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Applying principles of animal behavior to issues involving California sea lions interacting with  
Southern California fisheries and predation of endangered salmonids.

A dissertation submitted in partial satisfaction of the requirements  
for the degree Doctor of Philosophy in Biology

by

Zachary Schakner

2016

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## ABSTRACT OF THE DISSERTATION

Applying principles of animal behavior to issues involving California sea lions interacting with Southern California fisheries and predation of endangered salmonids.

by

Zachary Schakner

Doctor of Philosophy in Biology

University of California, Los Angeles, 2016

Professor Daniel T. Blumstein, Chair

The United States Marine Mammal Protection Act (MMPA 1972) resulted in federal protection and enhanced the recovery of California sea lion (*CSL--Zalophus californianus*) populations in the United States. As an unintended consequence of their protection, sea lion populations have expanded their range, negatively interacting with every commercial fishery on the west coast of the United States, predating endangered Pacific salmonids at upriver dams, and damaging docks/fishing vessels. Conservation and management problems with California sea lions can benefit from mechanistic insights into how individuals respond to stimuli and learn about biologically important events. This dissertation provides an in depth examination into how animal learning theory can be applied to conservation issues. I apply learning mechanisms to

enhance management of two conservation issues involving sea lions; depredation (removal of fish from fishing lines) and predation of endangered salmonids at the fish ladders below the Bonneville Dam. This dissertation is structured into two reviews, an empirical test of learning on deterrents on California sea lions (*Zalophus californianus*) interacting with fisheries, an analysis of social transmission and the impact of culling of California sea lions foraging at the Bonneville Dam. Chapter two unpacks the behavioral mechanisms involved in non-lethal deterrents and reviews their application for depredating marine mammals. This review makes the argument that Pavlovian fear conditioning can be applied to deterrents to enhance success in cases of human wildlife conflict and reduce management concerns over non-target animals. Chapter three presents a field experiment on Pavlovian fear conditioning for deterrents on wild California sea lions which examines whether conditioned individuals exhibit greater avoidance compared to control animals. Chapter four reviews how learning can be applied to solve conservation problems. Social learning, for instance, functions as a multiplier, rapidly spreading undesirable wildlife behaviors through populations, suggesting that target lethal or non-lethal management strategies may be necessary. Chapter five uses social network based diffusion analysis to show that social transmission is driving foraging of endangered salmonids by California sea lions. Social transmission has implications for management measures, and we used epidemiological models of behavioral transmission to assess current and potential lethal removal strategies.

The Dissertation of Zachary Schakner is approved.

Michael Fanselow

Gregory Grether

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles  
2016

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*Conservation and Management*, edited by Oded Berger-Tal and David Saltz, Cambridge University Press. Chapter 3 is a reprint. Schakner, Z. A., & Blumstein, D. T. (2013). Behavioral biology of marine mammal deterrents: A review and prospectus. *Biological Conservation*, 167, 380–389.

These chapters are the result of collaborations and all coauthors contributed considerably. All coauthors have given their permission to use publications in this dissertation.

## VITA

ZACHARY SCHAKNER

### RESEARCH INTERESTS

I am interested in how knowledge of animal behavior can be used to mitigate marine mammal/fishery conflict and predation on ESA-listed Salmonids

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Schakner, Z.A., et al 2015 Social transmission drives California sea lion foraging on endangered salmon at Bonneville Dam: assessing the impact of lethal removal using epidemiological models. 2015 Anadromous Fish Evaluation Program Annual Review. Walla Walla, Washington.

Schakner, Z.A. *et al.* 2013. Learning online: Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. 20<sup>th</sup> Biennial Conference on the Biology of Marine Mammals Dunedin, New Zealand

## CHAPTER 1

### GENERAL INTRODUCTION

Humans are rapidly altering the land and seascape through fishing, cultivation, and ranching, and urbanization. Anthropogenic alterations simultaneously reduce natural food availability and create novel resources in the form of crops, domesticated livestock, garbage cans, and fishing lines: forcing wildlife to rapidly adapt. Human-wildlife conflict arises when specific behaviors enhance exploitation of human resources. Crop raiding, depredation and other forms of human-wildlife conflict refers to the stealing of domesticated animals, garbage cans, or crops by wildlife and are an emerging problem for scientists, policy makers, and the local peoples whose livelihoods are affected by these behaviors. Conflict may ultimately threaten human safety and economic livelihood. There is growing awareness of wildlife managers to the advantages of using existing knowledge of animal behavior and physiology to improve conservation efforts. It is remarkable that while we have known about the mechanistic processes of learning for over a century, there are relatively few concrete examples of managers effectively applying such theory to address wildlife management problems. This dissertation bridges the gap from theory to application by explicitly testing mechanistic insights from animal learning to solve conservation problems.

Learning is an example of reversible plasticity (for review see Dukas and Ratcliff 2009). Learning typically remains open to change throughout life, old associations can be replaced, relearned, and reinstated facilitating behavioral modifications across an individual's lifetime. Knowledge of learning mechanisms is of use to managers who wish to modify animal behavior. Chapter 2 introduces the fundamentals of learning theory and reviews how learning can be applied to solve conservation problems. Training animals with basic learning mechanisms may

help repel animals from human resources, attract them to particular habitats/regions, or generate basic survival skills to enhance survival during translocations/reintroductions. Much of my focus in Chapter 2 is on the role of learning in behavior-based management of human wildlife conflicts.

Since anthropogenic resources, like fishing lines or crops, can reduce the costs compared to natural foraging, there is strong motivation for wildlife to rapidly form the association between humans and food reward. Chapter 2 highlights two unanswered questions within the field of human wildlife conflicts. First, how can learning enhance mitigation techniques (i.e., deterrents) designed to reduce the incidence the behavior? Second, what are the consequences of social learning of undesirable wildlife behaviors?

## ANIMAL LEARNING THEORY CAN ENHANCE DETERRENT TECHNIQUES

Understanding how animals learn to exploit human resources, and how they respond to and learn from painful stimuli may enhance conservation efforts aimed at reducing human wildlife conflicts. Deterrents and repellents produce noxious, aversive or painful stimuli to prevent animals from interacting with human habitat or resources (Ramp et al. 2011). Once wildlife associate humans with food resources, management efforts rely on raising the cost to the individual depredator. Because the association is difficult to extinguish, management efforts must rely on forming new negative associations. Chapter three unpacks the behavioral mechanisms involved in non-lethal deterrents and reviews their application for depredating marine mammals. I discuss the underlying behavioral basis of how deterrents generate avoidance. Deterrents capitalize on behavioral mechanisms such as threat detection, assessment and learning. Theoretically, effective deterrence relies on altering the relative costs and benefits to the individual depredator by creating a perceived risk associated with human resources.

During painful encounters, animals rapidly learn to identify the cues, context, or local conditions that are associated with that danger. This learning mechanism enables animals to learn from, respond, and detect danger. Thus, animals naturally fear condition themselves to avoid predators, threatening environments or dangerous stimuli. Repellents, therefore, should capitalize on insights from the fear conditioning literature to generate avoidance. Pavlovian fear conditioning is an associative form of learning in which individuals exposed to an aversive stimulus (the unconditioned stimulus) is paired to an innocuous stimulus (the conditioned stimulus, e.g., a neutral tone) (Grillon 2002; Fanselow and Ponnusamy 2008). Once conditioning has occurred, exposure to the unconditioned stimulus generates fear reactions to the conditioned stimulus. Training animals with basic associative learning mechanisms may produce long term-learned avoidance. By reviewing deterrents applied to mitigate conflict, I suggest in Chapter 3 that fear conditioning could be useful in this context. A deterrent that capitalizes on individual-specific learning mechanisms, like fear conditioning, may enhance success while simultaneously balancing welfare concerns and reduce noise pollution. I make the argument that Pavlovian fear conditioning should enhance the success of reducing human wildlife conflict and also reduce management concerns over harm to non-target animals.

#### SOCIAL LEARNING HAS CONSEQUENCES FOR MANAGING THE SPREAD OF BEHAVIORS THROUGH POPULATIONS.

When innovators initially learn to depredate or crop raid, social learning can have a multiplier effect by spreading behaviors through populations quickly (Lefevbre 1995). The creation of novel concentrations of resources such as garage cans, crops, or domesticated wildlife provide motivation for marine mammals to learn to exploit those resources. Wildlife learning to

associate humans with food resources is expected to occur quickly (Schakner and Blumstein 2016). In elephants (*Loxodonta africana*) for example, network analysis of crop raiders has demonstrated that the behavior appears to be socially learned through social networks (Chiyo et al. 2011). Correspondingly, social learning is believed to underlie the diffusion of depredation in sperm, killer whales, and pilfering black bears (Whitehead 2004; Mazur et al. 2008, Schakner et al. 2014). In these cases, it is important to know both the identity of innovators (age/sex) and the pattern of diffusion. This knowledge is useful to stop the spread and for targeted repellents or removals of individuals.

Understanding the transmission dynamics that underlies the spread of an undesirable behavior is essential toward controlling it with interventions. Socially transmitted behaviors, ideas, or information can be contagious, spreading through populations like an infectious disease. Interactions between individuals underlie transmission of both behaviors and diseases, creating similar patterns of spread across contact networks. Given the parallels between transmission of behavior and disease, wildlife managers may benefit from principles of infectious disease control. In the disease literature, cases of super spreaders, or a minority of individuals that infect a disproportionately more than other individuals (Lloyd-Smith et al. 2005; Stein 2011) requires targeted interventions like vaccines or removal. In animal societies, certain group members (e.g., older males) exhibit increased probability of behavioral transmission, suggesting target removal application of deterrents could prevent transmission. Predicting and identifying heterogeneities in behavioral transmission requires knowledge of the underlying social networks and association patterns.

The need for timely interventions is a well-known principle in infectious disease control (Cooper et al. 2006; Buhnerkempe et al. 2014). Similarly, there are consequences for delayed

action for social transmission of undesirable wildlife behaviors. Delayed action may make interventions like non-lethal deterrents or culling ineffective, because the behavior is too prevalent in the population. This also raises ethical questions (e.g., is it ethical to continue to culling when more and more individuals learn the behavior?). Social transmission functions as a multiplier, rapidly spreading behaviors through populations like an infectious disease. And, like an infectious disease, socially transmitted behaviors require early action to reduce their spread.

With the underlying theory of animal learning and how it can be applied to human wildlife conflicts reviewed in Chapter 2 and 3, I use my final two chapters to empirically test these ideas with issues arising with California sea lions.

## CALIFORNIA SEA LION AND FISHERY CONFLICT

The Marine Mammal Protection Act of 1972 (MMPA) offered sweeping protections for 125 species of marine mammals in US waters. Hailed as a conservation success story, the law has brought species from the brink of extinction and fully recovered many populations in the 40 years since it was enacted. In particular, California sea lion populations have grown considerably (Read and Wade 2000, Lowry and Maravilla-Chavez 2005, Carretta et al. 2011). An unintended consequence of the MMPA is increasing competitive interactions between sea lions and humans. Along the West Coast of the United States expanding California sea lion populations create conflicts from consumption of endangered salmonid species, interactions with fisheries, and damage to docks/personal vessels (Fletcher 2010; Scordino 2010). Conflicts with California sea lions can benefit from mechanistic insights into how individuals respond to stimuli and learn about biologically important events.

## FEAR CONDITIONING CALIFORNIA SEA LIONS WITH AN ACOUSTIC DETERRENT

In Southern California sea lion depredation, or the removal of fish from lines or nets, creates scientific, management, and conservation concerns that include socio-economic losses upon fisheries (Fletcher et al. 2010), increased entanglements, and potential (and realized) retaliatory actions by fisherman (Powell and Wells 2011; Read, 2008). As a consequence of these conflicts, there is increasing demand for effective non-lethal mitigation techniques, such as the development and application of effective deterrents to reduce conflicts (Gordon and Northridge 2002; Götz and Janik 2013). A range of different presumably aversive stimuli, such as intense acoustic signals, are used to elicit avoidance in marine mammals (Brandt et al. 2013). However, the use of such intense acoustic signals in marine environments to prevent depredation is controversial. There are concerns about their overall efficacy, ethical and conservation concerns over potential hearing damage, and ecological impacts on non-target wildlife (Gordon and Northridge 2002; Götz and Janik 2013). Focusing deterrents on species-specific sensory capabilities and individual learning mechanisms can potentially limit the effects on non-target species, as well as reduce an individual's exposure to painful stimuli (Götz and Janik 2013).

Chapter 3 is a field experiment on Pavlovian fear conditioning in wild California sea lions. I tested the efficacy of fear conditioning using aversive acoustic stimuli for reducing California sea lion interactions from two commercial fishing contexts in Southern California, USA; bait receivers and fishing vessels. The acoustic deterrent caused animals to increase distance and spend more time away from the bait barge but conditioned individuals showed less strong avoidance responses compared to control individuals. During playback from sport fishing vessels, both conditioned and unconditioned stimuli caused individuals to surface at a greater distance from the vessel during playback than on non-playback, but playback did not eliminate

interactions with the boat. Our observations suggest that the conditioned response to acoustic stimuli failed to create the desired management goal (avoidance) in this particular fishery, however, the unconditioned response holds some potential. There may be other fishery applications where increased surface activity effectively prevents foraging behavior, such as bottom net fishing where individuals have to forage at depth.

## SEA LION PREDATION OF SALMONIDS AT BONNEVILLE DAM

California sea lions have expanded their range into upriver dams and locks, creating invasive impacts on Pacific salmonids (Carey et al. 2012). California sea lions have discovered concentrated salmon at the fish ladders below the Bonneville Dam, and knowledge of this food source has diffused through a local California sea lion population. Increasing predation pressure impedes endangered salmonid recovery and has resulted in a controversial lethal removal of individual sea lions at the dam. The tailrace of the dam appears to offer heightened benefits compared to natural foraging because fish congregate below the dam before swimming up the fish ladders. But, not all sea lions in the Columbia River estuary visit the dam (Wright et al. 2010). My fifth chapter uses social network based diffusion analysis to show that social transmission is driving foraging of endangered salmonids by California sea lions. Social transmission has implications for management measures, and we used an epidemiological model of behavioral transmission to assess current and potential lethal removal strategies. We show that current levels of lethal control have substantially reduced the rate of social transmission, but failed to effectively reduce overall sea lion recruitment. We show that the implementation of culling efforts earlier could have substantially reduced the extent of behavioral transmission and, ultimately, resulted in fewer animals being culled.

## GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

The fundamental mechanisms involved in animal learning are of practical importance to conservation/management practitioners and central to integrating behavioral ecology with conservation and wildlife management. My goal for this dissertation was to demonstrate that basic learning mechanisms offer promise as tools to inform management policy for controlling human-wildlife conflicts. My field studies of fear conditioning in sea lions interacting with fishing boats showed that fear conditioning is possible in the wild. These experiments were modeled after the extensive fear conditioning literature on laboratory rats, where conditioning elicits avoidance of foraging contexts (Blanchard et al. 2011; Fanselow and Ponnusamy 2008). We found that the conditioned response to acoustic stimuli was surfacing/changing orientation, which is not a target response that effectively deters sea lions from fishing boats. Thus, while we were able to induce mild fear conditioning in individual Californian sea lions interacting with commercial fishing activities, we were unable to create the avoidance necessary to prevent the predation problem. However, it should be noted that increased surface swimming (even at close distances) is a useful conditioned response in other commercial fisheries (e.g., bottom set gillnets) or on fish farms where predators need to spend a significant amount of time underwater in order to obtain prey (e.g., by manipulating nets). In order for fear conditioning to reduce interactions, careful consideration has to be given to the behavior of individuals, the unconditioned/conditioned responses, and the overall management goal when designing deterrents.

Sea lions preying threatened and endangered salmon in the Columbia River garners national and international attention. In Chapter 5, our results suggest that epidemiological

analyses offer promise in understanding and controlling socially transmissible behaviors such as salmonid foraging. Managers can use the results of epidemiological models to reduce the spread of unwanted behaviors in wildlife because they can help predict the risk factors for potential outbreaks, estimate the future prevalence of infection/behavior in the population, and test the efficacy of interventions such as culling (i.e., lethal removal of specific individuals). We believe these results will shape both policy as well as public perceptions. Our analysis challenges the current lethal removal law because delayed action necessitates more culling in the long term with little effectiveness. An amendment to the current law, proposed independent of our analysis, calls for a temporary expedited procedure for culling of pinnipeds in the Columbia River. Chapter 5 suggests this new policy will be more effective and ultimately reduce the overall number of sea lions lethally removed.

Facilitating human-wildlife coexistence is an emerging challenge in a world where wildlife and human interactions are increasing. Reducing conflicts requires managers to alter wildlife behaviors by exposing individuals to aversive deterrents or by lethally removing nuisance animals. Conflicts with California sea lions highlight the challenges of managing charismatic predator species versus economically, culturally, and ecologically important fisheries resources. There is a demand for new tools to both understand and modify wildlife behavior so that both can coexist while simultaneously balancing ethical concerns associated with removing natural predators. I believe a cognition-based approach to managing wildlife may be both effective and ethical. Incorporating fear conditioning for non-lethal deterrents is individual specific, thereby limiting the amount of overall aversive stimuli and potential for non-target impacts to the ecosystem. Even in cases where lethal removal is required, targeted removal of

super spreaders or initiating culling before the behavior can spread is not only more effective, but more ethical in the long term because it results less culling overall.

## References

- Brandt, M. J., Höschle, C., Diederichs, A., Betke, K., Matuschek, R., Witte, S., & Nehls, G. (2013). Far-reaching effects of a seal scarer on harbour porpoises, *Phocoena phocoena*. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(2), 222–232.
- Buhnerkempe, M. G., Tildesley, M. J., Lindström, T., Grear, D. A., Portacci, K., Miller, R. S., & Webb, C.T. (2014). The impact of movements and animal density on continental scale cattle disease outbreaks in the United States. *PLoS ONE*, 9(3), e91724.
- Carey, M. P., Sanderson, B. L., Barnas, K. A., & Olden, J. D. (2012). Native invaders – challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment*, 10(7), 373–381.
- Carretta, J. V., Forney, K. A., & Oleson, E. (2011). U.S. Pacific marine mammal stock assessments: 2011. *NOAA-Technical Memorandum-NMFS-SWFSC-476*.
- Chiyo, P. I., Moss, C. J., & Alberts, S. C. (2012). The influence of life history milestones and association networks on crop-raiding behavior in male African elephants. *PLoS ONE*, 7(2), e31382.
- Cooper, B. S., Pitman, R. J., Edmunds, W. J., & Gay, N. J. (2006). Delaying the international spread of pandemic influenza. *PLoS Med*, 3(6), e212.
- Dukas, R., & Ratcliffe, J. M. (2009). *Cognitive ecology II*. University of Chicago Press.

- Fanselow, M. S., & Ponnusamy, R. (2008). The use of conditioning tasks to model fear and anxiety. In R. Blanchard, C. D. Blanchard, G. Griebel, & D. J. Nutt (Eds.), *Handbook of Anxiety and Fear* (Vol. Volume 17, pp. 29–48). Amsterdam, Netherlands: Elsevier.
- Fletcher, R. C. (2008). Exploding populations of California sea lions: a crisis with no political solution on the horizon. *Proc. Vert. Pest Conf.*, *23*, 178–180.
- Gordon, J., & Northridge, S. (2002). Potential impacts of acoustic deterrent devices on Scottish marine wildlife. *Scottish Natural Heritage Commissioned Report F01AA404*.
- Gotz, T., & Janik, V. M. (2013). Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. *Marine Ecology Progress Series*, *492*, 285–302.
- Grillon, C. (2002). Startle reactivity and anxiety disorders: Aversive conditioning, context, and neurobiology. *Biological Psychiatry*, *52*(10), 958–975.
- Lefebvre, L. (1995). The opening of milk bottles by birds - evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. *Behavioural Processes*, *34*(1), 43–53.
- Lloyd-Smith, J. O., Schreiber, S. J., Kopp, P. E., & Getz, W. M. (2005). Superspreading and the effect of individual variation on disease emergence. *Nature*, *438*(7066), 355–359.
- Lowry, M. S., & Maravilla-Chavez, O. (2005). Recent abundance of California sea lions in western Baja California, Mexico and the United States. *Proceedings of the Sixth California Islands Symposium*.
- Mazur, R., & Seher, V. (2008). Socially learned foraging behaviour in wild black bears, *Ursus americanus*. *Animal Behaviour*, *75*, 1503–1508.

- Powell, J. R., & Wells, R. S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science*, 27(1), 111–129.
- Ramp, D., Foale, C. G., Roger, E., & Croft, D. B. (2011). Suitability of acoustics as non-lethal deterrents for macropodids: the influence of origin, delivery and anti-predator behaviour. *Wildlife Res.*, 38(5), 408–418.
- Read, A. J., & Wade, P. R. (2000). Status of marine mammals in the United States. *Conservation Biology*, 14(4), 929–940.
- Schakner, Z. A., Lunsford, C., Straley, J., Eguchi, T., & Mesnick, S. L. (2014). Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. *PLoS ONE*, 9(10), e109079.
- Scordino, J. (2010). West Coast pinniped program investigations on California sea lion and Pacific harbor seal impacts on salmonids and other fishery resources. *Pacific States Marine Fisheries Commission, Portland, OR*.
- Stein, R. A. (2011). Super-spreaders in infectious diseases. *International Journal of Infectious Diseases*, 15(8), e510–e513.
- Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. *Learning & Behavior*, 38(3), 329–336
- Wright, B. E., Tennis, M. J., & Brown, R. F. (2010). Movements of male California sea lions captured in the Columbia River. *Northwest Science*, 84(1), 60–72.

## CHAPTER 2

### Learning and conservation behavior: An introduction and overview

#### **A. Conceptual Background**

Learning is a key aspect of behavior that may greatly enhance the survival and fecundity of animals, especially in a changing environment. Wildlife conservation problems often involve increasing the population of threatened or endangered species, decreasing the population of species deemed over-abundant, or encouraging animals to move to or from certain areas.

Learning is an example of reversible plasticity (for review see Dukas 2009), which typically remains open to change throughout life. Old associations can be replaced, relearned and reinstated, facilitating behavioral modifications across an individual's lifetime. Because learning is potentially demographically important, and because it can be used to modify individual's behavior, it may therefore be an important tool for conservation behaviorists (Blumstein & Fernández-Juricic 2010). Our aim in this chapter is to introduce the fundamentals of learning that will later be developed and applied in subsequent chapters.

Animal learning theory defines learning as experience that elicits a change in behavior (Rescorla 1988, Heyes 1994). There are three basic mechanisms, or types of experiences, that underlie animal learning. The simplest learning process is non-associative because it involves an individual's experience with a single stimulus. During this process, exposure to the single stimulus results in a change in the magnitude of response upon subsequent exposure to that stimulus. If the response increases, the process is called *sensitization*; if the response decreases, the process is called *habituation*. More complex associative learning mechanisms involve a change in behavior as a result of experience with two stimuli through *Pavlovian conditioning*

(also referred to as *classical conditioning*), or the relationship between a subject's own behavior in response to a stimulus, which is called *instrumental conditioning*. Finally, learning can also occur as a result of interactions or observations with other individuals through *social learning*, but it is currently unclear whether social learning actually represents separate learning mechanisms than individual learning (Heyes 1994). Below we will describe these in more detail and outline the conditions that influence them. Later we will explain how knowledge of mechanisms of learning can be applied to wildlife management and conservation.

### **Non-associative learning: Habituation and Sensitization**

*What is it?*

Single stimulus learning is the simplest learning process and involves a change in the frequency or intensity of response to a stimulus. Non-associative, single stimulus learning involving a reduction of a behavioral response to repeated exposure to stimuli that is not due to sensory fatigue is called habituation (Groves & Thompson 1970). Unlike generalized sensory adaptation or motor fatigue (which would exhibit generalized responses within a modality to stimuli), habituation is characterized by stimulus specificity, which can be tested by showing responsiveness to novel stimuli (Rankin *et al.* 2009). This specificity suggests the function of habituation is to filter harmless stimuli from novel stimuli (Rankin *et al.* 2009). In contrast to habituation, heightened responsiveness after repeated exposure is termed sensitization.

According to the *dual process theory of habituation*, an observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves & Thompson 1970).

### *Conditions influencing habituation*

Generally, simple parameters such as intensity, modality, and frequency influence single-stimulus learning in animals. More frequent exposure typically results in quicker or more pronounced habituation (Groves & Thompson 1970, Rankin *et al.* 2009). Correspondingly, repeated exposure to less intense stimuli results in a response decrement whereas repeated exposure to higher intensity stimuli may either elicit no habituation or may result in sensitization (Groves & Thompson 1970, Rankin *et al.* 2009). After becoming habituated, withholding the stimulus results in a partial recovery in responsiveness, a process termed *stimulus recovery*. Response decrement exhibits specificity within a modality, which can be demonstrated by restored responsiveness to novel stimuli. During the course of habituation, the presentation of another, strong stimulus results in *dishabituation*, or restored responsiveness to a previously habituated stimulus. These behavioral characteristics of habituation have been clearly described in Groves & Thompson (1970), and since refined in Rankin *et al.* (2009).

