Environmental Noise and Decision Making
Possible Implications of Increases in Anthropogenic Noise for Information Processing in Marine Mammals

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Recent increases in anthropogenic noise in the marine environment are a source of concern for the current welfare and future fitness of many marine mammal species. In this article I explore the specific question of how environmental noise could affect information processing. I also discuss the possible changes in behavior that would result, and how these changes could negatively impact the welfare and fitness of marine mammals. I identify two ways in which environmental noise could affect decision-making. First, environmental noise could add statistical noise to the detection of auditory signals, either masking them completely or rendering them ambiguous. Animals can respond to this problem either by moving away from the source of noise, or by altering the characteristics of their signal processing to increase the signal to noise ratio. Second, environmental noise could generate emotional states of fear or anxiety that cause biases in information processing. Anxiety is an emotion that functions as an early warning of potential threats, and is associated with a suite of changes in information processing including sensitization to stimuli potentially associated with threats, and pessimistic biases in decision-making resulting in increased risk aversion. Although these changes are clearly beneficial in the short term, chronic anxiety is likely to result in behavioral changes that will be detrimental to an animal's fitness in the longer term. Thus, there are likely to be subtle effects of noise on decision-making that have not so far been considered in relation to the effects of anthropogenic noise on marine mammal behavior.

The Problem

Anthropogenic noise has increased dramatically in the marine environment in recent years (Andrew, Howe, Mercer, & Dzieciuch, 2002; Hatch & Wright, this issue), and it is therefore important to consider how this change could affect the welfare and fitness (i.e. lifetime reproductive success) of marine mammals (Fair & Becker, 2000; Wright et al., this issue, b). Environmental noise can potentially impact the welfare and fitness of animals via a number of different mechanisms. For example, loud noises can directly damage animals' ears, and chronic exposure to moderate levels of environmental noise is associated with physiological and anatomical changes in both rats and humans that are associated with negative health consequences (Baldwin, this issue; Clark & Stansfeld, this issue; Wright et al., this issue, a). Environmental noise may also have less direct effects on behavior, and possibly also fitness, by causing alterations in information processing and consequent decision-making. These latter effects may be subtler than the direct effects of noise, however through the alterations in behavior that they cause they could be equally detrimental to animal welfare and long-term fitness. In the remainder of this article I will describe and discuss some of the effects of

noise on information processing. I should stress at this point that there is currently very little information about these effects in marine mammals, and consequently the majority of my examples will come from studies of other more easily studied animals such as laboratory rodents and birds. However, there is every reason to expect that marine mammals should respond in similar ways to other animals when confronted with increases in environmental noise, and the limited information that we do currently have for marine mammals supports this prediction (Wright et al., this issue, b).

Information Processing and Noise

The performance of adaptive behavior relies on an animal possessing accurate information about the world (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Natural selection has equipped animals with the cognitive mechanisms that they need to process information and generate adaptive behavior within the environments in which they have evolved. The brain receives information about the state of the environment via the senses and about the state of the body via its own internal monitoring mechanisms. On the basis of this information, decision mechanisms in the brain generate appropriate physiological and behavioral responses.

Sound is an extremely important source of information for marine animals. The superior propagation of sound in water as compared with air, coupled with reduced visibility in the sea have led to hearing becoming an important sense in many species of marine mammals and probably also fish. For example, many marine mammals use vocalizations for both intra-specific communication and for echolocation, meaning that auditory information is crucial to activities including locating food, making foraging decisions, avoiding predators, choosing mates and social behavior. As a consequence of the importance of sound in marine mammal ecology, it makes sense that marine mammals have evolved specialized mechanisms for processing sound-related information, and that these mechanisms might be particularly sensitive to changes in environmental noise.

The term information processing refers to everything that goes on between information entering an animal via its sense organs and observed behavior (see Figure 1 for a summary). Thus, the brain can be viewed as an information-processing organ. I will discuss two routes via which environmental noise could potentially alter information processing in marine mammals.

