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Abstract:

Preliminary experimental evidence shows that it is possible for an eavesdropping dolphin to discern object information from the returning echoes generated by the echolocation signals of conspecifics. Researchers have offered suggestions as to how this proposed ability may affect the behavior of wild dolphin species. A review of early and contemporary ideas, hypotheses and experiments concerning eavesdropping in dolphins is presented here, resulting in the development of a formalized, modern version of the 'echoic eavesdropping' hypothesis. The ecological implications of eavesdropping behavior remain unknown; refinement of the hypothesis and clarification of underlying assumptions are vital to our understanding of how echoic eavesdropping behavior might manifest itself in the social behavior of wild odontocetes. Suggestions for future research involving both echoic eavesdropping and a novel, alternative hypothesis (multi-source echoic eavesdropping) are offered. With the potential to elucidate many of the mysteries concerning dolphin biosonar use and dolphin behavior in general, echoic eavesdropping is an idea that deserves future attention.

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Do Dolphins Eavesdrop on the Echolocation Signals of Conspecifics?

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Preliminary experimental evidence shows that it is possible for an eavesdropping dolphin to discern object information from the returning echoes generated by the echolocation signals of conspecifics. Researchers have offered suggestions as to how this proposed ability may affect the behavior of wild dolphin species. A review of early and contemporary ideas, hypotheses and experiments concerning eavesdropping in dolphins is presented here, resulting in the development of a formalized, modern version of the 'echoic eavesdropping' hypothesis. The ecological implications of eavesdropping behavior remain unknown; refinement of the hypothesis and clarification of underlying assumptions are vital to our understanding of how echoic eavesdropping behavior might manifest itself in the social behavior of wild odontocetes. Suggestions for future research involving both echoic eavesdropping and a novel, alternative hypothesis (multi-source echoic eavesdropping) are offered. With the potential to elucidate many of the mysteries concerning dolphin biosonar use and dolphin behavior in general, echoic eavesdropping is an idea that deserves future attention.

Despite substantial knowledge of the structure and function of odontocete biosonar systems that has been revealed under experimental conditions, little is known about the way these systems function in a natural setting as part of the normal behavioral repertoire of wild dolphins (see discussions by Barrett-Lennard, Ford, & Heise, 1996; Evans & Awbrey, 1988; Herzing & dos Santos, 2004; Li, Wang, Wang, & Akamatsu, 2005; Madsen, Kerr, & Payne, 2004; Popper, 1980). In his definitive work on the subject of dolphin sonar, Au (1993, p. 271) went so far as to claim that, despite what we have learned in the lab, "we do not have the foggiest idea of how dolphins utilize their sonar in a natural setting." Many studies in recent years have sought to address this problem - new and more cost-effective technologies have allowed scientists to record the broadband echolocation signals of wild free-ranging odontocetes with enough accuracy to allow for a more comprehensive analysis of acoustic and behavioral data (Akamatsu, Wang, & Wang, 2005; Au, 2003; Au & Benoit-Bird, 2003; Dudzinski, Clark, & Würsig, 1995; Herzing & dos Santos, 2004; Lammers, Au, Aubauer, & Nachtigall, 2004; Madsen, Kerr, & Payne, 2004; Schotten, Whitlow Jr, Lammers, & Aubauer, 2004)

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Bat species are known to emit a near constant stream of echolocation clicks during their active periods (Tyack & Clark, 2000), and, in view of the wealth of information this kind of system is capable of providing, it might be assumed that dolphins would also engage their active sonar system on a frequent basis. However, many recent studies have revealed that, among dolphins, echolocation is employed much more sparingly in the wild than previously thought. Dolphins are capable of localizing and tracking prey using passive acoustic cues alone (Wood & Evans, 1980), and studies of passive listening foraging strategies (Barrett-Lennard, Ford, & Heise, 1996; dos Santos & Almada, 2004; dos Santos, Caporin, Moreira, Ferreira, & Coelho, 1990; Evans & Awbrey, 1988; Gannon et al., 2005) have led to the conclusion that silent hunting techniques may be prevalent, possibly serving as a primary means of prey detection in some foraging situations (Herzing, 2004; Herzing & dos Santos, 2004). Eavesdropping has also been implicated as a possible explanation for sparse echolocation usage (Götz, Verfuß, & Schnitzler, 2005). A special form of eavesdropping has been proposed for echolocating odontocetes (Dawson, 1991; Jerison, 1986; Xitco & Roitblat, 1996), and it is this hypothesized process, termed ‘echoic eavesdropping’, that is discussed here.

The echoic eavesdropping hypothesis for dolphin species proposes that a dolphin might not transmit any echolocation clicks of its own, but rather listen to the echolocation clicks and click echoes produced by conspecifics in order to gain information about its environment. Central to this discussion are two questions concerning echoic eavesdropping: 1) can the echoic eavesdropping hypothesis help us to better understand dolphin behavior as it relates to echolocation use, and 2) can it be used to understand the data showing sparse echolocation usage by wild dolphins? This review evaluates the strengths and weaknesses of the echoic eavesdropping hypothesis in answering these questions. We will begin by describing in more detail the hypothesis in its current form, specifying the earlier hypotheses and suggestions from which it is derived. We will then highlight some difficulties with the current hypothesis arising from the many untested assumptions upon which it rests. Lastly, we will present an alternative hypothesis that addresses some of the limitations of the current echoic eavesdropping hypothesis.

Echoic Eavesdropping

The term ‘eavesdropping’ is commonly used to describe a situation where one animal is able to discern valuable information by means of intercepting the signals generated by a conspecific, predator or prey (see review by Peake, 2005). It manifests itself in various forms and in various modalities across taxa: for example, female black-capped chickadees (*Poecile atricapilla*) eavesdrop on the territorial songs of males as a means of evaluating a mate (Mennill, Ratcliffe, & Boag, 2002); the female corn earworm moth, (*Helicoverpa zea*) whose pheromones, intended to attract males of the same species, are intercepted by parasitic female wasps of the chalcid genus *Trichogramma* (Stowe, Turlings, Loughrin, Lewis, & Tumlinson, 1995); and the tungara frog (*Physalaemus pustulosus*) whose calls attract the predatory fringe-lipped bat (*Trachops cirrhosus*) (Page & Ryan, 2005). However, a distinction must be made between the concept of eavesdropping in the traditional sense outlined above, and the ‘echoic eavesdropping hypothesis’ as it

relates to dolphin echolocation (Dawson, 1991; Götz, Verfuß, & Schnitzler, 2005; Xitco & Roitblat, 1996). The current form of the echoic eavesdropping hypothesis for dolphin species refers exclusively to a scenario wherein one dolphin does not transmit any echolocation clicks of its own, but rather listens to the echolocation clicks and click echoes produced by conspecifics in order to gain information about its environment. A dolphin, then, is eavesdropping specifically on the echolocation of other dolphins, and not on other sounds in the environment, nor on non-echolocation signals produced by conspecifics. It assumes a complex level of object and environmental information is available to the eavesdropping animal through the click echoes it receives. In this paper, the term 'echoic eavesdropping' is used to refer to the hypothesis outlined above, whereas 'eavesdropping' or 'classic eavesdropping' are used to refer to the traditional definition common to animal communication/signaling (see discussions of 'classic eavesdropping' in McGregor, 1993; 2005).