### **Pavlovian conditioning**

#### *What is it?*

Pavlovian learning is seen when individuals learn the relationship between two stimuli; it is also called classical conditioning and, broadly, is one type of associative learning (Mackintosh 1974, Dickinson 1980, Rescorla 1988). In this type of learning, a biologically relevant stimulus, called the *Unconditioned Stimulus* (abbreviated US) is preceded by another stimulus, the *Conditioned Stimulus* (abbreviated CS). According to contemporary animal learning theory successful classical conditioning depends upon the contingency between the CS and US. This contingency

can be positive, meaning that the US reliably follows the CS, or negative, meaning the CS reliably signals the absence of US. As a result of this pairing, animals are able to learn the relations between the two stimuli and generate an adaptive response (Dickinson 1980, Shettleworth 2010).

The capacity to learn about the relationship between two stimuli, such as sounds preceding the presence of a predator, or taste cues associated with edible food, is functional because it guides how an animal can adaptively respond to exogenous stimuli as well as anticipate future events (Domjan 2005, Shettleworth 2010). *Pavlovian fear conditioning* is an associative form of learning in which individuals are exposed to an aversive stimulus (US) paired with an innocuous stimulus (CS) (Fanselow 1984, Grillon 2002, Fanselow & Ponnusamy 2008). Once conditioning has occurred, exposure to the unconditioned stimulus generates fear reactions to the conditioned stimulus. For example, by learning the cues that predict a predator attack, prey are able to modify their behavior and reduce the probability of death (Domjan 2005). From this functional learning perspective, learning about the relationship between two stimuli influences the adaptive decision making process and can modify an individual's behavioral response (Hollis 1982).

### *Conditions influencing Pavlovian Conditioning*

Functionally, there are particular conditions in which animals are able to learn patterns or relationships between stimuli in the natural world. The temporal relationship between two stimuli influences the conditioning process. Generally, a CS that precedes a US in time leads to more robust conditioning (Domjan & Burkhard 1986, Rescorla 1988). This is intuitive because in nature it is adaptive to learn the cues that precede consequences (i.e. certain tastes may

precede sickness, or alarm calls are likely to precede predator presence).

The Rescorla-Wagner model (RW) is a generally accepted model for predicting the behavioral consequences and conditions driving associative learning between a CS and a US (Rescorla & Wagner 1972). According to the model, learning occurs as a result of the difference between what an animal expects to happen versus what happens. The RW-model suggests that all learning curves are similar and asymptotic (Fig. 3.1). For example, the first pairing of a CS (e.g. a neutral tone) followed by a US (e.g. a shock) is surprising, and results in a significant amount of learning (Fig. 3.1). After subsequent pairings, the amount that is learned decreases because the US is less surprising when it follows the CS, resulting in a negatively accelerating curve. At the asymptote, the past experience with the CS/US pairing means that the CS accurately predicts the US, and thus little more is learned. According to the model, learning curves may differ in their slope, which is determined by the values of the rate parameters (i.e. magnitude of US or CS and US salience). In other words, some relationships can be learned more quickly than others (e.g., taste aversion or fear conditioning). The model can be used to help understand differences between species (Trimmer *et al.* 2012) and help explain differences in the speed of learning. For instance, the value of alpha (the CS learning rate) for auditory cues may be higher in one species than another, which will then lead to the former learning more quickly than the latter when an auditory cue signals something like the imminent delivery of food. The RW model produces idealized learning curves during controlled conditions. In the wild, differences in parameter values across species may explain observed patterns of learning in different situations, although this requires further study.

Conditioning also depends on the nature and relationship of the stimuli being paired. Conditioning experiments confirm that learning particular combinations of stimuli can be

especially effective. For example, pigeons form effective associations when auditory cues are the CS preceding a shock and visual cues precede food (Shapiro *et al.* 1980). Taste aversion learning is a well-known example of selective associations. In Garcia & Koelling's (1966) experiment, rats with two cues, taste CS and audiovisual CS, were then exposed to a nausea inducing US or shock US. Shocked individuals associated the shock with the audiovisual cue and poisoned individuals associated the sickness with the taste cue (Garcia & Koelling 1966). There also is evidence of preparedness (Öhman & Mineka 2002), or evolved predispositions to associate particular stimuli (Griffin & Evans 2003). Animals form rapid associations between ecologically relevant CSs and certain aversive USs compared to fear irrelevant CSs (Mineka & Öhman 2002). Examples include fearful responses to foxes (*Vulpes vulpes*), but not goats (*Capra hircus*), by tamar wallabies (*Macropus eugenii*) (Griffin *et al.* 2001), or fear responses to snakes but not flowers by primates (including humans) (Öhman & Mineka 2002). These, and many other examples (Domjan 2005) have suggested animals are predisposed to learn the relationships between evolutionarily relevant stimuli; findings which help develop an ecologically relevant perspective on general learning theory.

## **Instrumental conditioning**

*What is it?*

In instrumental conditioning, the animal learns a relationship between an operant behavior and the consequence of that behavior, and behavioral frequencies are adjusted accordingly (Thorndike & Bruce 1911, Domjan & Burkhard 1986). This is a second type of associative learning. During conditioning, a stimulus, typically termed a *reinforcer* influences the likelihood

of a response. Thus, behaviors followed by positive consequences will increase in occurrence, whereas behaviors followed by negative consequences will decrease. Functionally, instrumental conditioning is a mechanism that enables individuals to modify, shape or create complex patterns of behavior

### *Conditions influencing instrumental conditioning*

The rate of instrumental conditioning is influenced by the reinforcer type, the reinforcement schedule, and the nature of the response (Domjan & Burkhard 1986). Generally, positive reinforcers, such as food or water, increase the frequency of a behavioral response, whereas negative reinforcers, such as shock or other pain inducing events, decreases the frequency of a behavioral response. Similar to Pavlovian conditioning, instrumental conditioning depends on the temporal association between the reinforcer and response as well as on the contingency between the response and occurrence of the reinforcer. Finally, instrumental conditioning is limited by the degree that reinforced behaviors fit into an animal's natural behavior patterns, as well as the *belongingness* (the fit between the animal's behavior and stimuli used to reinforce them—e.g. Shettleworth 1975)

## **Social learning**

### *What is it?*

We use Hoppitt & Laland's (2008) definition of social learning as “the process through which one individual influences the behavior of another individual in a manner that increases the probability that the observer learns” (further reviewed in Heyes 1994, Galef & Laland 2005).

Research has emphasized the adaptive value of social learning (Laland 2004, Rendell *et al.* 2010, Heyes 2012). Social learning can function as a multiplier, since new traits can spread more quickly socially than by individual learning alone. There is evidence that asocial and social learning rely on the same underlying associative and non-associative mechanisms (Heyes 1994, 2012).

For instance, stimulus enhancement has been proposed as a form of single stimulus social learning. It occurs when a demonstrator's presence exposes an observer to a stimulus, resulting in an increase or decrease in responsiveness in the observer's interaction with that stimulus (Heyes 1994). From this perspective, stimulus enhancement may sensitize or habituate a response to a stimulus following an observer's interaction with a stimulus. For example, Heyes *et al.* (2000) found that rats observing conspecifics pressing a lever increased the probability of the observer interacting with that lever. It should be noted, however, that it is difficult to rule out associative learning in many cases of stimulus enhancement, because individuals may be learning to associate a location or stimulus with a reward (Hoppit & Laland 2008).

Observational conditioning is another form of social learning that, in this case, involves associative learning. Learning occurs when an observer's exposure to a demonstrator enables it to learn the relationship between two stimuli. For example, classic work by Mineka & Cook (1984) on rhesus monkeys (*Macaca mulata*) showed that naïve monkeys, when exposed to videos of wild monkeys responding fearfully to snakes, quickly learned the relationship between the fear response and the snake stimulus. In this experiment, the demonstrator monkeys' fear response is believed to be an US and associative learning occurs when paired with the snake, a CS.

Finally, observational learning occurs when an observer's experience with a demonstrator facilitates the observer's learning of a stimulus and response. For example, Akins & Zentall's (1996, 1998) work on Japanese quail (*Coturnix japonica*) used a two-action test to show observer quail learn to peck or step on a treadle based upon the demonstrator's action and the observed reward for that specific action.

### *Conditions influencing social learning*

If we assume that asocial and social learning are governed by the same underlying fundamental learning mechanisms (Heyes 1994), then the conditions for both will be similar but with an added condition for social learning: the presence of conspecific or traces of conspecific stimuli. The components of an individual's social milieu provide opportunities for individuals to interact with and learn from conspecifics or traces of conspecifics (Coussi-Korbel & Fragaszy 1995). Variables such as rank, age, familiarity, and social group size, can influence how and from whom individuals learn, which is termed directed social learning (Coussi-Korbel & Fragaszy 1995, Swaney *et al.* 2001, Nunn *et al.* 2009).

A given individual is not equally exposed to all animals in space and time (Coussi-Korbel & Fragaszy 1995), so there is some uncertainty as to who can and should learn socially. Network based diffusion analysis (NBDA) use formal network statistics to test for social learning in social groups. NBDA tracks the passage of information along established social networks in animal groups (Franz & Nunn 2009) because behaviors are expected to be transmitted across existing social connections.

While social learning may be potentially adaptive, like many traits, whether or not animals that learn specific things enhance their fitness may depend on the specific situation. For

instance, social learning may lead to animals acting upon outdated information because they copied demonstrators who had learned something that is no longer valuable, and making the outdated behavioral response last longer within the population despite being less valuable (for review, see Laland 2004, Rendell *et al.* 2010).

## **B. Learning and conservation: How knowledge of learning mechanisms may help solve conservation problems**

With this fundamental review of learning behind us, we shall now go on to highlight some important conservation questions that will be enhanced by the study of learning. Numerous conservation and management problems can apply mechanistic insights into how animals learn about biologically relevant events. We organize this section according to the three conservation behavior themes (Berger-Tal *et al.* 2011, Chapter 1).

### **Theme 1. Anthropogenic impacts on behavior**

#### *1a. What constrains animal learning in response to anthropogenic change?*

Anthropogenic change may increase environmental variation and may create novel environments that animals may have not experienced before (Sih *et al.* 2011). When faced with variable environments, learning is an adaptive mechanism that permits individuals to acquire predictive information from local conditions to generate adaptive behavioral responses (Shettleworth 2010). But, there are constraints on learning, and there is variation in how species respond to environmental change (Sol *et al.* 2002). We divide constraints to learning as internal and external.

Internal constraints are largely cognitive, while external constraints include the rapidity of the stimulus exposure, the magnitude of the consequence and its consistency over time.

### Internal constraints

Differences in underlying input mechanisms, such as a species' perceptual abilities, the attention an individual can allocate to a task, or an individual's motivation (Macphail & Barlow 1985, Shettleworth 2010, Heyes 2012) are likely to influence learning capacities.

Non-detectable stimuli can't be learned. Some anthropogenic stimuli may simply not be detected, such as glass windows by birds. An animal that relies on vision might not learn to avoid a highway, compared to an animal with acute hearing that is disturbed by distant sounds. Sensory disturbances vary (Lowry *et al.* 2011) and so does the combination of sensory modalities during association formation (taste precedes sickness, sound precedes pain, etc.).

The Rescorla-Wagner model predicts that novel or surprising unconditioned stimuli will be more effective at strengthening CS-US associations than those that whose occurrence is not surprising. But this may be a double-edged sword to managers. Novel foraging resources, such as crops or fishing lines, can be attractive, highly rewarding and lead to accelerated learning of nuisance behaviors. By contrast, other novel anthropogenic disturbance stimuli are perceived as threatening, resulting in accelerated avoidance (Frid & Dill 2002). Thinking about stimuli with respect to their potential RW learning rate parameter values (such as salience, surprisingness, belongingness) may be a fruitful way to categorize anthropogenic stimuli particularly if the goal is to train animals to selectively make associations or to train animals to selectively avoid resources.

Motivational mechanisms mediate an individual's tolerance for conspecifics, heterospecifics (including humans), or other potentially novel stimuli. Ultimately, motivational mechanisms will influence the stimuli an animal encounters, and how effectively they are conditioned. Neophobia is defined as a propensity to avoid novel stimuli (Greenberg 2003). Differences in neophobia may underlie the propensity to learn (Sol 2013). For example, there is evidence that less neophobic urban zenaida doves (*Zenaida aurita*) that experience a highly dynamic environment, become less neophobic, learn faster and are more inclined to learn from conspecific demonstrators than less urbanized doves (Carlier & Lefebvre 1997, Seferta *et al.* 2001). Motivational mechanisms can also vary intraspecifically due to personality differences in boldness/shyness (Shettleworth 2010, Sih & Giudice 2012). In numerous species, such as guppies (*Poecilia reticulata*), trout, (*Oncorhynchus mykiss*), and black-capped chickadees (*Parus atricapillus*), bolder or more exploratory individuals learn quicker (Dugatkin & Alfieri 2003, Sneddon 2003, Guillette *et al.* 2009).

Comparative studies in birds and mammals suggest that the correlations between brain size, learning and overall behavioral flexibility enable species to respond to novel ecological challenges (Sol *et al.* 2002, 2008). Generating behavioral flexibility through learning may enable individuals to modify, copy, or create novel antipredator responses (Berger *et al.* 2001), prey choice (Estes *et al.* 1998), or habitat selection (Doligez *et al.* 2002). Comparative approaches suggest that species with larger brains (relative to body size) have enhanced survival in novel, disturbed, or dynamic environments (Sol *et al.* 2005, 2007, 2008; Amiel *et al.* 2011). Thus, while behavioral plasticity, generated by learning, is widespread in nature, there is variation in the degree to which animals can learn to respond to the new situations that are generated by anthropogenic change and relative brain size is a rough index of this flexibility. Managers should

be sensitive to this variation and future research should identify other correlates of flexibility. It is important to note, however, that the effect of brain size on behavioral complexity remains highly debatable (Healy & Rowe 2007), and no study that we know of has looked at the influence of brain size on the effectiveness of different learning mechanisms.

In some species, there may be a sensitive time period during which most learning about a particular biologically important process occurs (Hogan & Bolhuis 2005). The classic example is filial imprinting in precocial birds (Lorenz 1970). However, there is also strong evidence of sensitive periods for habitat (Davis & Stamps 2004) and sexual preferences (Bateson 1978). More generally, however, individuals at different life stages may be more or less likely to learn (Dukas 2008). Hawkins *et al.* (2008) demonstrated age dependent learning of predator cues in hatchery-reared salmon. Their results suggest heightened receptivity to learning predator cues during the life history stage at which juveniles would be undergoing a habitat shift and thus are particularly sensitive toward predation. Such variation in the ability to learn may allow young, but not older, animals to learn appropriate responses in an anthropogenically disturbed environment.

Learning during sensitive periods can be via individual associative learning mechanisms or via social learning from parents. These so called parental effects may be obligatory for survival in some species. However, parental effects can also act as multipliers, spreading maladaptive behaviors through populations. For instance, wild black bear (*Ursus americanus*) cubs raised by garbage pilfering sows were significantly more likely to rely on human resources (Mazur & Seher 2008)

Finally, managers should be mindful of sensitive periods to optimize reintroductions/translocations. For instance, if animals are to be moved to a new environment,

pre-exposure to that environment (or certain characteristics of that environment, such as food sources) during a sensitive period may be essential for successful establishment. Much work remains to be done to provide concrete examples that can help inform management.

### External constraints

Learning is adaptive because it enables individuals to track environmental variation. We know that the type of reinforcer, the temporal relationship between the reinforcer and the consequence, and the magnitude of the consequence will all constrain the rate of learning (Shettleworth 2010). Positive reinforcers, such as food, safety, or conspecifics tend to increase behavioral responses. Negative reinforcers such as painful, noxious or distracting stimuli may only require a single exposure to create long- term learning (Rau & Fanselow 2009).

Learning can only occur if the rate of learning is faster than the rate of environmental change (Johnston 1982). If anthropogenic change is too rapid, learning cannot occur and individuals in a population will be unable to modify their behavior and behaviorally track the changes. In such cases, given sufficient additive genetic variation, there will be strong selection against those animals with an inadequate behavioral response.

The magnitude of the consequence, the speed (rapidity) at which a stimulus reaches its full magnitude, and its consistency over time (anthropogenic noise, for instance, may cycle over 24 hours) will also influence learning. An event or stimulus that is always lethal will prevent any learning from occurring, whereas highly profitable food sources (such as crops or garbage cans), or painful/nearly lethal encounters, may stimulate rapid and complete learning after one or a few exposures. Intense stimuli with a rapid onset elicit startle responses (Yeomans *et al.* 2002). In organisms vulnerable to high intensity acoustic stimuli like sea turtles or cetaceans, rapid onset

exposures (seismic airgun arrays or sonar) may lead to sensitization of avoidance responses (Gotz & Janik 2011, DeRuiter & Doukara 2012).

*Ib. Anthropogenic impacts on behavior: Can we develop an evolutionary ecology of habituation?*

A fundamental question in wildlife conservation and management concerns the causes and consequences of habituation and sensitization. Why do some species habituate, while others sensitize to anthropogenic stimuli? The “life-dinner principle” suggests that for a prey species, the costs of getting predated far outweigh the costs of missing a meal (Dawkins & Krebs 1979). From a life-dinner principle perspective, there is an asymmetry between the fitness costs of failing to detect a predator (Type 1 error) and over-reacting to non-threatening stimuli (Type 2 error).

Habituation to non-threatening stimuli is somewhat expected since anxiety or stress from over-generalized threat recognition may be costly in terms of energy or time allocated to unnecessary defenses (Blanchard 2008). We therefore expect animals to show an initial heightened response, followed by rapid habituation to repeated un-reinforced exposures of even potentially threatening stimuli (Groves & Thompson 1970). Habituation is thus a mechanism to reduce the costs of false alarms (Thorpe 1956, Shalter 1984).

Remarkably, given how long we have known about mechanistic processes involved in habituation and sensitization (Groves & Thompson 1970), little is known about habituation in the wild, or what we will refer to as the evolutionary ecology of habituation. Perhaps this is in part because habituation has been extensively investigated under controlled experimental conditions. By contrast, in nature, an organism’s environment is noisy and filled with threatening

and non-threatening stimuli that occur in a variety of different contextual situations. To deal with this uncertainty, there is evidence that habituation under natural conditions is quite selective and enables individuals to learn what is not threatening (Deecke *et al.* 2002, Hemmi & Merkle 2009, Raderschall *et al.* 2011). In a series of studies of antipredator responses in wild hermit crabs, Hemmi (2011) demonstrated that habituated responses are recovered when the same predator stimulus is presented at a different distance or angle. Similar to laboratory investigations of dishabituation, this study shows that in the wild, even small changes in stimulus presentation can result in recovered responsiveness. Correspondingly, selective habituation is hypothesized to be the mechanism by which harbor seals (*Phoca vitulina*) discriminate between threatening and non-threatening killer whale (*Orcinus orca*) vocalizations (Deecke *et al.* 2002). Harbor seals responded with flight to playback of vocalizations from local marine mammal-eating killer whales and novel fish-eating killer whales, but not local fish-eating killer whales. These results suggest that the seals habituated to non-threatening local fish eating killer whales, but were fearful to unknown vocalizations. This specificity of habituation makes sense in terms of the fundamental characteristics of habituation described in our introduction and illustrates its evolutionary context.

Ultimately, to develop a natural history of habituation we will need to understand what sorts of stimuli in nature lead to habituation and then understand the what life history and natural history features are correlated with habituation or sensitization. As a step towards this, Li *et al.* (2011) developed a mixed-modeling statistical approach to identify how different anthropogenic stimuli (people, people on bicycles, people in cars) influenced flight initiation distance decisions in yellow-bellied marmots (*Marmota flaviventris*). Flight initiation distance (FID) is a

particularly sensitive assay for how animals respond to approaching threats and animals repeatedly exposed to humans often tolerate closer approaches before fleeing.

The nature, spatio-temporal pattern, and context of exposure to stimuli influence the rate of habituation and whether sensitization occurs. For example, yellow-eyed penguins (*Megadyptes antipodes*) show sensitized stress responses to tourists in Sandfly Bay (Ellenberg *et al.* 2009). The authors suggested that the unpredictable and abrupt behavior of tourists that ran, shouted and chased penguins prevented habituation and facilitated sensitization. During exposure to threatening stimuli, animals assess the type and risk of the threat, as well the contextual cues (whether or not escape was possible) and used these factors to generate an appropriate response (Blanchard 2008, Blanchard *et al.* 2011). Risk assessment studies using laboratory rats show that an individual's response is the result of the type and distance of threat, and the local environment, to produce the adaptive response (Blanchard 2008, Blanchard *et al.* 2011). In the wild, whether an animal habituates or not is likely to be influenced both by the immediate environment (for instance, is a safe place to escape available?) and its own locomotor abilities (can it escape?).

Species and individuals within species may vary in how quickly they habituate as a result of personality or sex differences (Rodríguez-Prieto *et al.* 2010a). In humans, personality traits like extroversion and impulsivity are correlated with a faster startle habituation response (LaRowe 2006). This suggests that over time there will be a non-random distribution of personalities in response to anthropogenic disturbance. Thus, we can predict that more tolerant species or individuals will be able to colonize more disturbed areas (Carrete & Tella 2010).

Habitat availability may be another factor that influences the likelihood of habitation or sensitization. Blumstein (2013) proposed the ‘contiguous habitat hypothesis’ to explain why some Southern California birds habituated while others sensitized. The contiguous habitat hypothesis predicts that species that find themselves in highly fragmented and rare habitats will be more likely to habituate to increased human disturbance. This might result from a process of sorting whereby individuals and species that were unable to tolerate increased disturbance have been eliminated while those that tolerated disturbance persisted in the patches. The net result would be that ‘tolerant’ species will be found in this highly patchy habitat while those in more contiguous habitat might be more variable and indeed might respond to increased disturbance by sensitizing. If generally true, the hypothesis suggests that the opportunity to move within habitat patches will be more often associated with sensitization than situations where animals are so constrained that they have no other choices than habituation.

*1c. Novel mismatches between cues and fitness: is learning important?*

Individuals may naturally learn to identify cues that help them detect suitable habitats in which they historically have had relatively high survival or reproductive success (reviewed in Davis & Stamps 2004, Stamps & Swaisgood 2007). In some circumstances, individuals may select suboptimal habitats because of a mis-match between the cues they evolved to evaluate and novel fitness consequences associated with those cues; this is referred to as an ecological trap (reviewed by Schlaepfer *et al.* 2002, Sih *et al.* 2011, chapter 4). Whether ecological traps are more or less likely in species that learn about their habitat (or other biologically important characteristics) is an open question. For instance, animals that disperse may rely on learning cues from their natal habitat to help them develop a template by which they can evaluate habitat

quality and determine where to settle while dispersing (Davis & Stamps 2004). The degree that animals learn would influence how those cues can be manipulated.

We expect that associative learning mechanisms (e.g. Pavlovian and instrumental associative learning) should enable individuals to select suitable habitats if learning is a mechanism underlying habitat selection. Even if learning is not a natural mechanism, it might be possible to generate positive experiences to train animals to use a desired habitat and/or negative experiences to train animals to avoid a particular habitat. Stimuli such as tastes, smells, or visual cues can give information on relative forage quality or risk of predation that will influence animal decisions.

Extensive work on learning and life skill training in hatchery reared fish represents an important application of learning theory that has translated to applied value. Hatchery fish that learn life skills such as predator recognition, prey handling, foraging locations exhibit enhanced post-release survival (reviewed in Brown & Laland 2001, Brown *et al.* 2003, Hawkins *et al.* 2008). Additionally, social learning can act as a multiplier of these skills, facilitating quicker learning and transmission, which is more efficient for the aquaculturist whose aim is to produce animals that will survive upon release.

## **Theme 2. Behavior-based management: Training for conservation**

Knowledge of learning mechanisms is also of use to managers who wish to modify animal behavior. Training animals with basic learning mechanisms may help repel animals from human resources, attract them to particular habitats/regions, or generate basic survival skills to enhance survival during translocations/reintroductions.

### *2a. Teaching attraction*

Animal learning principles can provide general rules on how animals can be taught specific behaviors or attraction to habitats as well as the conditions under which they may not be able to be taught. Positive reinforcers can be used to attract an animal, locate food source, or increase the frequency of a particular behavior. Stimuli used for positive reinforcement include food, shade, odors, shelter, or access to conspecifics. These stimuli can be manipulated to facilitate the learning of habitat preferences. Preferences can be taught via Pavlovian conditioning where the taste is associated with food quality, or via instrumental means where, for example, animals are trained to use tunnels beneath freeways. Additionally, conspecific or heterospecific stimuli can act as positive reinforcers during food source localization or habitat selection (for review see Avarguès-Weber *et al.* 2013). The constraints to learning mentioned above similarly apply - there may be certain critical periods for learning to develop certain preferences.