First, environmental noise could add statistical noise to the detection of auditory signals, masking the incoming information completely, changing it in some way, or rendering it ambiguous. Second, by generating an emotional state, such as fear or anxiety, environmental noise could provoke changes in decision-making mechanisms congruent with the induced state. Below I enlarge on each of these possibilities and provide examples of the changes in behavior that might result.
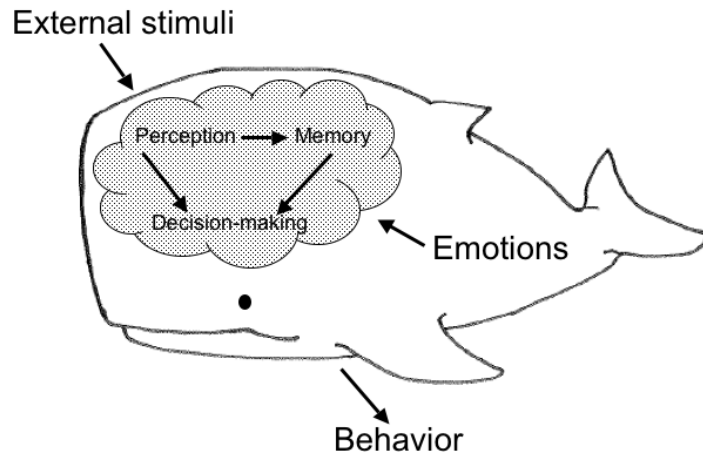
Figure 1. The basic elements of an information-processing model of behavior. Environmental noise could affect information processing in animals either by interfering with the in-coming information from the environment, or indirectly, by evoking internal emotional states such as anxiety that then bias information processing mechanisms.

Detecting Signals in Noise

Many animals face the problem of distinguishing biologically important stimuli, such as conspecific signals or returning echoes, from background noise (for a review see Brumm & Slabbekoorn, 2005). Some mistakes are inevitable, because most signals have some degree of variation associated with them, and natural environments are characterized by permanent background noise of biotic and abiotic origins. Figure 2 illustrates a typical signal detection problem in which an animal looking for a potential mate is faced with distinguishing conspecific calls from those of other species. Although I have chosen this particular example, it is important to realize that the same basic scenario could apply to discriminating any type of auditory information from background noise including returning echoes, sounds of other species and abiotic noises such as those produced by weather, seismic activity and boats. In Figure 2 both types of call are somewhat variable in frequency, as depicted by the normal distributions, and there is an area of overlap in which the two types of call cannot be distinguished on the basis of frequency alone. As a result, conspecific signals will sometimes be incorrectly ignored (misses) and calls of other species will sometimes be incorrectly identified as conspecifics (false alarms, see Table 1). Both types of mistakes have associated costs; in this example, misses will result in passing up a potential mate, whereas false alarms will result in time waste courting the wrong species and possibly infertile mating attempts. In different scenarios the costs will be different; for example in the situation where an animal has to detect the sound of an approaching boat from background environmental noise a miss could result in physical injury or even death, and a false alarm could result in prematurely leaving a good foraging patch.

The problem faced by natural selection is how to minimize the costs of misses and false alarms. Signal detection theory, originally developed in a military context to deal with the problem of identifying significant objects such as planes on noisy radar screens, can be used to quantify this trade-off (e.g. Wiley, 1994). In short, the position of the criterion for discriminating the two