Early speculation and the development of the hypothesis

The nature of the dolphin biosonar transmission and reception system inspired speculation early on as to its usefulness in allowing dolphins to eavesdrop on the echolocation activity of conspecifics. Caldwell and Caldwell (1977) suggested that dolphins would be alerted to the presence of a food source by monitoring the echolocation signals of conspecifics. An analogous situation is found in bats; echolocating microchiroptera species appear to monitor and respond to the echolocation signals of conspecifics and sympatric species as a means of locating feeding sites (Balcombe & Fenton, 1988; Barclay, 1982). The bats' responses seem predominantly cued to 'feeding buzzes', indicative of the presence of prey by bats actively involved in feeding. This process is not unlike traditional definitions of eavesdropping (see Bradbury & Vehrencamp, 1998), and is not exclusive to echolocation as such.

Later speculation considered the possibility that an eavesdropping dolphin may receive more detailed information from the outgoing click than simply being alerted to the presence of conspecifics or prey species. Penner (1988) discovered a predictable relationship in detection experiments between the distance an echolocating dolphin was to a target and the time delay between the dolphin's echolocation clicks. This inter-click interval was stable enough to allow a human researcher to determine the distance at which a dolphin was concentrating echolocation searches simply by monitoring outgoing clicks. Presumably, other dolphins should be capable of similar range estimations when monitoring the outgoing echolocation of conspecifics either by relying on echolocation computations or by simple learned associations.

An early test of a dolphin's ability to extract information exclusively from echoes was performed by Scronce and Johnson (1976) who required a bottlenose dolphin to report the presence or absence of a 7.62 cm diameter steel sphere. The dolphin was prevented from emitting echolocation clicks of its own by covering the melon with an acoustically impenetrable mask. An artificial click projector was used to ensonify the sphere with pulses resembling natural dolphin clicks, resulting in echoes that the dolphin could use to determine the presence of the sphere. The

sphere was ensonified at distances of 40 m and 80 m, with correct target detection by the dolphin well above what would be expected by chance for both distances. Detection must have been accomplished on the basis of information the dolphin received from the target backscatter. Scronce and Johnson concluded that a dolphin is able to detect and report the presence of an object by listening for the occurrence of target echoes that do not originate from its own biosonar.

In his discussion of dolphin perception, Jerison (1986) introduced essential components of the modern version of the echoic eavesdropping hypothesis. His discussion focused on speculation as to the nature of the dolphin's perceptual world (its '*Umwelt*'), and its relationship to echolocation. Linking echolocation to human language, psychological concepts of 'self' and implicating echolocation in a 'communal mode of reality' for dolphins, Jerison's arguments rely heavily on psychological conjecture. At the core of his more esoteric ideas was a proposal that dolphins may share information by listening to the echolocation activity of other dolphins. Inspired by Fenton's (1980) description of echolocation eavesdropping in bats, Jerison suggested that the echolocation signals and their echoes would provide eavesdropping dolphins with object information similar, if not identical, to the information received by the sender. In contrast to earlier speculation, this idea opened a new avenue for exploring eavesdropping – one where echoes might provide an eavesdropper with detailed information about the environment and objects in that environment.

Dawson's (1991) article concerning vocal communication in Hector's dolphins (*Cephalorhynchus hectori*) introduced a more formalized version of the echoic eavesdropping hypothesis, which he referred to simply as the 'eavesdropping' hypothesis. Much of Dawson's argument focuses on a suggestion for a communication system for Hector's dolphins that does not rely on frequency modulated and unmodulated pure tone 'whistle' structures, but rather on pulsed sounds as a mode for communication. Hector's dolphins are a non-whistling species, and Dawson's hypothesis was largely in response to the suggestion by Herman and Tavolga (1980) and others that whistles are the primary mode of communication for delphinid species. Herman and Tavolga (1980) had, however, pointed out that the suggestion that pulsed sounds are never the primary mode of communication for delphinid species may be unjustified and premature given that pulsed sounds for non-whistling species were likely to be an important form of communication, especially in light of the then existing evidence for burst-pulse sounds used in social interactions (the authors cited Bastian, 1967; Caldwell & Caldwell, 1977 as providing examples).

Dawson (1991) suggested that dolphins can detect the presence of conspecifics by listening to swimming sounds (passive listening), find food by listening to the echolocation activity of other dolphins (similar to 'classical eavesdropping'), but also "detect and interpret the echoes of each other's sonars". Based on Johnson's (1988) description of bionic sonar systems that do not require 'knowledge' of the outgoing signal, Dawson suggested that click echoes alone would provide the eavesdropper with detailed object information. This unintentional transfer of information between individuals, although not falling within traditional definitions of social communication, is the basis for Dawson's suggested communication system for Hector's dolphins.

Taken together, these early suggestions concerning a dolphin's potential ability to discern object information by listening to the echolocation activity of conspecifics (Caldwell & Caldwell, 1977; Dawson, 1991; Jerison, 1986; Penner, 1988; Scronce & Johnson, 1976) form what can be termed the 'modern echoic eavesdropping hypothesis'. The hypothesis could be formulated as follows: a dolphin in an appropriate listening position relative to an actively echolocating conspecific or conspecifics is able to receive and utilize detailed object and environmental information from the generated click echoes. With the exception of the two studies described in the following section, few data have been collected to test this hypothesis.

Experimental and observational support

The first and only experimental test to date to focus on the echoic eavesdropping hypothesis was conducted on two Atlantic bottlenose dolphins (*Tursiops truncatus*) housed at the Living Seas, Epcot (Xitco & Roitblat, 1996). Inspired by the hypotheses offered by Dawson (1991) and Jerison (1986), Xitco and Roitblat designed a series of experiments meant to test for 'passive echolocation object recognition'. It was assumed that the echo features most important to the eavesdropping dolphin are those that are most similar to the echo features available to the echolocating dolphin. Therefore, the two dolphins were positioned close together along the same axis to reduce distortion of off-axis echoes, in view of the fact that the spectral components of the receiving beam pattern differ considerably at various points along the horizontal and vertical axes (Au, 1993; Au & Moore, 1984). Additionally, Xitco and Roitblat suggested that if the eavesdropping dolphin was able to recognize objects by listening to the echoes generated by the inspecting dolphin's echolocation, it would imply that the eavesdropper does not need to produce echolocation clicks of its own in order for its own echo processing to occur, as has been suggested for both echolocating bats (Razak, Fuzessery, & Lohuis, 1999; Suga, 1990) and dolphins (Dubrovsky, 2004).