### *2b. Teaching avoidance*

The creation of novel concentrations of resources such as crops, garbage cans, fishing lines and domesticated livestock, provide motivation for animals to learn to exploit those resources, resulting in human/wildlife conflict. Since anthropogenic resources, like fishing lines or crops, can reduce the costs compared to natural foraging, the motivation to form the association between humans and food reward is not only high, but learning is expected to occur quickly (Schakner & Blumstein 2013). Once learned, the association is difficult to break and thus management efforts require foresight and a preventative mindset. Since learning to acquire human resources involves associative mechanisms, there are points in the learning process that management efforts should target to be most effective in teaching avoidance: pre-association formation, during association formation, and post association formation.

Animals require a contingency to form an association between two stimuli or stimulus/response (Rescorla 1968). In the wild, animals can learn the association between human resources and the cues that reliably precede them. For example, marine mammals, such as sperm whales (*Physeter macrocephalus*), have learned to associate vessel sounds (CS) with a food reward (US: fish on line) (Thode *et al.* 2007). In order to form that association, the vessel sounds must reliably predict the food reward. Therefore, the most effective management of depredation is preventing animals from learning the depredative behavior in the first place by reducing the contingency between stimulus and reward. This can be accomplished by decoupling the spatio-temporal overlap between potential depredators and the human resources. For example, in the Gulf of Alaska, demersal longline fisheries management shifted from a 10-day derby-style fishing season (vessels catch a year's quota in a set period of time) to an 8-month long individual fishing quota regime. As a result of the extended overlap between sperm whales and fishing vessels in space and time with the new quota fishing regime, there was ample opportunity for the animals to learn to exploit the resources and the whales are now attracted to boats setting and hauling in lines which results in a loss of valuable fishes (Hill *et al.* 1997). A lesson from this case study is that foresight may be necessary to prevent learning from occurring in the first place.

When innovators initially learn to depredate or crop raid, social learning can have a multiplier effect by spreading behaviors through populations quickly (Lefevbre 1995). In elephants (*Loxodonta africana*) for example, network analysis of crop raiders has demonstrated that the behavior appears to be socially learned through social networks (Chiyo *et al.* 2011). Correspondingly, social learning is believed to underlie the diffusion of depredation in sperm, killer whales, and pilfering black bears (Whitehead 2004, Mazur & Seher 2008, Schakner *et al.* 2014 ). In these cases, it is important to know both the identity of innovators (age/sex) and the

pattern of diffusion. This knowledge is useful to stop the spread and for targeted repellents or removals of individuals.

Once the association between humans and food reinforcers has formed, management efforts rely on raising the cost to the individual depredator. Because the association is difficult to extinguish, management efforts must rely on forming new negative associations or on decoupling the contingency between humans and reward. Deterrents and repellents produce noxious, aversive or painful stimuli to prevent animals from interacting with human habitat or resources (Ramp *et al.* 2011). Here we suggest that associative learning may produce long term-learned avoidance.

During painful encounters, animals rapidly learn the cues, context, or local conditions that are associated with that danger. This learning mechanism, i.e. fear conditioning, enables animals to learn from-, respond to-, and detect danger. Repellents, therefore, should capitalize on insights from the fear conditioning literature to generate avoidance. The use of painful stimuli such as rubber bullets or electric shocks are widespread for eliciting avoidance, but their effectiveness can be short term or impractical, and this raises ethical issues (e.g. is it ethical to continue to do something that's both painful and ineffective?). However, painful deterrent stimuli may be an integral part of a fear-conditioning program. Once conditioning has occurred, exposure to the conditioned stimulus generates fear reactions.

During painful encounters, an animal's unconditioned response is different from the conditioned response. For example, rats exposed to shock (US) react with a burst of motor activity. In contrast, rats exposed to a stimulus that predicts shock (CS such as context or experimenter), evoke behavioral responses such as fleeing, hyper-vigilance, or freezing. This

suggests a conditioning approach may offer promise, especially if the conditioned response to the target CS is avoidance.

What cues animals pick up on to avoid an area remains an open question. For instance, it is known that animals learn to avoid environments, stimuli, or conditions that are correlated with a decrease in fitness (i.e. death; Lima & Dill 1990, Frid & Dill 2002). Habitats, however, contain competing contextual stimuli such as landscape features, conspecifics, heterospecifics, and background noise. During an aversive event (a predator attack), individuals likely associate contextual cues (such as open space or shadows) as well as other stimuli (such as predator scents). According to the Rescorla-Wagner model, contextual cues compete with the CS for association with the US. In contrast to experimental contexts (a cage), the natural world is full of stimuli, and thus the animal may make associations between competing contextual cues and aversive stimuli. This means that managers should employ conditional stimuli that are obvious, discriminable, and detectable, preceding the biologically relevant aversive stimuli, when designing and implementing repellents. If habitat avoidance is the goal, diffuse CS stimuli, such as a strobe or sound, can be implemented (Table 3.1).

#### A checklist for US and CS selection

Effective deterrence relies on stimuli that are both aversive enough to cause rapid fear conditioning, and sufficiently aversive to prevent rapid habituation. To accomplish this, managers must tailor deterrent stimuli toward species-specific sensory modalities and sensory sensitivities. For example, sound is a fundamental channel for communication, foraging and predator detection in marine mammals and this makes it a useful modality in which to develop acoustic deterrents (Jefferson & Curry 1996). However, the input of aversive acoustic stimuli can impact non-target species, which should be considered during the development and

implementation of acoustic deterrents (T. Gotz, pers. comm.). Deterrents can be modulated to match a species sensory sensitivity while still being outside non-target animals' sensory range. Unconditioned stimuli that elicit pain must be practical as well and not cause permanent damage to the depredator. Finally, in social species, fearful responses by conspecifics can serve as a US (Mineka & Cook 1984).

There is evidence that CS which naturally 'belong' with US result in rapid and more long lasting associations (Domjan 2005). From this functional perspective, using biologically relevant stimuli like predator calls that precede painful stimuli may result in rapid and stronger associations. For example, Leigh & Chamberlain (2008) used barking dogs as a conditioned stimulus preceding rubber buckshot US on crop raiding bears, which yielded stronger responses than non-conditioned individuals. A conditioned stimulus that precedes the US must be discriminable, salient, and consistent. Additionally, the reinforcement schedule (how often to pair CS/US versus CS alone) can be modified depending on the nature of the conflict.

### **Theme 3. Behavioral indicators**

Our final section is brief: there may be a variety of behavioral indicators that can be used to reflect an animal's past experiences and knowledge of past experiences may be useful to wildlife management. The brevity of this section should not undermine its potential importance and future research should focus on identifying other situations and indicators that can be used to inform management.

#### *3a. Flight Initiation Distance*

As discussed above, in order to understand the behavioral imprint of humans, flight initiation distance can be used as a behavioral indicator of disturbance. Assuming that all else is equal

between sites (e.g. Gill *et al.* 2001), the difference in FID between two sites can provide a measure of the degree to which humans have modified risk assessment. When measured longitudinally, FID can also be used as a proxy for habituation (Ikuta & Blumstein 2003, Rodríguez-Prieto *et al.* 2010b).

### *3b. Socially-learned Traits*

Socially learned traits can diffuse through populations. After reintroductions or translocations, social transmission can be used track the spread of behaviors through groups. This may indicate how well reintroduced individuals are being incorporated or adapting behaviorally to life in the wild. In a well documented case of reintroduction, captive bred Arabian Oryx (*Oryx leucoryx*) foraging behavior was suggested to have been influenced by interactions with conspecifics (Tear *et al.* 1997). Social learning is believed to have enhanced foraging behaviors of reintroduced individuals during periods of low food availability (Tear *et al.* 1997). This study suggests that after reintroduction/translocation, managers can probe individuals in a group to assess whether behaviors have spread indirectly through social transmission.

In several species, social learning underlies stable inter-population behavioral variation. Apes, songbirds and cetaceans are believed to exhibit long-term, socially learned traditions or cultures (Whiten *et al.* 1999, Rendell & Whitehead 2001, Laiolo & Tella 2007). Since these socially learned behaviors are often functional (i.e. they are foraging tactics or social signals with fitness consequences) these traits could be used to indicate population viability (Laiolo & Tella 2007, Whitehead 2010). Laiolo & Tella (2005, 2007) were able to use bird song (a socially learned trait) diversity to show that fragmentation has eroded both cultural and population diversity. These studies suggest that cultural diversity can be used as a proxy for population viability as well as a tool for targeting subpopulations likely to be threatened (Whitehead 2010).

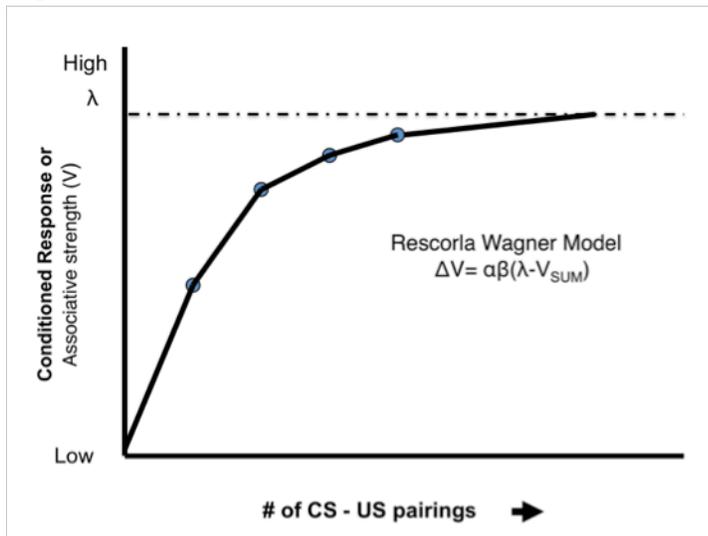
## **Summary**

We believe that the fundamental mechanisms involved in animal learning are of practical importance to conservation/management practitioners and central to integrating behavioral ecology with conservation and wildlife management. The necessity of incorporating learning into conservation is further discussed in subsequent chapters. In chapter 6, for instance, Fernández-Juricic describes how species-specific input channels and sensory systems influence which stimuli will be learned, which can be applied to repelling or attracting animals. The role of learning in behavioral modification is further discussed by Shier in chapter 10 including case studies involving reintroduction/translocations. From a broader perspective, learning is a mechanism of phenotypic plasticity, and the range and limits to plasticity in endangered and threatened species can be used to predict and manage species responses to anthropogenic change

Table 2-1. Advantages and disadvantages to a variety of stimuli that could be used as both conditioned and unconditioned stimuli for management-based training.

Stimulus	Advantages	Disadvantages
<i>Conditioned stimulus</i>		
Sound (e.g., Neutral tone)	Localized transmission	Non-target species impact
Light (e.g., Strobe light)	Discriminable	Limited to night or dark locations
Object (e.g., Flag or person)	Useful for place avoidance	Difficult associate object with US
Chemosensory (e.g., Taste or scent)	Salient cue for food aversion	Limited to nauseating US
<i>Unconditioned stimulus</i>		
Pain (e.g., Electric shock)	Long lasting associations after few exposures	Can cause physical damage
Distracting (e.g., White noise)	Wide-ranging	Impact non-target species
ecologically relevant stimuli (e.g., Predator cue)	Species-specific	Rapid habituation
Frightening stimuli (e.g., Looming, novel, or abrupt stimuli)	Can elicit fear responses	Rapid habituation
Nauseating (e.g., LiCl)	One trial learning	Unwanted prey avoidance

**Figure 2-1**



The Rescorla-Wagner model of learning. On the y-axis is the performance, which represents underlying learning (associative strength). The change in predictive value of a CS,  $\Delta V$ , is a result of the discrepancy between what is expected versus what actually happens ( $\lambda - V_{SUM}$ ).  $\alpha$  and  $\beta$  are learning rate parameters that correspond to salience of the CS and US, and  $V_{SUM}$  is the sum of current associative strengths of all the CSs present. During the first few trials of CS/US (x-axis), the associative strength is large because the US is surprising. With subsequent trials however, the associative strength decreases because it becomes less surprising. At the asymptote, the CS predicts the US with certainty, thus there is nothing more

## References

- Akins, C.K., Klein, E.D. & Zentall, T.R. 2002. Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Animal Learning & Behavior*, **30**:275–281.
- Akins, C.K. & Zentall, T.R. 1996. Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *Journal of Comparative Psychology*, **110**:316–320.
- Akins, C.K. & Zentall, T.R. 1998. Imitation in Japanese quail: The role of reinforcement of demonstrator responding. *Psychonomic Bulletin & Review*, **5**:694–697.
- Amiel, J.J., Tingley, R. & Shine, R. 2011. Smart Moves: Effects of Relative Brain Size on Establishment Success of Invasive Amphibians and Reptiles. *PLoS ONE*, **6**:e18277.
- Avarguès-Weber, A., Dawson, E.H. & Chittka, L. 2013. Mechanisms of social learning across species boundaries. *Journal of Zoology*, **290**:1-11
- Barton, R.A. 1996. Neocortex size and behavioural ecology in primates. *Proceedings of the Royal Society of London Series B*, **263**:173–177.
- Bateson, P. 1978. Sexual imprinting and optimal outbreeding. *Nature*, **273**:659–660.
- Berger, J., Swenson J.E. & Persson, I. L. 2001. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science*, **291**:1036–1039.
- Blanchard, C.D. 2008. Defensive behaviors, fear, and anxiety. In Blanchard, C.D., Blanchard, R.J., Griebel, G. & Nutt, D.J. (eds.), *Handbook of Anxiety and Fear*. pp. 63–79. Oxford: Elsevier.
- Blanchard, C.D., Griebel, G., Pobbe, R. & Blanchard, R.J. 2011. Risk assessment as an evolved threat detection and analysis process. *Neuroscience and Biobehavioral Reviews*,

35:991–998.

- Blumstein, D.T. & Fernández-Juricic, E. (2010). *A Primer of Conservation Behavior*. Sunderland: Sinauer Associates.
- Brown, C., Davidson, T. & Laland, K.N. 2003. Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon. *Journal of Fish Biology*, **63**:187–196.
- Brown, C. & Laland, K.N. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**:471–493.
- Carlier, P. & Lefebvre, L. 1997. Ecological differences in social learning between adjacent, mixing, populations of Zenaida doves. *Ethology*, **103**:772–784.
- Carrete, M. & Tella, J.L. 2010. Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters*, **6**:167–170.
- Chiyo, P.I., Moss, C.J. & Alberts, S.C. 2012. The influence of life history milestones and association networks on crop-raiding behavior in male African elephants. *PLoS ONE*, **7**:e31382.
- Coussi-Korbel, S. & Fragaszy, D.M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**:1441–1453.
- Davis, J.M. & Stamps, J.A. 2004. The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, **19**:411–416.
- Dawkins, R. & Krebs, J.R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **205**:489–511.
- Deecke, V.B., Slater, P.J.B. & Ford, J.K.B. 2002. Selective habituation shapes acoustic

- predator recognition in harbour seals. *Nature*, **420**:171–173.
- DeRuiter, S.L. & Doukara, K.L. 2012. Loggerhead turtles dive in response to airgun sound exposure. *Endangered Species Research*, **16**:55–63.
- Dickinson, A. 1980. *Contemporary Animal Learning Theory*. Cambridge: Cambridge University Press.
- Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science*, **297**:1168–1170.
- Domjan, M. 2005. Pavlovian conditioning: A functional perspective. *Annual Review of Psychology*, **56**:179–206.
- Domjan, M. & Burkhard, B. 1986. *The Principles of Learning & Behavior*. Monterey: Brooks/Cole Publication Company.
- Dugatkin, L.A. & Alfieri, M.S. 2003. Boldness, behavioral inhibition and learning. *Ethology Ecology & Evolution*, **15**:43–49.
- Dukas, R. & Ratcliffe, J.M. 2009. *Cognitive ecology II*. Chicago: University of Chicago Press.
- Dukas, R. 2008. Life history of learning: performance curves of honeybees in settings that minimize the role of learning. *Animal Behaviour*, **75**:1125–1130.
- Ellenberg, U., Mattern, T. & Seddon, P.J. 2009. Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour*, **77**:289–296.
- Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. 1998. Killer whale predation on sea otters: linking oceanic and nearshore ecosystems. *Science*, **282**:473–476.
- Fanselow, M.S. & Ponnusamy, R. 2008. The use of conditioning tasks to model fear and

- anxiety. In Blanchard, C.D., Blanchard, R.J., Griebel, G. & Nutt, D.J. (eds.), *Handbook of Anxiety and Fear*. pp. 29-48. Oxford: Elsevier.
- Fanselow, M.S. 1984. What is conditioned fear? *Trends in Neurosciences*, **7**:460–462.
- Franz, M. & Nunn, C.L. 2009. Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, **276**:1829–1836.
- Frid, A. & Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**:11–26.
- Galef, B. & Laland, K.N. 2005. Social learning in animals: empirical studies and theoretical models. *BioScience*, **55**:489–499.
- Garcia, J. & Koelling, R.A. 1966. Relation of cue to consequence in avoidance learning. *Psychonomic Science*, **4**:123–124.
- Gill, J.A., Norris, K. & Sutherland, W.J. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**:265–268.
- Gotz, T. & Janik, V.M. 2011. Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. *BMC Neuroscience*, **12**:1-12
- Greenberg, R. 2003. The role of neophobia and neophilia in the development of innovative behaviour of birds. In Reader, S. & Laland, K. (eds.), *Animal innovation*, pp. 175–196. New York: Oxford University Press.
- Griffin, A.S. & Evans, C.S. 2003. The role of differential reinforcement in predator avoidance learning. *Behavioural Processes*, **61**:87–94.

- Griffin, A.S., Evans, C.S. & Blumstein, D.T. 2001. Learning specificity in acquired predator recognition. *Animal Behaviour*, **62**:577–589.
- Grillon, C. 2008. Models and mechanisms of anxiety: evidence from startle studies. *Psychopharmacology*, **199**:421–437.
- Groves, P.M. & Thompson, R.F. 1970. Habituation a dual process theory. *Psychological Review*, **77**:419–450.
- Guillette, L.M., Reddon, A.R., Hurd, P.L. & Sturdy, C.B. 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes*, **82**:265–270.
- Hawkins, L.A., Magurran, A.E. & Armstrong, J.D. 2008. Ontogenetic learning of predator recognition in hatchery-reared Atlantic salmon, *Salmo salar*. *Animal Behaviour*, **75**:1663–1671.
- Healy, S.D. & Rowe, C. 2007. A critique of comparative studies of brain size. *Proceedings of the Royal Society B-Biological Sciences*, **274**:453–464.
- Hemmi, J.M. & Merkle, T. 2009. High stimulus specificity characterizes anti-predator habituation under natural conditions. *Proceedings of the Royal Society B-Biological Sciences*, **276**:4381–4388.
- Heyes, C. 2012. What's social about social learning? *Journal of Comparative Psychology*, **126**:193–202.
- Heyes, C.M. 1994. Social-learning in animals - categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, **69**:207–231.
- Heyes, C.M., Ray, E.D., Mitchell, C.J. & Nokes, T. 2000. Stimulus enhancement: controls for social facilitation and local enhancement. *Learning and Motivation*, **31**:83–

98.

- Hill, P.S., Laake, J.L. & Mitchell, E.D. 1999. Results of a pilot program to document interactions between sperm whales and longline vessels in Alaskan waters. U.S Department of Commerce, Report No. NOAA TM-NMFS-AFSC-108.
- Hogan, J.A. & Bolhuis, J.J. 2005. The development of behaviour: trends since Tinbergen (1963). *Animal Biology*, **55**:371–398.
- Hollis, K. 1982. Pavlovian conditioning of signal-centered action pattern and autonomic behavior: A biological analysis of function. *Advances in the Study of Behavior*, **12**:1.
- Hoppitt, W. & Laland, K.N. 2008. Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior*, **38**:105–165.
- Ikuta, L.A. & Blumstein, D.T. 2003. Do fences protect birds from human disturbance? *Biological Conservation*, **112**:447–452.
- Jefferson, T.A. & Curry, B.E. 1996. Acoustic methods of reducing or eliminating marine mammal-fishery interactions: Do they work? *Ocean Coastal Management*, **31**:41–70.
- Johnston, T.D. 1982. Selective costs and benefits in the evolution of learning. *Advances in the Study of Behavior*, **12**:65–106.
- Laiolo, P. & Tella, J.L. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark. *Journal of Applied Ecology*, **42**:1183–1193.
- Laiolo, P. & Tella, J.L. 2007. Erosion of animal cultures in fragmented landscapes. *Frontiers in Ecology and the Environment*, **5**:68–72.
- Laiolo, P., Vögeli, M., Serrano, D. & Tella, J.L. 2008 Song diversity predicts the viability of fragmented bird populations. *PLoS ONE*, **3**:e1822.
- LaRowe, S.D., Patrick, C.J., Curtin, J.J. & Kline, J.P. 2006. Personality correlates of

- startle habituation. *Biological Psychology*, **72**:257–264.
- Lefebvre, L. 1995. Culturally-transmitted feeding-behavior in primates - evidence for accelerating learning rates. *Primates*, **36**:227–239.
- Lefebvre, L. & Sol, D. 2008. Brains, lifestyles and cognition: are there general trends? *Brain, Behavior and Evolution*, **72**:135–144.
- Leigh, J. & Chamberlain, M. 2008. Effects of aversive conditioning on behavior of nuisance Louisiana black bears. *Human–Wildlife Interactions*, **51**:175–182
- Li, C., Monclús, R., Maul, T.L., Jiang, Z. & Blumstein, D.T. 2011. Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Applied Animal Behaviour Science*, **129**:146–152.
- Laland, K.N. 2004. Social learning strategies. *Learning & Behavior*, **32**:4–14.
- Lima, S.L. & Dill, L.M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology*, **68**:619J.
- Lorenz, K. 1970. Companions as factors in the bird's environment. In *Studies in Human and Animal Behaviour*. pp. 101—258. Cambridge: Harvard University Press.
- Lowry, H., Lill, A. & Wong, B.B.M. 2011. Tolerance of auditory disturbance by an avian urban adapter, the noisy miner. *Ethology*, **117**:490–497.
- Mackintosh, N. J. 1974. *The Psychology of Animal Learning*. Oxford: Academic Press.
- Macphail, E.M. & Barlow, H.B. 1985. Vertebrate intelligence: the null hypothesis [and discussion]. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, **308**:37–51.
- Mazur, R. & Seher, V. 2008. Socially learned foraging behaviour in wild black bears, *Ursus americanus*. *Animal Behaviour*, **75**:1503–1508.

- Mineka, S., Davidson, M., Cook, M. & Keir, R. 1984. Observational conditioning of snake fear in rhesus-monkeys. *Journal of Abnormal Psychology*, **93**:355–372.
- Mineka, S. & Ohman, A. 2002. Phobias and preparedness: the selective, automatic, and encapsulated nature of fear. *Biological Psychiatry*, **52**:927–937.
- Nunn, C.L., Thrall, P.H., Bartz, K., Dasgupta, T. & Boesch, C. 2009. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *Animal Behaviour*, **77**:1515–1524.
- Ohman, A. & Mineka, S. 2002. Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review*, **108**:483–522.
- Raderschall, C.A., Magrath, R.D. & Hemmi, J.M. 2011. Habituation under natural conditions: model predators are distinguished by approach direction. *The Journal of Experimental Biology*, **214**:4209–4216.
- Ramp, D., Foale, C.G., Roger, E. & Croft, D.B. 2011. Suitability of acoustics as non-lethal deterrents for macropodids: the influence of origin, delivery and anti-predator behaviour. *Wildlife Research*, **38**:408–418.
- Rankin, C.H., Abrams, T., Barry, R.J. *et al.* 2009. Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, **92**:135–138.
- Rau, V. & Fanselow, M.S. 2009. Exposure to a stressor produces a long lasting enhancement of fear learning in rats. *Stress-the International Journal on the Biology of Stress*, **12**:125–133.
- Rendell, L., Boyd, R., Cownden, D. *et al.* 2010. Why copy others? Insights from the social learning strategies tournament. *Science*, **328**:208–213.

- Rendell, L. & Whitehead, H. 2001. Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**:309
- Rescorla, R.A. 1968. Probability of shock in the presence and absence of cs in fear conditioning. *Journal of Comparative and Physiological Psychology*, **66**:1–5.
- Rescorla, R.A. & Wagner, A.R. 1972. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. *Classical conditioning II: Current research and theory* pp. 64–99.
- Rescorla, R.A. 1988. Behavioral studies of Pavlovian conditioning. *Annual Review of Neuroscience*, **11**:329–352.
- Rodríguez-Prieto, I., Martín, J. & Fernández-Juricic, E. 2010a. Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences*, **278**:266–273
- Rodríguez-Prieto, I., Martín, J. & Fernández-Juricic, E. 2010b. Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology*, **64**:1937–1945.
- Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**:474–480.
- Seferta, A., Guay, P.J., Marzinotto, E. & Lefebvre, L. 2001. Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, **107**:281–293.
- Schakner, Z.A. & Blumstein, D.T. 2013. Behavioral biology of marine mammal deterrents: A review and prospectus. *Biological Conservation*, **167**:380–389.

