

Studying Marine Mammal Cognition in the Wild: A Review of Four Decades of Playback Experiments

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Abstract

The playback of sounds to animals to assess their behavioural responses presents a powerful tool to study animal cognition in the wild. While playbacks are commonly used to study acoustic responses in birds and other terrestrial animals, their application to the study of marine mammal cognition so far has been limited. A survey of the published literature on field playback experiments with marine mammals identified 46 studies, with a trend towards increased use of playback approaches in recent years. Field playbacks to marine mammals have been used to address questions of wildlife management, the impact of anthropogenic noise, acoustic interactions between predators and prey, individual and kin recognition, as well as the function of communicative sounds. This paper summarizes the major findings of marine mammal playbacks to date and reviews recent advances in the design and execution of playback experiments, with special reference to marine mammals. Issues concerning appropriate presentation of acoustic stimuli, appropriate quantification of behavioural responses, as well as appropriate control and replication of treatments are discussed. An analysis of replication in marine mammal playbacks showed that the use of a small number of playback stimuli to conduct multiple playback trials (pseudoreplication) was common. This overview of playback experiments in the study of marine mammal cognition in the wild showed that such approaches contribute significantly to the field; however, in many cases, there appears to be substantial room for improvement of playback procedure and experimental design.

Key Words: playback experiment, response, marine mammal, cetacean, pinniped, mother-offspring recognition, communication, experimental design, pseudoreplication, controlled exposure experiment

Introduction

Playback is the experimental presentation of recorded sensory stimuli to animals to investigate their behavioural or psychophysiological responses. Test stimuli can be visual (using video projection; e.g., Ord et al., 2002; Rosenthal et al., 2004; Trainor & Basolo, 2006), but in practice, most playback experiments investigated responses to sounds. Playbacks of acoustic stimuli can be used to investigate responses to conspecific and/or heterospecific biological sounds as well as to anthropogenic noise. Playback has become an indispensable tool for researchers of animal behaviour and bioacoustics as well as for those conducting industrial noise mitigation studies. Cognition describes the higher-level processes involved in storing, editing, and integrating sensory information, such as memory, perception, and learning, and playback is probably the most commonly used method to study sound cognition and communication in wild animals. While its use is common in research on terrestrial animals, such as birds and anuran amphibians (see Falls, 1992, for an overview), playback is still only used infrequently to study marine mammal cognition, especially in the field. This fact may seem surprising in so far as most marine mammals rely primarily on sound to communicate and to obtain information about their environments.

In the austral spring of 1964, William Watkins and William Schevill of the Woods Hole Oceanographic Institution lowered an underwater speaker through a hole in the ice covering McMurdo Sound, Antarctica, to play recorded sounds from Weddell seals (*Leptonychotes weddellii*) back to these animals (Watkins & Schevill, 1968) and, thus, conducted one of the first field playbacks to a marine mammal in its natural habitat. Since this first field playback over four decades ago, there has been a slow, but steady, trickle of research using sound playbacks to study the acoustic cognition and communication of marine mammals with clear signs of an increasing trend since

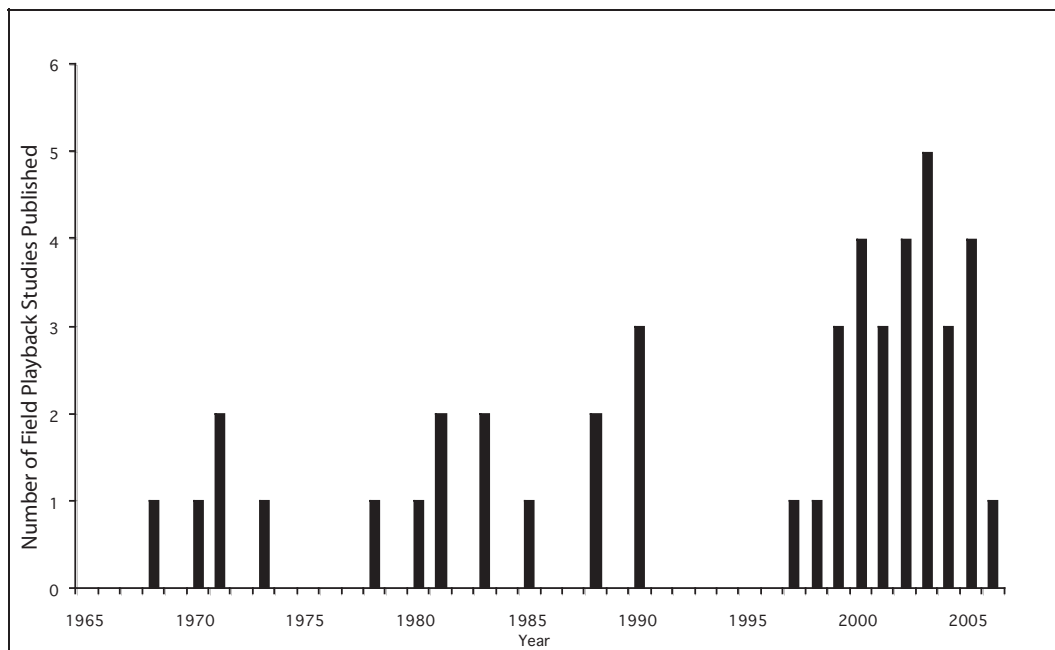


Figure 1. Histogram showing the number of studies involving field playbacks to marine mammals in the refereed literature (including academic theses, if not published elsewhere)

1999 (see Figure 1). Field playback experiments have brought about substantial progress in some areas of cognitive research, such as the study of acoustic mother-offspring recognition in otariids (e.g., Trillmich, 1981; Insley, 2001; Charrier et al., 2002a), and this success validates the usefulness of this approach. Yet, researchers in other areas of marine mammal cognition appear to be hesitant to use playbacks to answer cognitive questions. Field playbacks to odontocetes have been largely limited to two species: the bottlenose dolphin (*Tursiops truncatus*) (e.g., Sayigh et al., 1999; Gannon et al., 2005) and the beluga (*Delphinapterus leucas*) (Morgan, 1970, 1973; Fish & Vania, 1971). While several species of mysticetes have been studied using field playback experiments (gray whales, *Eschrichtius robustus*; humpback whales, *Megaptera novaeangliae*; right whales, *Eubalaena* spp., bowheads, *Balaena mysticetus*; and rorquals, *Balaenoptera* spp.), the majority of these studies have been controlled exposure experiments to assess responses to anthropogenic noise. The number of playback studies to learn about mysticete cognition and communication is limited. For sirenians, a single preliminary playback trial investigated acoustic recognition in a captive mother-offspring pair of Amazonian manatees (*Trichechus inunguis*) (Sousa-Lima et al., 2002) and a field experiment assessed the response of Florida manatees (*Trichechus manatus latirostris*) to boat noise (Miksis-Olds, 2005). A single controlled exposure

experiment has been conducted with polar bears (*Ursus maritimus*) to assess the impact of human noise (Eckhart, 2005). To date, no playback studies on sea otters (*Enhydra lutris*) have been published in the peer-reviewed literature.

Compared to the study of bird acoustic communication, where over 200 playback studies have been published in the last five years alone, it appears that researchers of marine mammals are slow to include playback components in their research projects. The reasons for the limited use of playbacks in marine mammal science are primarily the logistic challenges of studies at sea or at remote haulouts and rookeries, the high cost of conducting field research on marine mammals, and the difficulty of quantifying behavioural responses to underwater playbacks. In addition, many field studies into acoustic communication of marine mammals were only initiated relatively recently and therefore still provide insufficient background information to phrase complex cognitive questions. Additional research using playbacks has been conducted on marine mammals in captivity, and the results of this research underscore the value of the playback approach (e.g., Morgan, 1973; Thomas et al., 1990; Miksis et al., 2001; Shapiro et al., 2004). Captive playbacks have revealed much about the perceptive and cognitive abilities of marine mammals, information that could not have been obtained easily in the wild. Even so, learning how marine mammals apply their perceptive and cognitive abilities to find

food and evade predators in their aquatic habitat, and to function in their often complex social environments, requires studying wild marine mammals in their natural surroundings and social context. Framing questions about cognition, including those best answered with playbacks, requires a large amount of groundwork. As an example, formulating hypotheses about the function of vocalizations requires good description and sound understanding of the vocal repertoire and social interactions of a species. Quantifying changes in behaviour in response to playback experiments requires baseline information on normal patterns of behaviour and their variation from observational studies. Finally, conducting playbacks of biological sounds with adequate replication requires sufficient numbers of high-quality recordings of the sound stimulus, something that is currently available for only a very small number of marine mammal species.

As a number of long-term studies on wild populations of marine mammals reach maturity, this groundwork has been completed for a number of species from a variety of taxonomic backgrounds. Therefore, the time is ripe to take cognitive research into the wild, and the recent increase in the number of playback studies conducted with free-ranging marine mammals (see Figure 1) may well be reflective of this. At this point, it is valuable to take stock of the progress made so far as well as to examine research on terrestrial animals to learn from the expertise and knowledge gained here. The first objective of this paper is to provide an overview of the peer-reviewed literature on the use of playbacks to assess responses of wild marine mammals spanning four decades. The second objective is to discuss the design of playback trial and the analysis of the collected data with a special focus on issues and considerations relevant to marine mammalogy. Finally, I synthesize this information to point out solutions to common problems and new ways to integrate playback approaches into existing research projects. By assessing the contribution of field playbacks to the study of marine mammal cognition and establishing standards for sound playback design, I hope to better delineate the role of playbacks in the future of cognitive research on free-ranging marine mammals.

A Survey of Marine Mammal Playbacks

A Brief History of Playbacks to Marine Mammals in the Field

Since the publication of the first field playback study on marine mammals (Watkins & Schevill, 1968), there has been slow but steady progress in the application of playback techniques in the wild. The 1970s saw the first attempts to use playbacks of killer whale (*Orcinus orca*) calls as a tool in wildlife

management to exclude marine mammals from certain areas (Fish & Vania, 1971; Anderson & Hawkins 1978), as well as the first playbacks of conspecific calls to captive and free-ranging belugas (Morgan, 1970, 1973). During the 1980s, playback studies investigated mother-pup recognition by means of in-air sounds in pinnipeds (Trillmich, 1981), a line of research that has since undergone rapid expansion. In this decade, researchers conducted the first playbacks of conspecific sounds to mysticetes to gain an understanding of the function of acoustic communication in these species (Clark & Clark, 1980; Tyack, 1983; Mobley et al., 1988). The foundations for the study of impacts of anthropogenic noise on marine mammals using controlled exposure experiments were also laid at this time (Malme et al., 1983, 1988; Richardson et al., 1985). During the 1990s, all aspects of playback research on marine mammals expanded. Some of the long-term studies on marine mammals were reaching maturity, and this allowed researchers to address more complex cognitive questions (e.g., individual recognition: Sayigh, 1992; Sayigh et al., 1999). Dahlheim & Ljungblad's (1990) exploratory use of projected sounds to determine the hearing sensitivity of free-ranging baleen whales presents an innovative use of field playbacks conducted at this time.