In the Xitco and Roitblat experiment, an eavesdropping dolphin was positioned at a bite plate with its melon held above water, making it impossible to transmit echolocation clicks because of the impedance mismatch between air and water. The inspecting dolphin was positioned underneath the eavesdropper, and was allowed to inspect objects using echolocation, the click echoes of which were available to the eavesdropping dolphin. In a variety of trials in a series of two experiments with both familiar and unfamiliar stimulus objects presented behind a visually opaque but echoically transparent screen, the eavesdropper and the inspecting dolphin performed a match-to-sample task. Overall, the eavesdropper performed significantly above chance level with accuracy that closely reflected the performance of the inspecting dolphin. Alternative explanations for the eavesdropper's performance were rejected; for example, covert echoic inspections of the target object by the eavesdropper, or transmission of information via whistles. The authors concluded that "the listener's performance was guided by object-specific or feature-specific information that he received by listening to echoes generated as the inspector examined the sample." This is strong evidence that a dolphin is able

to extract object information by processing the echoes generated by the echolocation activity of conspecifics.

The only observational test of the echoic eavesdropping hypothesis in wild dolphins so far reported is that by Götz et al. (2005). These authors suspected that the tight swimming formations and synchronous swimming behavior exhibited by rough-toothed dolphins (*Steno bredanensis*) could actually be a strategy meant to facilitate echoic eavesdropping. Based on the assumption that close swimming proximity and silence is necessary for dolphins to acquire useful information from the returning click echoes generated by conspecifics, they tested to see if there was a correlation between synchronous swimming and reduced group echolocation production. Their study found that of 80% of the synchronous swimming sequences recorded, only a single dolphin appeared to be echolocating. In the sequences where asynchronous swimming was recorded, there was always more than one dolphin echolocating. The putative 'eavesdropping' dolphins in the synchronous swimming scenario were assumed to be able to listen to and process the pulse-echo pairs; that is, both the outgoing click and returning click echo generated by the actively echolocating dolphin. This then would have provided the eavesdropping dolphins with useful target information – resulting in concomitant behaviors: such as maintaining close swimming proximity, alignment, and not producing echolocation signals of their own. This observational study was the first of its kind to provide evidence to suggest that dolphins may engage in echoic eavesdropping behaviors in the wild.

Influence of the hypothesis

With only one experimental and one observational study of the echoic eavesdropping hypothesis reported in the literature to date, the idea is still largely untested. Nonetheless, there has been ample speculation as to how the potential for echoic eavesdropping may manifest itself in the behavior of dolphin species. As described earlier, synchronous behavior may be a strategy employed by dolphins in order to maximize received echo information generated by conspecifics (Götz, Verfuß, & Schnitzler, 2005; Kuc, 2002; Xitco & Roitblat, 1996). Others have suggested that echoic eavesdropping may influence swimming formations used during foraging (Janik, 2005). Norris and Dohl (1980) discussed how echolocation by a group of dolphins may result in 'shared information' and 'sensory integration', concepts similar to, and perhaps facilitated by, echoic eavesdropping. This 'sensory integration', including the rapid transmission of acoustic sensory information between members of a group, has also been discussed by Fellner et al. (2006). Herzing (2006) has discussed the need to understand echoic eavesdropping and its relationship to swimming positions as it relates to the analysis of shared cognitive information. Group echolocation strategies (including echoic eavesdropping) must then lead to social behavior that dictates which dolphin echolocates and when, possibly resulting in echolocation 'emission rules' like those discussed by dos Santos and Almada (2004). Echoic eavesdropping behavior may influence the social hierarchies and the rotating social roles that facilitate shared echolocation duties suggested by Johnson and Norris (1986; 1994). The relationship between echoic eavesdropping, shared information, group synchrony, and a dolphin's proposed

ability to utilize complicated cognitive processes related to a theory of mind have been discussed by Harley et al. (1995). It has been suggested that the echelon swimming position commonly seen for mother-calf pairs may facilitate echoic eavesdropping, and possibly provide immature dolphins an opportunity to develop echolocation skills (Herzing, 2004). Finally, echoic eavesdropping has been implicated as a major component of conceivable communication systems for odontocetes (Dawson, 1991; Jerison, 1986).

We return to the questions posed at the beginning of this discussion: is the echoic eavesdropping hypothesis capable of explaining dolphin behavior as it relates to echolocation use, and does it explain the data showing sparse echolocation usage by wild dolphins? To properly explore these questions, it is necessary to consider some of the conceptual problems with the current hypothesis and its underlying assumptions.

Conceptual Challenges

The listening position problem

It is not clear what listening positions provide an eavesdropping dolphin with sufficient echolocation detail to facilitate object detection, identification, classification, and discrimination. In their experiment, Xitco and Roitblat (1996) noted that the eavesdropping dolphin often “slid along the bite plate to position himself even closer to the inspector”, presumably to increase the quality of the received echo information. It is assumed that the closer the eavesdropper is to the axis of the investigator’s (term ‘investigator’ equivalent to Xitco and Roitblat’s term ‘inspector’) beam, and the closer the two dolphins are to each other on the whole, the more useful the received echoes will be for the eavesdropper, as the information will likely be ‘comparable’ to that of the investigator. Furthermore, the closer the eavesdropper is to the investigator, the higher the received level of the echo returns will be. ‘Comparable’ in this sense implies that the investigator is, by default, always in an optimal listening position, and that the closer an eavesdropper is to this position, the better the echo-information will be. This, however, might not be the case. Xitco and Roitblat (1996) point out that ‘comparable’ information might not be essential for the eavesdropper to glean sufficient information from the echoes in order to acquire ‘useful’ object information. Any variety of listening angles relative to the investigator and the object might yield echo structures that are of use to the eavesdropper. Scronce and Johnson’s (1976) experiments revealed that echoes received from an object being ensonified at oblique angles and originating 80 m from an eavesdropping dolphin nonetheless produced enough echoic information for the dolphin to perform basic detection tasks (i.e., to report if it heard reflected acoustic energy or not).