- Sevenster, P. 1973. Incompatibility of response and reward. In Hinde, R.A. & Stevenson-Hinde, J. (eds), *Constraints on learning: Limitations and Predispositions*, pp.265-283. Oxford: Academic Press.
- Shalter, M. 1984. Predator–prey behavior and habituation. In *Habituation, Sensitization, and Behavior*. pp. 349–391. Orlando: Academic Press Inc.
- Shapiro, K.L., Jacobs, W.J. & Lolordo, V.M. 1980. Stimulus-reinforcer interactions in Pavlovian conditioning of pigeons - implications for selective associations. *Animal Learning & Behavior*, **8**:586–594.
- Shettleworth, S.J. 1975. Reinforcement and the organization of behavior in golden hamsters: Hunger, environment, and food reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, **1**:56–87.
- Shettleworth, S.J. 2010. *Cognition, evolution, and behavior*. Second edition. New York: Oxford University Press.
- Sih, A., Ferrari, M.C.O. & Harris, D.J. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**:367–387.
- Sih, A. & Giudice, M.D. 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society of London B*, **367**:2762–2772.
- Sneddon, LU. 2003. The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology*, **62**:971–975.
- Sol, D. 2003. Behavioral innovation: a neglected issue in the ecological and evolutionary literature. In Reader, S. & Laland, K. (eds.), *Animal innovation*, pp. 63-82. New York: Oxford University Press.

- Sol, D., Bacher, S., Reader, S.M. & Lefebvre, L. 2008. Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist*, **172**:S63–S71.
- Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, **102**:5460–5465.
- Sol, D., Timmermans, S. & Lefebvre, L. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour*, **63**:495–502.
- Stamps, J.A. & Swaisgood, R.R. 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, **102**:392–409.
- Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K.N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, **62**:591–598.
- Tear, T.H., Mosley, J.C. & Ables, E.D. 1997. Landscape-Scale foraging decisions by reintroduced Arabian oryx. *The Journal of Wildlife Management*, **61**:1142–1154.
- Thode, A., Straley J., Tiemann, C.O., Folkert, K. & O’Connell, V. 2007. Observations of potential acoustic cues that attract sperm whales to longline fishing in the Gulf of Alaska. *Journal of the Acoustical Society of America*, **122**:1265–1277.
- Thorpe, W.H. 1956. *Learning and Instinct in Animals*. Cambridge: Harvard University Press.
- Thorndike, E.L. & Bruce, D. 1911. *Animal Intelligence: Experimental Studies*. Lewiston: Macmillan Press.
- Trimmer, P.C., McNamara, J.M., Houston, A.I. & Marshall, J.A.R. 2012. Does natural

- selection favour the Rescorla–Wagner rule? *Journal of Theoretical Biology*, **302**:39–52.
- Whitehead, H. 2010. Conserving and managing animals that learn socially and share cultures. *Learning and Behavior*, **38**:329–336.
- Whiten, A., Goodall J., McGrew, W.C. *et al.* 1999. Cultures in chimpanzees. *Nature*, **399**:682–685.
- Yeomans, J.S., Li, L., Scott, B.W. & Frankland, P.W. 2002. Tactile, acoustic and vestibular systems sum to elicit the startle reflex. *Neuroscience and Biobehavioral Reviews*, **26**:1–11.

## CHAPTER 3

# Behavioral biology of marine mammal deterrents: A review and prospectus

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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 predator 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 predator, 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 reduced fish stock/increased 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

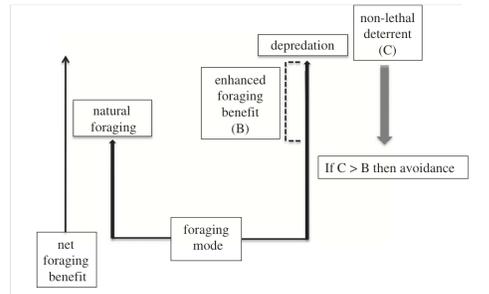


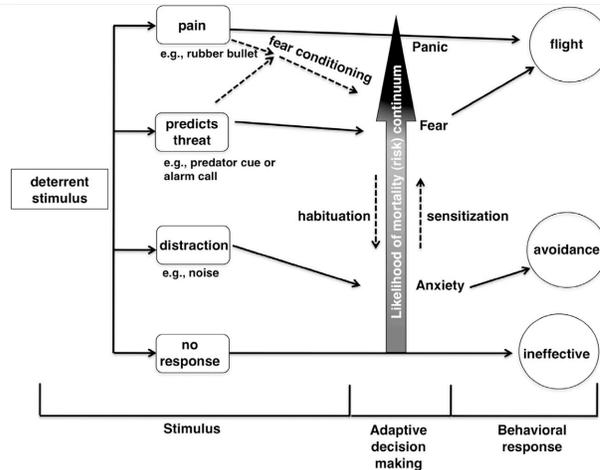
Fig. 1. How deterrents work. When the costs created by a non-lethal deterrent (C) exceed the benefits of depredation (B), animals should resume 'natural' foraging.

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 Öhman, 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).

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).



**Fig. 2.** A mechanistic framework of the behavioral biology of deterrents. The stimulus component involves the mechanisms by which deterrents elicit aversion: pain, threat (direct or predicted), or distraction. Upon detection, the deterrent stimulus is assessed in terms of mortality risk, which ultimately guides the behavioral response. Learning mechanisms are illustrated (with the dotted lines) and either act by decreasing (habituation) or increasing (sensitization) a deterrent’s perceived risk.

**Table 1**  
Relevant behavioral principles for wildlife deterrence.

Behavioral principle	Definition
Fear	A short-term fight or flight response to direct threat involving heightened physiological arousal (Grillon, 2008)
Anxiety	Response to potential/ambiguous danger or treat (Marks, 1987)
Habituation	Non-associative learning involving a reduction of behavioral response to repeated exposure to stimuli that is not due to sensory fatigue (Groves and Thompson, 1970)
Sensitization	Non-associative learning exemplified by a heightened sensory responsiveness after exposure to aversive stimuli (Plappert et al., 1999)
Dual process theory of habituation	An observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves and Thompson, 1970)
Fear conditioning	Associative learning process after pairing of aversive stimulus (unconditioned stimulus, US, e.g., a shock) to an innocuous stimulus (conditioned stimulus, e.g., a neutral tone—(Fanselow, 1984; Grillon, 2008))
Extinction	Decrease in learned responsiveness because the CS is no longer reinforced with the unconditioned stimulus (Domjan and Burkhard, 1986)

The distinction between proximate mechanisms of fear and anxiety are well recognized by those who study laboratory animals, but there is no reason to believe these distinctions are a laboratory artifact. Fear is seen when an individual responds to a direct threat (e.g., an attacking predator), whereas anxiety is induced with potential or contextual threat such as response to olfactory cues that signal possible predator presence (Blanchard et al., 1993; Blanchard, 2008). These two mechanisms of behavior are unique, and believed to be governed by distinct neural mechanisms (Charney and Deutch, 1996; Grillon, 2002, 2008; Davis, 2006). Behaviorally, anxiety is associated with increased risk assessment (vigilance), avoidance of anxiety-associated stimuli or areas, and increased sensory sensitivity that is designed to better

evaluate the true threat, whereas fear involves immediate flight responses (Blanchard et al., 1993; Eilam et al., 2011).

Non-lethal deterrent stimuli elicit fear or anxiety to create behavioral avoidance of human resources. Ultimately, the pathway to avoidance behaviors (Fig. 2) depends on the characteristics of the aversive stimulus as well mechanisms of threat analysis and learning.

### 3. Decision making is often adaptive

After detecting a threatening stimulus, individuals analyze the characteristics of the stimulus as well as the environmental context to assess the level of risk to generate an adaptive behavioral response (Blanchard et al., 1990; Lima and Dill, 1990). The process of risk assessment can be described as a continuum with stimuli that pose no risk at the bottom and stimuli that signal imminent danger at the top (Fig. 2). Fanselow and Lester (1988) describe this as the “predatory imminence continuum” and show that a given behavioral response depends upon where an individual perceives its own location on the continuum. For example, when exposed to scent cues that predict predator presence, anxiety is elicited in laboratory rats and behavioral responses involve avoidance strategies that reduce the likelihood of encounter. Conversely, direct encounters with a real threat (an approaching experimenter) elicit flight (Blanchard et al., 1990). We extend Fanselow and Lester’s (1988) predatory imminence continuum concept for non-lethal deterrents to include aversive stimuli other than predators (Fig. 2). Ultimately, where an individual perceives its location on the likelihood of mortality (risk) continuum guides the individual’s behavioral response (Fanselow and Lester, 1988).

### 4. What are the characteristics of threatening or aversive stimuli?

Stimuli that are recognized as threatening or aversive can disrupt behavior and create long-term avoidance (Frid and Dill, 2002; Rianne, 2007; Rau and Fanselow, 2009). Defensive behaviors

are observed in response to a variety of different stimuli such as pain, predator cues, or dangerous contexts (Blanchard et al., 1990). In addition to incorporating relevant sensory modalities of threat detection, generating avoidance depends upon the characteristics of the stimulus that elicits aversion (Talling et al., 1998). Deterrent stimuli are either inherently aversive or are learnt through conditioning. Thus, responses to deterrents fall naturally into (1) simple exposure to painful stimuli (2) stimuli that are predictive of threat, (3) or stimuli that are aversive through distraction. We classify non-lethal deterrent stimuli by these mechanisms (Fig. 2): pain (e.g., rubber bullets); stimuli that are predictive of threat (e.g., predator sound or alarm calls); or disruption (e.g., noise – Bomford and Obrien, 1990). These mechanisms evoke varying levels of risk and thus elicit varying responses and they can be viewed somewhat continuously along a continuum of mortality risk (Fig. 2), which we will discuss below.

#### 4.1. Painful stimuli

Pain in animals is defined as a harmful sensory event from damage or potential injury (Zimmermann, 1986). From a functional perspective, pain is adaptive because it signals danger and elicits immediate escape behaviors (Patrick, 1991). Thus, a painful stimulus signals imminent risk (predator attack) and falls on the upper end of the perceived level of risk continuum (Fig. 2). Pain provokes fear responses and flight behaviors designed to immediately remove the individual from the situation. For example, high intensity shocks on laboratory rodents are shown to induce species-specific defense involving a burst of motor responses (Fanselow and Lester, 1988). These captive experiments emphasize that painful stimuli elicit fear associated defense responses characteristic of predator attack in lab rats (*Rattus norvegicus*).

Physical characteristics of painful stimuli include intensity, loudness, suddenness, or duration (Boissy, 1995). Painful stimuli are often tactile but can span other modalities. For example, harsh acoustic stimuli can be painful (Bomford and Obrien, 1990). Psychophysical investigations are useful in understanding the characteristics of acoustic stimuli that induce aversion in animals (Gotz and Janik, 2010). Novel acoustic stimuli may be inherently threatening (Gray, 1987), but the structure of the sound in an acoustic deterrent should incorporate species-specific psychophysical characteristics that contribute to aversion. Zwicker and Fastl (1999) developed a model that identified increased sharpness, increased loudness, increased roughness and decreased tonality as the four contributors to perceived unpleasantness of sound in humans. Gotz and Janik (2010) tested this model and demonstrated that the same characteristics contribute to aversion of sound in captive grey seals.

#### 4.2. Stimuli that predict threat

In nature, animals are expected to be sensitive to stimuli or environments that are correlated with threat or danger. Historically, they include stimuli that are from salient predators or other threats or stimuli that arise from conspecific aggression (Gray, 1987). Stimuli that indicate a threat (sight or sound of attacking predator), elicit defensive responses (Gray, 1987). Animals may innately recognize threatening predator cues, or may have evolved predispositions to learn from specific cues preferentially (Griffin and Evans, 2003). Examples include fearful responses to foxes (*Vulpes vulpes*), but not goats (*Capra hircus*), by tammar wallabies (*Macropus eugenii*) (Griffin et al., 2001), fearful responses to cat odor in rats (Dielenberg and McGregor, 2001), or fearful responses to snakes by primates (including humans) (Öhman and Mineka, 2003). Killer whales have been observed preying on all species of marine mammals except manatees and river dolphin species

(Jefferson et al., 1991), and can elicit fearful responses in marine mammals (Cummings and Thompson, 1971; Baird and Stacey, 1989; Deecke et al., 2002).

#### 4.2.1. Conditioned stimuli

Conditioned stimuli arise when animals learn to associate a previously neutral stimulus with an aversive event and subsequently exhibit conditioned fear. Threatening encounters cause an immediate type of associative learning that enables animals to acquire predictive information from a threatening cue or context (Fanselow and Ponnusamy, 2008). There is a clear adaptive benefit of learning from threatening situations because cues or context provide information how to respond and detect future dangerous events. This learning process, called *fear conditioning*, is a Pavlovian form of associative learning.

*Pavlovian fear conditioning* has been extensively studied in laboratory animals. Experimentally, individuals are exposed to an aversive stimulus, (unconditioned stimulus, US, typically a shock) which is paired to an innocuous stimulus (conditioned stimulus or CS, e.g., a neutral tone (Grillon, 2002; Fanselow and Ponnusamy, 2008). The unconditional stimulus facilitates conditioning of fear reactions to the conditional stimulus. Conditioning occurs quickly in just one or several pairings in part because the aversive stimulus facilitates rapid fear learning. Following conditioning, the individual will subsequently show fear and anxiety when exposed to the neutral stimulus (CS) or environmental context because of associative learning (Grillon, 2002). *Fear conditioning* has been extensively studied in rats, which exhibit long lasting fear responses, over weeks or months, to neutral stimuli associated with shocks (Gale et al., 2004; Rianne, 2007).

The physical characteristics of threatening stimuli such as the modality, movement, suddenness and proximity also influence the magnitude of a fear response (Gray, 1987). The direction of approach and whether it looms or fills the visual field all are examples of movement features of stimuli that may modify flight distance (Gray, 1987; Ellison et al., 2012). Additionally, sudden stimuli can elicit startle responses that potentiate flight (Gray, 1987; Yeomans et al., 2002; Gotz and Janik, 2011).

#### 4.3. Masking, disruptive or distracting stimuli

A stimulus that prevents or distracts animals from biologically important tasks, like assessing predation risk or communication can be perceived as aversive and may elicit avoidance. For instance, the *distracted prey hypothesis* predicts that stimuli (in any modality) can distract and divert attention away from risk assessment (Chan et al., 2010). Animals are expected to exhibit anxiety and avoidance of distracting stimuli because of their impact on proper risk assessment. In odontocetes, a masking stimulus may reduce effectiveness of echolocation and thus prevent the individual from locating the fishing resource (Mooney et al., 2009). Marine mammals avoid anthropogenic acoustic stimuli from a variety of sources including ship noise or geophysical surveys (Nowacek et al., 2007), suggesting that a deterrent signal can capitalize on mechanisms of distraction.

### 5. Learning and motivation influence the response to deterrent stimuli through time

The capacity to learn from threatening encounters is functional because it guides how an animal can adaptively respond to an immediate threat and anticipate/avoid future danger. For example, by learning the cues that predict a predator attack, a prey species is able to modify its behavior and through avoidance, it reduces the probability of death (Domjan, 2005). From this functional learning

perspective, learning about deterrent stimuli influences the adaptive decision making process and can modify an individual's behavioral response to deterrent stimuli through time. Each learning mechanism can produce increases or decreases in (defensive) responsiveness (Fig. 2). Incorporating the learning mechanisms involved in animal response to threat is necessary for long-term deterrence.

Failure to recognize a predator may have substantial fitness costs (Lima and Dill, 1990). Conversely, anxiety or stress from over-generalized threat recognition may be costly in terms of energy or time allocated to unnecessary defenses. Animals may habituate to repeated exposures of potentially threatening stimuli with recurring exposure (Groves and Thompson, 1970). *Habituation* involves single stimulus learning involving a reduction of behavioral response to repeated exposure to stimuli that is not due to sensory fatigue. Habituation to deterrent stimuli in cases of human wildlife conflict represents a major limitation toward long-term deterrent success (Shivik, 2006), thus, detailed knowledge of how habituation occurs is necessary if we are to reduce the likelihood of its occurrence (Blumstein and Fernández-Juricic, 2010).

Generally, simple parameters such as intensity, modality, and frequency of exposure influence single-stimulus learning in animals (Groves and Thompson, 1970). Additionally, response decrement can be generalized to stimuli within the same modality that are similar to the original stimulus. These parameters have practical significance for managers deciding which stimuli as well as the schedule at which depredators are exposed. All else equal, the more frequent exposure results in more pronounced habituation (Groves and Thompson, 1970; Rankin et al., 2009). Correspondingly, less intense stimuli result in a response decrement whereas greater intensities may show no habituation (Groves and Thompson, 1970; Rankin et al., 2009). Painful stimuli signal imminent threat (Fig. 2) and are the least likely to be habituated to. Rapid habituation is expected in response to continuous playback of less intense signals (predator sounds) versus sudden and intense stimuli.

Habituation, however, is not ubiquitous and repeated stimulation could lead to sensitization (Groves and Thompson, 1970; Rankin et al., 2009). *Sensitization* refers to a form of non-associative learning exemplified by a heightened sensory responsiveness after exposure to aversive stimuli (Plappert et al., 1999). Thus, in contrast to habituation, sensitization involves heightened risk after repeated exposure. According to the dual process theory of habituation, an observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves and Thompson, 1970). Deterrents should incorporate some sensitizing mechanism to delay or prevent habituation (Gotz and Janik, 2011).

Habituation and sensitization are the behavioral outcome of the interaction between two underlying neurobiological pathways (Groves and Thompson, 1970; Domjan and Burkhard, 1986). Sensitization is underpinned by the state system. The state system is made up of the components of nervous system that determine overall responsiveness and arousal (Domjan and Burkhard, 1986). Stimuli that are particularly intense, emotionally salient, or startling may activate the state system (Groves and Thompson, 1970). Increased responsiveness is expected to occur if the individual is exposed to the startling stimuli repeatedly while still sensitized from the previous exposure. Gotz and Janik (2011) exposed individual gray seals to harsh, startle-reflex eliciting acoustic stimuli. After just several exposures, the individuals showed heightened flight reflexes whereas individuals exposed to non-startle stimuli habituated. This suggests that sensitizing the startle reflex arc results in increased flight/avoidance responses, which can be used to create effective deterrents (V. Janik pers. Comm.).

Motivation is the behavioral mechanism underlying an individual's assessment of costs/benefits of a given foraging situation. In the case of depredation, the foraging benefits are high, and costs are low, (Fig. 2) resulting in motivation to exploit fisheries. Thus, if a deterrent stimulus repels animals away from a resource, motivation to forage may drive them back to depredation. Learning modifies assessment of the cost/benefit ratio and changes behavior via motivational change, ultimately shaping the frequency of exposure to deterrent stimuli. Habituation occurs after repeated exposure to a stimulus and is rapid when there is short amount of time between exposures to stimuli (Staddon and Higa, 1996). Since the motivation to depredate increases the rate at which an individual is exposed to deterrent stimuli, it accelerates habituation.

## 6. Review of marine mammal deterrents

A deterrent should exploit animal sensory mechanisms of threat detection to raise the real or perceived costs or risks involved in depredation (Shivik et al., 2003; Biedenweg et al., 2011). There has been a significant effort to develop, implement, and test numerous deterrents that exploit marine mammal sensory modalities, including tactile harassment, chemosensory deterrents that either induces fear or disgust, and acoustic deterrence. Here, we review the basic modalities of deterrents tested in cases of marine mammal depredation. The purpose of this review is to summarize cases of deterrent application, identify knowledge gaps and highlight management concerns of application of non-lethal deterrents. Finally, we propose deterrent strategies that may be useful to manage marine mammal depredation.

### 6.1. Marine mammal sensory modality background

Generally, mammals use visual, acoustic, and chemosensory modalities to detect threatening stimuli (Apfelbach et al., 2005). The physical characteristics of the aquatic medium (e.g., increased sound transmission and light attenuation) have translated into a reliance on sound for marine mammal detection of predators, communication, and navigation (Schusterman, 1981). Overall, marine mammals exhibit aural sensitivity, visual acuity in the limited portion of water that transmits light, and decreased olfaction (Watkins and Wartzok, 1985; Wartzok and Ketten, 1999). This suggests that acoustic, visual, chemosensory (taste), and tactical are the relevant sensory modalities for marine mammal deterrents. Additionally, deterrent stimuli should incorporate the sensory sensitivity of a given modality (Gilsdorf et al., 2003).

### 6.2. Chemosensory deterrents

From first principles, the lack of olfactory capacity in marine mammals suggests that deterrents that use of predator scents should be unsuccessful. Chemosensory deterrent mechanisms have focused on taste as a mechanism for inducing aversion. Conditioned taste aversion methods in human/wildlife conflict have produced mixed results in terrestrial systems (Shivik, 2006). While further testing in cases of marine mammal/fishery conflict is necessary, CTA methods had limited effectiveness when tested on sea lions preying salmon from Ballard locks dam in Seattle. Steelhead (*Salmo gairdneri*) laced with an emetic, lithium chloride, were tethered and fed to sea lions to elicit aversion. The animals were observed to have fled the area and believed to have become ill (Gearin et al., 1986). However, the same individuals returned an hour later to continue foraging in the area (Gearin et al., 1986). Further information is needed as to whether marine mammals would generalize their aversion from fishing resources into the wild, but we believe that these strategies are unlikely to be successful.

Pre-exposure to the food before conditioning delays or prevents taste aversion learning. Additionally, as a generalist forager, sea lions may learn that this particular fish species is not good to eat (the taste and smell of a prey item serves as the CS), rather than the animal learning where not to forage.

### 6.3. Acoustic deterrents

Marine mammals may avoid anthropogenic sounds (Kastelein et al., 2008; Morton and Symonds, 2002; Nowacek et al., 2007) and thus sounds have been used to manage marine mammal/fishery conflict. Acoustic deterrent devices (ADDs) are one of the most widespread non-lethal deterrent methods implemented for marine mammal/fishery conflict (Fjalling et al., 2006; Graham et al., 2009; Jacobs and Terhune, 2002; Jefferson and Curry, 1996; Sepulveda and Oliva, 2005; Shaughnessy et al., 1981). They are primarily used to protect stationary resources such as aquaculture pens or salmon spawning sites.

The basic goal of an ADD (also termed acoustic harassment device AHD) is to create a sound that is painful or distracting enough that it creates aversion and makes the animal flee or prevent it from visiting the area altogether (Jefferson and Curry, 1996). Their use is expected to be effective because marine mammals are particularly sensitive to high intensity sound because of specialized hearing adaptations for underwater sound (Wartzok and Ketten, 1999). Marine mammal species have variable hearing thresholds, as well as variable responsiveness to novelty. This information is essential to properly design an ADD because different hearing sensitivities across species will result in differential behavioral responses (Götz, 2008).

Despite short-term successes in creating aversion, ADDs have not been useful in the long-term because animals seemingly habituate to them or continue depredating (Anderson and Hawkins, 1978; Mate and Harvey, 1987). The low cost prey resources offered by fishing lines or aquaculture pens likely accelerate sea lion habituation to ADDs. After repeated exposure to the ADD, habituation essentially makes the sound a salient neutral stimulus that the animal can learn to associate with fishery resources. This so-called 'dinner bell effect' is observed when the depredators learn to associate the deterrent sound with food resources (Jefferson and Curry, 1996; Mate and Harvey, 1987).

Acoustic deterrent device usage remains controversial because of the risk of harming pinniped hearing and disturbing non-target wildlife (Gordon and Northridge, 2002; Morton and Symonds, 2002). The high source pressure levels of most ADDs on the market can potentially influence hearing by causing temporary threshold shifts (TTS) or even risk permanent hearing damage (Gordon and Northridge, 2002). ADDs aimed at deterring pinnipeds often produce mid-to high frequency high intensity noise that is within the sensitive hearing range of odontocetes. Consequently, ADD usage can cause habitat exclusion in odontocete species such as killer whales and harbour porpoises (*Phocoena phocoena*) (Morton and Symonds, 2002; Olesiuk et al., 2002; Brandt et al., 2013). A successful deterrent should be sufficiently aversive so that it creates avoidance but does not cause hearing damage or excludes or interferes with non-target species.