With the turn of the millennium came a distinct increase in the interest in marine mammal playback research. Whereas before 1999, less than two field playback studies were published on average in the marine mammal literature in a given year, this number has since increased to consistently between three and six playback publications annually (see Figure 1). One area of increased interest has been the study of mother-pup acoustic recognition in pinnipeds (e.g., McCulloch et al., 1999; McCulloch & Boness, 2000; Charrier et al., 2001, 2002a; Insley, 2001). Here, several populations have been studied intensively for decades, providing a rich background of information that may explain the increase in playback studies. Another area that has shown a distinct increase in productivity is the study of responses of marine mammals to anthropogenic noise using controlled exposure experiments (e.g., Frankel & Clark, 2000; Miller et al., 2000; Fristrup et al., 2003). This increase in publications may well be due to heightened awareness and increased use of high-amplitude sounds for scientific (e.g., Acoustic Thermography of Ocean Climate [ATOC]) and military purposes (e.g., Low-Frequency Active Sonar [LFA]). Whether this recent trend towards more frequent use of field playback experiments in marine mammal bioacoustics represents a temporary phenomenon or whether it will continue into the future is currently difficult to say; however, the advances brought about in some areas of

marine mammal behaviour and cognition by the increased use of field playback experiments should make one hopeful that this trend continues.

Types of Marine Mammal Playback Studies

Sound playbacks to marine mammals have been used for a variety of purposes. In a few studies, playbacks served primarily as a research tool. For example, Deutsch et al. (1990) used in-air playbacks of sounds of aggressive males in combination with other stimuli to entice male Northern elephant seals (*Mirounga angustirostris*) to move onto a weighing platform to document changes in body weight over the course of the breeding season. Similarly, Hayes et al. (2004a) used underwater playbacks of vocalizations of male Pacific harbour seals (*Phoca vitulina richardii*) to identify territorial males and to map their territories. In the vast majority of studies, however, playback experiments were used to study the responses of marine mammals to acoustic stimuli and thus to gain insights into their behaviour and cognition. The primary areas of marine mammal science that have incorporated playback experiments are wildlife management, research into the impact of anthropogenic noise, the study of individual and kin recognition, the study of predator-prey interactions, and the study of the function of communicative vocalizations (see Figure 2). To assess the current state of marine mammal playback research, I summarize the 46 playback experiments conducted with marine mammals cited in Table 1 and will discuss their contribution to the different areas of research in more detail.

The Role of Playbacks in Marine Mammal Management

The role of sound playbacks in the management of marine mammals is to elicit behavioural responses in certain individuals to prevent them

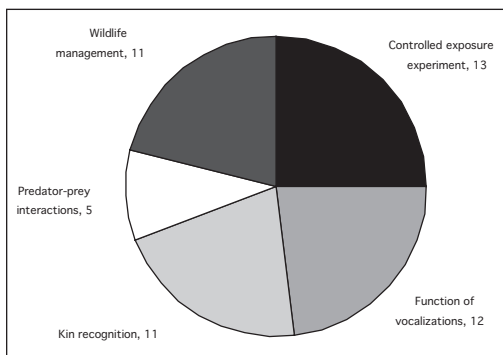


Figure 2. Pie chart showing the number of field playback experiments with marine mammals in five different areas of cognitive research

from interfering with human industrial activities (e.g., fishing), to save them from negative impacts caused by human activity (e.g., seismic testing, underwater explosions), or to prevent stranding or other accidental death. While the primary purpose of playbacks conducted for management reasons is not necessarily to learn about the animals' behaviour and cognition, such playbacks nonetheless often generate information that is highly relevant to cognitive or behavioural questions, thus warranting their discussion here.

One of the first playback experiments with cetaceans in the field was conducted by Fish & Vania (1971), who played recordings of killer whales to belugas in the Kvichak River, Alaska, with the objective to exclude them from the river to reduce predation on outmigrating salmon (*Oncorhynchus nerka*) smolts. While underwater playbacks of noise or music appeared to have little effect on the belugas' behaviour, they showed a strong avoidance response to playbacks of killer whale calls. While the playbacks clearly were successful from a management perspective, it remains unclear whether the belugas recognized the sounds as coming from killer whales; they also responded to two preliminary playbacks of 2.5 kHz randomly pulsed tones.

Anderson & Hawkins (1978) tested the effectiveness of underwater broadcasts of various synthesized and recorded sounds (killer whale calls as well as banging and shouting) to keep grey seals (*Halichoerus grypus*) away from salmon nets in Scotland. They found that none of the sounds was consistently effective at deterring seals from approaching or depredating nets. Shaughnessy et al. (1981) conducted underwater playbacks of killer whale calls to Cape fur seals (*Arctocephalus pusillus*) to test if such playbacks could be used to prevent fur seal depredation and interference with fishery operations off southern Africa. Fur seals showed distinctive and consistent behavioural responses to the playback of killer whale calls, but responses were of short duration. The animals dove for 10 to 30 s and oriented towards the sound source after which they typically resumed their previous activity. If playbacks were conducted to fur seals inside a set purse-seine net, 48 to 100% of the seals left the net, but most returned within 1 min of the start of the playback. Additional presentation of a visual stimuli (models of killer whale dorsal fins) had no recognizable effect. It therefore seems that the responses of the fur seals were too transitory for playback of killer whale calls to prevent depredation and interference in the long term. Iida et al. (2006) tested the effectiveness of in-air and underwater playbacks of artificially generated frequency sweeps and strobe lights to drive Steller sea lions (*Eumetopias jubatus*) away from

Table 1. Summary of field playback experiments with marine mammals, giving the species and research topic of each study; the column “Pseudoreplication” indicates whether trials were replicated to ensure statistical independence (simple = a single playback sequence was used per treatment; sacrificial = a few playback sequences were used for each treatment to conduct multiple trials, or focal individuals were used repeatedly; true replication = all trials were statistically independent or non-independence was addressed statistically).

Taxon species	Study	Primary research topic	Pseudoreplication
Balaenidae			
<i>Balaena mysticetus</i>	Richardson et al., 1985	Response to anthropogenic noise	Simple
	Richardson et al., 1990	Response to anthropogenic noise	Simple
<i>Eubalaena glacialis</i>	Parks, 2003	Function of vocalizations	Sacrificial
	Nowacek et al., 2004	Wildlife management	Simple
		Function of vocalizations	
<i>E. australis</i>	Clark & Clark, 1980	Function of vocalizations	Simple
Balaenopteridae			
<i>Balaenoptera physalus</i> & <i>B. musculus</i>	Croll et al., 2001	Response to anthropogenic noise	True replication
<i>Megaptera novaeangliae</i>	Tyack, 1983	Function of vocalizations	Sacrificial
	Mobley et al., 1988	Function of vocalizations	Sacrificial
		Wildlife management	
	Frankel & Clark, 1998	Response to anthropogenic noise	True replication
	Frankel & Clark, 2000	Response to anthropogenic noise	True replication
	Miller et al., 2000	Response to anthropogenic noise	True replication
	Fristrup et al., 2003	Response to anthropogenic noise	True replication
Eschrichtiidae			
<i>Eschrichtius robustus</i>	Cummings & Thompson, 1971	Predator-prey interactions	Simple
	Malme et al., 1988	Response to anthropogenic noise	Simple
	Dahlheim & Ljungblad, 1990	Response to anthropogenic noise*	True replication
Physeteridae			
<i>Physeter macrocephalus</i>	André et al., 1997	Wildlife management	Simple
	Goold, 1999	Wildlife management	N/A
	Rendell & Whitehead, 2005	Function of vocalizations	Sacrificial
Monodontidae			
<i>Delphinapterus leucas</i>	Morgan, 1970	Function of vocalizations	Simple
	Fish & Vania, 1971	Wildlife management	Simple
		Predator-prey interactions	
	Morgan, 1973	Function of vocalizations	Simple
Phocoenidae			
<i>Phocoena phocoena</i>	Olesiuk et al., 2002	Response to anthropogenic noise	True replication
	Koschinski et al., 2003	Response to anthropogenic noise	Simple
Delphinidae			
<i>Tursiops truncatus</i>	Sayigh et al., 1999	Individual and kin recognition	True replication
	Gannon et al., 2005	Predator-prey interactions	True replication
Otariidae			
<i>Arctocephalus galapagoensis</i> & <i>Zalophus californianus</i> <i>wollebaeki</i>	Trillmich, 1981	Individual and kin recognition	True replication
<i>Arctocephalus pusillus</i>	Shaughnessy et al., 1981	Wildlife management	Sacrificial
<i>A. tropicalis</i>	Charrier et al., 2001	Individual and kin recognition	True replication
	Charrier et al., 2002a	Individual and kin recognition	True replication
	Charrier et al., 2002b	Individual and kin recognition	Sacrificial
	Charrier et al., 2003a	Individual and kin recognition	True replication

Taxon species	Study	Primary research topic	Pseudoreplication
<i>A. tropicalis</i> (cont.)	Charrier et al., 2003b	Individual and kin recognition	Sacrificial
<i>Callorhinus ursinus</i>	Insley, 2000	Individual and kin recognition	Sacrificial
	Insley, 2001	Individual and kin recognition	True replication
<i>Eumetopias jubatus</i>	Iida et al., 2006	Wildlife management	Sacrificial
Phocidae			
<i>Mirounga angustirostris</i>	Deutsch et al., 1990	Wildlife management	N/A
<i>Halichoerus grypus</i>	Anderson & Hawkins 1978	Wildlife management	Insufficient information
	McCulloch et al., 1999	Individual and kin recognition	True replication
	McCulloch & Boness, 2000	Individual and kin recognition	True replication
<i>Phoca vitulina richardii</i>	Deecke et al., 2002	Predator-prey interactions	True replication
	Hayes et al., 2004a	Function of vocalizations	N/A
	Hayes et al., 2004b	Function of vocalizations	Simple
<i>Leptonychotes weddellii</i>	Watkins & Schevill, 1968	Function of vocalizations	Sacrificial
	Thomas et al., 1983	Function of vocalizations	Simple
Ursidae			
<i>Ursus maritimus</i>	Eckhart, 2005	Wildlife management	Sacrificial
Sirenia			
<i>Trichechus manatus latirostris</i>	Miksis-Olds, 2005	Wildlife management	Sacrificial

* This is a study to assess the hearing sensitivity of free-ranging animals.

haul-outs and fishing gear; they found that in-air playbacks resulted in the greatest avoidance followed by strobe lights and underwater playbacks.

Mobley et al. (1988) reported the first use of playbacks to prevent cetaceans from accidental stranding. A humpback whale had been sighted in the Sacramento River, California, in October 1985 for more than three weeks, causing concerns about its well-being. After playbacks of conspecific feeding calls from a vessel downstream, the animal turned and continued to follow the vessel for over 7 h until it reached the open ocean. During this time, the playback vessel broadcast the feeding calls only sporadically to avoid habituation. The same individual was sighted off the Farallon Islands, California, the following summer, suggesting that the attempt to return it to its normal habitat had been successful in the long term. Goold (1999) attempted to use playback of sperm whale (*Physeter macrocephalus*) codas to entice a group of six juvenile sperm whales to leave a narrow confined bay in the Orkney Islands, Scotland. A single playback trial was conducted in poor visibility and elicited a close approach to the playback vessel by one individual. These preliminary results suggest that playbacks of conspecific sounds may be an effective means to influence the movements of cetaceans in situations where the animals are disoriented or in danger of accidental stranding.