The propagation of click echoes vis-à-vis the contours and composition of the ensonified object must also be considered when conceptualizing efficacious listening positions. Echo structures vary considerably depending on the structural makeup and relative aspect of the target (Au & Hammer, 1980; Helweg, Roitblat, Nachtigall, & Hautus, 1996). Therefore, a scenario wherein the bulk of the reflected energy generated from an investigator’s transmitting beam might be di-

rected at an angle away from its own receiving beam can be constructed. A dolphin ensonifying a highly reflective flat surface at an oblique incident angle will have the bulk of the energy from that beam directed away from its position along the angle of reflection, and little energy will be contained within the investigator's receiving beam. This creates a scenario wherein the investigator's received echoes will not contain as much energy as those received by a potential eavesdropper positioned on-axis along the angle of reflection some distance away from the investigator. Would this mean that the eavesdropper is receiving 'better' echoic information from the investigator's echolocation signals than the investigator? An eavesdropping scenario must then take into account all of the potential reflective properties of the environment including surface and substrate reflections and reflections created by highly variant object structures and aspects. One problem with this sort of speculation is our lack of knowledge as to what exactly a dolphin requires from an echo structure in order to glean useful object information. Perhaps the above scenario would not facilitate eavesdropping, as the echo structure with 'more energy' overall may not be as useful to the dolphin as other features in the echo structure. The question as to what type of echo structure is 'useful' to a dolphin depends on the nature of the experimental task, or the demands of a specific ecological scenario. In some scenarios, what is 'useful' may simply be an ability to detect enough backscatter energy to determine the presence of an object (as in the Scronce and Johnson experiment). For other scenarios, an ability to discriminate between different types of objects is required (as in the Xitco and Roitblat experiment). Perhaps in natural foraging situations, groups of dolphins do not require ideal discrimination performance from an echoic-eavesdropping scenario (e.g., I detect a cod/I detect a salmon) as often as simple detection performance (e.g., I detect nothing/I detect something).

Currently, it is not known how variations in listening position might affect discrimination or detection performance. Additional experimental tests might reveal that any number of listening positions could produce similar discrimination performance results for the eavesdropper. If echoic eavesdropping can occur at distances beyond the current constraints of the hypothesis, it may not be necessary to limit our search for potential eavesdropping behaviors to tightly spaced synchronous events as described by Götz et al. (2005). Furthermore, echoic eavesdropping might occur over larger distances if dolphins require only basic detection as opposed to complex discrimination. As this problem is yet unresolved, the echoic eavesdropping hypothesis is not yet useful in answering our question about how echoic eavesdropping may influence the echolocation behavior of dolphins in the wild in terms of listening positions that may affect group swim formations, spacing, etc.

The off-axis problem

The listening position problem is further complicated by the unknown role that lower frequencies (i.e., < 60kHz) found in the 'off-axis' portion of the transmission/receiving beam play in the performance of the dolphin's biosonar. The many experiments testing a dolphin's ability to detect, recognize and classify objects based on their echo structure have led to the conclusion that 'the use of

broadband short-duration transient-like sonar signals that can encode important target information also plays an important role in the dolphins' discrimination capabilities' (Au, 1993). Given that, for healthy individuals, the majority of spectral energy and peak frequencies for many dolphin species occur in the higher frequencies (i.e., > 60kHz, Au, 1993), it has previously been assumed that these higher frequencies are critical to the process of object discrimination. There are obvious theoretical benefits for a wideband echolocation signal in helping to reduce target ambiguity in general (Altes, Dankiewicz, Moore, & Helweg, 2003). Higher frequency sounds with shorter wavelengths are required in order to promote reflections and minimize refraction around smaller objects and object features. A 150 kHz tone for example should be appropriate for resolving a sphere with a radius of 1.55 mm (Tyack & Clark, 2000). Given that the highest echolocation frequencies are contained exclusively within the on-axis portion of the transmitting beam, the usefulness of the off-axis beam (containing lower frequencies) for object recognition or discrimination has been called into question. Based on Au's (1993) work with directional hearing, Madsen et al. (2004) concluded that "while the off-axis part of sonar clicks may play an important role in eavesdropping by conspecifics, predators, and prey, it has probably little relevance to the performance of the sonar".

Existing demonstrations (Xitco & Roitblat, 1996) and observations (Götz, Verfuß, & Schnitzler, 2005) of echoic eavesdropping have been limited to on-axis scenarios. A dolphin's echolocation transmission beam is highly directional becoming more directional (narrow) as frequency increases with both the horizontal and vertical beam at -3dB measuring $\sim 10^\circ$ at 120 kHz (Au, Moore, & Pawloski, 1986). The receiving beam is also highly directional, with the vertical beam at -3dB measuring $\sim 10^\circ$ at 120 kHz, and the horizontal beam at -3dB measuring $\sim 14^\circ$ at 120 kHz (Au, 1993). Given these narrow beam patterns for high frequencies, this would suggest that dolphins in an eavesdropping scenario need to be positioned close together for optimal discrimination performance, assuming optimal discrimination requires access to undistorted frequencies at ~ 120 kHz.

However, the dependence of improved object discrimination on the use of clicks with high frequency energy peaks has not been established. In a summary of various experiments concerning frequency spectra and investigative tasks, Au (1993) noted that dolphins do not appear to alter frequency components of their outgoing clicks in response to targets with features varying in complexity. The broad changes in frequency spectra that have been recorded for individual dolphin echolocation seem more closely associated with changes in source level to compensate for noise and masking rather than discrimination difficulty. Madsen et al. (2004) suggested that centroid frequency is a more robust indicator of spectral components vital to dolphin sonar. This often lower center frequency tends to remain stable despite source level changes (Au & Würsig, 2004). Furthermore, the large variation for typical peak frequencies (ranging from 5 kHz to 160 kHz (Au, 1993)) across species does not seem to be correlated with an increase or decrease in discrimination ability. Tyack and Clark (2000) pointed out that although often suggested (see for example Au & Würsig, 2004), there does not appear to be a clear correlation between body size of the odontocete and peak frequency, nor prey

size and peak frequency, as had been previously suggested (see Li, Wang, Wang, & Akamatsu, 2005).

A potentially vital theme was discussed by Tyack and Clark (2000) concerning the notion that the majority of the biological targets that dolphins will encounter in 'real life' situations (i.e., fish or organisms in the deep scattering layer) will contain gas-filled organs or other structures with much lower resonant frequency characteristics than the artificial targets used in experimental tests. Many of these structures will respond best to the lowest frequencies emitted by an echolocating dolphin, allowing the possibility that dolphins may use lower frequency echolocation for detection of these types of targets. This ambiguity could lead to speculation that the higher frequencies present in the click spectra could aid in discrimination, but are not essential for it to occur. It has not been ruled out that the lower frequencies contained in an echolocation click and its corresponding click echo can provide a dolphin with 'adequate' object information. Herzing and dos Santos (2004) suggested that "although echolocation is traditionally thought of as high-frequency sound production, high frequency sound is not essential for echolocation".