types of call will depend on the relative costs of the two types of mistakes: if misses are cheap or false alarms particularly costly then it will pay to set a conservative criterion (i.e. further towards the right) and only initiate mating or stop foraging if the sound is highly characteristic of a conspecific vocalization or a boat engine, whereas if the reverse is true and misses are costly or false alarms cheap, then it will pay to set a less stringent criterion (i.e. further towards the left) and classify a wider range of signals as those of potential mates or dangerous boats. The optimal position for the criterion will depend on the specific context and the relative costs and benefits of errors versus correct responses.
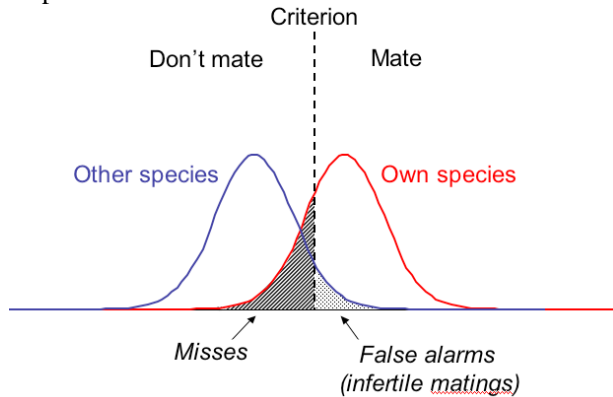

Figure 2. In this example, the x-axis describes the frequency of a call, and the y-axis describes the probability of a call of a given frequency appearing. Two probability distributions are shown: the one on the left corresponds to the calls of other species, and the one on the right to conspecific calls. The dotted line is the criterion below which calls are classified as other species and above which calls are classified as conspecific. The probability of missing a conspecific call is indicated by the hatched area, and probability of a false alarm by the shaded area.

Table 1
Types of possible response in a signal detection task.

	Signal	
Response	Present	Absent
Signal detected	Hit	False alarm
No signal detected	Miss	Correct rejection

We can use the basic framework established above to think about the possible effects of increased environmental noise on decision-making. Figure 3a shows a hypothetical example in which additional environmental noise increases the variance of the distribution of signals that should be rejected. If the criterion for rejection is unchanged (as shown in Figure 3a), then the number of misses will remain unchanged, but the number of false alarms will increase. The fitness consequences of such a change will depend on the costs of a false alarm, but if, as in the case of the above example, a false alarm translates into an infertile mating, then they could be considerable. In the most extreme cases environmental noise could completely mask biologically significant signals depriving animals of sources of information vital for their fitness.

Animals faced with an increase in environmental noise can respond in various ways to reduce the probability of errors in signal detection. Broadly speaking, either signalers can alter some aspect of their signal production to reduce the probability of errors, or signal receivers can change some feature of

their signal to reduce the probability of errors. In both cases these responses could either be adaptive plasticity within the individual, or take place by natural selection over evolutionary time. However, the long life spans and generation times of many marine mammal species may severely limit their capacity to keep up with rapid environmental changes via the latter mechanism.
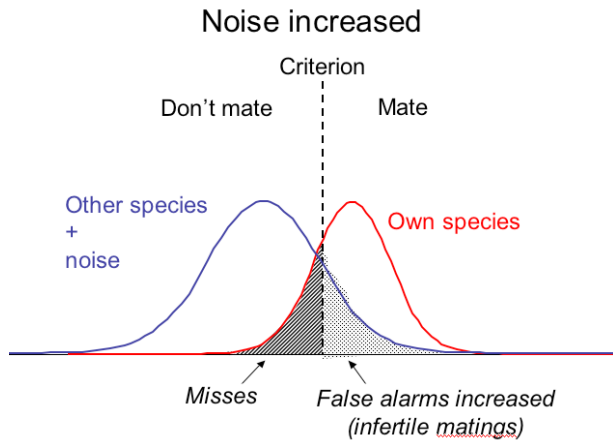

Figure 3a. Increased environmental noise makes the signal detection problem described in Figure 2 more difficult by increasing the variance of the sounds from which conspecific calls must be discriminated.

Hearing may initially appear a passive sense in which the signal receiver has little latitude for improving signal detection. However, there are a number of mechanisms involving both perception and behavior via which signal receivers can reduce the probability of errors in detection. At the behavioral level, it may be possible to improve the signal to noise ratio by moving closer to the source of a signal or away from the source of noise. At the information processing level, the signal receiver could change the criterion for classification. For example, moving the criterion to the right will serve to reduce the false alarm rate at the expense of increasing the miss rate (Figure 3b). Many perception adaptations have also been identified in species as diverse as insects, frogs, birds and bats (reviewed in Brumm & Slabbekoorn, 2005). Research on perception is usually derived from laboratory studies, making it difficult in marine mammals, however recent research on hearing in fish under noise conditions has the potential to identify the strategies used in fish (Wysocki & Ladich, 2005).