Three studies used playback experiments to investigate avoidance responses of marine

mammals to decrease the risk of vessel collisions. André et al. (1997) played various artificial and natural sounds to sperm whales off the Canary Islands, Spain, with the goal to use these sounds to reduce collisions with high-speed ferries in the region. They found little or no detectable response to killer whale calls, vessel noise, or percussive sounds. Playbacks of frequency sweeps and artificial codas caused some animals to stop vocalizing temporarily. Playback of a 10-kHz pulsed sound caused avoidance in some animals (strong avoidance in some cases); however, the animals appeared to respond only in certain behavioural contexts and there was evidence for habituation. To investigate means to reduce the number of ship strikes involving Northern right whales (*Eubalaena glacialis*), Nowacek et al. (2004) tested the response to playbacks of ship noise, conspecific social sounds, and a signal designed to alert the whales to an approaching vessel. The whales reacted strongly to the alert signal by swimming to the surface—unfortunately, this response was more likely to increase rather than decrease the risk of collision. The animals reacted mildly to the social sounds of conspecifics, but showed no response to recordings of approaching vessels or to actual vessels in their environment. Miksis-Olds (2005) used playbacks of recorded noise of small vessels and personal watercraft (jet skis) to test how and when Florida manatees detect approaching boats. She found that the animals generally responded to playbacks by moving towards deeper water. Responses to

playbacks of sounds of personal watercraft tended to be more drastic than to those of small boats at idle or at planing speeds. These three studies showed that playback experiments can be extremely useful to learn about how and when marine mammals detect and respond to approaching vessels.

These findings suggest that sound playback approaches should be considered in the development of effective management strategies for marine mammals. While the playback of predator sounds to exclude marine mammals from a given area may be effective in the short term, the results of playback trials of killer whale calls to Pacific harbour seals (Deecke et al., 2002) suggested that these animals are likely to habituate to such playbacks. Further research into the number and schedule of exposures leading to habituation is needed. The results of playbacks of conspecific sounds to remove cetaceans from locations where they may be in danger of accidental stranding are encouraging, but further controlled and replicated experimentation is required. Playback of predator sounds is not advisable in such situations since it is likely to evoke strong responses that could lead to further disorientation. The playback of vessel noise can help determine the extent to which different marine mammals rely on acoustic cues to detect vessels as well as to identify the mechanics of their escape response. In cases where this escape response occurs too late or is inappropriate to prevent collisions, transducers on ships could broadcast alerting sounds to warn the animals. More research is required into which types of sound could serve this purpose for different species, however. The stimuli tested so far (André et al., 1997; Nowacek et al., 2004) proved to be largely ineffective.

Controlled Exposure Experiments: Using Playbacks to Assess Responses of Marine Mammals to Anthropogenic Noise

Anthropogenic noise generated by increasing human activity in the marine environment has the potential to negatively affect marine mammals—animals that have sensitive underwater hearing and rely extensively on sound for orientation and communication. Increasing awareness of the potential effects of noise pollution has led to calls for experimental approaches to quantify the impacts of different types of anthropogenic noise. Controlled exposure experiments are field studies designed to broadcast controlled doses of an acoustic stimulus to assess behavioural and/or physiological responses of animals with the ultimate goal to determine population-level impacts of the noise source (Tyack et al., 2003; but see Bejder et al., 2006). They are therefore playback experiments in the wider sense of the word. While their primary purpose is not to learn about animal

cognition, they nonetheless often provide data on the hearing sensitivity, response thresholds, nature of avoidance responses, and other information relevant to the study of cognition and, therefore, are included here.

The first controlled exposure experiments were conducted in the 1980s to assess the effect of noise associated with offshore oil and gas extraction (airgun sounds and drilling noise) on grey whales off California and in the Bering Sea (Malme et al., 1983, 1988), as well as on bowhead whales in the Beaufort Sea (Richardson et al., 1985, 1990). These studies documented some avoidance when animals were exposed to playbacks of drill ship noise, although feeding grey whales appeared to be more tolerant compared to migrating animals. The fact that certain individual bowheads were regularly observed near drill ships and dredges (Richardson et al., 1990) in spite of documented avoidance by most animals suggests that either there is substantial variation among individuals in their tolerance to anthropogenic noise or animals will eventually habituate to it. All studies found significant avoidance in response to airgun blasts.

Most controlled exposure experiments with marine mammals to date have been conducted with humpback whales in the Hawaiian Islands. The first experiments here were conducted to assess the effect of a low-frequency (60 to 90 Hz) sound source used in the Acoustic Thermometry of Ocean Climate (ATOC) experiment to measure long-term changes in ocean temperature. Playbacks of ATOC sequences with a reduced source level showed that the time between surfacings and the distance covered under water increased with higher received sound level (Frankel & Clark, 1998). Experimental broadcasts using the full experimental source level (195 dB re. 1 μ Pa) confirmed this finding (Frankel & Clark, 2000). From a cognitive perspective, the suggestion that humpbacks exposed to low-frequency noise spend more time at depths may seem counterintuitive since this response will actually increase their exposure to the sound.

In the 1990s, the U.S. Navy developed a powerful sonar (SURTASS-LFA) based on frequency sweeps in the range of 150 to 320 Hz, with reported source levels of up to 215 dB re. 1 μ Pa. One controlled exposure experiment has investigated the behaviour and distribution of fin (*Balaenoptera physalus*) and blue (*B. musculus*) whales off California (Croll et al., 2001) and did not find any obvious responses to the sound. Two experiments have investigated the effect of SURTASS-LFA on the singing behaviour of male humpback whales. Miller et al. (2000) followed and recorded focal singers for at least two full songs before broadcasting sonar signals with received sound levels of 150 dB re. 1 μ Pa or less at 6 min intervals.

The six individuals that continued to sing during exposure increased the length of their songs by 29% during playback compared to pre-playback songs. Song length returned to normal after playbacks. Fristrup et al. (2003) measured diel variation in song length and also conducted playbacks of sonar signals (received sound pressure level for the nearest animal: 120 to 155 dB re. 1 μ Pa). Song length was highly variable and increased during the course of the day. Song length also increased on days with higher local whale density and at times of heightened social activity. Playbacks showed that males increased the length of their songs if these were overlapped by sonar signals, and that the increase was greater than expected if singers simply compensated for song time masked by the signal. There also appeared to be a significant delay in the response; songs 1 to 2 h after the last playback in a series were longest. These two studies make an interesting contribution to the field of marine mammal cognition since they provide the first information on how noise interference affects acoustic signalling behaviour.

Two studies investigated the response of harbour porpoises (*Phocoena phocoena*) to anthropogenic noise. Olesiuk et al. (2002) studied the response of this species to acoustic harassment devices used by aquaculture operations to prevent pinniped depredation of farmed fish. They documented a drastic avoidance response, and exclusion extended substantial distances from the sound source. Even at distances of 2.5 to 3.5 km from the source, the observed number of porpoises was typically 8% of what would be expected had there been no response. Koschinski et al. (2003) investigated the response of harbour porpoises and Pacific harbour seals to underwater playbacks of noise generated by an offshore wind generator; they documented a significant shift in the distribution of porpoises and seals away from the sound source. The response of the harbour porpoises was not as drastic as their response to acoustic harassment devices. To date, the study by Koschinski et al. is the only controlled exposure experiment to have been published on pinnipeds. This is rather surprising given the abundance of certain pinniped species around centres of human activity. Eckhart (2005) conducted in-air playbacks with polar bears to test their response to recordings of human voices to determine the impacts of ecotourism operations. This study did not find a detectable response to the playbacks.

In an interesting variant of a controlled exposure experiment, Dahlheim & Ljungblad (1990) used an underwater loudspeaker to play tonal sounds to free-ranging gray whales on the Mexican breeding grounds in order to determine their hearing sensitivity and thus assess impacts of anthropogenic

noise. While the study is preliminary in nature due to limited sample size, this approach has the potential to obtain audiogram information from species that are difficult to keep in captivity.

Playback Experiments in the Study of Individual and Kin Recognition

Many marine mammals live in environments where vision and olfaction are limited and, therefore, they rely primarily on acoustic cues to detect or recognize each other. Playback experiments have provided an excellent tool to determine the mechanisms and functions of kin recognition, to identify the acoustic features that code individual or group-specific variation, and to establish the distance over which recognition can occur as well as the time over which vocal features are remembered. While acoustic analysis can help to test whether vocalizations of a species exhibit individual or group-specific variation, playback presents the only means to establish whether such variation is actually used for recognition (e.g., see McCulloch et al., 1999).

Most research on vocal recognition in marine mammals so far has focused on mother-pup recognition by means of in-air calls in pinnipeds. Many species breed in crowded rookeries, and females and pups often have to find each other over distances beyond the range where visual or olfactory recognition are possible. While female phocids generally have short maternal care, and mothers stay with their pups for the entire time in many species, otariids typically have a lactation period that lasts several months during which mothers leave for extended foraging trips. Trillmich (1981) first used in-air playbacks to investigate mother-pup recognition in two species of otariid: the Galápagos fur seal (*Arctocephalus galapagoensis*) and the Galápagos sea lion (*Zalophus californianus wollebaeki*). He demonstrated that acoustic recognition was mutual—not only did mothers discriminate between calls of their own pups and those of strange pups, but pups also discriminated between calls of their mothers and those of an unrelated female. Mutual recognition has since been documented in a variety of otariid species (Charrier et al., 2001; Insley, 2001).

Playback research conducted with fur seals has helped clarify important cognitive aspects of parent-offspring conflict. Parent-offspring conflict results primarily from the fact that the relative costs and benefits of parental investment are not equal for parents and for offspring (Trivers, 1974) and has implications for the relative importance of effective mother-pup recognition. Wiley (1994) provided a valuable framework for the analysis of errors in animal communication based on the premise that animals cannot simultaneously minimize both false

alarms (responding to an inappropriate signal) and missed detections (failing to respond to an appropriate signal). Instead, they are forced to make compromises with respect to the relative importance of either error. For a female fur seal, the cost of responding to the call of a strange pup (a false alarm) is a waste of a valuable resource (milk) likely causing her own pup to starve. The cost of failing to respond to calls of her own pup (a missed detection) similarly causes the loss of her pup. For a pup, the cost of a false alarm is possible injury caused by aggression from an unrelated female, while the much greater cost of a missed detection is certain death by starvation. The large asymmetry in the cost of false alarms and missed detections in pups suggests that pups should have a more liberal response criterion compared to females. This has indeed been demonstrated both in Northern (*Callorhinus ursinus*) and Subantarctic (*Arctocephalus tropicalis*) fur seals through playbacks of in-air calls (Insley, 2001; Charrier et al., 2002b, 2003b). In addition, Subantarctic fur seal pups increase their likelihood to respond to calls from an unrelated female the longer their mothers remain absent (Charrier et al., 2002a), probably reflecting an increasing cost for missed detections. Presumably because the costs of recognition errors are so high, fur seals have evolved impressive abilities for acoustic discrimination. Newborn Subantarctic fur seals learn to recognize their mothers' calls within a matter of days (Charrier et al., 2001). Females in this species are able to account for maturational changes in the structure of their pup's call and recognize it after up to three weeks of absence (Charrier et al., 2003a), and young Northern fur seals are able to retain maternal calls in memory for at least four years (Insley, 2000).