The central problem in this debate is an inability to characterize what 'adequate', 'useful', or 'detailed' object information is for a dolphin's echolocation process. If we accept that higher frequencies are capable of providing dolphins with better object detail, at what point does a lack of high frequency echoes lead to an inability to detect or identify an object or its features? Large objects like the ocean floor, surface, or rock outcroppings will certainly respond easily to the lowest frequencies in an echolocation click. It seems likely then that a dolphin could detect and classify these biologically relevant targets without using high frequency clicks. Does this mean that a dolphin's off-axis beam containing limited high frequency energy but ample lower frequency energy could be used to gather 'useful' environmental and target information from large targets? The findings of a recent study by Akamatsu et al. (2005) support this notion. The authors recorded echolocation signals from the free-ranging Yangtze finless porpoise (*Neophocaena phocaenoides asiaorientalis*) using a stereo acoustic data logger. It was calculated that the porpoise was capable of receiving surface echoes from the off-axis portion of its beam at depths of 50 m. Moreover, Akamatsu et al. estimated that a porpoise would be able to detect a 10 cm fish positioned 3 m above itself using the off-axis portion of its echolocation beam with energy at 38 kHz. Not only does it appear that the porpoise is capable of receiving very general information concerning the location of large targets like the surface (useful in orientation) at considerable distance, but the porpoise is capable of resolving the presence of small prey species using lower frequencies from the off-axis portion of their echolocation beam. Presumably, this information might not be 'detailed' object information, but it may be considered 'adequate' and 'useful'.

Additional support for the notion that dolphins do not necessarily require higher frequencies for 'useful' object information is described in experiments with free-swimming bottlenose dolphins involved in open water search and detection tasks (Houser et al., 2005; Martin, Phillips, Bauer, Moore, & Houser, 2005). For these experiments, dolphins were fitted with a device capable of recording echolocation clicks and click echoes, as well as swim position. The dolphins were re-

quired to report the presence or absence of an object located on the sea floor. One of the two dolphins involved in the experiment had significant hearing loss above 50 kHz, and, consequently, produced echolocation clicks during detection tasks with peak frequencies between 30-60 kHz (Houser et al., 2005). Despite using these 'lower' frequencies, the dolphin was successful during these detection tasks. This confirms prior reports that dolphins with profound hearing loss that rely on lower frequency echolocation clicks are, nonetheless, able to perform well in detection tasks (e.g., Houser, Helweg, & Moore, 1999; Moore, Finneran, & Houser, 2004). For these experiments, on-axis clicks with peak frequencies far below the 120 kHz typical for healthy dolphins nevertheless resulted in 'adequate' detection ability.

Further eavesdropping listening position experiments will shed light on the problem of where the boundaries lie between 'adequate' object information allowing a dolphin to report the presence or absence of an object (object detection), and 'detailed' object information allowing for complex object discrimination. If dolphins eavesdrop on the low-frequency echoes propagating in a much wider receiving beam pattern, they may be capable of swimming in widely spaced formation and still be able to receive useful, biologically relevant echo information from conspecifics. In this sense, the off-axis 'problem' may in fact be an 'opportunity' for an echolocating dolphin. Unraveling the extent to which dolphins can use this low-frequency off-axis echo information will alter our ideas as to how echoic eavesdropping might manifest itself in the behaviors of wild dolphins. Currently, the off-axis problem creates a critical challenge to the assumption that echoic eavesdropping can only occur over short distances.

The features problem

Solving both the listening position problem and the off-axis problem will shed light on components critical to our understanding of echoic eavesdropping. However, both of these problems are complicated by a more fundamental issue: it is still not known what features in the returning echo structure are used by either the eavesdropping dolphin or the investigator to perform object discrimination in the first place.

Click echoes are capable of providing a dolphin with considerable environmental and object information, allowing dolphins to perform remarkable perceptual feats beyond simple orientation and obstacle object avoidance tasks (see reviews by Kellogg, 1970; Moore, 1980) and basic object detection (Au & Snyder, 1980; Helweg, Au, Roitblat, & Nachtigall, 1996). They can distinguish objects based on size, shape, and composition (Au & Hammer, 1980; Au, Schusterman, & Kersting, 1980; Nachtigall, 1980), despite changes in aspect (Au & Turl, 1991; Helweg, Roitblat, Nachtigall, & Hautus, 1996). Sensory information received from both echolocation and visual modalities is evidently sufficiently comparable to lead to successful object matching across the two modalities, suggesting that echolocation may be functionally equivalent to vision for some object discrimination tasks (Harley, Putman, & Roitblat, 2003; Herman & Pack, 1992; Herman, Pack, & Hoffmann-Kuhnt, 1998; Pack & Herman, 1995).

How are dolphins able to accomplish these feats? Experimental work has been done to clarify this point, but much uncertainty remains. A few suggested essential features within the echo structure that allow for complex recognition include energy highlights (amplitude differences) for frequency components of individual echoes and across time for the echo train (Au, Moore, & Pawloski, 1988; Dankiewicz, Helweg, Moore, & Zafran, 2002; Helweg, Moore, Dankiewicz, Zafran, & Brill, 2003), general spectral qualities (Johnson, 1980), echo arrival times and time separation pitch (Au & Hammer, 1980; Moore, Hall, Friedl, & Nachtigall, 1984), range profiles (Herman, Pack, & Hoffmann-Kuhnt, 1998; Pack & Herman, 1995), and click echo and click train duration (Au & Turl, 1991). Suggestions for possible neural processing mechanisms (Johnson, 1980; Popper, 1980), and neural network models (Altes, 1995; Au, 1994; Roitblat, Au, Shizumura, & Moons, 1995) relating to echo processing have been offered. It appears that dolphins are able to construct global mental object representations based on object shape, contours, and composition from these features contained in the echo structure (Harley, Putman, & Roitblat, 2003; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002), revealing a high level of complexity in the dolphin's perceptual system (for an overview of the problem see Roitblat, 2004). Despite this experimental work, a comprehensive theory as to how received echo structure stimuli lead to perception has not yet been proposed. It could be said that a search for the germane echo features facilitating object recognition is a red herring, equivalent to constructing a theory of vision in humans based on analysis of retinal processing of light ray stimuli, thus ignoring the 'behind the scenes' processing taking place at higher levels of neurological function resulting in perception. Neurological top-down processing theories might be our only avenue for understanding how object recognition takes place for dolphins, demanding a different computational framework that is "more like a dynamic system than like a standard computation algorithm", as Roitblat (2004) suggested.