Signalers can respond by shifting the signal away from the noise by altering its frequency (Figure 3c), or sharpening the discriminability of the conspecific signal (Figure 3d), which will reduce the number of misses. An example of altering the frequency of a signal is found in urban great tits (*Parus major*), in which a correlation is observed between the amplitude of background noise and the average minimum frequency of male birds' songs (Slabbekoorn & Peet, 2003). Animals have used a number of different strategies for improving the discrimination of a signal without changing its frequency. Perhaps the most obvious way to counteract the masking effects of background is to increase the amplitude, a response referred to as the "Lombard effect". There is abundant evidence that many birds sing louder in response to increases in background noise. For example, male nightingales

(*Luscinia megarhynchos*) regulated the intensity of their songs according to the level of masking noise, thus maintaining a specific signal-to-noise ratio that is favorable for communication (Brumm & Todt, 2002). Another approach is to increase the duration of the signal or repeat the same signal more often. For example, killer whales (*Orcinus orca*) produced more easily perceived, long calls when noise from boats exceeded a threshold level (Foote, Osborne, & Hoelzel, 2004), and beluga whales (*Delphinapterus leucas*) increased the repetition of specific calls when a boat was nearby (Lesage, Barrette, Kingsley, & Sjare, 1999). It is important to realize that these compensatory strategies are not likely to be without cost. In the case of the killer whales for example, making longer calls must take either time or attention away from other important activities such as foraging, and will involve an increased energetic cost.
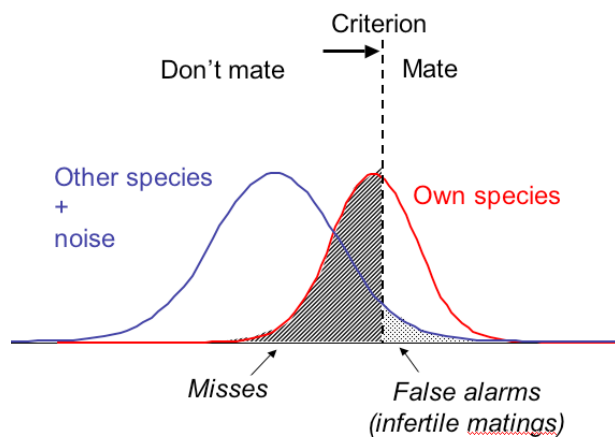

Figure 3b. Animals might respond to increased environmental noise by shifting the criterion to the right and hence reducing the possibility of false alarms at the expense of increasing the probability of misses.

Finally, both signalers and signal receivers can attempt to escape increased environmental noise either spatially or temporally. Spatial escape would involve moving to a different location where environmental noise is reduced. It is now well established that whales choose to avoid areas of high whale watching activity, and one explanation for this preference could lie in the signal detection difficulties imposed by boat noise (Wright et al., this issue, b). A major cost of using a spatial avoidance strategy is that it is likely to force animals into areas that are otherwise suboptimal. For example, whales might be forced into less good foraging areas in order to escape anthropogenic noise, which is likely to have welfare and fitness consequences. Temporal escape involves altering the timing of signaling to correspond with the time when there is least environmental noise. An example of this latter strategy was recently reported in urban robins that have shifted to singing during the night in areas where there is high traffic noise during the day (Fuller, Warren, & Gaston, 2007). Again, it is unlikely that this strategy will be without cost, because by singing at night robins may be exposing themselves to increased predation risks or depriving themselves of sleep. A possible case of temporal escape has been described in beluga whales (*Delphinapterus leucas*) that reduce their calling rate while vessels are approaching (Lesage, Barrette,

Kingsley, & Sjar, 1999). It is hard to speculate about the possible costs of this change in behavior without knowing the precise function of the vocalizations involved.