#### 6.3.1. Pingers

Pingers are a specific type of ADD that uses lower acoustic output (<150 dB (re: 1  $\mu$ Pa)) sounds to prevent bycatch (Götz, 2008). Bycatch represents another form of marine mammal fishery conflict in which marine mammals, commonly small odontocetes like porpoises, fail to detect fishing nets and ultimately become trapped. This incidental mortality is a significant conservation problem, resulting in several hundred thousand animals lost per year and threatening several species with extinction (Jefferson

and Curry, 1994, 1996; Read and Wade, 2000; Reeves et al., 2003; Read, 2008). This prompted the development of pingers, devices that give off high frequency but lower intensity acoustic stimuli, with the goal of either alerting the marine mammals to the presence of the net or creating aversion to the net (Dawson et al., 1998). Controlled field experiments have demonstrated that pingers significantly reduce harbour porpoise and common dolphin bycatch (Barlow and Cameron, 2003; Kraus et al., 1997; Carretta and Barlow, 2011) and effectively eliminated beaked whale bycatch in gillnets (Carretta et al., 2008).

The success of pingers and the ineffectiveness of ADDs illustrate the importance of motivation in aversion. In species that actively depredate from gillnets such as bottlenose dolphins and sea lions, pingers fail to induce avoidance (Carretta and Barlow, 2011; Gazo et al., 2008). It is not fully understood how porpoises become entangled in gillnets, but it is likely that porpoises are feeding in the vicinity and are unable to locate the net. Because porpoises appear to not be depredating, there is no heightened benefit to associate/habituate to the pinger, which is evidenced by long-term pinger success. The difference in the effectiveness of pingers is not only related to the benefits of depredation, but probably also with the sensitivity of different species to sound. For instance, the 100% reduction of bycatch in beaked whales suggests enhanced vulnerability of these whales to acoustic pollution (Carretta et al., 2008).

### 6.4. Tactile deterrents

Tactile deterrent methods vary, but typically involve physically creating pain or discomfort in depredators to induce aversion. Examples of tactile harassment methods include shooting rubber bullets, blunt-tipped arrows, or rubber buckshot at depredators (Scordino, 2010). The goal of tactile harassment methods is to elicit flight behaviors by creating pain. Illustrative examples of the long-term tactile harassment involve the depredation of spawning salmon in Bonneville dam in the Northwest United States. During tactile hazing individuals exhibit an immediate flight response, but frequently return and learn to either surface infrequently or avoid the shooter (Scordino, 2010).

The creation of a pulsed, low voltage DC electric field aimed to deter pinnipeds predated salmon is a novel tactile harassment technique, analogous to the use of electric fencing to control livestock in terrestrial ecosystems. In both captive setting and wild settings, seals exhibited avoidance to an electrical gradient, but the seals returned to the net once the electric field was turned off (Forrest et al., 2009). Overall, it appears that the electric field deterrent can generate a highly localized and temporary aversion because food motivation drives the animals to return (Shivik et al., 2003). Additional effects on non-pinniped species, especially fish requires further investigation.

The benefit of tactile harassment methods is that painful stimuli create immediate flight responses and are difficult to habituate to. Additionally, pain causes instantaneous and long-term learning (Fig. 2). Fear conditioning enables the animal to derive learned associations and subsequently exhibit fear responses to the stimuli or contexts that predict the tactile deterrent. The goal of tactile deterrents should explicitly be to promote fear conditioning rather than to continuously produce aversive stimuli (e.g., a constant electric fence or permanent presence of shooters).

### 6.5. Visual deterrents

There is evidence that pinnipeds and dolphins possess sophisticated visual systems (Schusterman, 1981; Kuczaj et al., 2008) and there are observations of pinnipeds using vision to detect predators (Baird and Stacey, 1989). However, visual deterrents have

Summary of some management concerns for non-lethal deterrents.

Management concerns for deterrents	Factors that reduce success (costs)	Factors that enhance success (benefits)
Animal welfare	<ul style="list-style-type: none"> <li>– Stimuli cause permanent damage</li> <li>– Stimuli deter animals completely from habitats of biological importance</li> </ul>	<ul style="list-style-type: none"> <li>– Use perceived aversive signals over intensity</li> <li>– Implement conditioning procedure to reduce exposure to painful stimuli</li> </ul>
Applicability	<ul style="list-style-type: none"> <li>– Cost prohibitive for fishermen</li> <li>– Depredation widespread geographically</li> <li>– Risk to human safety</li> </ul>	<ul style="list-style-type: none"> <li>– Localized depredation</li> <li>– Depredation only exhibited by rogue individuals</li> </ul>
Effectiveness	<ul style="list-style-type: none"> <li>– Behavior prevalent in population</li> <li>– Alternate food sources unavailable</li> <li>– Habituation</li> </ul>	<ul style="list-style-type: none"> <li>– Alternate food sources available</li> <li>– Sensitization</li> <li>– Target rogue individuals or individuals most likely to innovate (e.g., adult males or juveniles)</li> <li>– Prevent or limit association with fishery resources</li> </ul>
Impacts on non-target wildlife	<ul style="list-style-type: none"> <li>– Animals have too much previous experience</li> <li>– Unknown sensory mechanisms</li> <li>– Sensory sensitivity overlap with other marine mammals or fish</li> <li>– Pollution produced by deterrents (e.g., rubber bullets)</li> </ul>	<ul style="list-style-type: none"> <li>– Optimize signal for target animal sensory sensitivity</li> <li>– Multi-modal and varying stimuli deterrent strategy</li> </ul>

not been extensively tested in cases of marine mammal/fishery conflict. Fiberglass models of killer whales placed around aquaculture pens (Sepulveda and Oliva, 2005) had a limited effect in deterring depredating pinnipeds. Novel or intense light stimuli elicit aversive responses in sea turtles interacting with gill nets (Wang et al., 2010), but this strategy has not yet been tested on marine mammals.

## 7. Conclusions

### 7.1. Implications of deterrents

There are often conflicts between wildlife management and wildlife conservation (e.g., Blumstein 2010a,b; McMahon et al., 2012). Aversive stimuli can elicit fear or anxiety resulting in long term avoidance of an area or a resource (Frid and Dill, 2002; Morton and Symonds, 2002). Based on our review, we suggest that deterrents must incorporate first principles of animal behavior and learning for long-term success. We suggest that there are at least four potential management concerns (Table 2) that require consideration before implementing non-lethal deterrents: impacts on non-target wildlife; animal welfare; applicability; and overall effectiveness.

Because deterrent stimuli are potentially aversive to other taxa, successful application of deterrents must weigh the potential cost to other species with the overall management benefit. Marine mammals are equipped with species-specific sensory mechanisms and sensitivity to assess and detect threats. We, and others (e.g., Gilsdorf et al., 2003; Southwood et al., 2008; Gotz and Janik, 2010; Biedenweg et al., 2011; Ramp et al., 2011), have suggested that non-lethal deterrents should tailor signals toward the particular species' sensory mechanisms and sensitivities. Acoustic pollution has negative impacts (for review see Kight and Swaddle, 2011), especially for marine fauna (Rolland et al., 2012). Different deterrents will have different effects on marine fauna. Acoustic devices differ in their frequency range and acoustic output (emitted level and duty cycle) and the receivers (marine mammal species targeted or not by the deterrents) vary in their acoustic sensitivity and behavioral reactions to sound. The active space of acoustic stimuli will vary based upon the signal characteristics, as well as the receivers' hearing thresholds and responsiveness (i.e., seal scaring devices may deter porpoises 7.5 km away (Brandt et al., 2013)). The differences in sensory abilities, responsiveness to novelty (neophobia), and the learning capacity of other non-target species potentially exposed to deterrent stimuli should be taken into ac-

count before and during application to mitigate non-target wildlife impacts.

Deterrents are not only used to mitigate interactions of marine mammals with human activities (aquaculture or stealing fish from human fisheries), but also to deter marine mammals from natural habitats and natural prey in order to prevent competition with other top-predators: humans. This raises ethical concerns over the appropriate application of deterrents and how widespread their usage should be. Using deterrents for cases of natural foraging may be justified if there is clear documentation of negative impacts and the availability of alternative habitat/resources. Also, the target species should not be declining or endangered. Whether it is acceptable to use deterrents to elicit aversion from fishing gear versus using them to deter marine mammals from feeding in natural habitats over natural prey to avoid competition with humans for the same resource is an open question.

The degree of discomfort animals experience from deterrents raises animal welfare concerns. Exposure hinges upon whether alternative resources/habitat are available. If not, the individuals will have no choice but to continue to forage and be exposed to the deterrents. Deterrent stimuli should never cause permanent damage. The intensity and duration of deterrent stimuli (especially acoustic) are relevant parameters than can be modified to prevent damage.

We believe that deterrents will enhance success and minimize non-target impacts when used in situations where depredation has a narrow spatial extent and can be targeted to nuisance animals. Acoustic deterrents, by their very nature are applied over a relatively broad area and may include marine protected areas or large-scale aquaculture facilities. There is no register of the number of devices in use or lost at sea (some pingers can be active for a year upon being lost) and collecting these data should be a priority because this information can help mitigate the use of such devices. In Scotland, for example, ADD use may contribute to large-scale acoustic pollution (Gordon and Northridge, 2002). In the Rogue River in Southern Oregon, targeted hazing of individual sea lions with cracker shells, rubber bullets and seal bombs successfully reduced depredation of commercial and recreational salmon fishers in the river (Scordino, 2010). This is a sharp contrast with less successful deterrent efforts on sea lions that swim toward salmon ladders in Northern Oregon and Washington. The degree to which the behavior has spread through the population and the geographic extent that requires deterrence may contribute to their effectiveness.

## 7.2. Enhancing conservation success through fear conditioning—learning matters

Avoidance of possible or potential threat reduces the likelihood of attack whereas fight/flight behaviors are defenses from impending attack. These are distinct functional and behavioral pathways that animals evolved to avoid danger (McNaughton and Corr, 2004). Each is governed by unique proximate mechanisms (anxiety and fear). The capacity of painful or aversive stimuli to induce fear (flight) responses has made them common for managers (Shivik et al., 2003). Fear, however, is short term, and is terminated following the direct escape from threat (Eilam et al., 2011). In other words, once the animal has fled and is out of the immediate vicinity of the stimulus, fear subsides, and motivation will drive the depredator to return. In contrast, anxiety is sustained and can create chronic avoidance as seen in animal models of post-traumatic stress syndrome (Siegmund and Wotjak, 2006). The goal of deterrent stimuli should not be the continual use of stimuli that elicit short-term flight responses, but rather the promotion of anxiety that results in avoidance of potential danger. Thus, first principles strongly suggest that a Pavlovian fear conditioning paradigm will enable depredators to learn the cues/contexts that precede the dangerous/painful stimuli, ultimately resulting in anxiety and avoidance of the anxiety-producing situation.

A Pavlovian fear-conditioning paradigm for deterrents is an ethologically inspired deterrent. Fear conditioning, by facilitating learning of the cues that precede threat, enables individuals to use behavioral responses to move down the risk continuum (Fanselow and Lester, 1988) from fear (flight) to anxiety (avoidance). The application of fear conditioning for deterrents should be species specific, tailoring the stimuli used as US and CS to a species' sensory sensitivities, as well as include combinations of stimuli that belong together. For marine mammals, sound is a salient stimulus that can be used as a CS and a US if sufficiently startling (Gotz and Janik, 2011). Painful or startling stimuli are difficult to habituate to, especially if a once conditioned individual avoids exposure through avoidance. *Extinction*, the decrease in responsiveness to a previously acquired conditioned stimulus with repeated non-reinforced exposure, could be delayed with partial reinforcement. The reinforcement schedule (i.e., when to expose individuals to the CS and US pairing) can be tailored to suit particular situations. If there are many animals depredating (sea lions depredating purse seine nets) and a large turnover of individuals, learning will vary across individuals. This situation will likely require regular reinforcement to ensure new individual conditioning. Alternatively, if a small number of animals feed and repeatedly return it is likely that less regular, but nonetheless periodic, reinforcement schedules will suffice to prevent extinction. Managers should tailor reinforcement schedules to appropriate contexts and some effort must go into identifying the number and diversity of potential depredators.

Given management and conservation concerns, we recommend a cautious approach to deterrents. There are difficulties in designing US and CS and there is the real possibility of impacting non-target organisms or displacing target animals from essential habitat. There is much to learn to optimize deterrent application and to mitigate marine mammal conflict with fisheries. We emphasize that the value of using threatening or painful stimuli is that if effectively conditioned, it can create long-term learned avoidance that does not require using the painful stimulus in the future. Once the animals learn the association (and animals may learn these associations with only a few trials), they will never experience the painful stimuli as long as they avoid the protected resource. We view this, ultimately, as a welfare-friendly solution to human-wildlife conflict.

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## References

- Anderson, S.S., Hawkins, A.D., 1978. Scaring seals by sound. *Mammal Rev.* 8, 19–24.
- Apfelbach, R., Blanchard, C.D., Blanchard, R.J., Hayes, R.A., McGregor, I.S., 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neurosci. Biobehav. Rev.* 29, 1123–1144.
- Baird, R.W., Stacey, P.J., 1989. Observations on the reactions of sea lions, (*Zalophus californianus*) and (*Eumetopius jubatus*), to killer whales, (*Orcinus orca*) – evidence of prey having a search image for predators. *Can. Field Nat.* 103, 426–428.
- Barlow, J., Cameron, G.A., 2003. Field experiments show that acoustic pingers reduce marine mammal bycatch in the California drift gill net fishery. *Mar. Mammal Sci.* 19, 265–283.
- Biedeweg, T.A., Parsons, M.H., Fleming, P.A., Blumstein, D.T., 2011. Sounds scary? Lack of habituation following the presentation of novel sounds. *PLoS ONE* 6 (1), e14549.
- Blanchard, C.D., 2008. Defensive behaviors, fear, and anxiety. In: Blanchard, C.D., Blanchard, R.J., Griebel, G., Nutt, D.J. (Eds.), *Handbook of Anxiety and Fear*. Elsevier, Oxford, England, pp. 63–79.
- Blanchard, D., Blanchard, R.J., Rodgers, R.J., 1990. Pharmacological and neural control of anti-predator defense in the rat. *Aggressive Behav.* 16, 165–175.
- Blanchard, R.J., Yudko, E.B., Rodgers, R.J., Blanchard, C., 1993. Defense system psychopharmacology: an ethological approach to the pharmacology of fear and anxiety. *Behav. Brain Res.* 58, 155–165.
- Blumstein, D.T., Fernández-Juricic, E., 2010. *A Primer of Conservation Behavior*. Sinauer Associates, Sunderland, MA.
- Blumstein, D.T., 2010a. Conservation and animal welfare issues arising from forestry practices. *Anim. Welfare* 19, 151–157.
- Blumstein, D.T., 2010b. Flush early and avoid the rush: a general rule of antipredator behavior? *Behav. Ecol.* 21, 440–442.
- Boissy, A., 1995. Fear and fearfulness in animals. *Q. Rev. Biol.* 70, 165–191.
- Bomford, M., Obrien, P.H., 1990. Sonic deterrents in animal damage control – a review of device tests and effectiveness. *Wildlife. Soc. B* 18, 411–422.
- Bouskila, A., Blumstein, D.T., 1992. Rules of thumb for predation hazard assessment – predictions from a dynamic-model. *Am. Nat.* 139, 161–176.
- Brandt, M.J., Höschele, C., Diederichs, A., Betke, K., Matuschek, R., Witte, S., Nehls, G., 2013. Far-reaching effects of a seal scarer on harbour porpoises, *Phocoena phocoena*. *Aquat. Conserv.* 23, 222–232.
- Brodie, E.D., Formanowicz, D.R., 1991. Predator avoidance and antipredator mechanisms – distinct pathways to survival. *Ethol. Ecol. Evol.* 3, 73–77.
- Carretta, J.V., Barlow, J., 2011. Long-term effectiveness, failure rates, and “dinner bell” properties of acoustic pingers in a gillnet fishery. *Mar. Technol. Soc. J.* 45, 7–19.
- Carretta, J.V., Barlow, J., Enriquez, L., 2008. Acoustic pingers eliminate beaked whale bycatch in a gill net fishery. *Mar. Mammal Sci.* 24, 956–961.
- Chan, A.A., Giraldo-Perez, P., Smith, S., Blumstein, D.T., 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biol. Lett.* 6, 458–461.
- Charney, D.S., Deutch, A., 1996. A functional neuroanatomy of anxiety and fear: implications for the pathophysiology and treatment of anxiety disorders. *Crit. Rev. Neurobiol.* 10, 419–446.
- Cummings, W., Thompson, P., 1971. Gray whales, (*Eschrichtius robustus*), avoid underwater sounds of killer whales, (*Orcinus orca*). *Fish. Bull.* 69, 525–530.
- Davis, M., 2006. Neural systems involved in fear and anxiety measured with fear-potentiated startle. *Am. Psychol.* 61, 741–756.
- Dawson, S.M., Read, A., Slooten, E., 1998. Pingers, porpoises and power: Uncertainties with using pingers to reduce bycatch of small cetaceans. *Biol. Conserv.* 84, 141–146.
- Deecke, V.B., Slater, P.J.B., Ford, J.K.B., 2002. Selective habituation shapes acoustic predator recognition in harbour seals. *Nature* 420, 171–173.
- Dielenberg, R.A., McGregor, I.S., 2001. Defensive behavior in rats towards predatory odors: a review. *Neurosci. Biobehav. Rev.* 25, 597–609.
- Domjan, M., 2005. Pavlovian conditioning: a functional perspective. *Annu. Rev. Psychol.* 56, 179–206.
- Domjan, M., Burkhard, B., 1986. *The Principles of Learning & Behavior*. Brooks/Cole Pub. Co., Monterey, CA.
- Eilam, D., Izhar, R., Mort, J., 2011. Threat detection: behavioral practices in animals and humans. *Neurosci. Biobehav. Rev.* 35, 999–1006.
- Ellison, W.T., Southall, B.L., Clark, C.W., Frankel, A.S., 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conserv. Biol.* 26, 21–28.
- Endler, J.A., 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.

- Fanselow, M.S., 1994. What is conditioned fear? Trends Neurosci. 7, 460–462.
- Fanselow, M.S., Lester, L.S., 1988. A functional behavioristic approach to aversively motivated behavior: predatory imminence as a determinant of the topography of defensive behavior. In: Bolles, R.C., Beecher, M.D. (Eds.), Evolution and Learning. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ, pp. 185–212.
- Fanselow, M.S., Ponnusamy, R., 2008. The use of conditioning tasks to model fear and anxiety. In: Blanchard, R., Blanchard, C.D., Griebel, G., Nutt, D.J. (Eds.), Handbook of Anxiety and Fear. Elsevier, Amsterdam, Netherlands, pp. 29–48.
- Fjalling, A., Wahlberg, M., Westerberg, H., 2006. Acoustic harassment devices reduce seal interaction in the Baltic salmon-trap, net fishery. ICES J. Mar. Sci. 63, 1751–1758.
- Forney, K.A., Kobayashi, D.R., Johnston, D.W., Marchetti, J.A., Marsik, M.G., 2011. What's the catch? Patterns of cetacean bycatch and depredation in Hawaii-based pelagic longline fisheries. Mar. Ecol. -Evol. Persp. 32, 380–391.
- Forrest, K.W., Cave, J.D., Michielsens, C.G.J., Haulena, M., Smith, D.V., 2009. Evaluation of an electric gradient to deter seal predation on salmon caught in gill-net test fisheries. N. Am. J. Fish. Manage. 29, 885–894.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 16.
- Gale, G.D., Anagnostaras, S.G., Godsil, B.P., Mitchell, S., Nozawa, T., Sage, J.R., Wiltgen, B., Fanselow, M.S., 2004. Role of the basolateral amygdala in the storage of fear memories across the adult lifetime of rats. J. Neurosci. 24, 3810–3815.
- Gazo, M., Gonzalo, J., Aguilar, A., 2008. Pingers as deterrents of bottlenose dolphins interacting with trammel nets. Fish. Res. 92, 70–75.
- Gearin, P., Pfeifer, B., Jeffries, S., 1986. Control of California sea lion predation of winter-run steelhead at the Hiram M. Chittenden Locks, Seattle, December 1985–April 1986 with observations on sea lion abundance and distribution in Puget Sound. Washington Dep. Game, Fishery Manage. Rep. 86–20, 108 p. (Available from Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501).
- Gillman, E., Brothers, N., McPherson, G., Dalzel, P., 2006. A review of cetacean interactions with longline gear. J. Cetac. Res. Manage. 8, 215–223.
- Gilsdorf, J.M., Hygnstrom, S.E., VerCauteren, K.C., 2003. Use of frightening devices in wildlife damage management. Integr. Pest Manage. Rev. 7, 29–45.
- Gordon, J., Northridge, S., 2002. Potential impacts of acoustic deterrent devices on Scottish marine wildlife. Scottish Natural Heritage Commissioned, Report FO1AA404.
- Götz, T., 2008. Aversiveness of sound in marine mammals: psycho-physiological basis, behavioural correlates and potential applications (Ph.D. Dissertation). University of St. Andrews.
- Gotz, T., Janik, V.M., 2010. Aversiveness of sounds in phocid seals: psycho-physiological factors, learning processes and motivation. J. Exp. Biol. 213, 1536–1548.
- Gotz, T., Janik, V.M., 2011. Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. BMC Neurosci. 12.
- Graham, I., Harris, R.N., Denny, B., Fowden, D., Pullan, D., 2009. Testing the effectiveness of an acoustic deterrent device for excluding seals from Atlantic salmon rivers in Scotland. ICES J. Mar. Sci. 66, 860–864.
- Gray, J.A., 1987. The Psychology of Fear and Stress. Cambridge University Press, New Rochelle, New York, USA.
- Griffin, A.S., Evans, C.S., 2003. The role of differential reinforcement in predator avoidance learning. Behav. Process. 61, 87–94.
- Griffin, A.S., Evans, C.S., Blumstein, D.T., 2001. Learning specificity in acquired predator recognition. Anim. Behav. 62, 577–589.
- Grillon, C., 2002. Startle reactivity and anxiety disorders: aversive conditioning, context, and neurobiology. Biol. Psychiatry 52, 958–975.
- Grillon, C., 2008. Models and mechanisms of anxiety: evidence from startle studies. Psychopharmacology 199, 421–437.
- Groves, P.M., Thompson, R.F., 1970. Habituation a dual process theory. Psychol. Rev. 77, 419–450.
- Jacobs, S.R., Terhune, J.M., 2002. The effectiveness of acoustic harassment devices in the Bay of Fundy, Canada: seal reactions and a noise exposure model. Aquat. Mammal. 28, 147–158.
- Jefferson, T.A., Curry, B.E., 1994. A global review of porpoise (Cetacea, Phocoenidae) mortality in gillnets. Biol. Constr. 67, 167–183.
- Jefferson, T.A., Curry, B.E., 1996. Acoustic methods of reducing or eliminating marine mammal-fishery interactions: do they work? Ocean Coast. Manage. 31, 41–70.
- Jefferson, T.A., Stacey, P.J., Baird, R.W., 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Rev. 21, 151–180.
- Kastlein, R.A., Verboom, W.C., Jennings, N., de Haan, D., 2008. Behavioral avoidance threshold level of a harbor porpoise (*Phocoena phocoena*) for a continuous 50 kHz pure tone. J. Acoust. Soc. Am. 123, 1858–1861.
- Kight, C.R., Swaddle, J.P., 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol. Lett. 14, 1052–1061.
- Kraus, D., Read, A.J., Solow, A., Baldwin, K., Spradlin, T., Anderson, E., Williamson, J., 1997. Acoustic alarms reduce porpoise mortality. Nature 388, 525.
- Krebs, J.R., Davies, N.B. (Eds.), 1987. An Introduction to Behavioural Ecology, second ed. Sinauer Associates, Sunderland, MA.
- Kuczaj, S., Solangi, M., Hoffland, T., Romagnoli, M., 2008. Recognition and discrimination of human actions across the senses of echolocation and vision in the bottlenose dolphin: evidence for dolphin cross-modal integration of dynamic information. J. Comp. Psychol. 21, 84–95.
- Lang, P.J., Davis, M., Ohman, A., 2000. Fear and anxiety: animal models and human cognitive psychophysiology. J. Affect. Disord. 61, 137–159.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation – a review and prospectus. Can. J. Zool. 68, 619–640.
- Madden, F., 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. Hum. Dimens. Wildl. 9, 247–257.
- Marks, I.M., 1987. Fears, Phobias, and Rituals: Panic, Anxiety, and their Disorders. Oxford University Press, New York, NY, US.
- Mason, J.R., Shivik, J.A., Fall, M.W., 2001. Chemical repellents and other aversive strategies in predation management. Endang. Spec. Update 18, 175–181.
- Mate, B.R., Harvey, J.T., 1987. Acoustical Deterrents in Marine Mammal Conflicts with Fisheries: A Workshop Held February 17–18, 1986 at Newport, Oregon. Sea Grant College Program, Oregon State University.
- Mathias, D., Thode, A., Straley, J., Folkert, K., 2009. Relationship between sperm whale (*Physeter macrocephalus*) click structure and size derived from videorecorder images of a depredating whale (sperm whale prey acquisition). J. Acoust. Soc. Am. 125, 3444–3453.
- McMahon, C.R., Harcourt, R., Bateson, P., Hindell, M.A., 2012. Animal welfare and decision making in wildlife research. Biol. Constr. 153, 254–256.
- McNaughton, N., Corr, P.J., 2004. A two-dimensional neuropsychology of defense: fear/anxiety and defensive distance. Neurosci. Biobehav. Rev. 28, 285–305.
- Minaka, S., Ohman, A., 2002. Phobias and preparedness: The selective, automatic, and encapsulated nature of fear. Biol. Psychiatry 52, 927–937.
- Mooney, T.A., Pacini, A.F., Nachtigall, P.E., 2009. False killer whale (*Pseudorca crassidens*) echolocation and acoustic disruption: implications for longline bycatch and depredation. Can. J. Zool. 87, 726–733.
- Morton, A.B., Symonds, H.K., 2002. Displacement of (*Orcinus orca*) by high amplitude sound in British Columbia. Canada. ICES J. Mar. Sci. 59, 71–80.
- Naughton-Treves, L., 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conserv. Biol. 12, 156–168.
- Northridge, S.P., 1991. An updated world review of interactions between marine mammals and fisheries. FAO Fisheries Technical Paper, P.L., 2007. Responses of cetaceans to anthropogenic noise. Mammal Rev. 37, 81–115.
- O'Connell-Rodwell, C.E., Rodwell, T., Rice, M., Hart, L.A., 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. Biol. Constr. 93, 381–391.
- Ohman, A., 1997. As fast as the blink of an eye: evolutionary preparedness for preattentive processing of threat. In: Lang, P.J., Simons, R.F., Balaban, M.T. (Eds.), Attention and Orienting: Sensory and Motivational Processes. Erlbaum, Mahwah, NJ, pp. 165–184.
- Ohman, A., Mineka, S., 2003. The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. Curr. Dir. Psychol. 12, 5–9.
- 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. Mar. Mammal. Sci. 18, 843–862.
- Parsons, M.H., Blumstein, D.T., 2010. Familiarity breeds contempt: kangaroos persistently avoid areas with experimentally deployed dingo scents. PLoS ONE 5, 7.
- Patrick, B., 1991. Assessment of pain in animals. Anim. Behav. 42, 827–839.
- Pemberton, D., Shaughnessy, P.D., 1993. Interaction between seals and marine fish-farms in Tasmania, and management of the problem. Aquat. Conserv.: Mar. Freshwater Ecosyst. 3, 149–158.
- Plappert, C.F., Pilz, P.K.D., Schnitzler, H.U., 1999. Interaction between acoustic and electric sensitization of the acoustic startle response in rats. Behav. Brain Res. 103, 195–201.
- Ramp, D., Foale, C.G., Roger, E., Croft, D.B., 2011. Suitability of acoustics as non-lethal deterrents for macropodids: the influence of origin, delivery and anti-predator behaviour. Wildlife Res. 38, 408–418.
- Rankin, C.H., Abrams, T., Barry, R.J., Bhatnagar, S., Clayton, D.F., Colombo, J., Coppola, G., Geyer, M.A., Glanzman, D.L., Marsland, S., McSweeney, F.K., Wilson, D.A., Wu, C.-F., Thompson, R.F., 2009. Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. Neurobiol. Learn. Mem. 92, 135–138.
- Rau, V., Fanselow, M.S., 2009. Exposure to a stressor produces a long lasting enhancement of fear learning in rats. Stress 12, 125–133.
- Read, A.J., Wade, P.R., 2000. Status of marine mammals in the United States. Conserv. Biol. 14, 929–940.
- Read, A.J., 2008. The looming crisis: interactions between marine mammals and fisheries. J. Mammal. 89, 541–548.
- Reeves, R.R., Smith, B.D., Crespo, E.A., Notarbartolo di Sciara, G., 2003. Dolphins, Whales and Porpoises: 2002–2010 Conservation Action Plan for the World's Cetaceans.
- Rianne, S., 2007. PTSD and stress sensitisation: a tale of brain and body Part 2: animal models. Neurosci. Biobehav. Rev. 31, 558–584.
- Rolland, R.M., Parks, S.E., Hunt, K.E., Castellote, M., Corkeron, P.J., Nowacek, D.P., Wasser, S.K., Kraus, S.D., 2012. Evidence that ship noise increases stress in right whales. Proc. R. Soc. B 279, 2363–2368.
- Schusterman, R.J., 1981. Behavioral capabilities of seals and sea lions – a review of their hearing, visual, learning and diving skills. Psychol. Rec. 31, 125–143.
- Scordino, J., 2010. West Coast pinniped program investigations on California sea lion and Pacific harbor seal impacts on salmonids and other fishery resources. Pacific States Marine Fisheries Commission, Portland, OR.