Eavesdropping experiments have the potential to tell us not only more about the critical features in the echo structure that are necessary for object recognition, but also to increase our knowledge as to how natural dolphin behavior facilitates echolocation use in general, and to give us deeper insight into the dynamic process of object recognition. For example, movement of the dolphin's head in three dimensions during echolocation inspection tasks increases echo complexity and would be a useful strategy to increase the effectiveness of target resolution (Azzali, 1992). Furthermore, unlike most laboratory experiments, free-swimming dolphins are not required to remain in a fixed swimming position when inspecting a target; distance to the target may vary considerably as the dolphin approaches during inspection (see discussion on free-swimming detection tasks by Azzali, 1992; Houser et al., 2005; Martin, Phillips, Bauer, Moore, & Houser, 2005; Pack & Herman, 1995). The question arises, therefore, as to whether when the echolocating dolphin changes its head and swimming position relative to the target during inspection, 'predictable' changes in the highlights of the returning echo structure (e.g., changes in peak frequency, number of received echoes) are created, thus facilitating object recognition? If echolocating dolphins employ this strategy when inspecting objects (Altes, Dankiewicz, Moore, & Helweg, 2003; Houser et al., 2005), would an eavesdropping dolphin still be able to use this echoic information

if it had not initiated the changes in swim and head positions? Given the results of Xitco and Roitblat's (1996) experiment, it appears that an eavesdropping dolphin is able to make use of the information contained in the returning echoes despite small changes in swim and head position initiated by the echolocating dolphin.

An understanding of the echo features necessary and the behaviors facilitating object discrimination by an inspecting dolphin will help to construct a better hypothesis relating to echoic eavesdropping. Beyond simply knowing optimal or sufficient listening positions, understanding what additional behaviors are critical for the process as a whole (e.g., head movement) will allow scientists to better evaluate the behaviors of wild dolphins involved in potential echoic eavesdropping scenarios.

The outgoing click problem

For their experiment, Xitco and Roitblat (1996) addressed a secondary debate regarding the extent to which a dolphin requires knowledge of the outgoing click in order to process echo information. Dubrovsky (2004) argued that outgoing clicks, or signals similar to dolphin echolocation clicks, are necessary for the proper 'activation' of the 'active hearing mode' in dolphins. In this sense, proper echo processing would not be possible without the availability of some manner of outgoing click. This may be analogous to the situation described for echolocating bats, where echo processing can not take place without the information derived from the outgoing click (Razak, Fuzessery, & Lohuis, 1999; Suga, 1990). In contrast to this scenario, the results from Xitco and Roitblat's (1996) experiment suggests that a dolphin does not need to generate its own echolocation clicks to be able to derive object information from an echo structure. This does not, however, exclude the possibility that a dolphin must in some way hear the outgoing clicks of another dolphin in order to properly process associated echo information.

If, in an echoic eavesdropping scenario, the eavesdropper needs to be positioned in such a way as to be able to hear the outgoing click before echo processing can occur, this may again constrain potential listening positions. If the eavesdropper is required to have access to the outgoing click, presumably there are features within the click that are vital to echo processing. It is not known what these features might be (e.g., frequency spectra, amplitude). Perhaps the eavesdropper must be able to match the outgoing click to its echo, as has been suggested by Kuc (2002), possibly restricting the distance at which an eavesdropper can be positioned from an investigator. The role of the outgoing click in an echoic eavesdropping situation remains ambiguous, and is in need of further data for confirmation of its role.

The silence problem

We now turn to the question concerning to what extent the data showing sparse echolocation usage by wild dolphins can be explained by the current echoic eavesdropping hypothesis. The current hypothesis predicts that an eavesdropping dolphin will remain silent in order to maximize information it can gain from reception of click echoes resultant from the biosonar of conspecifics. Observations of

reduced echolocation use by wild odontocetes has led to speculation that echoic eavesdropping behavior could be implicated (dos Santos & Almada, 2004; Götz, Verfuß, & Schnitzler, 2005) and assumes that silence is an integral component of echoic eavesdropping. There are two arguments as to why silence would be correlated with eavesdropping. First, we assume that there are significant costs associated with echolocation production, prompting dolphins to employ strategies meant to reduce the need to use echolocation. Example costs include a metabolic expense or unwanted detection by predators and conspecifics. Thus, eavesdropping is a selfish strategy on the part of the eavesdropper; we would expect dolphins to employ this strategy whenever an appropriate situation presents itself. Second, remaining silent might actually facilitate eavesdropping by reducing the chance that conflicting echoes from two or more click trains will hinder the effectiveness of the echo processing system (i.e., to prevent jamming). We will discuss the strength of these two arguments in turn.

Limited data on odontocete echolocation use in the wild restricts the scope of speculation as to the influence of ecological costs in an echoic eavesdropping scenario, although some benefits to remaining echoically silent have been discussed. Although largely unstudied, predator detection was deemed unlikely in one study of passive listening in *Tursiops* (dos Santos & Almada, 2004). Also, it is possible that some known dolphin predators (e.g., sharks) would be unlikely to hear echolocation clicks (Gannon et al., 2005). The exception, of course, relates to predation from other echolocating odontocetes. Food competition and the cost of detection by conspecifics have not been studied (Gannon et al., 2005), although Janik (2000) noted that dolphins do respond to echolocation activity of feeding conspecifics. Barrett-Leonard et al. (1996) observed that transient, mammal-eating orca (*Orcinus orca*) populations employed a variety of strategies including total silence during prey detection and approach. This is an apparent effort by the group to minimize the costs associated with prey species' ability to detect orca biosonar. It could be argued that costs associated with detection by prey, predators, and conspecifics are irrelevant factors in this discussion given that a silent echoic eavesdropping dolphin will be positioned in close proximity to an actively echolocating dolphin, thus the likelihood of detection will be the same, or similar, whether or not the eavesdropper remains silent. However, it is possible that the summed effect of multiple echolocation signals contributes to higher detection levels by prey, predator, or conspecifics. Still, this increase is likely to be negligible when compared to the effects of the difference between a single individual echolocating and absolute silence from all individuals.

In addition to ecological costs, silence strategies may be influenced by the metabolic expense of echolocation production. There is an energetic cost for the production of echolocation signals; therefore, it is possible that social strategies have evolved that optimize echolocation use for individuals in group situations. Unfortunately, metabolic costs for dolphin biosonar have received limited experimental attention with the exception of a study by Cole and Speakman (1993). Speculation ranges from negligible to potentially significant predicted costs (Au, 1993; Cranford & Amundin, 2004; Gannon et al., 2005; Herzing & dos Santos, 2004; Johnson & Norris 1986; Norris, Würsig, Wells, & Würsig, 1994). Further experimental work is needed to clarify the true costs associated with echolocation

production before it can reasonably be implicated in the evolution of complex social behavior linked with echoic eavesdropping.