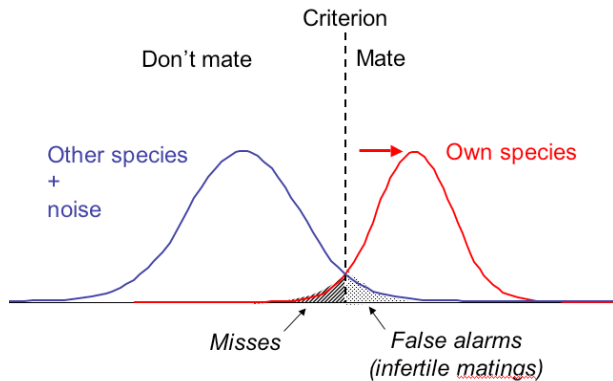## Shift signal away from noise

Figure 3c. Animals might respond to increased environmental noise by shifting their own signals away from the noise hence reducing the number of misses.
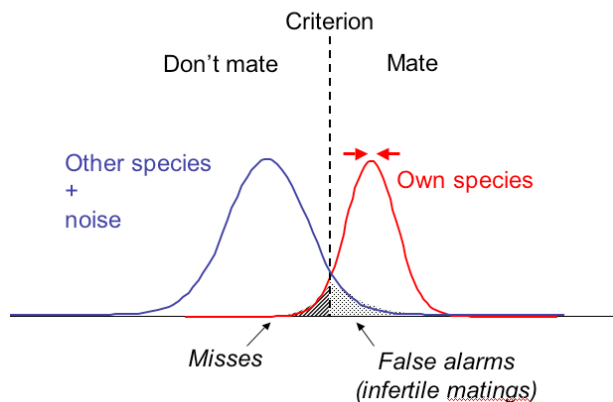
Sharpen discrimination

Figure 3d. Animals might respond to increased environmental noise by sharpening the discrimination of their own signals. This could be affected by reducing the variance in conspecific calls. The effect is to reduce the number of misses.

Cognitive Bias and Noise

For many animals environmental noise is an important cue that danger could be imminent. For example, many animals will rely on sound to provide them with information about the possible approach of a predator or other threat. It therefore makes sense that many animals will respond to unusual or unexpected noises with adaptive emotional reactions such as fear and anxiety. Increased levels of background noise are also associated with a stress response in humans (Clark & Stansfeld, this issue). Anxiety is an emotion that functions as an early warning of potential threats, and is associated with a suite of changes that prepare the animal for dealing with the threat. The physiological and behavioral changes that come with anxiety such as increased heart rate and vigilance are well known, however these are also accompanied by changes in information processing, referred to as "cognitive biases", that prepare the

animal cognitively for dealing with the threat (Clore & Huntsinger, 2007; Mathews, Mackintosh, & Fulcher, 1997). For example, anxious humans show selective attention to threatening words (Williams, Mathews, & McLeod, 1996), and will detect an angry face amongst a large array of neutral faces more rapidly (Bryne & Eysenck, 1995). Anxious humans are also more likely to assume a negative or threatening interpretation when presented with ambiguous stimuli such as homophones (e.g. die/dye or pain/pane, (Eysenck, MacLeod, & Matthews, 1987; Eysenck, Mogg, May, Richards, & Matthews, 1991)).

Recently, "pessimistic" cognitive biases have also been reported in non-human animals housed in suboptimal cages. For example, Harding et al. (2004) trained rats on a go/no-go task to press a lever to obtain a food reward on hearing a positive stimulus (the food-delivery tone), but to refrain from pressing the lever to avoid unpleasant white noise on hearing a negative stimulus (the noise-avoidance tone). Once trained on this task, rats were allocated to either predictable or unpredictable (depression-inducing) housing. Following this manipulation the rat were tested with non-reinforced stimuli intermediate between the food-delivery and noise-avoidance tones. The animals' anticipation of the positive and negative outcomes was estimated by measuring the probability with which they lever-pressed in response to the ambiguous tones. Rats in the unpredictable group showed fewer and slower responses than rats in the predictable group. Thus, the depressed rats showed reduced anticipation of a positive event.