In contrast to otariids, phocids typically lack extended lactation periods, and mothers and pups typically remain together until weaning in many species. Many phocid seals also breed in dense aggregations, however, and ice-breeding species cannot always rely on landmarks to relocate mothers or pups should separation occur. McCulloch et al. (1999) analysed calls of grey seal pups on the Isle of May, Scotland, for individual variation and conducted playback experiments to test whether females used such variation to discriminate between the in-air calls of their own pup and strange pups. The analysis detected pronounced individual variation in call structure, but playbacks showed that females failed to discriminate between calls of filial and nonfilial pups. Observations showed that suckling of strange pups (allosuckling) was common in this colony, which suggests that non-acoustic means of pup recognition are also rudimentary in this population. In contrast, playback trials conducted with grey seals on Sable Island, Canada, showed that females consistently

recognized the calls of their own pups (McCulloch & Boness, 2000). This is surprising in so far as separations of mother-pup pairs are far less common on Sable Island than on the Isle of May. The two studies illustrate the point that the presence of individual variation alone is insufficient evidence for discrimination and show that abilities for acoustic discrimination can vary tremendously among different populations of the same species.

Mother-offspring recognition only requires that the mother and the offspring memorize a single vocalization type and discriminate between it and all other vocalizations. In its simplest expression, such recognition could be achieved by discrimination between familiar and unfamiliar vocalizations (but playback experiments using calls of neighbouring unrelated females or pups argue against this possibility; see McCulloch & Boness, 2000). True individual recognition in contrast requires that animals are able to discriminate between vocalizations of several individuals not based on familiarity alone, thus demonstrating a mental association between the vocalization and the identity of the caller. Such true individual recognition is thought to be a prerequisite for much social behaviour. Sayigh et al. (1999) played signature whistles back to temporarily restrained female bottlenose dolphins and their independent offspring in Sarasota Bay, Florida. Females reacted significantly stronger to underwater playbacks of whistles of their independent offspring compared to those of an unrelated, but familiar individual of similar age. Similarly, offspring reacted significantly stronger to playbacks of whistles of their mothers compared to those of an unrelated, familiar adult female. The fact that independent offspring only travel with their mothers infrequently in this population in combination with the lack of responses to whistles of familiar, unrelated individuals rules out familiarity as the sole basis of recognition and, therefore, makes a strong case for true individual recognition. Janik et al. (2006) recently obtained the same responses from playbacks of artificially resynthesized signature whistles demonstrating that individual identity is encoded in the shape and frequency contour of the whistle rather than some other acoustic feature.

The study of individual and kin recognition in marine mammals is a research area where playback approaches have been employed with the most success to investigate the cognitive abilities of marine mammals in the wild. By no means has this field been researched exhaustively, however. Mother-offspring recognition has been studied only in a small number of species from a narrow taxonomic range. Additional research into recognition abilities of phocid seals may be especially rewarding. While several species of odontocetes exhibit

complex group-specific variation in their vocal repertoires (e.g., killer whales: Ford, 1991; Yurk et al., 2002; sperm whales: Rendell & Whitehead, 2003), the use of playback studies to determine the possible function of such variation has been limited to a single study—Rendell & Whitehead (2005). Rendell & Whitehead played codas back to social groups of sperm whales in Chilean waters to assess the function of variation in coda patterns but found few consistent responses. Given the amount of information provided by the application of playbacks to the study of other marine mammal recognition systems, further playback studies seem especially timely here.

Playback Experiments in the Study of Predator-Prey Interactions

Many marine mammals rely primarily on sound to localize prey or to detect the approach of predators. To date, little research has investigated the acoustic dimension of predator-prey interactions; however, the few studies conducted in this field have demonstrated that certain species employ complex cognitive abilities to evade predators or to detect and capture prey. So far, all field playback experiments to marine mammals as potential prey have investigated responses to playbacks of killer whale calls. Cummings & Thompson (1971) played a recording of killer whale calls to migrating grey whales off California and documented strong avoidance—gray whales approaching the playback vessel turned around and headed away from the playback source. The animals remained cryptic by surfacing low and creating little surface disturbance. Some individuals headed for kelp beds and stayed there until playbacks ceased, spy-hopping frequently. This study showed that gray whales rely at least in part on acoustic cues to locate their main predator and that they possess the ability to precisely localize the source of a sound. As discussed earlier, Fish & Vania (1971) played the same recordings to belugas similarly eliciting strong avoidance.

Deecke et al. (2002) investigated the response of Pacific harbour seals to underwater calls of different types of killer whales and found that the seals were able to discriminate between the calls of local fish-eating and mammal-eating killer whale populations. Given the fact that the fish-eating populations show a complex system of group-specific variation in vocal repertoires (Ford, 1991), the seals' ability to discriminate between populations is an impressive cognitive feat. While the seals did not respond to the calls of local fish-eating populations, playbacks of calls of a closely related and ecologically similar fish-eating population found 600 km to the north elicited a strong response. The fact that the seals ignored the calls of familiar fish-eating killer whales but responded

to the calls of fish-eating killer whales with which they had no prior experience showed that the discrimination is the result of selective habituation. The seals started with a general acoustic predator image that presumably includes all killer whale calls from which they have eliminated certain irrelevant cues, namely the calls of harmless fish-eating killer whales, by habituating to them. The seals therefore learned what not to fear and thus focused their fear on local threats identified by learning and experience.

The fact that harbour seals selectively habituated to calls of harmless familiar killer whales raises interesting questions about the earlier playback experiments with gray whales and belugas. Comparison of the spectrograms provided by Cummings & Thompson (1971) with those of Ford (1991) shows that both playbacks were of a recording of Southern Resident killer whales, a population known to feed exclusively on fish (Ford et al., 1998). The fact that belugas and gray whales responded so strongly to the calls of killer whales that pose no threat to them suggests either that they had insufficient experience with the calls of Southern Resident killer whales or that gray whales are unable to habituate to killer whale vocalizations.

Gannon et al. (2005) conducted the first and so far only playback experiment to study prey detection by a marine mammal predator. Although bottlenose dolphins have sensitive echolocation abilities, they echolocate surprisingly little in the wild, raising the possibility that they may localize prey through passive listening. To test this possibility, Gannon et al. played recordings of different sound-producing fish to bottlenose dolphins in Sarasota Bay. Recordings of snapping shrimp (*Alpheus* spp.) served as a control. Focal dolphins responded to the playback of fish sounds by orienting significantly more towards the sound source and increasing their echolocation output. These results could be partially explained by a response to a novel sound stimulus (snapping shrimp were recorded in Sarasota Bay, while fish sounds came from a variety of locations), but, nonetheless, the playback experiments showed that wild dolphins exhibit interest in the fish sounds, which provided some of the first evidence in support of the passive listening hypothesis.

Given how little is known about prey localization in marine mammals, it is surprising that similar playback approaches have not been used more often. We currently have no information on the mechanisms by which baleen whales detect concentrations of fish or crustaceans. Playbacks of sounds recorded from crustacean swarms or fish schools would be comparatively easy to conduct to determine the role of passive listening. In the northeast Pacific, mammal-eating killer whales use

echolocation extremely sparingly, and Barrett-Lennard et al. (1996) suggested that these predators may similarly rely on passive listening for sounds generated by their marine mammal prey. Again, testing this hypothesis using playbacks of sounds recorded from potential prey (echolocation clicks, breathing sounds, and communicative vocalizations) would be relatively straightforward.

Playback Experiments to Determine the Function of Communicative Vocalizations

Testing hypotheses about responses to conspecific sounds using playback experiments is one of the most powerful approaches to determine the function of such vocalizations. Indeed, the first field playback experiment on marine mammals was conducted with such a hypothesis in mind. Watkins & Schevill (1968) played back recordings of different conspecific underwater sounds to Weddell seals to test the prediction that trills function in dominance, low pulses are threat displays, and chirps may represent inquiry. While the observed responses did not necessarily confirm these predictions, the experiments showed for the first time that it is possible to elicit realistic responses from marine mammals using underwater playbacks. This study also provided some of the first evidence for vocal matching in a free-ranging marine mammal. Focal animals often responded to playbacks by emitting a vocalization of the same type. Thomas et al. (1983) expanded on this research by investigating vocal responses of Weddell seals to playbacks of sequences of conspecific calls at breeding sites and nonbreeding haulouts at McMurdo Sound, Antarctica. They were able to assign function (such as territorial advertisement, aggression, threat, and submission) to several vocalization types as well as document a difference in the vocal response from breeding and nonbreeding animals.

Hayes et al. (2004b) used playbacks to determine the function of underwater sounds produced by Pacific harbour seals during the breeding season. At this time, male harbour seals produce distinctive low-frequency vocalizations thought to form part of a lek display or play a role in male-male competition. The structure of these vocalizations appears to be correlated with the dominance status of vocalizing males. Juvenile males of low status produce calls of higher frequency and shorter duration than dominant individuals. To determine whether these vocalizations play a role in male-male competition, Hayes et al. conducted underwater playback experiments at eight locations in an estuarine channel. To test whether males use structural features of the call to obtain information about the dominance status of the calling individuals, short, high calls as well as long,

low calls were played. The playback trials showed that males held territories—the same individual always responded to playbacks at the same location, and where sex could be established it was always found to be a male. The results also suggested that call structure codes information about the caller's dominance status, and that territorial males use this information to make behavioural decisions—that is, male seals responded more often with territorial behaviour (approaching and slapping the water surface with hind or pectoral flippers) to playbacks of short, high-frequency calls indicating a subdominant intruder.

Morgan (1970, 1973) used playbacks to both free-ranging and captive belugas to investigate the function of different vocalizations. All playbacks to free-ranging belugas in the St. Lawrence Estuary, Canada, caused a decrease in vocal activity but elicited no change in the dive behaviour of the group. Playbacks of certain sounds, such as jaw claps, caused some individuals to approach the boat and inspect the sound source. Playback of a stereotyped call type recorded from a captive individual back to the same animal consistently caused the animal to respond with the same call type. This provides evidence for call matching and suggests that this particular call type may serve as a contact call. The fact that the captive animals showed very little response to vocalizations of free-ranging animals and vice versa caused Morgan to suspect geographic variation in beluga vocalizations. This has been confirmed since then through analysis of vocal repertoires (e.g., Angiel, 1997; Bel'kovich & Sh'ekotov, 1993).

Clark & Clark (1980) conducted the first playbacks of conspecific sounds to mysticetes to test if Southern right whales (*Eubalaena australis*) respond differently to recordings of their species' calls compared to artificial sounds of similar frequencies, human imitations of Southern right whale calls, or humpback whale sounds. Playbacks were started when a single whale or small group had passed a loudspeaker moored 100 m offshore and were headed away from it. When conspecific calls were played, right whales consistently turned and moved towards the speaker, increasing their vocal output. The single broadcast of human imitations of Southern right whale calls produced a similar response. Southern right whales that were exposed to broadcasts of artificial signals, humpback whale sounds, or control playbacks (recordings of water noise) continued to move away from the speaker and did not vocalize more. The study therefore showed that Southern right whale vocalizations attract conspecifics. More recently, Parks (2003) investigated whether calls recorded from surface active groups of Northern right whales and lone individuals attract conspecifics. Surface active groups are typically

composed of a single adult female with two or more males engaged in surface active behaviour. They are thought to play a role in reproduction and are accompanied by a distinctive type of vocal behaviour thought to originate from the female. Another type of vocalization called the "gunshot sound" is thought to be produced exclusively by males. Parks found that playbacks of sounds from surface active groups typically elicited approaches by nearby individuals. This response appeared equally strong for recordings of conspecific (Northern right whale) and heterospecific (Southern right whale) surface active groups. All identified individuals approaching after playbacks of calls from conspecific surface active groups were male, but playbacks of heterospecific calls elicited approaches by females and juveniles as well as males. Right whales did not respond with approach to playbacks of gunshot sounds. These results suggest that Northern right whales approach playbacks of conspecific and heterospecific calls for different reasons. Males presumably move towards playbacks of sounds of conspecific surface active groups because they perceive them as a mating opportunity, whereas the approach of all age and sex classes to sounds of heterospecific surface active groups may represent inquisitiveness towards a novel stimulus. The lack of responses to playbacks of gunshot sounds showed that whales do not respond indiscriminately to all right whales sounds.