- Sepulveda, M., Oliva, D., 2005. Interactions between South American sea lions (*Otaria flavescens*) and salmon farms in southern Chile. *Aquacult. Res.* 36, 1062–1068.
- 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. *Biol. Constr.* 21, 141–158.
- Shivik, J.A., 2006. Tools for the edge: what's new for conserving carnivores. *Bioscience* 56, 253–259.
- Shivik, J.A., Treves, A., Callahan, P., 2003. Nonlethal techniques for managing predation: primary and secondary repellents. *Conserv. Biol.* 17, 1531–1537.
- Siegmund, A., Wotjak, C.T., 2006. Toward an animal model of posttraumatic stress disorder. In: Yahuda, R. (Ed.), *Psychobiology of Posttraumatic Stress Disorder: a Decade of Progress*. pp. 324–334.
- Sigler, M.F., Lunsford, C.R., Straley, J.M., Liddle, J.B., 2008. Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. *Mar. Mammal. Sci.* 24, 16–27.
- Sih, A., 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* 139, 1052–1069.
- Southwood, A., Fritsches, K., Brill, R., Swimmer, Y., 2008. Sound, chemical, and light detection in sea turtles and pelagic fishes: sensory-based approaches to bycatch reduction in longline fisheries. *Endang. Species Res.* 5, 225–238.
- Staddon, J.E.R., Higa, J.J., 1996. Multiple time scales in simple habituation. *Psychol. Rev.* 103, 720–733.
- Talling, J.C., Waran, N.K., Wathes, C.M., Lines, J.A., 1998. Sound avoidance by domestic pigs depends upon characteristics of the signal. *Appl. Anim. Behav. Sci.* 58, 255–266.
- Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* 17, 1491–1499.
- Wang, J.H., Fisler, S., Swimmer, Y., 2010. Developing visual deterrents to reduce sea turtle bycatch in gill net fisheries. *Mar. Ecol. Prog. Ser.* 408, 241–250.
- Wartzok, D., Ketten, D.R., 1999. Marine mammal sensory systems. In: Reynolds, J., Rommel, S. (Eds.), *Biology of Marine Mammals*. Smithsonian Institution Press, Washington D.C., pp. 117–175.
- Watkins, W.A., Wartzok, D., 1985. Sensory biophysics of marine mammals. *Mar. Mammal. Sci.* 1, 219–260.
- Yano, K., Dahlheim, M.E., 1995. Killer whale, (*Orcinus orca*), depredation on longline catches of bottomfish in the southeastern Bering sea and adjacent waters. *Fish. Bull.* 93, 355–372.
- Yeomans, J.S., Li, L., Scott, B.W., Frankland, P.W., 2002. Tactile, acoustic and vestibular systems sum to elicit the startle reflex. *Neurosci. Biobehav. Rev.* 26, 1–11.
- Zimmermann, M., 1986. Behavioural investigations of pain in animals. *Assessing Pain Farm Anim.* 9742, 16–27.
- Zwicker, E., Fastl, H., 1999. *Psychoacoustics: Facts and Models*. Springer, Berlin, New York.

## CHAPTER 4

### Can fear conditioning repel California sea lions from fishing activities?

#### **Abstract**

Marine mammal interactions with fisheries create human wildlife conflicts that can threaten human safety, economic interests, and marine mammal survival. Marine mammal/fishery conflicts highlight the demand for effective non-lethal deterrents that repel marine mammals with minimal impacts on non-target species. A deterrent that capitalizes on individual-specific learning mechanisms, like fear conditioning, may enhance success while simultaneously balancing welfare concerns and reduce noise pollution. During fear conditioning, individuals learn the cues/contexts that precede the dangerous/painful stimuli, and respond by avoiding the dangerous/painful situations. We tested the efficacy of fear conditioning using aversive acoustic stimuli for reducing California sea lion (*Zalophus californianus*) interactions from two commercial fishing contexts in Southern California, USA; bait barges and fishing vessels. We performed conditioning trials on 24 individual sea lions interacting with bait barges. We tested for acquisition of conditioned fear by pairing a neutral tone with a startle stimulus. The unconditioned stimulus caused animals to increase distance and spend more time away from the bait barge but conditioned individuals had weaker avoidance responses compared to control individuals. From actively fishing commercial passenger fishing vessels we tested for fear conditioning by exposing sea lions to paired neutral tone/startle, startle pulse alone, and no sound controls over 226 fishing sets. We performed playback from 146 (including 48-no sound control) stops over two summer fishing seasons (2013, 2014). During playback from sport fishing vessels,

both conditioned stimulus and the unconditioned stimulus caused individuals to surface at a greater distance from the vessel during playback than on non-playback, but playback did not eliminate interactions with the boat. Taken together, our results suggest that the fear conditioning method has some promise for the development of non-lethal deterrents, but careful consideration has to be given to the behavior of individuals, the unconditioned/conditioned responses, and the overall management goal when designing acoustic deterrents.

## **1. Introduction**

To adjust to rapid anthropogenic environmental change, wildlife are increasingly turning to human-derived resources such as fish from fishing lines or nets (Zollett and Read, 2006), domesticated livestock (Muhly and Musiani, 2009) or garbage cans (Baruch-Mordo et al., 2013). Animals exploiting these resources create human-wildlife conflicts, ultimately threatening human safety, economic interests, and their own survival (Woodroffe et al., 2005). Marine mammal depredation, or the removal of fish from lines or nets, creates scientific, management, and conservation concerns that include socio-economic losses upon fisheries (Hamer et al., 2012), increased marine mammal entanglements, and potential (and realized) retaliatory actions by fisherman (Powell and Wells, 2011; Read, 2008). As a consequence of these conflicts, there is increasing demand for effective non-lethal mitigation techniques, such as effective deterrents to reduce conflicts (Berrow et al., 2008; Forrest et al., 2009; Gordon and Northridge, 2002; Götz and Janik, 2015, 2016).

Deterrents use aversive stimuli to prevent animals from acquiring human resources (Ramp et al., 2011). Deterrent stimuli use a variety of mechanisms to elicit defensive responses in animals (Götz and Janik, 2010; Schakner and Blumstein, 2013). A range of different presumably aversive

stimuli, such as intense acoustic signals, can elicit avoidance in marine mammals (Berrow et al., 2008; Brandt et al., 2013; Cosgrove et al., 2009). However, the use of such intense acoustic signals in marine environments to prevent depredation is controversial. There are concerns about their overall efficacy, ethical and conservation concerns over potential hearing damage, and ecological impacts on non-target wildlife (Gordon and Northridge, 2002; Götz and Janik, 2013). Focusing deterrents on species-specific sensory capabilities and individual learning mechanisms can potentially limit the effects on non-target species, as well as reduce an individual's exposure to painful stimuli (Götz and Janik, 2013). Individuals rapidly learn the cues, context, or conditions that predict threatening situations (e.g., predator attack). This suggests that a deterrent which capitalizes on individual-specific learning mechanisms may enhance success while simultaneously balancing welfare concerns and potential deleterious impacts on non-target species if the aversive stimulus does not elicit avoidance responses in non-target species.

*Pavlovian fear conditioning* is a form of associative learning in which individuals are exposed to an aversive, unconditioned stimulus (US) that is paired with an innocuous conditioned stimulus (CS) (Fanselow and Ponnusamy, 2008; Fanselow, 1984). Once conditioning has occurred, exposure to the unconditioned stimulus generates fear reactions to the conditioned stimulus. After painful encounters, however, conditioned responses to cues that signal pain (i.e., tone or context) are different from unconditioned response to the US itself (Blanchard and Blanchard, 1969; Fanselow, 1980; Hollis et al., 1997). For instance, rats' unconditioned response to aversive electric shock (US) involves a burst of motor activity (Fanselow, 1982). In contrast, rats exposed to a stimulus that predicts shock or threat (CS such as context or experimenter) react by fleeing, engaging in hyper-vigilance, or exhibiting generalized avoidance (Blanchard, 1997; Bolles and Collier, 1976; Fanselow, 1980). Conditioned responses

involve behaviors like vigilance or avoidance designed to circumvent threat that can also be the target responses for an effective deterrent (Hollis et al., 1997). These, deterrents use painful or aversive deterrent stimuli that are designed to elicit unconditioned responses. If effectively conditioned however, individuals will learn the cues that precede the painful stimulus so as to avoid the painful stimulus entirely. Employing fear conditioning to create deterrents might be a very effective way to reduce human-wildlife conflicts in a relatively humane way, especially if the conditioned response to the target CS is avoidance (Greggor et al., 2014; Mazur, 2010; Rossler et al., 2012; Schakner et al., 2014). This is because when properly conditioned, predators learn the cues/contexts that precede the aversive stimuli, ultimately resulting avoidance of the threatening situation without the need for continuous exposure to the aversive stimuli.

The acoustic startle reflex is a response from the sudden onset of a sharp acoustic stimulus that results in eyelid closure, contraction of neck and skeletal muscles, and sympathetic activation (Koch 1999). It also disrupts ongoing behavioral patterns, and reduces sensory and cognitive functioning (Graham 1979). In a captive setting, Janik & Götz (2011) demonstrated startle stimuli elicited flight responses and conditioned avoidance in grey seals (*Halichoerus grypus*) even when highly motivated to feed and in the presence of food (Götz & Janik, 2011). Seals were successfully fear-conditioned when a startle stimulus was paired with a non-startling tone (Götz & Janik 2011). This startle method (without fear conditioning) has succeeded in reducing seal approaches and seal depredation on salmon farms (Götz & Janik 2015, 2016). Here we test a fear conditioning approach to acoustic deterrents using a tone paired with an acoustic startle stimuli on free-living California sea lions (*Zalophus californianus*) interacting with commercial fishing activities in southern California. By doing so, we evaluate the efficacy of fear conditioning in two different contexts than had previously never been studied.

California sea lion depredation of commercial passenger fishing vessels and bait receivers— barges and docks where live bait is sold to sport fishers (hereafter bait barges) off the west coast of the United States has been observed for decades and has increased as pinniped populations have increased dramatically since the 1970's (Fletcher, 2008; Keledjian and Mesnick, 2013; Lowry and Maravilla-Chavez, 2005). Our objective was to test the efficacy of fear conditioning in reducing sea lion interactions from two commercial fishing contexts; bait barges and fishing vessels. We tested whether: (1) individual sea lions interacting with bait barges can be fear conditioned using aversive acoustic stimuli, (2) fear-conditioned individuals' responses differ from those of non-conditioned individuals and (3) fear conditioning reduces interactions between sea lions and commercial passenger fishing vessels in southern California.

## **2. Materials and methods**

### *2.1 Study site*

California sea lions on bait barges in Southern California's Mission Bay were used for conditioning trials. We conducted playback trials on sea lions interacting with commercial passenger fishing vessels off Southern California, that were based in San Diego Bay, Mission Bay, Dana Point, San Pedro, and Marina Del Rey.

### *2.2 Playback equipment and stimuli*

We broadcast acoustic stimuli through a Lubell 9162T underwater loudspeaker (Lubell Labs Inc, Columbus, Ohio), using a Vibe 292 power Amplifier (Lanzar Inc.), from a Tascam DR40 player. The loudspeaker was calibrated using variety of test signals at broadband source levels. Playback signals were then readjusted digitally using Adobe Audition (Adobe® Systems,

Mountain View, CA, USA). The Conditioned Stimulus (CS) was a 6 s long, 120 dB (re1  $\mu$  Pa) sine wave tone (shaped with a fade in 1.5 s to be non-startling), with a frequency range of 1-2 kHz (Figure 1). The Unconditioned Stimulus (US) was centered around 10-11 kHz with a bandwidth from 2 kHz to 18kHz. It is 190 dB (re1  $\mu$  Pa) 200 ms long with a rise time of 2ms (figure 1). The pulse was shaped white noise synthesized in Adobe Audition software with a band-pass filter and an envelope gain function. During pairings, the US was played 2 seconds after the CS.

### *2.3. Experimental design*

#### *2.3.1 Conditioning trials on bait barges*

Two observers were stationed at the end of the bait barge to control the acoustic apparatus and perform focal follows. Individual sea lions were marked with non-toxic paint pellets. After marking, a focal individual was flushed into the water by walking towards it. Observers recorded the focal individual's behavior (surface time and distance to barge using a laser rangefinder). Following a 2 min pre-trial observation period, playback trials commenced. Each trial consisted of a sound exposure followed by observation of the subject's response. The first surfacing of the animal within a 20 m radius of the deterrent initiated the next trial. This continued until all trials were completed for the focal animal's treatment. Each individual was randomly assigned to a paired playback or control treatment. For the paired group, treatment consisted of 6 trials of CS/US training followed by 6 trials of CS-alone (CS-) test phase (Figure 2). The unpaired control group was presented with the same total number of CS and US sounds (control-CS or

control-US) as the paired group during training, but in a predetermined random order so there was no consistent association between the CS and US (Figure 2).

### *2.3.2 Bait barge conditioning trials analysis*

To study factors that predicted response during observation, we fitted generalized linear mixed effects models (GLMMs) with distance fled (in m) and time spent away (in min) as response variables, using a gamma error distribution. Fixed effects included treatment (factor levels: CS/US training, CS- testing, Control US-Alone and Control CS-alone), trial number, and sex and the interaction between trial number and treatment. We tested the following random effect combinations (here shown in R notation); random intercept term for individual (1 | ID) as well as random slope terms for treatment (treatment | ID) and trial number (Trial | ID) within individual.

For all statistical analyses, we used R 2.14 (R Development Core Team 2014) using the package lme4 (Bates et al. 2011). We used a two-step (Zuur et al., 2009) model selection procedure using Akaike Information Criterion for small sample sizes (AICc). The fixed and random effects combination retained in the final selected model are shown in supplementary table 1. 95% confidence intervals calculated using the ‘confint’ function (method “Wald”) in lme4. Model assumptions were validated by examining the distribution of residuals and quantile-quantile plots. Table S1 lists the information on the random and fixed effects included in the full model and distributions. All model parameter coefficients and CIs are shown on the scale of the response variable.

### *2.3.3 Conditioning trials on fishing boats*

A single CPFV fishing trip was composed of multiple fishing stops. At each stop, the playback apparatus was deployed at the stern of the fishing vessel where fishing was concentrated. The acoustic stimuli were broadcast only when sea lions were observed interacting with the vessel. Three conditions were randomly selected for playback: Pairing (CS/US), US-alone, or control with no sound.

Two observers, one stationed on the observation deck and one on the stern recorded the amount of time and number of sea lions within 50 m of the vessel while scanning for other marine mammals > 50 m away. Behavioral observations included orientation, surface movements, and time spent around the boat. Surface distances from vessel were measured with a laser range finder. The second observer focused on quantifying the following variables: time spent fishing at each fishing stop, bait foraging (the amount of time sea lions were within 30 m of the stern actively taking bait from fishing lines or chum while swimming back and forth), surface take (when sea lions removed a hooked fish as evidenced by movement on the fishing line indicating that a fish was no longer hooked, and a sea lion surfaced immediately with a fish), surfacing behavior (number and distance of surfacings), and the number of sea lion-vessel interactions (number of sea lions and time spent within 50 m of vessel). Additional variables recorded included the fishing stop number, as well as number and species of fish caught at each fishing location.

### *2.3.4 Analysis of conditioning trials on fishing boats*

To study the factors that influenced sea lion surfacing behavior during playback, we fitted a GLMM with surfacing frequency as a response variable and a GLM with surfacing distance as a

response variable. Fixed effects included treatment (factor levels: control, CS/US pairing, US-alone) and time spent fishing was included as an offset term. Location and the fishing stop number were included as random effects for all GLMMs. To study how playback influenced sea lion bait foraging, we fitted a GLM with bait foraging presence as the binomial response variable. Bait foraging occurred when sea lions were stern foraging for at least 50% time fishing at a single stop (absence defined as a CSL bait foraging for less than 50% time fishing at a stop). Fixed effects included treatment and time spent fishing.

### **3. Results**

#### *3.1 Conditioning trials on bait barges*

Conditioning trials took place from September through November 2014. A total of 24 individual California sea lions were marked and used for playback (12 treatment, 12 control). The only factor to significantly predict the distance and time spent away in response to playback was the US when played alone in the control group (Table 1; Figure 2). Individual sea lions surfaced 7.7x farther and spent nearly 8x more time away from the bait dock in response to the US-alone (Table 1, Figure 2) than in response to the control CS. The interaction between trial number and CS/US treatment was significant for both distance and time spent away, suggesting that conditioned individuals had diminished responses with each successive trial (CS/US pairings) compared to control individuals.

#### *3.1.2 Conditioning trials on fishing boats*

We monitored 226 fishing stops across five locations in southern California during two summer fishing seasons (2013, 2014). Fishing time at a stop ranged from 0.08 h to 1.9 h with a mean of 0.73 h ( $\pm 45$  h SD). Over the two seasons of observations, interactions with sea lions occurred during 62% of the 226 fishing stops. Playbacks were performed on 98 fishing stops; in addition, we had 48 control (no sound) observations. Surface takes occurred too infrequently to be included in analyses.

Compared to no-sound control treatment, playback of the startle pulse (US-alone) caused sea lions to surface 2.7 times farther from the vessel and reduced surfacing frequency by 23% (Table 2). The paired playback caused a 26% decrease in surfacing but had no effect on distance compared to control treatments (Table 2).

The US-alone treatment reduced the presence of sea lion bait foraging behavior causing an 83% reduction in the number of events when bait foraging was present (more than 50% of the time). There was no significant effect of the paired playback bait foraging behavior (Supp. Table 1).

#### **4. Discussion**

Playback of intense, impulsive signals evoked strong unconditioned behavioral responses in California sea lions that included rapid flight and increased distance from sport fishing activities around bait docks and vessels. These results are consistent with earlier studies that showed avoidance responses to startling stimuli in grey seals (Götz & Janik, 2015). The pairing of a neutral tone with the intense startling pulse produced conditioned responses in individual sea lions interacting with bait barges. In contrast to our prediction that conditioning would create avoidance, conditioned individuals spent more time at closer distances to the bait barge compared to control individuals. Correspondingly, sea lions responded differently to the CS/US

playback compared to the US alone from the sport fishing vessels. While not specifically quantified, we hypothesize that sea lions were learning to surface surreptitiously, or change their orientation when they heard the warning sound, so as to avoid exposure to the potentially painful startle sound without swimming away. Götz & Janik (2015) also reported reduced dive times in their fear-conditioning paradigm applied to captive grey seals.

According to adaptive-evolutionary perspectives on learning theory, the nature of the conditioned response is determined by the unconditioned stimulus (Fanselow and Lester, 1988; Timberlake, 1994). Learned responses are tailored to the particular US. For instance, response to sickening food involves taste aversion (Garcia et al., 1955), whereas responses to CS preceding tactile pain, like a shock, include the avoidance of the context where pain occurred. For our study, the unconditioned stimulus was an intense, startle-eliciting acoustic pulse. We predicted that the behavioral responses to intense acoustic stimuli would include avoidance of the site of sound exposure, as observed in captive experiments (Finneran et al., 2003; Götz & Janik, 2011). Rather, the diminished spatial avoidance responses suggest that sea lions were learning to avoid the underwater sound by surfacing so as to avoid the sound. One difference between this and previous studies was a relatively long CS tone. This provided the animals with a relatively long warning period. Thus, the specific duration of the CS might have helped sea lions develop successful avoidance strategies. In some cetacean species, the Pavlovian response to a warning signal preceding intense acoustic stimuli reduces hearing sensitivity (Nachtigall and Supin, 2014, 2013), a possibility that has not been explored with pinnipeds. Our observations suggest that the conditioned response to acoustic stimuli failed to create the desired management goal (avoidance) in this particular fishery, however, unconditioned response hold some potential. The

situation may be different in other applications where increased surface activity effectively prevents foraging behavior.

The deterrent changed the behavior of sea lions interacting with fishing vessels. Sea lions surfaced at greater distances from vessels during playback than during non-playback periods. However, the average distance of surfacing during playback was still within the 50 m of boats. It appears therefore, that the deterrent modifies bait foraging behavior in sea lions but does not prevent interactions with the boat entirely. It may be that individuals surface further out to avoid being near the sound source while stern foraging. In some cases, the startle deterrent did not influence sea lion behavior. Identifying the specific mechanisms underlying the lack of response (habituation, increased motivation, higher hearing thresholds, or indeed a high turnover of animals) requires further investigation. Generally speaking, one problem with otariids (which include California sea lions) is that they have less sensitive underwater hearing than most phocid seals (which include grey seals) limiting the applicability of acoustic startle (Schusterman 1981).