We used a similar approach to ask whether European starlings (*Sturnus vulgaris*) deprived of environmental enrichment in their cages show biases in their classification of ambiguous signals (Bateson & Matheson, 2007). On the basis of the previous findings in humans and rats discussed above, we hypothesized that starlings in enriched cages should be more likely to classify ambiguous signals as being associated with a positive outcome than starlings housed in standard, unenriched cages. Starlings were trained on a go/no-go procedure to discriminate between two visual stimuli (cardboard lids of white and dark grey) associated with outcomes of a different value (palatable and unpalatable mealworms hidden underneath). Individual birds' responses to unreinforced, intermediate stimuli (various shades of grey between white and dark grey) were subsequently examined while each bird was housed sequentially in both standard and enriched cages. The probability of a bird classifying an ambiguous pale grey lid as hiding a palatable mealworm was lower in standard cages than enriched cages, but this difference was only found in birds that received enriched cages first (Figure 4). Our results can be interpreted as showing a pessimistic bias in birds that have recently experienced a decline in environmental quality (see also Matheson, Asher & Bateson, 2008).

The above studies show that animals experiencing anxiety or depression induced by poor housing conditions are more pessimistic in their interpretation of ambiguous information resulting in more risk-averse decision-making. The pessimistic animals were less ready to expose themselves to unpleasant events such as white noise or quinine-tainted food. It is reasonable to hypothesize that similar risk-averse biases may be present in marine mammals rendered anxious by recent increases in anthropogenic noise. While increased risk-aversion is an adaptive response in the face of real threats,

chronic pessimism is unlikely to be adaptive since it may cause animals to pass up opportunities beneficial to their long-term fitness.
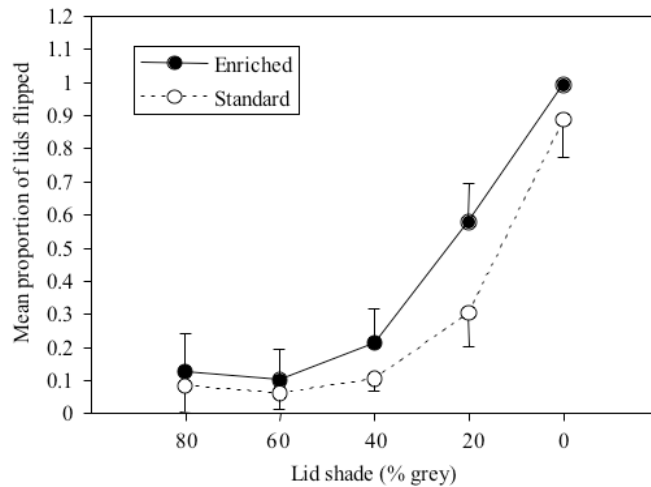

Figure 4. An example of a pessimistic cognitive bias . The x-axis shows the shade of the lid used to hide a worm. 80% grey lids were associated with unpalatable quinine-injected mealworms whereas white lids (i.e. 0% grey) were associated with palatable mealworms. Intermediate lid shades were never reinforced with either type of mealworm. The y-axis shows the proportion of times birds investigated Petri dishes by flipping off the lid (from Bateson & Matheson (2007), with permission).

Conclusions

Increases in anthropogenic noise are likely to have subtle effects on the cognition and behavior of marine mammals via at least two different mechanisms. First, noise may interfere with or mask the auditory signals available to marine mammals depriving them of important sources of information. Although evidence suggests that animals will compensate for such interference via a range of strategies, this is unlikely to be without costs. Second, noise may evoke emotional states that bring about biases in information processing and decision-making. Although these biases may have been adaptive in the environments in which the animals evolved, it is possible that they may be maladaptive in the radically different environments present in today's oceans. Further research is needed to identify the extent to which marine mammal behavior is affected by increased levels of anthropogenic noise, and to quantify the potential welfare and fitness consequences of these changes.

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