Tyack (1983) and Mobley et al. (1988) conducted underwater playbacks of different types of conspecific vocalizations to humpback whales off Hawaii. Tyack played recordings of songs: long patterned sequences of stereotyped vocalizations exclusively produced by males, and social sounds, which are vocalizations and percussive sounds produced by groups of five to eight individuals in which males were fighting, probably for access to a female in the group. Focal males that were singing during playback trials typically stopped upon hearing both songs and social sounds. Whales occasionally approached the boat rapidly after playback of social sounds but never after the playback of songs. Instead, whales typically moved away after the playback of songs, as did all animals that did not charge when exposed to social sounds. The results showed that, much like right whales, sounds of surface active groups attract humpback whales. Attraction may not be the primary purpose of the social sounds, however. Instead, they may function in the interactions between males in a surface active group, and other males may cue in on these sounds to locate groups. Mobley et al. (1988) similarly played recordings of songs and social sounds and, in addition, presented whales with synthesized sounds as well as recordings of feeding calls recorded in southeastern Alaska during the summer

months. At 163 dB re. 1 μ Pa, the sound level of the playbacks of Mobley et al. was 8 dB higher than that of Tyack, but both playback levels fall within the range of normal peak source levels of humpback song (151 and 173 dB re. 1 μ Pa, respectively; Au et al., 2006). Unlike Tyack, Mobley et al. found no evidence that animals moved away from playbacks. The presentation of feeding calls elicited the largest number of fast approaches followed by social sounds, synthetic sounds, and songs. Only 8% of focal animals responded with fast approaches to playbacks of social sounds compared to 55% in the study of Tyack. This difference could be due to the difference in playback volume, perhaps signalling a difference in the perceived urgency or threat of the playback stimulus. Although fast approach responses to songs were extremely infrequent, it appears that playback of old versions of songs (recorded four years prior to playback) elicited more fast approaches compared to playbacks of recently recorded songs. The finding of both studies that song playbacks did not attract focal animals suggests that one important function of humpback song is territoriality and male-male competition. This does not, however, preclude a role in mate attraction and female choice.

These studies illustrate the usefulness of a playback approach to answer functional questions about marine mammal vocalizations. While observational studies provide a valuable contribution towards formulating hypotheses about the function of vocalizations, testing these hypotheses requires experimental manipulation best done using playback procedures. It is therefore not surprising that the most revealing playback studies discussed here were those in which clear hypotheses about the functional significance of sounds were formulated *a priori* from observational data and tested using playback trials (e.g., Parks, 2003; Hayes et al., 2004b). Since we are only beginning to understand the acoustic behaviour of many marine mammal species sufficiently to be able to formulate such hypotheses, playback experimentation will continue to play a strong role in this field for years to come.

Methodological Considerations of Playback Experiments

The Challenge of Conducting Marine Mammal Playbacks in the Field

Compared to studies of terrestrial animals, such as songbirds or anuran amphibians, conducting field playbacks with marine mammals can be challenging. Equipment for the recording and broadcast of underwater sound tends to be costly. Boat-based research in exposed areas can be limited to extremely short time windows. Animals

can be difficult to localize and detect, and quantifying behavioural responses under water can be difficult or impossible. These logistical constraints are probably an important reason why playback experiments to study marine mammal cognition in the wild have been so limited in number. Even so, the review of marine mammal field studies that have used playback techniques to date has shown that the logistical challenge of conducting field playbacks is a small price to pay for the analytical power of the approach. In fact, it is exactly because of this logistical challenge and the high cost of field research of marine mammals that it is important that researchers in this field follow sound playback protocol and analytical procedure to avoid frustration, the misdirection of funds and research effort, and the collection of meaningless data and presentation of erroneous conclusions. I will point out some of the considerations involved in designing and conducting playback experiments

of high scientific quality with marine mammals. Much discussion has focused on improving the quality of playback experiments with terrestrial animals (e.g., Kroodsma, 1989; Gerhardt, 1992; McGregor, 1992b), and it seems timely to draw on the experiences gained to address the same issues for marine mammals. Issues to consider when designing and conducting field playback experiments with marine mammals are summarized in Table 2 and discussed in detail below.

Appropriate Presentation of Playback Stimuli

Whether a focal individual will perceive a playback stimulus as realistic enough to exhibit an appropriate response depends on the urgency of the signal, the fidelity of the stimulus, its source level, as well as the context in which it is presented. The urgency of any signal is determined by the importance of an appropriate response to the receiving individual's fitness. Signals have high urgency if an appropriate

Table 2. Checklist for experimental design and protocol for conducting playback experiments with marine mammals in the field

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1. Appropriate presentation of playback stimuli
 - a. The urgency of the presented stimulus should be high enough to expect a response.
 - b. The frequency response of the recording and playback equipment should be adequate to cover the frequency band audible to the study species.
 - c. The source levels of the playback must be determined and should fall within the range typical for the stimulus.
 - d. The playback stimulus should be presented in the behavioural context in which the animal(s) would normally experience it.
 - e. The playback stimulus should be presented from a distance similar to that at which first detection would normally occur.

 2. Quantifying responses to playbacks
 - a. Acoustic indicators of response variables, such as inspection behaviour, orientation, and communication, should be considered in situations where visual documentation of responses is difficult.
 - b. Use of telemetry or data-logging devices can provide valuable information about responses to playbacks.
 - c. Observational studies and pilot playback trials can help identify responses and choose appropriate response variables.
 - d. A multivariate analysis of many behavioural parameters should be performed in situations where the relevant response variables are difficult to identify *a priori*.

 3. Appropriate control of playback stimuli
 - a. All equipment and personnel used to broadcast sound and document behavioural responses must be in place and operational during the control condition to control for observer effects.
 - b. Sound sequences used as controls must contain background noise of similar amplitude and spectral composition as the treatment sequences to control for extraneous stimuli.
 - c. Positive controls using stimuli known to evoke responses can provide valuable information in situations where it is unclear whether a treatment will elicit a response.

 4. Appropriate replication
 - a. Playback trials treated as independent in the statistical analysis should each be conducted with different, independent exemplars of the playback stimulus.
 - b. Playback trials treated as independent should be conducted with different, independent focal individuals or groups.
 - c. If independence of replicate trials cannot be achieved due to logistical constraints, this should be addressed in the statistical analysis.
 - d. If independence of trials cannot be achieved, published results should clearly identify which trials are truly independent and which are not.

response is required to ensure an animal's survival or reproduction, and signals have low urgency if an appropriate response brings only a minor fitness benefit. Animals are much more likely to respond to playbacks of urgent signals of relatively poor fidelity. The difference in response to manipulated calls by female and pup fur seals observed by Charrier et al. (2002b, 2003b) illustrates this point. This fact can explain the relative success of eliciting realistic responses by playbacks of predator calls compared to playbacks of conspecific communicative vocalizations not immediately related to reproduction or survival.

Fidelity describes the acoustic quality (in terms of signal-to-noise ratio, frequency range, and distortion) of a recorded and broadcast signal. Watkins & Schevill (1968) already noted the importance of fidelity in playback experiments. While broadcasts of conspecific calls of poor acoustic quality elicited aggressive responses but no vocalizations from Weddell seals, playbacks of higher fidelity elicited vocal rather than physically aggressive responses. Many marine mammals have excellent high-frequency hearing, and the playback stimulus should ideally be recorded and broadcast in the entire frequency band audible to the study species. High frequencies experience greater attenuation under water. Therefore, it may be possible in a few cases to realistically broadcast playback stimuli using equipment with an upper-frequency limit below that of the study species' hearing by designing the playback set-up to re-create the perception of distant sounds rather than ones generated right next to the focal individual. In any case, it is important to know as much as possible about the hearing abilities of the study species before purchasing equipment to record and broadcast playback stimuli. It is also good procedure to re-record several examples of the playback stimulus and to analyze them for frequency content and fidelity (e.g., Rendell & Whitehead, 2005).

Similar considerations apply to choosing the appropriate source level for playback. Choosing a source level that is too low may result in animals failing to detect the playback stimulus or ignoring it because they do not perceive it as realistic or urgent. The latter possibility is a concern especially with sounds used in mate attraction or intrasexual competition where source levels may code information on the quality of the calling individuals. Conversely, choosing a source level that is too high and thus creating a supernatural stimulus may equally elicit unrealistic responses or result in the animals failing to respond at all. Adjusting source levels of playbacks to simulate distant stimuli may be possible to a degree. However, doing so may elicit an equivocal response since marine mammals are likely to rely on additional cues,

such as signal degradation and differential decay, to determine their distance to the sound source (see Tyack et al., 2003). While measuring source levels in the terrestrial environment is relatively inexpensive and easy, obtaining such measurements in the aquatic environment requires the use of calibrated hydrophones. The potential dangers associated with using inappropriate source levels for playbacks make this extra investment of money and effort well worthwhile. For descriptions of different methods to measure source levels of sounds produced by marine mammals, see Janik (2000), Wahlberg et al. (2002), and Miller (2006). Due to the complexities of sound propagation under water, it is also useful to take sound-level measurements at various distances from the playback source to map the generated sound field empirically and estimate received levels for focal animals at various locations (e.g., Malme et al., 1988; Frankel & Clark, 1998, 2000).

An important consideration when conducting playback experiments is the behavioural context in which animals are exposed to the stimulus. Many communicative signals are associated with specific contexts, and presenting them outside of their contexts can evoke responses quite different from those typically observed. For example, the fact that Mobley et al. (1988) observed very strong responses to playbacks of Alaskan feeding calls from humpback whales on the breeding grounds in Hawaii, a context in which these animals would not normally experience these sounds, does not mean that the animals would necessarily respond in the same manner on the Alaskan feeding grounds. Similarly, the playback of sounds associated with reproductive behaviour (e.g., Hayes et al., 2004b) may elicit very different responses (or fail to elicit any response) from nonbreeding animals (see also Thomas et al., 1983). External sound stimuli, such as heterospecific sounds or anthropogenic noise, can also elicit very different responses depending on the behaviour state of the focal animal before and during playback (e.g., Malme et al., 1983, 1988). For animals with both underwater and in-air hearing, sounds that are typically heard under water may elicit very different responses when presented in the air and vice versa. Determining the appropriate context for a playback stimulus requires a good understanding of the behavioural repertoire and communication system of the study species—information that can be obtained from observational studies.

A related issue concerns the appropriate distance of the playback source to the focal animal. Many underwater acoustic signals of marine mammals are audible over many kilometres (e.g., Janik, 2000; Møhl et al., 2000; Zimmer et al., 2005; Miller, 2006). Projecting such long-range

signals at natural source levels in close proximity to a focal animal creates an unnatural situation since under normal circumstances the animal would likely have perceived faint degraded versions of the signal long before hearing it at close range. This unnatural situation can elicit responses not representative of normal behaviour. The lack of consistent responses of sperm whales to coda playbacks reported by Rendell & Whitehead (2005) may be attributable to the fact that playbacks were conducted as close as 50 m to the nearest whale when sperm whales can probably detect coda vocalizations over many kilometres. Simulating long-range detection in underwater playbacks to marine mammals requires a great spatial distance between the focal animal and the playback source and, therefore, often necessitates the use of a separate observation platform to document responses. The possibility of simulating long-range detection by decreasing source level is limited since this fails to provide other range cues such as signal degradation and differential decay (Tyack et al., 2003).