The second argument is that eavesdroppers remain silent in order to prevent sonar 'jamming'. Data collected from some echolocating bat species (e.g., *Tadarida teniotis*, *Tadarida brasiliensis*) suggest that they may employ a jamming avoidance response (JAR) by changing parameters of their echolocation calls (Fenton, 2003), including shifting their dominant frequency when jammed with the calls of conspecifics (Gillam, Ulanovsky, & McCracken, 2007; Ulanovsky, Fenton, Tsoar, & Korine, 2004). In contrast, studies of other species (e.g., *Taphozous perforatus*) did not find evidence of JAR behaviors (Ulanovsky, Fenton, Tsoar, & Korine, 2004). JAR has not been studied in marine mammals (Gillam, Ulanovsky, & McCracken, 2007), although suggestions for potential JAR behaviors have been offered for dolphins. For dolphin groups, echolocation 'emission rules' that compensate for too many simultaneous biosonar signals in the water have been suggested (dos Santos & Almada, 2004). The limited observations on wild dolphin populations suggest a negative correlation between group size and echolocation activity; the larger the group, the less relative echolocation use (Barrett-Lennard, Ford, & Heise, 1996; dos Santos & Almada, 2004). Götz et al. (2005) reported for their study of *Steno bredanensis* that no more than one animal was recorded echolocating in 80% of recorded synchronous swimming sequences. Additional data collected from free swimming spinner dolphins (*Stenella longirostris*) revealed minimal concurrent echolocation activity among closely spaced animals (Lammers, Schotten, & Au, 2006). This suggests that if echoic eavesdropping is the cause of the described behavior then a JAR response of limiting outgoing echo trains for the group to a few or just one animal may occur in order to prevent confusing returning echo structures as Götz et al. (2005) point out.

Although the above observations could be interpreted to mean that silence is important to eavesdropping if individual members of these groups are indeed eavesdropping on each other, it also reveals that groups of echolocating odontocetes (with the exception of the study by Götz et al. (2005)) are able to echolocate en masse, presumably without affecting foraging effectiveness. If the echo reception process were compromised by the presence of conspecifics' echolocation activity, one would expect to record far less echolocation activity from such groups. Furthermore, experimental studies have also shown that potentially disruptive acoustic activity including noise and reverberation does not have a serious negative impact on dolphin echolocation performance (Au, 1993; Dubrovsky, 2004). Experiments with man-made models have even shown that dolphins should theoretically be able to extract useful target information from multiple biosonar sources (Kuc, 2002). This ambivalence reminds us again that we still do not understand what the salient features in the echo structure necessary for object detection and recognition are. At what point does a combination of click trains emitted from nearby conspecifics hinder an animal's ability to extract necessary object information? Does this number change as a consequence of the type of task at hand (e.g., simple object or obstacle detection vs. acquisition of detailed object information)? Considerably more experimental and observational work needs to be conducted before a clear picture of the sonar jamming problem will emerge for odontocetes.

It is not certain that significant costs, metabolic or otherwise, could be the cause of silent behavior in an echoic eavesdropping scenario - there is insufficient observational or experimental supportive evidence. Nor is sonar jamming convincingly implicated as a problem for odontocetes. It could be argued that silence is putatively inferred as a factor in echoic eavesdropping given its importance to traditional definitions of eavesdropping. For orca, group silence while hunting vigilant marine mammals through passive listening is probably a necessary strategy to avoid detection. However, echoic eavesdropping does not predict group silence in the way that passive listening might, rather it predicts individual silence; as a result these group detection costs seem an inappropriate factor to consider. Intuitively, silence seems a necessary condition for eavesdropping - for example, it is hard to imagine an effective eavesdropping scenario where songbirds can successfully eavesdrop on the songs of conspecifics while themselves singing. These limitations, however, may be misplaced for dolphin species where the presence of simultaneous biosonar signals may not compromise individuals' sonar success, and may even contribute to its efficiency (Kuc, 2002). Preliminary data gathered from Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Gregg, et al., in prep.) suggest that, in some situations, dolphin dyads swimming in close proximity are more likely to echolocate on a target in unison, even when an eavesdropping scenario where one dolphin could remain silent presents itself (i.e., synchronous swimming and close proximity). If data from wild populations reveal that an appropriately positioned potential eavesdropper is more likely to commence echolocation than remain silent, this will require modification to the current echoic eavesdropping hypothesis. If the arguments for silence as an integral component of the echoic eavesdropping hypothesis are not viable, then observations of sparse echolocation use by wild odontocetes can not be explained by this hypothesis.

The social problem

When discussing how echoic eavesdropping might help explain dolphin behavior in relation to echolocation, an additional element that is not related to the performance of the biosonar system must be considered. Some researchers have discussed how social rules and roles may influence the production or suppression of echolocation activity in dolphin groups (e.g., dos Santos & Almada, 2004; Johnson & Norris 1986; Johnson & Norris, 1994). Perhaps echolocation production or suppression may be involved in displays of dominance or fitness, either by an individual, dyads (e.g., male alliances), or smaller groups, wholly divorced from the possible negative or positive impacts on the biosonar system of the individuals involved. Or perhaps, as Johnson and Norris (1986; 1994) suggest, rotating social roles may dictate which dolphin echolocates and when. Complex behavioral accounts involving kin selection, reciprocity, and inclusive fitness may be involved, as has been proposed for explaining geese flight formations (e.g., Andersson & Wallander, 2004). Understanding wild dolphin echolocation behavior may require that we look beyond the mechanics of echoic eavesdropping and take into account social explanations.