The lack of the ability to mark individual sea lions foraging in the open ocean remains a major limitation of our and other studies that require individual identification (e.g., studies of habituation to repeated exposure of stimuli).

Thus, while we were able to induce mild fear conditioning in individual Californian sea lions interacting with commercial fishing activities, we were unable to create the desired avoidance necessary to mitigate the predation problem in the tested industries. However, it may be worth to consider that increased surface swimming (even at close distances) may well be a useful conditioned response in other commercial fisheries (e.g., bottom set gillnets) or on fish farms where predators need to spend a significant amount of time underwater in order to obtain prey (e.g., by manipulating nets). Taken together, our results suggest that the fear conditioning

method has some promise for the development of non-lethal deterrents, but careful consideration has to be given to the behavior of individuals, the unconditioned/conditioned responses, and the overall management goal when designing acoustic deterrents.

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**Table 4-1**

Generalized linear mixed effects models for individual California sea lions response (time spent away and distance fled) during conditioning trials on bait barges. Model coefficients for fixed effects are presented on the scale of the response variable. Significant ( $p < 0.05$ ) variables are highlighted in bold.

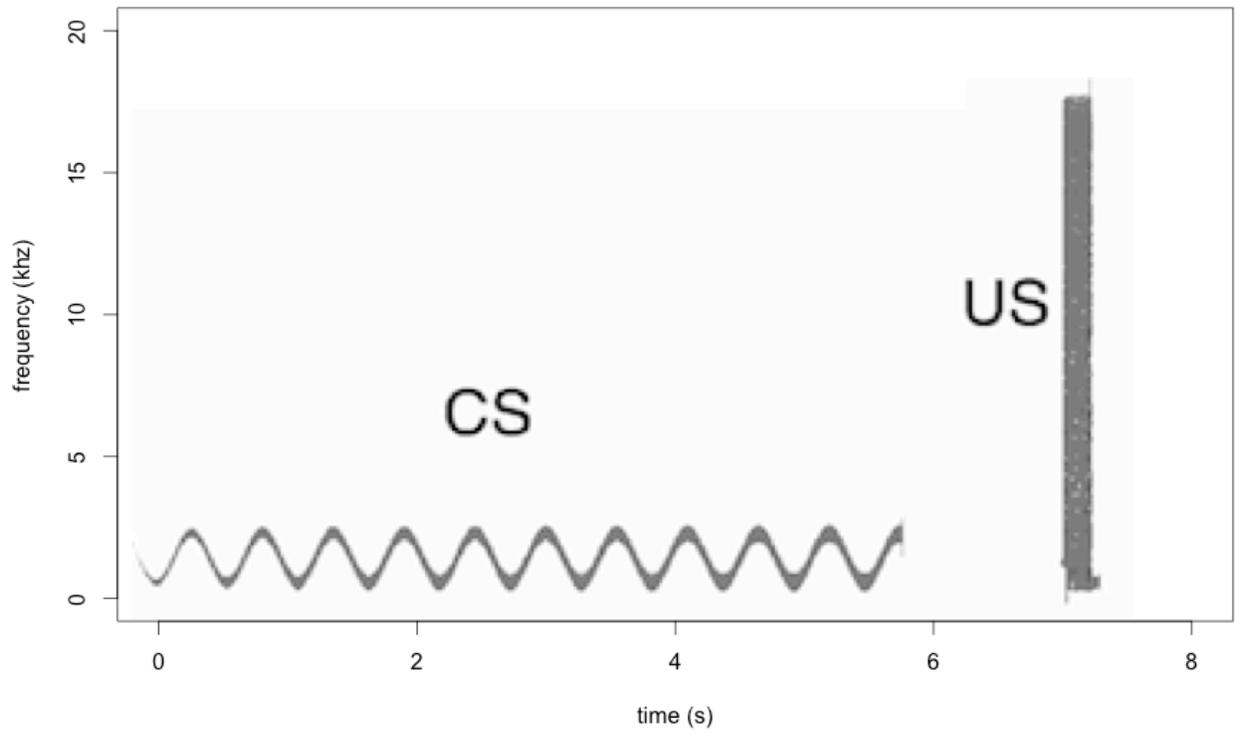
	model	Model Coefficient	95% CI	<i>P-value</i>
(intercept)	time	1.96	1.17, 3.28	<b>&lt;0.05</b>
	distance	10.11	6.4, 15.95	<b>&lt;0.001</b>
Control Treatment: US-Along	time	7.92	4.47, 14.00	<b>&lt;0.001</b>
	distance	7.74	3.59, 16.65	<b>&lt;0.001</b>
Treatment: CS/US training	time	1.60	0.79, 3.27	0.37
	distance	2.32	1.20, 4.37	<b>0.01</b>
Treatment: CS- Testing	time	0.73	0.36, 1.47	0.37
	distance	1.71	0.93, 3.14	0.08
Trial number	time	1.16	1.03,1.30	<b>&lt;0.01</b>
	distance	1.22	1.08,1.37	<b>&lt;0.001</b>
US-Along × Trial number	time	0.87	0.75,1.03	0.10
	distance	0.87	0.78,0.97	<b>&lt;0.05</b>
CS/US × Trial number	time	0.82	0.71,0.95	<b>&lt;0.05</b>
	distance	0.80	0.69, 0.93	<b>&lt;0.01</b>
CS-Testing × Trial number	time	0.92	0.80,1.06	0.216
	distance	0.77	0.66, 0.89	<b>&lt;0.01</b>

**Table 4-2**

Generalized linear mixed effects models for sea lion surfacing behavior (frequency and distance) during playback from active fishing vessels. Model coefficients presented on the scale of the response variable. Significant ( $p < 0.05$ ) variables are highlighted in bold. 'nr' indicates the variable was not retained in the model selection process.

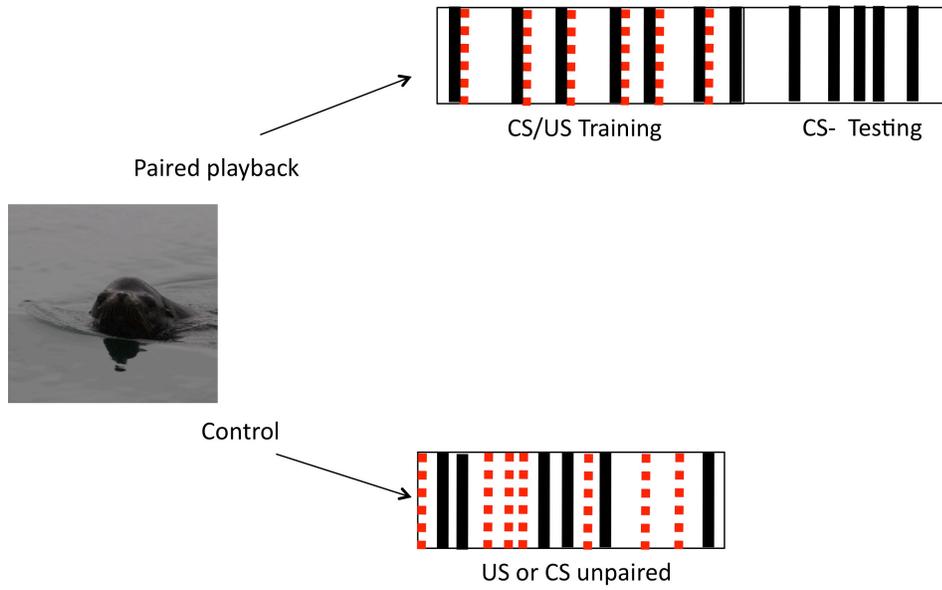
	model	Model Coefficient	95% CI	<i>P-value</i>
(intercept)	Surfacing frequency	22.1	14.2, 34.2	<b>&lt;0.001</b>
	Distance	19.1	13.6, 27.1	<b>&lt;0.001</b>
Treatment: US- Alone	Surfacing frequency	0.77	0.71, 0.83	<b>&lt;0.001</b>
	Distance	2.70	1.99, 3.62	<b>&lt;0.001</b>
Treatment: CS/US training	Surfacing frequency	0.74	0.67, 0.80	<b>&lt;0.001</b>
	Distance	1.06	0.75, 1.50	0.72
Time spent fishing	Surfacing frequency	1.08	1.02, 1.10	<b>&lt;0.001</b>
	Distance	nr	nr	nr
Stop N	Surfacing frequency	nr	nr	nr
	Distance	0.88	0.78, 0.99	0.051

**Fig. 4-1**



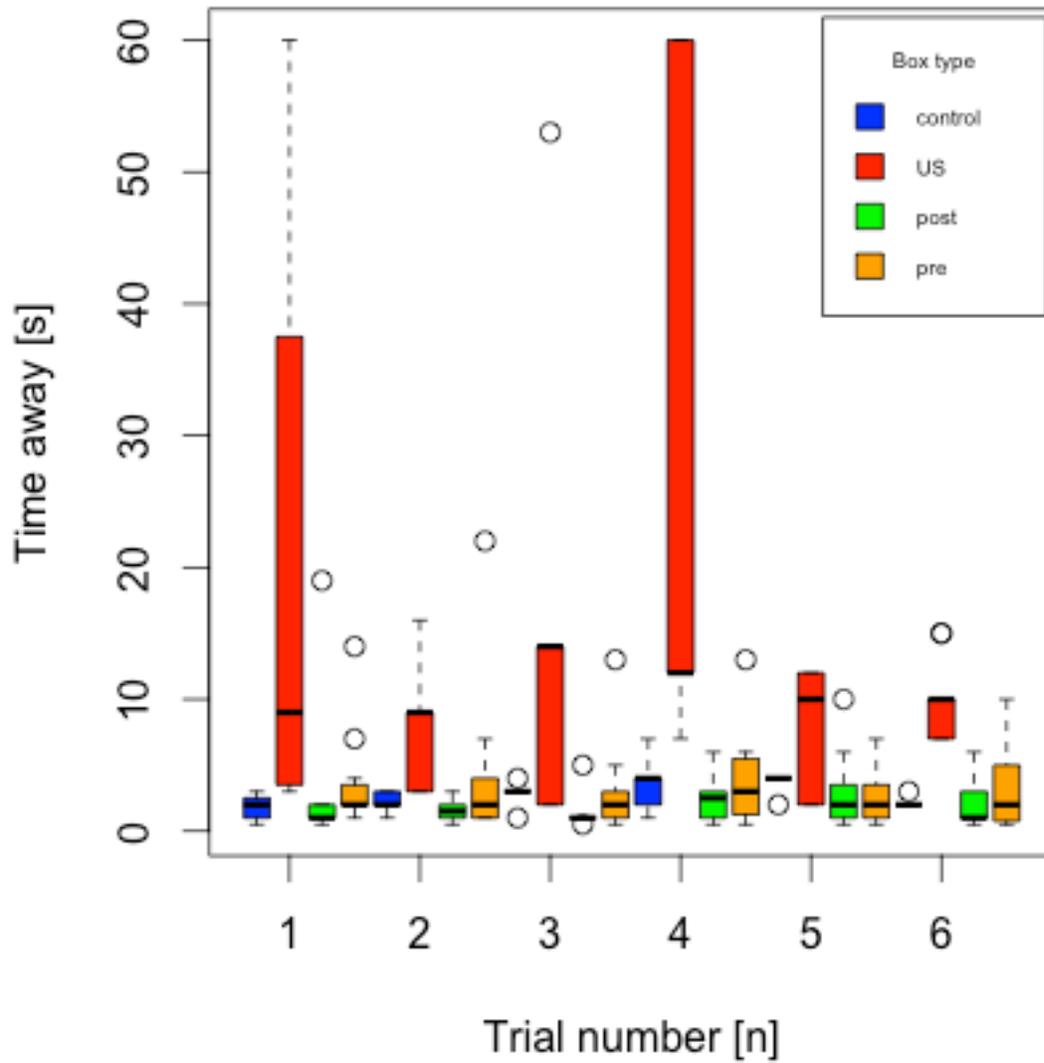
Conditioned Stimulus (CS) and Unconditioned Stimulus (US) playback sounds.

**Fig. 4-2**



Reinforcement schedules for individuals in paired playback or control treatments. Dotted Red dotted lines refer to US and black solid lines represent CS.

Fig. 4-3



Average ( $\pm$  95% confidence interval) sea lion response (time spent away from bait barge) during conditioning trials.

**Appendix A. Generalized linear mixed models used in this study**

Dependent variable	Factors	Random Factors	Model
<i>Conditioning trials on bait barges</i>			
Time away from dock	Sex, trial, treatment	(1  ID) ,(treatment   ID) ,(Trial   ID)	Gamma distribution with log-link function
Distance fled from dock	Sex, trial, treatment	(1  ID) ,(treatment   ID) ,(Trial   ID)	Gamma distribution with log-link function
<i>Conditioning trials on fishing boats</i>			
Bait Foraging	treatment, time spent fishing	n/a	Binomial Poisson distribution with log-link function
Surfacing Frequency	treatment, time spent fishing	(1 stop),(1 Site)	Gamma distribution with log-link function
Surfacing Distance	treatment, fishingtime, stop	n/a (GLM)	Gamma distribution with log-link function

**Supplemental Table 1**

Influence of playback on sea lion foraging behavior during active fishing.

Model: Presence of Bait foraging			
Variable	<i>Coefficient</i>	<i>CI (95%)</i>	<i>P</i>
(Intercept)	5.40	2.27, 15.9	<b>&lt; 0.001</b>
Treatment: US-alone	0.27	.08, 0.72	<b>&lt;0.01</b>
Treatment: CS/US pairing	6.30	0.94, 124.5	0.10

## References

- Baruch-Mordo, S., Webb, C.T., Breck, S.W., Wilson, K.R., 2013. Use of patch selection models as a decision support tool to evaluate mitigation strategies of human–wildlife conflict. *Biol. Conserv.* 160, 263–271.
- Berrow, S., Cosgrove, R., Leeney, R.H., Arata, J., McGrath, D., Dalgard, J., Le Gall, Y., 2008. Effect of acoustic deterrents on the behaviour of common dolphins. *J. Cetacean Res. Manag.* 10, 227–233.
- Blanchard, C.D., 1997. Stimulus, environmental, and pharmacological control of defensive behaviors, in: Bouton, M.E., Fanselow, M.S. (Eds.), *Learning, Motivation, and Cognition: The Functional Behaviorism of Robert C. Bolles*. American Psychological Association, Washington, DC, US, pp. 283–303.
- Blanchard, R.J., Blanchard, D.C., 1969. Passive and active reactions to fear-eliciting stimuli. *J. Comp. Physiol. Psychol.* 68, 129–135.
- Bolles, R.C., Collier, A.C., 1976. The effect of predictive cues on freezing in rats. *Anim. Learn. Behav.* 4, 6–8.
- Brandt, M.J., Höschle, C., Diederichs, A., Betke, K., Matuschek, R., Witte, S., Nehls, G., 2013. Far-reaching effects of a seal scarer on harbour porpoises, *Phocoena phocoena*. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 23, 222–232.
- Cosgrove, R., Browne, D., Rihan, D., Robson, S., 2009. Assessment of acoustic deterrent devices “pingers” and porpoise by catch rates in Irish gillnet fisheries in the Celtic Sea.
- Fanselow, M.S., 1984. What is conditioned fear? *Trends Neurosci.* 7, 460–462.
- Fanselow, M.S., 1982. The postshock activity burst. *Anim. Learn. Behav.* 10, 448–454.

- Fanselow, M.S., 1980. Conditional and unconditional components of post-shock freezing. Pavlov. J. Biol. Sci. Off. J. Pavlov. 15, 177–182.
- Fanselow, M.S., Lester, L.S., 1988. A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior, in: Bolles, R.C., Beecher, M.D. (Eds.), *Evolution and Learning*. Lawrence Erlbaum Associates, Inc, Hillsdale, NJ, England, pp. 185–212.
- Fanselow, M.S., Ponnusamy, R., 2008. The use of conditioning tasks to model fear and anxiety, in: Blanchard, R., Blanchard, C.D., Griebel, G., Nutt, D.J. (Eds.), *Handbook of Anxiety and Fear*. Elsevier, Amsterdam, Netherlands, pp. 29–48.
- Finneran, J.J., Dear, R., Carder, D.A., Ridgway, S.H., 2003. Auditory and behavioral responses of California sea lions (*Zalophus californianus*) to single underwater impulses from an arc-gap transducer. *J. Acoust. Soc. Am.* 114, 1667–1677.
- Fletcher, R.C., 2008. Exploding populations of California sea lions: a crisis with no political solution on the horizon. *Proc Vert Pest Conf* 23, 178–180.
- Forrest, K.W., Cave, J.D., Michielsens, C.G.J., Haulena, M., Smith, D.V., 2009. Evaluation of an electric gradient to deter seal predation on salmon caught in gill-net test fisheries. *North Am. J. Fish. Manag.* 29, 885–894.
- Garcia, J., Kimeldorf, D.J., Koelling, R.A., 1955. Conditioned aversion to saccharin resulting from exposure to gamma radiation. *Science* 122, 157–158.
- Gordon, J., Northridge, S., 2002. Potential impacts of acoustic deterrent devices on Scottish marine wildlife. *Scott. Nat. Herit. Comm. Rep.* F01AA404.
- Götz, T., Janik, V.M., 2010. Aversiveness of sounds in phocid seals: psycho-physiological factors, learning processes and motivation. *J. Exp. Biol.* 213, 1536–1548.

- Götz T., Janik V.M. 2011. Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. *BMC Neurosci.* 12: 30.
- Götz, T., Janik, V.M., 2013. Acoustic deterrent devices to prevent pinniped depredation: efficiency, conservation concerns and possible solutions. *Mar. Ecol. Prog. Ser.* 492, 285–302. doi:10.3354/meps10482
- Götz, T., Janik, V.M., 2015. Target-specific acoustic predator deterrence in the marine environment. *Anim. Conserv.* 18, 102–111. doi:10.1111/acv.12141
- Götz, T., Janik, V.M., 2016. Non-lethal management of carnivore predation: long-term tests with a startle reflex-based deterrence system on a fish farm. *Anim. Conserv.* doi: 10.1111/acv.12248
- Greggor, A.L., Clayton, N.S., Phalan, B., Thornton, A., 2014. Comparative cognition for conservationists. *Trends Ecol. Evol.* 29, 489–495.
- Hamer, D.J., Childerhouse, S.J., Gales, N.J., 2012. Odontocete bycatch and depredation in longline fisheries: A review of available literature and of potential solutions. *Mar. Mammal Sci.* 28, E345–E374.
- Hollis, K.L., Pharr, V.L., Dumas, M.J., Britton, G.B., Field, J., 1997. Classical conditioning provides paternity advantage for territorial male blue gouramis (*Trichogaster trichopterus*). *J. Comp. Psychol.* 111, 219–225.
- Keledjian, A.J., Mesnick, S., 2013. The impacts of el Niño conditions on California sea lion (*Zalophus californianus*) fisheries interactions: predicting spatial and temporal hotspots along the California coast. *Aquat. Mamm.* 39, 221–232.
- Lowry, M.S., Maravilla-Chavez, O., 2005. Recent abundance of California sea lions in western Baja California, Mexico and the United States. *Proc. Sixth Calif. Isl. Symp.*

- Mazur, R.L., 2010. Does aversive conditioning reduce human-black bear conflict? *J. Wildl. Manag.* 74, 48–54.
- Muhly, T.B., Musiani, M., 2009. Livestock depredation by wolves and the ranching economy in the Northwestern US. *Ecol. Econ.* 68, 2439–2450.
- Nachtigall, P.E., Supin, A.Y., 2014. Conditioned hearing sensitivity reduction in a bottlenose dolphin (*Tursiops truncatus*). *J. Exp. Biol.* 217, 2806–2813.
- Nachtigall, P.E., Supin, A.Y., 2013. A false killer whale reduces its hearing sensitivity when a loud sound is preceded by a warning. *J. Exp. Biol.* 216, 3062–3070.
- Powell, J.R., Wells, R.S., 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Mar. Mammal Sci.* 27, 111–129.
- Ramp, D., Foale, C.G., Roger, E., Croft, D.B., 2011. Suitability of acoustics as non-lethal deterrents for macropodids: the influence of origin, delivery and anti-predator behaviour. *Wildl. Res* 38, 408–418.
- Read, A.J., 2008. The looming crisis: Interactions between marine mammals and fisheries. *J Mammal* 89, 541–548.
- Rossler, S.T., Gehring, T.M., Schultz, R.N., Rossler, M.T., Wydeven, A.P., Hawley, J.E., 2012. Shock collars as a site-aversive conditioning tool for wolves. *Wildl. Soc. Bull.* 36, 176–184.
- Schakner, Z.A., Blumstein, D.T., 2013. Behavioral biology of marine mammal deterrents: A review and prospectus. *Biol. Conserv.* 167, 380–389. doi:10.1016/j.biocon.2013.08.024
- Schakner, Z.A., Petelle, M.B., Berger-Tal, O., Owen, M.A., Blumstein, D.T., 2014. Developing effective tools for conservation behaviorists: Reply to Greggor et al. *Trends Ecol. Evol.* 29, 651–652.

- Schusterman, R.J., 1981. Behavioral capabilities of seals and sea lions - a review of their hearing, visual, learning and diving skills. *Psychol. Rev.* 31, 125–143.
- Timberlake, W., 1994. Behavior systems, associationism, and Pavlovian conditioning. *Psychon. Bull. Rev.* 1, 405–420.
- Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. *People and Wildlife, Conflict Or Co-existence?* Cambridge University Press.
- Zollett, E.A., Read, A.J., 2006. Depredation of catch by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery. *Fish. Bull.* 104, 343–349.
- Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

## CHAPTER 5

### Epidemiological models to control the spread of information in marine mammals

#### **Abstract:**

Socially transmitted wildlife behaviors that create human-wildlife conflict are an emerging problem for conservation efforts that also provide a unique opportunity to apply principles of infectious disease control to wildlife management. As an example, California sea lions (*Zalophus californianus*) have learned to exploit concentrations of migratory adult salmonids below the fish ladders at Bonneville Dam impeding endangered salmonid recovery. Proliferation of this foraging behavior in the sea lion population has resulted in a controversial culling program of individual sea lions at the dam, but the impact of such culling remains unclear. To evaluate the effectiveness of current and alternative culling strategies, we used network-based diffusion analysis on a long-term dataset to demonstrate that social transmission is implicated in the increase in dam foraging behavior and then studied different culling strategies within an epidemiological model of the behavioral transmission data. We show that current levels of lethal control have substantially reduced the rate of social transmission, but failed to effectively reduce overall sea lion recruitment. Implementation of culling efforts earlier could have substantially reduced the extent of behavioral transmission and, ultimately, resulted in fewer animals being culled. Epidemiological analyses offer a promising tool to understand and control socially transmissible behaviors.

## **Introduction**

Socially transmitted behaviors, ideas, or information can be contagious, spreading through populations like an infectious disease (Bettencourt *et al.* 2006; Christakis and Fowler 2007; Hill *et al.* 2010). Interactions between individuals underlie transmission of both behaviors and diseases, creating similar patterns of spread across contact networks (Hill *et al.* 2010), and conservation biologists and wildlife managers increasingly need to control the spread of unwanted wildlife behaviors (Chiyo *et al.* 2012; Schakner *et al.* 2014). Human-wildlife conflict arises when specific behaviors increase exploitation of human resources (Madden 2004), which may threaten human safety and economic livelihood and ultimately result in wildlife culling to eliminate the conflict (Bergstrom *et al.* 2014). Unfortunately, such culling strategies often have deleterious consequences for wildlife populations and raise technical, ethical, and scientific questions as to their scope and effectiveness. Understanding the transmission mechanisms that underlie the spread of detrimental behaviors may lead to science-based recommendations on culling strategies to limit the impact of these behaviors and potentially reduce absolute culling levels to a socially acceptable level. However, new tools are needed to integrate these mechanistic insights with the impacts of culling on unwanted wildlife behavior.

To motivate the development of such tools, we use foraging behavior in California sea lions as a case study. In the early 2000s, California sea lions (*Zalophus californianus*) discovered concentrations of salmonids migrating upriver below the entrances to fish ladders at Bonneville Dam (located 235 km up the Columbia River, 45.6442° N, 121.9406° W). Increasing sea lion

predation pressure impedes the recovery of the Columbia River's declining salmon and steelhead (*Oncorhynchus* spp.) runs, of which 13 evolutionarily significant units are federally listed under the U.S Endangered Species Act (NMFS 2014). Near the mouth of the river is a major haulout for migratory male California sea lions with aggregations of 10s to 1000s of individuals (Figure 1)(Wright *et al.* 2010). Sea lions were observed sporadically at Bonneville Dam from when it was built in 1938 until the late 1990s (Stansell *et al.* 2010), but the number of individuals foraging at the dam has increased sharply starting in 2002 (Figure 1). The rapid increase in dam-foraging behavior among a subgroup of the population is consistent with social transmission of learned exploitation of this novel food source, as opposed to random asocial learning (Aplin *et al.* 2015). Sea lion foraging at the dam is a known source of salmonid mortality. This impedes endangered salmonid recovery and has created local, regional, and national management conflicts because California sea lions are also federally protected under the U.S. Marine Mammal Protection Act (16 USC Chapter 31). Culling of sea lions preying on salmon at Bonneville Dam began in 2008, but was halted in 2011 during an injunction while being challenged in a lawsuit from the Humane Society of United States (*Humane Society vs Locke. 2010*). This highlights the challenges of culling charismatic predator species versus the threat of extinction of economically, culturally, and ecologically important salmon (Marshall *et al.* 2015).