Quantifying Behavioural Responses

One of the biggest challenges of conducting underwater playbacks to marine mammals lies in the difficulty inherent in documenting behavioural responses in animals that spend the majority of their time under water. In animals such as odontocetes, however, that navigate and communicate primarily using sounds, behavioural responses typically have an acoustic component, and acoustic responses are relatively straightforward to document and measure (e.g., Thomas et al., 1983; Gannon et al., 2005). Classic response variables in terrestrial playbacks include the following: (1) inspection of the playback source, (2) orientation or movement towards or away from the playback source, and (3) acoustic responses. In most odontocetes, the occurrence of inspection is easily documented by listening for echolocation clicks. The vocalizations of many marine mammals have directional components (e.g., Møhl et al., 2000; Miller, 2002; Lammers & Au, 2003) so that orientation with respect to the sound source can be inferred acoustically in cases where focal animals vocalize. Use of hydrophones for acoustic localization of focal animals can help to document movement away from or towards the sound source in these situations. Finally, most marine mammals rely primarily on sound for underwater communication, making any communication in response to playbacks easy to document.

Recent advances in the development of telemetry techniques and data-logging devices have greatly improved the ability of researchers to document underwater and surface behaviour of

marine mammals. These techniques are especially valuable when assessing responses to field playbacks. Miksis et al. (2001) described the use of a tag to measure cardiac responses to playbacks in captive bottlenose dolphins. Similar tags to measure psychophysiological responses could soon be available for deployment in the field and would prove to be a great asset to the study of marine mammal cognition using playbacks. Johnson & Tyack (2003) designed a digital recording tag for temporary attachment to cetaceans using suction cups that records sounds received and emitted by the tagged animal and documents its movement in three dimensions. Nowacek et al. (2004) used this tag in playback experiments to Northern right whales with the added advantage that the animals' received levels during the playbacks were recorded. Costa et al. (2003) used tags capable of recording received levels in addition to the depth and movements of the tagged animals to assess the response of Northern elephant seals to ATOC sounds. These examples illustrate the usefulness of data-logging technology in the study of marine mammals, and its role in marine mammal playbacks is likely to increase further in the near future.

A final consideration with respect to quantifying responses to playbacks lies in the choice of which response variables to measure. Analyzing a limited number of behavioural parameters can mean missing significant behavioural responses. For example, an analysis of the response of Pacific harbour seals to playbacks of killer whale sounds (Deecke et al., 2002) documented a significant decrease in the number of seals visible at the surface but no consistent change in the distance of the nearest animal to the sound source. This was presumably because after diving away from the surface, the seals moved towards areas of shallow water or kelp beds that provided refuge from predation, and the movement with respect to the sound source depended on where these refuges were located. The choice of response variables is often limited by which behavioural parameters can actually be measured, but observational studies and pilot playback trials can help identify responses and choose appropriate response variables.

McGregor (1992b) reviewed the advantages and disadvantages of using multiple measures to quantify responses to playbacks. Relying on multiple behavioural parameters increases the likelihood of describing the behavioural response adequately, but this leads to statistical problems as many of the parameters collected are likely to be correlated (e.g., dive duration and distance covered during a dive in Frankel & Clark, 1998, 2000). An effective method to circumvent this problem is to use multivariate statistics such as principal

components analysis to reduce multiple measures to variables that are statistically independent of each other. This method has the disadvantage that it can be difficult to determine the nature of the response from published results. It does present a statistically sound approach towards quantifying behavioural responses in playback experiments, however, where the nature of behavioural change in response to playback is difficult to predict *a priori*.

Appropriate Controls in Playback Studies

There is considerable debate on what constitutes an appropriate control for playback experiments, and the type of control used often depends on the exact phrasing of the research question. For example, if playback experiments of killer whale calls are conducted to harbour seals to test whether mammal-eating killer whales pay a cost for calling in terms of alerting potential prey, an appropriate control would be a recording of silent killer whales (i.e., segments of background noise without calls extracted from a recording of killer whales; Deecke et al., 2002). If, however, the question is whether harbour seals respond to killer whale calls (rather than to any sound of similar loudness and frequency composition), recordings of a nonthreatening sound stimulus with a similar frequency composition, such as the social sounds of humpback whales, may be more appropriate as a control (see Gannon et al., 2005, for a similar use of a biological sound as a control).

Regardless of the research question, all playback experiments need to control for two confounding factors: (1) observer effects and (2) equipment effects. Observer effects result from responses of focal animals to the presence of the researchers or vessels involved in broadcasting the sounds or measuring the response variables (such as vessels following focal animals or groups, e.g., Malme et al., 1988). Equipment effects are generated by responses to the presence of the playback equipment, to extraneous noise or other stimuli generated during playback, and to equipment used to quantify behavioural responses (e.g., tag effects). Extraneous noise includes the background noise invariably present in any field recordings of marine mammals as well as any noise artefact generated by the playback equipment. Controlling for these two types of effects means that all personnel and equipment used to broadcast sound and measure responses must also be in place during the control condition. It also means that the playback equipment must be switched on and fully operational during the control condition and that sound sequences used as controls must contain background noise of similar amplitude and spectral composition as treatment

sequences. In experiments where information is hypothesized to be encoded in the frequency modulation of a signal over time, playing the signal backwards can constitute a valuable control since the overall frequency composition of both signal and noise is maintained but the temporal modulation is not. Paired experimental designs can be especially powerful—for example, if the same recording sessions are used to generate treatment and control sequences (e.g., Deecke et al., 2002). The most convincing results come from studies where the same stimulus can be used as a treatment in one trial but as a control in another, as is the case in the study of mother-offspring recognition in otariids and odontocetes (McCulloch et al., 1999; Sayigh et al., 1999).

In situations where it is unclear whether a given treatment will elicit a detectable response, including a positive control in the experimental design can provide valuable information. A positive control includes a stimulus with a high degree of urgency that is likely or known to elicit a response. In cases where the presentation of a treatment stimulus fails to elicit a response, a positive control can help determine whether the failure to detect a response is due to inappropriate playback equipment or design or whether the tested stimulus simply does not evoke a response. Gannon et al. (2005) provided a good example for the appropriate use of a positive control. They used recordings of conspecific whistles, which were known to elicit orientation responses from bottlenose dolphins (Sayigh et al., 1999), as a positive control in their study to investigate the response of this species to recordings of fish sounds. In any case, the numerous challenges involved in conducting appropriately controlled playback studies demonstrate that when designing and executing playback experiments, the amount of thought and effort invested into control and treatment trials should be roughly equal.

Appropriate Replication

Kroodsma (1989, 1990) first pointed out the dangers of pseudoreplication of trials in playback experiments. While his papers sparked a lively discussion on the issue (e.g., Catchpole, 1989; Searcy, 1989), the general consensus was that pseudoreplication should be a serious concern (McGregor et al., 1992). Pseudoreplication means the treatment of replicate trials as statistically independent when in reality they are not. The most common forms of pseudoreplication in playback experiments are (1) testing different focal animals in multiple trials with the same playback stimulus and then considering the response observed in each trial as statistically independent and (2) testing the same individual with different playback stimuli and treating its responses as statistically independent.

The first form of pseudoreplication tends to be far more common in field playback experiments, while the second form is often a concern in captive studies where the number of study subjects is limited.

The main problem with pseudoreplication is that it endangers the external validity of the documented response. In cases where a single playback stimulus is presented in multiple trials and statistically compared to a control, the results adequately reflect the response of the animals to that particular exemplar of the stimulus, but they do not necessarily reflect the response to the class of sounds from which the stimulus came. For example, before one can conclude that harbour seals respond to calls of a particular population of killer whales in a certain way, one has to expose many harbour seals to many different call types from that population. Failing to do so raises the possibility that it was something about the particular exemplar used, but not about killer whale calls in general, that elicited the specific response. The second type of pseudoreplication is probably more obvious—conducting multiple playback trials with the same individual allows one to determine the response of that particular individual to the stimuli but does not allow one to make inferences about the population as a whole.

All studies that use playbacks to determine the responses of animals to certain sound types (and not simply as a tool to modify an animal's behaviour) should therefore present many independent playback sequences to many individuals or independent groups to ensure that their conclusions are valid outside the narrow framework of the study. The relatively common protocol of combining several independent playback stimuli into a single playback sequence and presenting this sequence to many individuals and groups does not avoid pseudoreplication (Kroodsma et al., 2001). The entire response observed in such a playback experiment could be elicited by a single abnormal stimulus in the sequence rather than the signal class tested as a whole. Independent stimuli should ideally be recorded from different individuals (or noise sources in the case of controlled exposure experiments) in different locations (to account for differences in the noise background). In situations where the number of independent playback sequences is limited for logistical reasons, averaging all response variables collected with the same playback sequence and using the number of independent sequences, not trials, to determine the degrees of freedom avoids the problem of pseudoreplication (Deecke et al., 2002). This procedure reduces the statistical power of the analysis compared to complete replication but still provides greater power than if only a single

trial had been conducted with each sequence since much of the extraneous individual or group-specific variation in the response is eliminated. In any case, when presenting results of playback experiments, researchers should clearly identify which responses were obtained with the same and which with different playback sequences (e.g., Parks, 2003) to allow the reader to assess possible effects of pseudoreplication. In summary, the need for appropriate replication suggests that when designing playback experiments with marine mammals and other species, at least as much research effort and money must be budgeted for obtaining sufficient numbers of independent playback stimuli as for conducting the actual playback experiment.

Marine Mammal Playbacks and Pseudoreplication

Kroodsma et al. (2001) surveyed the literature on playback experiments conducted with terrestrial animals to assess the frequency of pseudoreplication ten years after the problem was first identified. He found that the large majority of studies (75%) had not truly replicated treatments primarily because they had used limited playback sequences for each treatment to conduct a multitude of trials but had subsequently treated each trial as statistically independent. I have similarly analysed the 46 field playback studies on marine mammals published to date to identify cases of inappropriate replication. Like Kroodsma et al., I have divided the studies into cases of simple pseudoreplication, sacrificial pseudoreplication, and true replications. Simple pseudoreplication designates studies using only a single exemplar of a playback stimulus for each treatment. Studies in which several independent playback stimuli were combined into a single playback sequence for each treatment are included here. Sacrificial pseudoreplication designates studies where several stimuli were used for each treatment, but trials were pooled for each treatment and treated as statistically independent. Studies in which several trials were conducted with the same individual but treated as statistically independent are also included here. True replication finally identifies studies where all trials are truly independent or where non-independence was addressed statistically.