An alternative eavesdropping scenario

Given the considerable ambiguity present in many of the fundamental concepts underpinning echoic eavesdropping, there is opportunity for reformulation of the hypothesis. Although Götz et al. (2005) observed a potential echoic eavesdropping scenario where silence appeared to play an important role, with potentially similar data presented by Lammers et al. (2006), it has not been convincingly argued that an eavesdropping dolphin must remain silent in order to receive valuable echo information. Like Jerison's (1986) suggestion that multiple individual dolphins echolocating in unison may enhance perception, it may be possible that a dolphin is able to resolve adequate or possibly even enhanced object information by combining backscatter originating from a multi-source system, even while itself actively echolocating. Similar to the scenario envisioned by Kuc (2002), if a dolphin's echo processing system 'knows' the distance to the sources and if this distance remains near constant, and if the system can match echoes to sources, enhanced target information might be possible. It is important to note that when faced with an experimental target identification task of increased complexity, dolphins are known to emit more echolocation clicks than for easier tasks (Helweg, Roitblat, Nachtigall, & Hautus, 1996). Given that the number of clicks, in addition to signal strength, is one of only two features a dolphin manipulates for difficult identification tasks of this nature (Roitblat, Penner, & Nachtigall, 1990), it could be assumed that more information resulting in better resolution is achieved through emission of an increasing number of clicks. Detection ability has been shown to increase as the number of click echoes available to the dolphin increases (Altes, Dankiewicz, Moore, & Helweg, 2003). Dolphins appear to recognize objects by integrating information found across multiple echoes in an echo train (Helweg, Au, Roitblat, & Nachtigall, 1996). Therefore, multiple sources ensonifying a target simultaneously could result in a faster and more efficient means of increasing target identification if a dolphin can process multiple echo structures in this manner. Swimming in predictable and stable formations while concurrently emitting multi-source echolocation clicks could be a group strategy for rapidly increasing target resolution; this would certainly be a substantial benefit to both the individual and the group. This could also result in earlier detection of remote prey, obstacles and predators, increasing foraging efficiency, and threat identification.

It is still not certain that a dolphin involved in echoic eavesdropping must remain close to the actively echolocating dolphin in order to receive useful echo information. This is based on ambiguity concerning appropriate listening positions, the role of the outgoing click, and the role of off-axis frequencies for echolocation performance. If close proximity is not necessary for echoic eavesdropping, why then would foraging dolphin groups need to remain in tight formations? Would it not then be advantageous to spread out the group (for appropriate foraging scenarios), as has been seen for large aggregates of some species (Norris & Dohl, 1980)? If multi-source echolocation is a strategy used to increase target resolution efficiency for the group, remaining in tight formation may help to eliminate target ambiguity. If the group is widely spaced, echolocation activity would be spread over a wider area, perhaps reducing the number of useful echo structures originating from too many targets. Through a strategy of remaining close together, there would be a

higher likelihood that each of the individuals in the group would be echolocating on the same target, increasing the chance that the echoes are returning from one target or area of the target, possibly enhancing the usefulness of the returning echoes for individuals within the group.

This forms an alternative to the echoic eavesdropping hypothesis as has been presented in this review: 'multi-source echoic eavesdropping'. Like echoic eavesdropping, this alternative hypothesis suggests that dolphins are able to glean useful object information from listening to the returning echoes generated by the echolocation activity of conspecifics. However, it predicts that a dolphin will receive enhanced object information by listening to the echolocation activity of conspecifics in combination with its own echolocation. This suggests that dolphins will swim in tight and regular swimming formation as a means of directing the group's echolocation on a specific target, increasing target feature recognition and reducing target ambiguity, although other explanations for tight swimming formations are also possible (e.g., safety, forcing schooling behavior of prey species). In contrast to echoic eavesdropping, the multi-source echoic eavesdropping hypothesis predicts that 1) dolphins will be more likely to echolocate than remain silent when an eavesdropping scenario presents itself, and 2) close swimming positions, while advantageous in some group foraging situations, are not essential for echoic eavesdropping to occur. Importantly, the echoic eavesdropping hypothesis and the multi-source echoic eavesdropping hypothesis may not necessarily be mutually exclusive. Dolphins may in fact be capable of single or multi-source eavesdropping, and could switch between either depending on the appropriateness of the behavior to the given situation.

Future Research

Before a clearer picture emerges of how echoic eavesdropping might influence behavior in wild populations, many questions must be answered concerning the function of the mechanisms involved:

1. What listening positions are capable of producing useful echo information to the eavesdropper? Must an eavesdropper be positioned close to the investigator?
2. Can lower frequencies in the click structure be used by a dolphin for object detection/discrimination? What features in the click structure are necessary for object detection/discrimination in general?
3. What is the role of the outgoing click for the echolocation system for both an inspecting dolphin and an eavesdropper?
4. Can dolphins process echoes resulting from the echolocation of conspecifics in conjunction with their own echolocation? If this is possible, does this decrease or increase target recognition performance?
5. What are the metabolic costs for echolocation production? How might other costs influence the eavesdropping behavior of dolphins?

Answers to these questions will facilitate a more detailed discussion as to the possible role that echoic eavesdropping plays in the social lives of wild dolphin spe-

cies. Studies of wild populations can contribute to this discussion by revealing the following:

1. Under what circumstances do individual dolphins and groups of dolphins use echolocation, and when do they remain silent?
2. How does swimming formation and group synchrony relate to echolocation use? When positioned in an 'ideal echoic eavesdropping position', as has been revealed under experimental conditions, will wild dolphins engage in behaviors correlated with echoic eavesdropping?
3. Can the 'multi-source echoic eavesdropping' hypothesis be used to explain group echolocation behavior?

Testing both the echoic eavesdropping hypothesis and the multi-source echoic eavesdropping hypothesis requires first and foremost considerable experimental work. Knowledge as to what listening positions produce above chance discrimination performance by the listener will be vital to our understanding of the eavesdropping process, and will help resolve questions concerning the role of the outgoing click and off-axis frequencies within the echo process. Testing the multi-source echoic eavesdropping hypothesis will require eavesdropping experiments where the eavesdropper and the investigator are both allowed to inspect an object with echolocation. This type of experiment will determine to what extent multiple echolocation signals hamper or enhance discrimination performance. Perhaps the most straightforward method for testing both effective listening positions and multi-source jamming issues is to use an artificial click projector during a discrimination/detection task involving a single dolphin. By varying the position of the projector in relation to the dolphin, we may learn the importance of on-axis echo reception as it relates to the dolphin's ability to use (artificial) click echoes for object discrimination/detection. The artificial click projector can also be used to investigate a dolphin's ability to perform active echolocation discrimination/detection tasks while being 'jammed' by the projector. In addition to these types of experiments, observational work will need to focus on when and in what situations groups of dolphins engage their echolocation. If multi-source echoic eavesdropping occurs, one would expect groups of foraging dolphins to engage their echolocation en masse. If echoic eavesdropping occurs, less echolocation for a foraging group should be observed. Echolocation use for situations other than foraging (e.g., resting, traveling etc.) will also shed light on this issue. A capacity for object discrimination through echoic eavesdropping has been demonstrated (Xitco & Roitblat, 1996), but how this capacity manifests itself in the behavior of wild dolphins remains unknown. With the potential to contribute to our understanding of dolphin behavior and biosonar use in general, echoic eavesdropping is a valuable idea that deserves future attention.

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