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Review

Behavioral biology of marine mammal deterrents: A review and prospectus

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ABSTRACT

Marine mammal depredation of fisheries is a concern from a scientific, management, and conservation perspective. This conflict has prompted the development of non-lethal deterrents, a management technique that uses aversive stimuli to elicit avoidance. Animals are expected to be sensitive to cues of danger to avoid sources of mortality. Deterrents capitalize on behavioral mechanisms such as threat detection, assessment and learning. A deterrent must create enough risk, or cost, that it overcomes the heightened foraging benefits of depredation. Theoretically, effective deterrence relies on altering the relative costs and benefits to the individual depredator by creating a perceived risk associated with human resources. Here we discuss the underlying behavioral basis of how deterrents generate avoidance. We review deterrents applied to marine mammals to mitigate conflict with fisheries and suggest that fear conditioning could be useful in this context. This is discussed in the context of some potential management concerns of application of non-lethal deterrents in the wild.

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1. Introduction

The recovery of certain animal populations, combined with the expansion of human populations and the fragmentation of habitats, has caused substantial overlap between humans and wildlife. This spatial and temporal overlap creates direct conflicts over human resources and products, including livestock, crops, fish, and garbage. Human wildlife conflict (HWC), defined broadly, refers to wildlife behaviors that negatively influence human goals or vice versa (Madden, 2004). HWC occurs when wildlife kill domesticated animals, or eat garbage or crops. It is well documented in terrestrial ecosystems and seen when carnivores prey upon livestock and elephant/primate forage in crops (Naughton-Treves, 1998; O'Connell-Rodwell et al., 2000; Treves and Karanth, 2003).

In marine ecosystems, HWC is globally distributed and taxonomically widespread because of commercial fishing (Northridge, 1991). Numerous mammals, including pinnipeds, false killer whales (*Pseudorca crassidens*), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and bottlenose dolphins (*Tursiops truncatus*) have been reported to steal fish from fishing lines, nets, fish ladders or aquaculture pens (Yano and Dahlheim, 1995; Gillman et al., 2006; Sigler et al., 2008; Read, 2008; Forney et al., 2011). This behavior is referred to as depredation.

The alteration of wildlife habitat whereby fishing lines or aquaculture pens are introduced to animals' environments has shifted the costs and benefits of natural mammal foraging by creating novel concentrations of prey. To the individual depredator, exploiting fishing resources represents a more efficient feeding strategy than natural foraging. There are lower costs in terms of energy, time, and travel for locating/acquiring prey. For example, when depredating demersal, long-line fishing vessels, sperm whales do not have to dive to forage at their typical depth and fishing lines also offer a high concentration of debilitated prey (Mathias et al., 2009). However, depredation incurs (potentially lethal) costs from entanglement with, or ingestion of fishing gear. In addition to creating novel concentrations of prey, human activities may reduce foraging resources previously available to natural predators, via direct take (and in some cases overfishing) or via a number of indirect paths altering the trophic web. Because animals seek to maximize foraging efficiency by reducing time, energy, or distance travelled while foraging (Krebs and Davies, 1987), the low cost of depredating from fishing lines/aquaculture pens or higher costs of searching for food in a disturbed habitat offer heightened motivation for learning to associate foraging resources with humans/human habitat.

Marine mammal depredations of fisheries resources are a concern from both scientific, management, and conservation perspectives because there are direct socio-economic impacts upon fisheries, a potential for reducedfishstocincreased marine mammal mortality, and potential (and realized) retaliatory actions by fisherman. This conflict has stimulated to the development of non-lethal deterrents designed to ward off wildlife (Pemberton and Shaughnessy, 1993; Read, 2008).

Deterrents, defined broadly are management techniques that use aversive stimuli to prevent animals from utilizing human resources (Ramp et al., 2011). A deterrent stimulus is defined as an aversive, harmful, fearful, or noxious stimulus that elicits defensive responses in animals (Gotz and Janik, 2010). A deterrent must create enough risk (real or perceived) so that the costs of using a resource are greater than the foraging benefits of depredation (Fig. 1).

The goal of a deterrent is to create aversive stimulus that excludes wildlife from human resources and/or habitats (Mason et al., 2001). Animal threat detection and response mechanisms evolved to identify environmental cues of danger and then to activate appropriate defense responses and avoidance (Lang et al., 2000; Frid and Dill, 2002; Eilam et al., 2011). From a functional (i.e., evolutionary) perspective, there is often a survival advantage for the early and rapid detection of threatening stimuli (Öhman, 1997; Blumstein 2010a,b). In many circumstances, the costs of failing to respond to threatening stimulus far outweigh costs of a false positive response (over-reaction to innocuous stimuli (Bouskila and Blumstein, 1992; Sih, 1992; Mineka and Ohman, 2002). Animals are therefore expected to be sensitive to cues of danger (predation, conspecific aggression, or dangerous environmental features) because death leads to an abrupt reduction in future direct fitness (Endler, 1986; Blanchard, 2008). The capacity to detect threatening stimuli therefore, has been under intense selection, resulting in evolution of specialized mechanisms of threat assessment, learning, and behavioral response (Blanchard, 2008; Eilam et al., 2011). Deterrent stimuli capitalize upon the mechanisms of threat detection and avoidance (Frid and Dill, 2002; Parsons and Blumstein, 2010; Biedenweg et al., 2011).

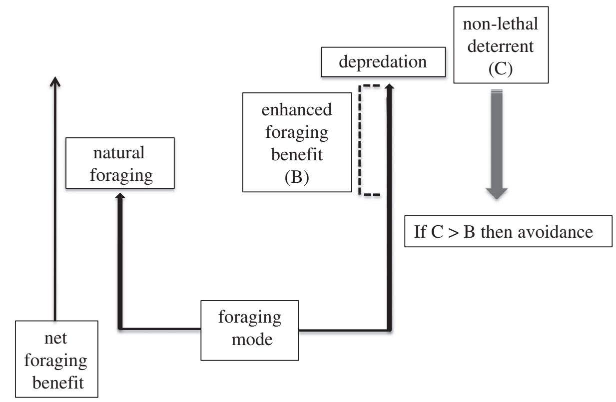

Fig. 1. How deterrents work. When the costs created by a non-lethal deterrent (C) exceed the benefits of depredation (B), animals should resume 'natural' foraging.

Below we discuss the underlying behavioral basis of how deterrents generate avoidance and review deterrents applied to marine mammals to mitigate conflict with fisheries. Schematically, Fig. 2 breaks down animal response to deterrent stimuli into mechanisms of aversion, decision-making and learning. Table 1 provides relevant definitions of behavioral principles that will be referred to throughout this review. What follows is a discussion of these underlying behavioral mechanisms.

2. Avoidance mechanisms

Defensive behaviors describe the responses of individuals to threatening stimuli (Blanchard, 2008). In nature, defensive responses to risky situations or stimuli, such as a predatory encounters, can broadly be divided into two categories; immediate defensive responses to a direct encounter (flight), or avoidance behaviors that decrease the probability of encountering danger based upon indirect cues (Lima and Dill, 1990; Brodie and Formanowicz, 1991). The two categories are underpinned by two distinct mechanisms, fear and anxiety (Blanchard et al., 1993; Blanchard, 2008). Fear and anxiety are reliant upon two separate neurochemical pathways (McNaughton and Corr, 2004). Fear is defined as a short-term fight or flight response involving heightened physiological arousal that reduces impact of impending threat (Grillon, 2008). By contrast, anxiety is sustained and precipitated by potential, ambiguous, or contextual threats (Blanchard, 2008; Grillon, 2008; Eilam et al., 2011).