The results of this analysis are given in Table 1 and in Figure 3. Pseudoreplication was not an issue for three studies since playbacks were simply used to modify the animals' behaviour for research or management purposes. In one additional study, insufficient information was provided to assess whether playbacks were replicated properly. From the remaining 42 studies, 25 (60%) showed evidence for some form of pseudoreplication while

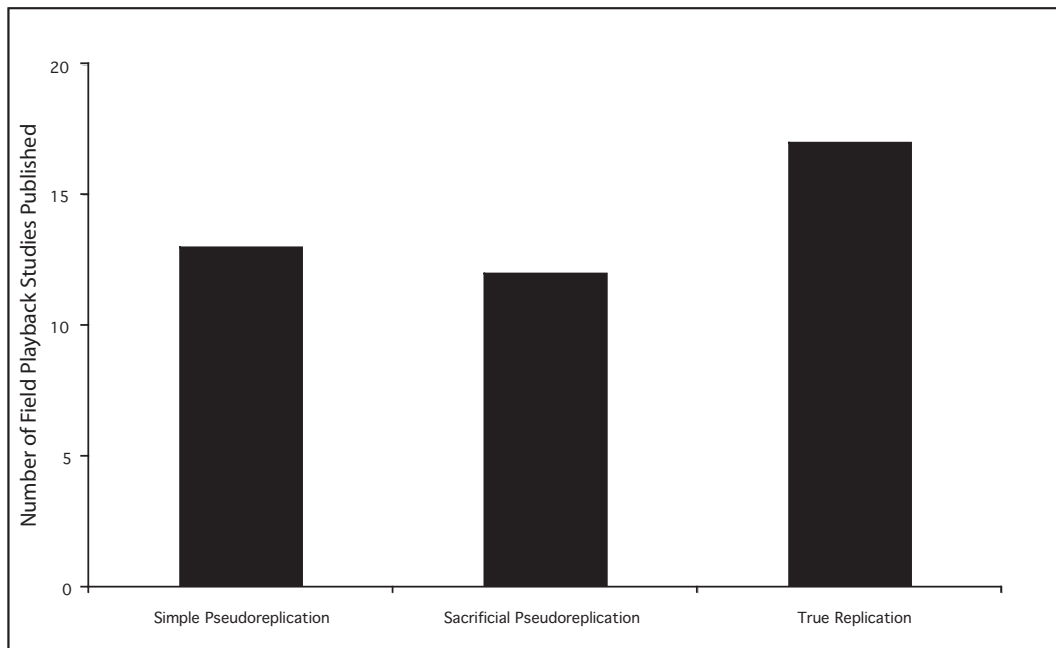


Figure 3. Histogram showing the number of field playback experiments with inappropriate (left two columns) and appropriate (right column) replication; simple pseudoreplication refers to studies in which a single playback stimulus was used for each treatment; sacrificial replication refers to studies where several stimuli were used per treatment to conduct multiple trials, or where the same individuals were treated as independent replicates; and true replication refers to studies where independent playback stimuli were used for each trial or where non-independence was addressed statistically. See text for details.

in 17 of the studies (40%), all trials were truly independent or non-independence was addressed in the statistical analysis. The fact that these figures are better than those for terrestrial playbacks (Kroodsma et al., 2001) is encouraging; however, a large number of studies (eight) in the true replication category come from the field of individual or kin recognition where pseudoreplication is inherently rare since the nature of the question requires that the sound recorded from each individual (offspring or mother) can only serve as a treatment stimulus for a single individual. An additional seven studies in this category were controlled exposure experiments in which pseudoreplication is not an issue because the actual sound source investigated was used to broadcast the stimulus (Frankel & Clark, 2000; Miller et al., 2000; Croll et al., 2001; Olesiuk et al., 2002; Fristrup et al., 2003) or because the stimulus was a synthetic signal bound to exhibit almost no variation (Frankel & Clark, 1998). This means that in the remaining research areas of wildlife management, the study of predator-prey interactions, and the study of the function of vocalizations, only two studies avoided pseudoreplication by conducting each trial with an independent stimulus (Gannon et al., 2005) or by addressing non-independence statistically (Deecke et al., 2002).

These findings are by no means meant to suggest that all conclusions drawn from experiments that were not appropriately replicated are meaningless—non-independence becomes a problem only when a stimulus or individual tested is in some way not representative of the population as a whole. The frequent occurrence of pseudoreplication in the field of marine mammal playback experiments, however, makes it close to impossible to determine which conclusions are valid and which are not. This analysis of replication in marine mammal playback experiments has therefore shown that there is much room for improvement in terms of experimental design procedure, and it underscores the need for researchers to budget sufficient resources, effort, and time to obtain adequate samples of playback stimuli.

Summary and Conclusions

Playback is one of only a handful of experimental tools to study cognition in free-ranging animals, and sound playbacks appear to be especially suited for learning about marine mammals, a group of animals that rely extensively on sound to obtain information about their environment and to transmit information through it. Captive research fulfills an important

role in identifying and delineating the cognitive abilities of marine mammals. Descriptive studies are essential for formulating meaningful hypotheses about how the marine mammals interact with their environment as well as with each other, and on how they apply their cognitive abilities to do so. Testing these hypotheses, however, requires experimentation in the wild, and sound playback provides a powerful experimental technique. Although the use of playback experiments in marine mammal science has been rather limited, the contribution from playback studies so far has been substantial. Much of what we know to date about how marine mammals apply their cognitive abilities to meet the challenges of their aquatic environment comes from research using sound playback.

Field research on marine mammals entails many logistical challenges. Incorporating a playback component into a field research project can add yet another set of challenges to an already extensive list. Even so, the review of the marine mammal playback literature has shown that these challenges are worth meeting. In addition, the section on playback protocol has hopefully pointed out ways to overcome some of the obstacles on the way towards sound playback design and procedure and has shown that other obstacles are not as formidable as they may initially seem. A growing amount of information about the behaviour of marine mammals in the wild from an increasing number of long-term studies provides a rich background against which to frame cognitive questions. Many of these long-term studies incorporate an acoustic component, and the resulting databases of recordings will increase the availability of acoustic stimuli for future playback experiments. Acoustic monitoring and innovative technologies, such as digital tags and telemetry techniques, are making it easier to document the behaviour of marine mammals in response to underwater playbacks. All these developments will help to make playback experimentation on wild marine mammals less challenging and more effective in the future. The logistical and financial constraints of marine mammal field research make it difficult to repeat studies in order to confirm the validity of conclusions drawn or to correct experimental mistakes. This means that great care must be taken to “get it right the first time”—to apply sound experimental design and playback procedure from the beginning. Researchers of marine mammals can benefit much from the extensive literature on terrestrial animals, where playback is a standard experimental tool and many excellent texts on experimental design and procedure are available (e.g., McGregor 1992a). The review of the marine mammal literature on playbacks suggests that there is currently room for improvement, especially with respect to appropriate replication.

Given how little we know about cognition in many species of marine mammals, there is a substantial need for further playback experiments. Research into the extent to which species such as baleen whales, deep-diving pinnipeds, or mammal-eating killer whales rely on passive listening for sounds generated by their prey is required to understand the foraging process of the animals and to assess the degree to which anthropogenic noise interferes with their ability to detect and obtain food. Research on bottlenose dolphins and several species of otariids has documented exceptional capabilities for individual and kin recognition. Many other species of marine mammals are known to exhibit individual variation in their vocalizations, and the possible function of such variation in delineating interactions between individuals in these species remains to be tested. The same is true for the group-specific variation in the vocalizations of some marine mammals. Group-specific variation in vocal repertoires that is correlated with social parameters rather than geographic distance is rare among birds and primates, but it has been described in great detail for some odontocetes (e.g., Ford, 1991; Yurk et al., 2002; Rendell & Whitehead, 2003). It remains to be tested, however, whether such variation plays a role in influencing behavioural decisions. These are just a few examples of numerous cognitive questions that remain to be answered using playback approaches. The potential for sound future playback experiments in the field of marine mammal cognition research, as well as the larger field of marine mammalogy, is bound to be substantial.

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Literature Cited

- Anderson, S. S., & Hawkins, A. D. (1978). Scaring seals by sound. *Mammal Review*, 8, 19-24.
- André, M., Terada, M., & Watanabe, Y. (1997). Sperm whale (*Physeter macrocephalus*) behavioural response after the playback of artificial sounds. *Reports of the International Whaling Commission*, 47, 499-504.

- Angiel, N. M. (1997). *The vocal repertoire of the beluga whale in Bristol Bay, Alaska*. Unpublished Master of Science thesis, University of Washington, Seattle.
- Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., & Andrews, K. (2006). Acoustic properties of humpback whale songs. *Journal of the Acoustical Society of America*, *120*(2), 1103-1110.
- Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, *51*(3), 553-565.
- Bejder, L., Samuels, A., Whitehead, H., & Gales, N. (2006). Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour*, *72*(5), 1149-1158.
- Bel'kovich, V. M., & Sh'ekotov, M. N. (1993). *The belukha whale: Natural behavior and bioacoustics* (M. A. Svanidze, Trans.). Woods Hole, MA: Woods Hole Oceanographic Institution.
- Catchpole, C. K. (1989). Pseudoreplication and external validity: Playback experiments in avian bioacoustics. *Trends in Ecology and Evolution*, *4*(10), 286-287.
- Charrier, I., Mathevon, N., & Jouventin, P. (2001). Mother's voice recognition by seal pups: Newborns need to learn their mother's call before she can take off on a fishing trip. *Nature*, *412*(6850), 873.
- Charrier, I., Mathevon, N., & Jouventin, P. (2002b). How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, *205*(5), 603-612.
- Charrier, I., Mathevon, N., & Jouventin, P. (2003a). Fur seal mothers memorize subsequent versions of developing pups' calls: Adaptation to long-term recognition or evolutionary by-product? *Biological Journal of the Linnean Society*, *80*(2), 305-312.
- Charrier, I., Mathevon, N., & Jouventin, P. (2003b). Vocal signature recognition of mothers by fur seal pups. *Animal Behaviour*, *65*(3), 543-550.
- Charrier, I., Mathevon, N., Hassnaoui, M., Carraro, L., & Jouventin, P. (2002a). The subantarctic fur seal pup switches its begging behaviour during maternal absence. *Canadian Journal of Zoology*, *80*(7), 1250-1255.
- Clark, C. W., & Clark, J. M. (1980). Sound playback experiments with southern right whales (*Eubalaena australis*). *Science*, *207*(4431), 663-665.
- Costa, D. P., Crocker, D. E., Gedamke, J., Webb, P. M., Houser, D. S., Blackwell, S. B., et al. (2003). The effect of a low-frequency sound source (Acoustic Thermometry of the Ocean Climate) on the diving behavior of juvenile northern elephant seals, *Mirounga angustirostris*. *Journal of the Acoustical Society of America*, *113*(2), 1155-1165.
- Croll, D. A., Clark, C. W., Calambokidis, J., Ellison, W. T., & Tershy, B. R. (2001). Effect of anthropogenic low-frequency noise on the foraging ecology of *Balaenoptera* whales. *Animal Conservation*, *4*(1), 13-27.
- Cummings, W. C., & Thompson, P. O. (1971). Gray whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. *Fishery Bulletin*, *69*(3), 525-530.
- Dahlheim, M. E., & Ljungblad, D. K. (1990). Preliminary hearing study on gray whales *Eschrichtius robustus* in the field. In J. A. Thomas & R. A. Kastelein (Eds.), *Sensory abilities of cetaceans* (pp. 335-346). New York: Plenum Press.
- Deecke, V. B., Slater, P. J. B., & Ford, J. K. B. (2002). Selective habituation shapes acoustic predator recognition in harbour seals. *Nature*, *420*(6912), 171-173.
- Deutsch, C. J., Haley, M. P., & Le Boeuf, B. J. (1990). Reproductive effort of male Northern elephant seals: Estimates from mass-loss. *Canadian Journal of Zoology*, *68*(12), 2580-2593.
- Eckhart, G. (2005). *The effect of ecotourism on polar bears*. Unpublished Master of Science thesis, University of Central Florida, Orlando.
- Falls, J. B. (1992). Playback: A historical perspective. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 11-33). New York: Plenum Press.
- Fish, J. F., & Vania, J. S. (1971). Killer whale, *Orcinus orca*, sounds repel white whales, *Delphinapterus leucas*. *Fishery Bulletin*, *69*(3), 531-535.
- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia, Canada. *Canadian Journal of Zoology*, *69*(6), 1454-1483.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R., & Balcomb, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, *76*(8), 1456-1471.
- Frankel, A. S., & Clark, C. W. (1998). Results of low-frequency playback of M-sequence noise to humpback whales, *Megaptera novaeangliae*, in Hawai'i. *Canadian Journal of Zoology*, *76*(3), 521-535.
- Frankel, A. S., & Clark, C. W. (2000). Behavioral responses of humpback whales (*Megaptera novaeangliae*) to full-scale ATOC signals. *Journal of the Acoustical Society of America*, *108*(4), 1930-1937.
- Fristrup, K. M., Hatch, L. T., & Clark, C. W. (2003). Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. *Journal of the Acoustical Society of America*, *113*(6), 3411-3424.
- Gannon, D. P., Barros, N. B., Nowacek, D. P., Read, A. J., Waples, D. M., & Wells, R. S. (2005). Prey detection by bottlenose dolphins, *Tursiops truncatus*: An experimental test of the passive listening hypothesis. *Animal Behaviour*, *69*(3), 709-720.
- Gerhardt, H. C. (1992). Conducting playback experiments and interpreting their results. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 59-77). New York: Plenum Press.
- Goold, J. C. (1999). Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the UK*, *79*(3), 541-550.

- Hayes, S. A., Costa, D. P., Harvey, J. T., & Le Boeuf, B. J. (2004a). Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): Are males defending the hotspot? *Marine Mammal Science*, 20(3), 639-656.
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., et al. (2004b). Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour*, 67(6), 1133-1139.
- Iida, K., Park, T-G., Mukai, T., & Kotani, S. (2006). Avoidance of artificial stimuli by the Steller sea lion. In A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, et al. (Eds.), *Sea lions of the world* (pp. 535-549). Fairbanks: Alaska Sea Grant College Program, University of Alaska.
- Innsley, S. J. (2000). Long-term vocal recognition in the northern fur seal. *Nature*, 406(6794), 404-405.
- Innsley, S. J. (2001). Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour*, 61(1), 129-137.
- Janik, V. M. (2000). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *Journal of Comparative Physiology A*, 186(7-8), 673-680.
- Janik, V. M., Sayigh, L. S., & Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the USA*, 103(21), 8293-8297.
- Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, 28(1), 3-12.
- Koschinski, S., Culik, B. M., Henriksen, O. D., Tregenza, N., Ellis, G. M., Jansen, C., et al. (2003). Behavioural reactions of free-ranging porpoises and seals to the noise of a simulated 2 MW windpower generator. *Marine Ecology Progress Series*, 265, 263-273.
- Kroodsma, D. E. (1989). Suggested experimental design for song playbacks. *Animal Behaviour*, 37(4), 600-609.
- Kroodsma, D. E. (1990). Using appropriate experimental designs for intended hypotheses in song playbacks, with examples for testing effects of song repertoire sizes. *Animal Behaviour*, 40(6), 1138-1150.
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W. C. (2001). Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour*, 61(5), 1029-1033.
- Lammers, M. O., & Au, W. W. L. (2003). Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): A signal feature to cue direction of movement? *Marine Mammal Science*, 19(2), 249-264.
- Malme, C. I., Würsig, B., Bird, J. E., & Tyack, P. L. (1988). Observations of feeding gray whale responses to controlled industrial noise exposure. In W. M. Sackinger & M. O. Jeffries (Eds.), *Proceedings of the Ninth International Conference on Port and Ocean Engineering under Arctic Conditions* (pp. 55-73). Fairbanks: The Geophysical Institute, University of Alaska.
- Malme, C. I., Miles, P. R., Clark, C. W., Tyack, P. L., & Bird, J. E. (1983). *Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behaviour: Final report for the period of 7 June 1982-31 July 1983* (No. 5366). Cambridge, MA: Bolt, Beranek and Newman Inc. for U. S. Minerals Management Service.
- McCulloch, S., & Boness, D. J. (2000). Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *Journal of Zoology*, 251(4), 449-455.
- McCulloch, S., Pomeroy, P. P., & Slater, P. J. B. (1999). Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Canadian Journal of Zoology*, 77(5), 716-723.
- McGregor, P. K. (Ed.). (1992a). *Playback and studies of animal communication*. New York: Plenum Press.
- McGregor, P. K. (1992b). Quantifying responses to playback: One, many, or composite multivariate measures. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 79-96). New York: Plenum Press.
- McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusabi, L., Gerhardt, H. C., et al. (1992). Design of playback experiments: The Thornbridge Hall NATO ARW consensus. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 1-10). New York: Plenum Press.
- Miksis, J. L., Grund, M. D., Nowacek, D. P., Solow, A. R., Connor, R. C., & Tyack, P. L. (2001). Cardiac responses to acoustic playback experiments in the captive bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology*, 115(3), 227-232.
- Miksis-Olds, J. L. (2005). *Manatee response to environmental noise*. Unpublished Ph.D. thesis, University of Rhode Island, Kingston.
- Miller, P. J. O. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, 52(3), 262-270.
- Miller, P. J. O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, 192(5), 449-459.
- Miller, P. J. O., Biassoni, N., Samuels, A., & Tyack, P. L. (2000). Whale songs lengthen in response to sonar. *Nature*, 405(6789), 903-903.
- Mobley, J. R., Herman, L. M., & Frankel, A. S. (1988). Responses of wintering humpback whales (*Megaptera novaeangliae*) to playback of recordings of winter and summer vocalizations and of synthetic sound. *Behavioral Ecology and Sociobiology*, 23(4), 211-223.
- Möhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., & Surlykke, A. (2000). Sperm whale clicks: Directionality and source level revisited. *Journal of the Acoustical Society of America*, 107(1), 638-648.
- Morgan, D. W. (1970). *The reactions of belugas to natural sound playbacks*. Paper presented at the Seventh Annual Conference on Biological Sonar and Diving Mammals, Menlo Park, CA.

- Morgan, D. W. (1973). The vocal and behavioral reactions of the beluga *Delphinapterus leucas* to playback of its sounds. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals: Current perspectives in research. Vol. 3: Cetaceans* (pp. 311-343). New York: Plenum Press.
- Nowacek, D. P., Johnson, M. P., & Tyack, P. L. (2004). North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proceedings of the Royal Society of London B*, 271(1536), 227-231.
- Olesiuk, P. F., Nichol, L. M., Sowden, M. J., & Ford, J. K. B. (2002). Effect of the sound generated by an acoustic harassment device on the relative abundance and distribution of harbor porpoises (*Phocoena phocoena*) in Retreat Passage, British Columbia. *Marine Mammal Science*, 18(4), 843-862.
- Ord, T. J., Peters, R. A., Evans, C. S., & Taylor, A. J. (2002). Digital video playback and visual communication in lizards. *Animal Behaviour*, 63(5), 879-890.
- Parks, S. E. (2003). Response of North Atlantic right whales (*Eubalaena glacialis*) to playback of calls recorded from surface active groups in both the North and South Atlantic. *Marine Mammal Science*, 19(3), 563-580.
- Rendell, L., & Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London B*, 270(1512), 225-231.
- Rendell, L., & Whitehead, H. (2005). Coda playbacks to sperm whales in Chilean waters. *Marine Mammal Science*, 21(2), 307-316.
- Richardson, W. J., Würsig, B., & Greene, C. R. (1990). Reactions of bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort Sea. *Marine Environmental Research*, 29(2), 135-160.
- Richardson, W. J., Fraker, M. A., Würsig, B., & Wells, R. S. (1985). Behaviour of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities. *Biological Conservation*, 32(3), 195-230.
- Rosenthal, G. G., Rand, A. S., & Ryan, M. J. (2004). The vocal sac as a visual cue in anuran communication: An experimental analysis using video playback. *Animal Behaviour*, 68(1), 55-58.
- Sayigh, L. S. (1992). *Development and function of signature whistles of free-ranging bottlenose dolphins, Tursiops truncatus*. Unpublished Ph.D. thesis, Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, MA.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D., & Irvine, A. B. (1999). Individual recognition in wild bottlenose dolphins: A field test using playback experiments. *Animal Behaviour*, 57(1), 41-50.
- Searcy, W. A. (1989). Pseudoreplication, external validity and the design of playback experiments. *Animal Behaviour*, 38(4), 715-717.
- Shapiro, A. D., Slater, P. J. B., & Janik, V. M. (2004). Call usage learning in gray seals (*Halichoerus grypus*). *Journal of Comparative Psychology*, 118(4), 447-454.
- Shaughnessy, P. D., Semmelink, A., Cooper, J., & Frost, P. G. H. (1981). Attempts to develop acoustic methods of keeping Cape fur seals *Arctocephalus pusillus* from fishing nets. *Biological Conservation*, 21(2), 141-158.
- Sousa-Lima, R. S., Paglia, A. P., & da Fonseca, G. A. B. (2002). Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, 63(2), 301-310.
- Thomas, J. A., Kastelein, R. A., & Awbrey, F. T. (1990). Behavior and blood catecholamines of captive belugas during playbacks of noise from an oil drilling platform. *Zoo Biology*, 9(5), 393-402.
- Thomas, J. A., Zinnel, K. C., & Ferm, L. M. (1983). Analysis of Weddell seal (*Leptonychotes weddelli*) vocalizations using underwater playbacks. *Canadian Journal of Zoology*, 61(7), 1448-1456.
- Trainor, B. C., & Basolo, A. L. (2006). Location, location, location: Stripe position effects on female sword preference. *Animal Behaviour*, 71(1), 135-140.
- Trillmich, F. (1981). Mutual mother-pup recognition in Galápagos fur seals *Arctocephalus galapagoensis* and sea lions *Zalophus californianus wollebaeki*: Cues used and functional significance. *Behaviour*, 78(1-2), 21-42.
- Trivers, R. L. (1974). Parent offspring conflict. *American Zoologist*, 14(1), 249-264.
- Tyack, P. L. (1983). Differential response of humpback whales, *Megaptera novaengliae*, to playback of song or social sounds. *Behavioral Ecology and Sociobiology*, 13(1), 49-55.
- Tyack, P. L., Gordon, J. C. D., & Thompson, D. (2003). Controlled exposure experiments to determine the effects of noise on marine mammals. *Marine Technology Society Journal*, 37(4), 39-51.
- Wahlberg, M., Lunnerdy, S-G., & Westerberg, H. (2002). The source level of harbour seal flipper slaps. *Aquatic Mammals*, 28(1), 90-92.
- Watkins, W. A., & Schevill, W. E. (1968). Underwater playback of their own sounds to *Leptonychotes* (Weddell seals). *Journal of Mammalogy*, 49(2), 287-296.
- Wiley, R. H. (1994). Errors, exaggeration, and deception in animal communication. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology* (pp. 157-189). Chicago: University of Chicago Press.
- Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in Southern Alaska. *Animal Behaviour*, 63(6), 1103-1119.
- Zimmer, W. M. X., Tyack, P. L., Johnson, M. P., & Madsen, P. T. (2005). Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. *Journal of the Acoustical Society of America*, 117(3), 1473-1485.