Given the parallels between social transmission of a behavior and of a pathogen, models from disease ecology (e.g. Susceptible-Infected (SI) models) provide an ideal tool to conduct retrospective analyses of current and potential culling strategies. Here, we used social network analysis to describe the transmission of salmonid foraging preferences by sea lions. We analyzed long term observations of individual sea lions in the Columbia River using network-based diffusion analysis (NBDA) (Hoppitt *et al.* 2010) to estimate the social-transmissibility of the

dam-foraging behavior. The parameters derived from the NBDA analysis were then translated into an SI model, where social transmission of behavior was equivalent to transmission of disease through direct contact between individuals and asocial acquisition of behavior mirrored random acquisition of infection (e.g. from an environmental reservoir). We used the model to examine whether culling was necessary, as well as the effect of alternative lethal control strategies by analyzing the impact of timing and level of culling on sea lion abundance at Bonneville.

## **Materials and Methods**

### Data collection

Sight-resight data of branded individual California sea lions were collected at the main haulout near the mouth of the Columbia river; the East Mooring Basin of Astoria, Oregon USA (river kilometer 25). Pacific States Marine Fisheries Commission and Oregon Department of Fish and Wildlife observers collected the number of individuals at each jetty/haulout from 1997-2014. Sampling occurred by performing counts of all individuals hauled out, followed by observing branded individuals at each haulout, and occasionally flushing all animals at specific haulouts and observing branded individuals during re-haulout. This data set spans 17 years (1997-2014) and includes 64,900 sighting records of 1439 unique, branded individuals. We used a ‘gambit of the group’ approach (Franks *et al.* 2010) with individuals considered associated if they were observed occupying the same dock or jetty. A simple-ratio association index was calculated in SOCPROG 2.4 (Whitehead 2009), with association strengths ranging from 0 (never observed hauled out together) to 1 (always observed hauled out together). We estimated the

association index for any individuals that were observed more than once (for alternate sighting threshold see Supporting Information and Figs. S1-S2).

Seasonal Bonneville Dam observation effort commenced each year with the first appearance of sea lions at the dam and continued until their absence. The timing of branded individuals foraging at the Bonneville Dam was collected by the United States Army Corps of Engineers sea lion observers program from 2002-2014. Observation effort methods are detailed elsewhere (Stansell *et al.* 2010).

#### Network-based diffusion models

We used network-based diffusion analysis (NBDA) (Hoppitt *et al.* 2010) of the association indices between individuals with the time at which an individual first arrived at Bonneville treated as a continuous variable. NBDAs were run to derive learning rates for two different models: (1) different social and asocial learning rates prior to and after instituting culling in 2008, and (2) constant social and asocial learning rates for the entire time series (2002-2014). Sample-size corrected Akaike Information Criterion ( $\Delta AICc$ ) was used to compare models, with a value of zero indicating the best model and values under two indicating preferred models (Hoppitt *et al.* 2010).

#### Discrete-time disease ecology model

To assess the impact of culling on sea lion foraging at Bonneville Dam, we translated the results of the NBDA into a discrete-time disease ecology model that tracked the number of sea lions foraging at Bonneville,  $Y(t)$ , over weekly time steps (Equation 1; see Supporting Information).

$$Y(t + 1) = Y(t) + a\lambda_0(t)X(t) + a\lambda_0(t)s(t)cX(t)Y(t) - \mu Y(t) - \gamma(t)Y(t) \quad (1)$$

We forced the number of non-foragers in the model,  $X(t)$ , using the count data on the number of sea lions hauled out in Astoria, OR (Fig. S9; see ‘Data collection’ and Supporting Information). Non-foragers learn to forage asocially at a baseline rate at time  $t$ ,  $\lambda_0(t)$  and socially according to  $s(t)$ , which is the strength of social learning relative to asocial learning at time  $t$ . Social learning was also influenced by the average contact rate between any two individuals,  $c$  (See Supporting Information). Because the learning parameters ( $\lambda_0(t)$  and  $s(t)$ ) were estimated from a sample of foragers, we also included a scaling factor,  $a$ , that provides a final model of the total accumulation of foragers (see Supporting Information for a test of this assumption). Sea lions were removed from the foraging population either naturally at rate  $\mu$  (e.g. through death or finding alternate foraging grounds) or through lethal removals at rate  $\gamma(t)$  (See Supporting Information).

### Culling strategies

To assess the impact of culling, we looked at both the year of implementation as well as estimates of the number of animals removed each year.

#### *Year of implementation*

We assessed eight different culling strategies relative to the timing of implementation (Table S1). The first was the actual culling strategy employed, which began in 2008 with a court-mandated break in 2011. We then assessed the impact of this one-year break by allowing for the mean number of animals removed in 2008-2010 and 2012-2014 to be removed in 2011 (i.e., 12;

Table S1). Finally, we allowed for earlier removals beginning in 2007 and progressing back to 2002, again using the mean number of animals removed in 2008-2010 and 2012-2014 (Table S1).

To assess these strategies, we calculated the total number of foragers across all years as well as the total number of animals culled. We also calculated the predicted total number of foragers if there had been no culling to determine the reduction in foragers achieved by each culling strategy (dashed, black line in Figure 2B). From these, we calculated the net benefit (i.e., the reduction in foragers minus the total number culled) to determine the effect of each strategy over current management time-scales (Figure 2B).

### *Target removals*

Twelve animals are currently removed on average per year, but it is unknown if this level of removal effort suitably balances reductions in foragers with the obvious ethical concerns over increased lethal removals. As a way to evaluate this, we used the eight culling strategies specified above (Table S1) but assumed that the number of yearly removals was constant across all years where removal occurred. Starting with no removals, we then calculated the marginal net benefit of removing one additional sea lion per year (e.g., net benefit of one removal per year minus the net benefit of no removals per year). Minimizing the derivative of marginal net benefit provided the point at which an additional yearly removal yielded the largest drop in benefit and thus, an ad hoc target culling strategy that balanced increasing reductions in foragers with the need to keep lethal removals to a minimum (Figure 3C). We note, however, that target strategies are a function of the management goal, where a desire for complete control of foraging behavior will necessitate increasing yearly removals as long as the marginal net benefit is positive.

## Results

There was strong support for models with social transmission of the dam foraging behavior compared to those without (Table 1). In addition, the start of culling appeared to coincide with a change in the learning process for dam foraging behavior, because models that allowed for different learning rates before and after January 1, 2008 were strongly favored (Table 1). This change in learning patterns led to a 91% decrease in the estimated social transmission effect after culling (i.e., 11.23 before and 1.05 after; Table 1). Thus, culling at least reduces the absolute number of foragers socially transmitting the behavior but may also alter contact patterns to reduce the relative rate of transmission.

The disease model fit the observed data (the maximum number of sea lions observed at Bonneville Dam in any one day during the year) well providing a good description of the total number of foragers present at Bonneville (Figure 2A). The current culling policy has reduced the transmission rate (Table 1) and has yielded positive benefits when comparing number of lethal removals to the reduction in overall foragers (Figure 2B). Had culling taking place during the 2011 injunction (Figure 2B labeled 'Actual+2011'), it would have yielded little additional reduction in the total number of foragers (Figure 2B). In contrast, beginning removal policies in any year before 2008 caused more substantial reductions in the total number of foragers compared to the actual policy but with increasing costs in terms of the total number of animals removed (Figure 2B). However, culling implemented before 2004 showed increased benefits but with decreased numbers of lethal removals relative to strategies implemented in 2004 or later, despite the longer duration of control (Figure 2B). The need for timely interventions is a well-known principle in infectious disease control (Buhnerkempe *et al.* 2014; Cooper *et al.* 2006), and

this result was robust to model assumptions and uncertainties, including parameter uncertainty and imperfect detection of foragers at Bonneville (See Supporting Information and Figs. S1-S8). These results show that earlier initiation of culling can lead to markedly fewer overall foragers than delayed implementation.

Even though early culling consistently yielded positive benefits, it is important to consider whether current culling levels sufficiently balance reductions in foragers with increasing ethical costs of lethal removals. Here, increasing numbers of yearly removals continued to reduce the number of foragers, to a point, but then additional culling produced rapidly diminishing returns (Figure 3). We defined the target yearly removal strategies as the point of diminishing returns that balances reduction of foragers versus overall culling (Figs. 3A,B). Current culling levels appear to be below this target strategy for the actual policy timeframe (Figure 3C), although a 57% increase in the total number of removals during this timeframe would have only reduced overall foragers by 28% (Figs. 3A,B). Full implementation of the target strategy in 2002 would have resulted in a 63% reduction in foragers with only a 43% increase in lethal removals (Figs. 3A,B). Similarly, if removals were implemented in 2005 or before, target strategies would have required fewer annual removals than currently employed (Figure 3C).

## **Discussion**

Taken together, our results suggest that immediate implementation of culling during the period of sharp increase in sea lions foraging at the dam could have reduced the extent of behavioral transmission and recruitment to the dam. Rapid proliferation of dam-foraging behavior through social transmission leads to more salmonid predation and ultimately requires

more sea lions to be removed annually than when removal actions are delayed. We note, however, that our model does not address impacts on the endangered salmonid population. Future models should incorporate a consumer-resource component to determine how lethal removal of sea lions relates to salmonid conservation. However, our current results highlight the necessity for early culling efforts from both a conservation and management perspective to prevent the spread of a detrimental behavior and to ultimately minimize the number of animals removed.

Although the conclusion that earlier implementation of lethal removals leads to fewer removals is based on a simple model framework, this management strategy is robust to model assumptions and uncertainties. First, imperfect detection of sea lion foragers at Bonneville Dam is likely to lead to underestimates in the number of removals necessary to curb the spread of the behavior. However, target strategies changed little as long as more than half of foragers were observed. Under this threshold, the qualitative pattern still held generally, although the target number of yearly removals increased to compensate for the greater number of foragers (Extended Data Fig. 2). Similarly, when assessing the impact of parameter uncertainty, we found that parameter combinations that generated greater numbers of foragers resulted in higher target numbers of yearly removals (Extended Data Figs. 3-7). This result highlights the importance of developing accurate estimates of the total number of foragers at Bonneville Dam to minimize culling.

Our results also have broader policy implications for the region. Recently, Steller sea lions (*Eumetopias jubatus*), a larger competitor of California sea lions, have begun to forage at Bonneville Dam. Also, California sea lions are increasing their presence at other dams, such as Willamette Falls, to forage on salmonids in the lower Columbia River. For both species, we

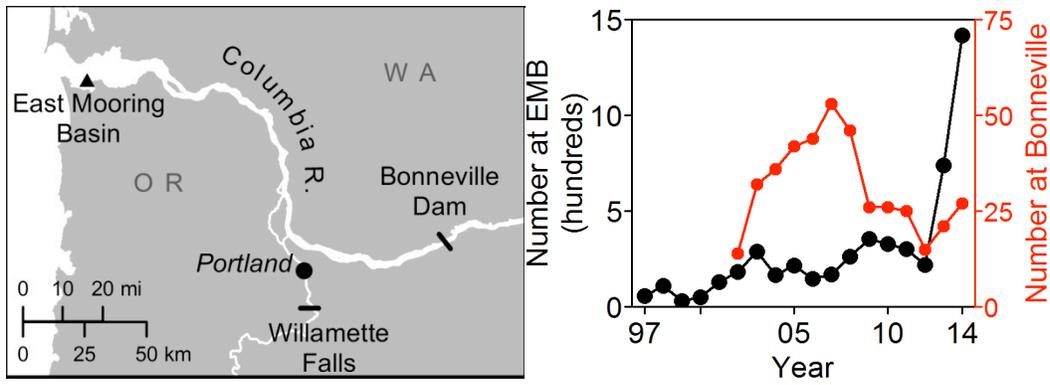
suggest that when socially transmitted foraging is expected, a shift in policy from delayed culling after assessment to early culling, with a hiatus if needed to assess efficacy, will ultimately result in fewer animals being culled. Culling protected predators to recover threatened and endangered salmonids stirs public emotions while raising legal and political concerns. Early application of lethal removal, while potentially controversial, is the most effective of the culling strategies we evaluated to control socially-mediated transmission.

## **Conclusions**

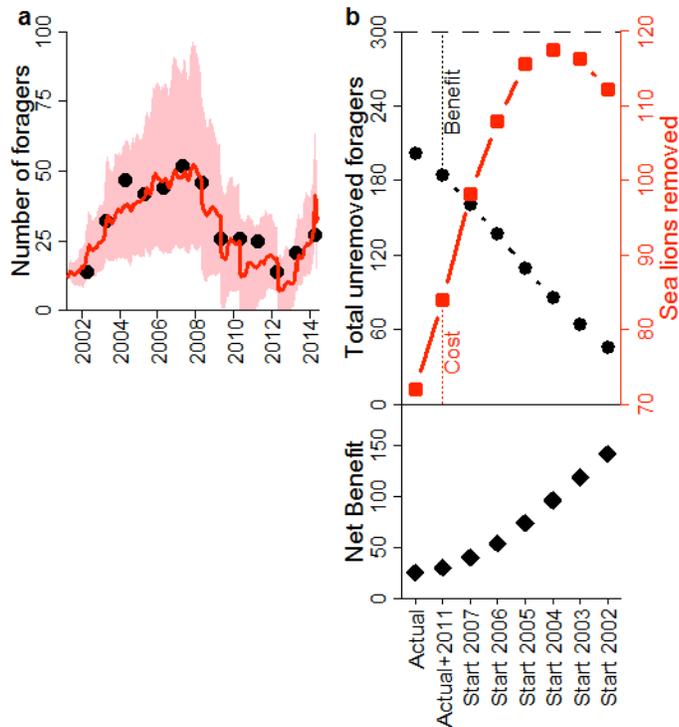
New techniques are required to facilitate human-wildlife coexistence in a world where wildlife and human interactions are increasing. Models from disease ecology offer a promising tool to understand behavioral transmission and can inform management policy for controlling human-wildlife conflicts. We developed a novel procedure for translating the output of a social network-based diffusion analysis into an epidemiological model. This novel synthesis provides a flexible framework that can be applied across a diversity of animal and human systems in order to test alternative management strategies in the containment of undesirable behaviors. We show that epidemiological models can reduce the spread of unwanted behaviors in wildlife because they can help predict the risk factors for potential outbreaks, estimate the future prevalence of infection/behavior in the population, and test the efficacy of interventions such as culling (i.e., lethal removal of specific individuals). Social transmission rapidly spreads behaviors through populations like an infectious disease. And, like an infectious disease, socially transmitted behaviors require early action to reduce their spread.

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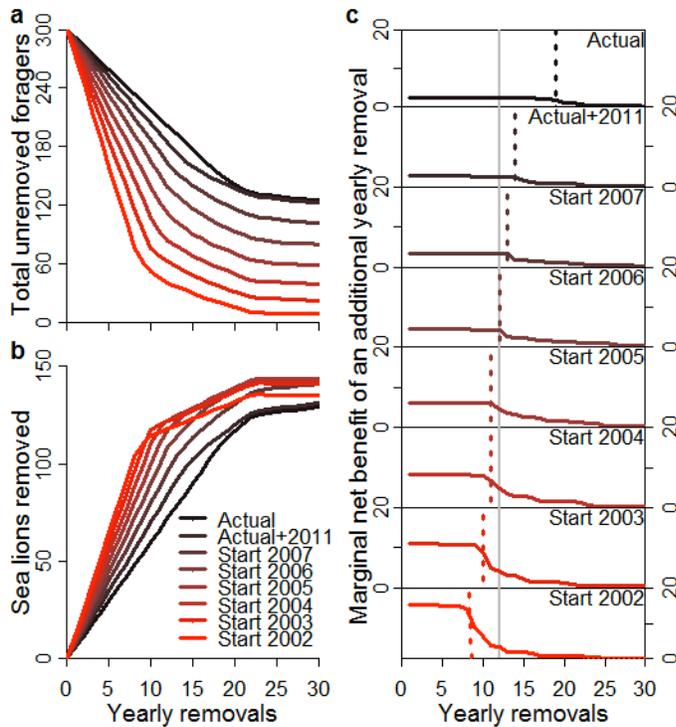
The study was conceived by Z.A.S. and M.G.B. M.G.B. and J.O.L-S. developed the model structure and developed the statistical methodology. Results were discussed and interpreted by Z.A.S., M.G.B., J.O.L-S. and D.T.B. The manuscript was drafted by Z.A.S., D.T.B, J.O.L-S. and M.G.B., with important contributions made by all of the other authors. M.J.T., B.K.V, and R.J.S. collected the data. We declare no competing financial interests



**Fig. 5-1: Columbia River and incidence of California sea lions at East Mooring Basin (EMB) and Bonneville Dam.** The maximum California sea lions observed at EMB (black) and average daily number of Bonneville foragers in each year (red).



**Fig. 5-2: Total number of foragers at Bonneville Dam and the benefits of early implementation of culling.** (A) Projected number of foragers through time for the model (solid red line) fit to the maximum daily number of foragers in each year (black circles). Light red shaded area is the 95% CI for model projections generated using Poisson errors. (B) The upper part of the graph depicts the total number of foragers to ever visit Bonneville Dam without culling (dashed, black line), the effect of different culling strategies (Table S1) on the total number of unremoved foragers (black circles), and the number of sea lions removed (red squares). The lower part of the graph depicts the net benefits of these strategies (benefits minus the cost; red and black diamonds). The actual culling strategy used (Actual) began in 2008 with an injunction on culling in 2011. Alternate strategies included: 1) Actual+2011 – the actual strategy used but with the average number culled from 2008-2014 implemented in 2011 and 2) Start 2002-2007 – same as the Actual+2011 strategy but with the average yearly cull from 2008-2014 implemented beginning in the year specified until 2008 (Table S1).



**Fig. 5-3: Target number of yearly removals.** (A) The total number of unremoved foragers and (B) the number of sea lions removed across different numbers of yearly removals. The years during which removals occurred were the same as for the culling strategies in Figure 2 and Table S1 (ranging from Actual in black to Start 2002 in red). The number of removals in each year however, was set equal and varied from 0 to 30. (C) The marginal net benefits of removing an additional sea lion a year (marginal benefit minus marginal cost). Dashed line denotes the target number of yearly removals that balances maintaining high benefits against the cost of an additional individual culled (i.e., target strategies were chosen to minimize the derivative of the marginal net benefit which represents the steepest decline in benefits when adding an additional yearly removal), while the solid gray line indicates the average number of animals culled since 2008.

**Table 5-1: Comparisons of NBDA models with and without social transmission and with and without a change in learning parameters in 2008 using the change in sample-size corrected Akaike Information Criterion ( $\Delta AICc$ ; zero indicates the best model). Parameter estimates and their 95% confidence intervals (in brackets) for each model are given.**

Model	Pre-2008 social learning coefficient <sup>1</sup>	Pre-2008 asocial learning rate <sup>2</sup>	Post-2008 social learning coefficient <sup>1</sup>	Post-2008 asocial learning rate <sup>2</sup>	$\Delta AICc$
Social transmission + Change in learning	11.23 [3.96, 19.02]	$1.22 \times 10^{-5}$ [ $4.07 \times 10^{-6}$ , $2.42 \times 10^{-5}$ ]	1.05 [ $6.66 \times 10^{-5}$ , 3.67]	$2.57 \times 10^{-5}$ [ $1.42 \times 10^{-5}$ , $3.98 \times 10^{-5}$ ]	0
No social transmission + Change in learning	-	$4.42 \times 10^{-5}$	-	$3.64 \times 10^{-5}$	31.4
Social transmission + No change in learning	6.79 [3.35 <sub>3</sub> , 7.50] <sup>3</sup>	$7.70 \times 10^{-6}$ [ $4.38 \times 10^{-6}$ , $1.19 \times 10^{-5}$ ] <sup>3</sup>	-	-	307.7
No social transmission + No change in learning	-	$(2.18 \times 10^{-5})^3$	-	-	357.8

<sup>1</sup>Unitless parameter

<sup>2</sup>Daily rates.

<sup>3</sup>Estimates are for the entire period 2002-2014.

## **Supporting Information**

### **SI Methods**

#### **Translating NBDA into an epidemiological model**

To better understand how sea lion culling impacts the total number of foragers at the Bonneville Dam over time, we sought to translate the results of our network-based diffusion analysis (NBDA) into an epidemiological model. Epidemiological models are useful for this type of analysis, because (1) they provide useful insights into transmission of an agent (i.e., pathogen or behavior) through a population; (2) they can incorporate multiple mechanistic hypotheses about the system (e.g. does the implementation of removal change learning rates); (3) they can be used retrospectively to assess the impact of control strategies that were never implemented; and (4) they are relatively simple and well-understood.

Because a learned behavior can be viewed as an infectious process, we aim to translate the NBDA into a susceptible-infected model (i.e., non-forager – forager), where we define the total rate of change in the infected (foraging) population,  $Y$ , as:

$$\frac{dY}{dt} = \alpha X + \beta XY - \mu Y - \gamma Y \quad (1)$$

Where,  $X$  is the number of susceptible individuals (non-foragers);  $\alpha$  is the transmission coefficient due to a background source of infection (asocial learning); the transmission coefficient due to contact between susceptible (non-foraging) and infected (foraging) individuals (social learning);  $\mu$  is the mortality rate of infected (foraging) individuals; and  $\gamma$  is the lethal removal rate of infected (foraging) individuals. Here, we note that the asocial learning component will create a constant arrival of individuals displaying the behavior. However, a true

‘outbreak’ of the behavior can only occur when the social learning component is supercritical (i.e., individuals with the behavior transmit it to more than one individual on average). Thus, knowledge of the social learning component is crucial to understanding outbreak dynamics.

To translate NBDA into this form, we start with rate of acquisition of a behavior by individual  $i$  at time  $t$ ,  $\lambda_i(t)$ , as defined by (Hoppitt *et al.* 2010):

$$\lambda_i(t) = \lambda_0(t)(1 - z_i(t)) \left[ s(t) \sum_{j=1}^N \alpha_{i,j} z_j(t) + 1 \right] \quad (2)$$

Where,  $\lambda_0(t)$  is the asocial learning rate at time  $t$ ;  $z_i(t)$  is an indicator function for whether individual  $i$  has learned the behavior at time  $t$  ( $z_i(t) = 1$ ) or not ( $z_i(t) = 0$ );  $s(t)$  is the strength of social learning relative to asocial learning at time  $t$ ;  $\alpha_{i,j}$  is association strength between individuals  $i$  and  $j$ ; and  $N$  is the total number of individuals.

Thus, the total rate of acquisition of the behavior in the population is given by:

$$\frac{dY}{dt} = \sum_{i=1}^N \lambda_0(t)(1 - z_i(t)) \left[ s(t) \sum_{j=1}^N \alpha_{i,j} z_j(t) + 1 \right] \quad (3)$$

Equation 3 requires individual-based methods incorporating contact information for all individuals. As such, for systems without complete contact data, this model cannot be used to track the total number of foragers. If, however, the association network is well-connected (Fig. S10A), and foragers do not occupy more central positions within the association network, as measured by the total number of associations (degree, Fig. S10A) or the number of shortest paths between any two individuals in the association network that an individual sits on (betweenness, Fig. S10B), the specific network structure will not be as important in modeling the total number

of foragers. Rather, only previous associations with foragers will be important in determining spread of the behavior (Fig. S10C). Thus, we assume that contacts between any two individuals in the population occur at random and at a constant strength (i.e.,  $a_{i,j} \approx c$  for all  $i \neq j$ ), equation 3 simplifies to:

$$\begin{aligned} \frac{dY}{dt} &\approx \sum_{i=1}^N \lambda_0(t)(1 - z_i(t))[s(t)cY + 1] \\ &= \lambda_0(t)X + \lambda_0(t)s(t)cXY \end{aligned} \quad (4)$$

Because the total number of individuals foraging in our case is not always increasing, we add in removals of foraging individuals through both natural removals at rate  $\mu$  (i.e., natural mortality or dispersal to other foraging grounds) and human removals (which includes live capture and transfer to captivity in addition to culling), which vary in rate through time,  $\gamma(t)$ , to get a translation of NBDA into an epidemiological model that describes the total rate of change in foragers:

$$\frac{dY}{dt} = \lambda_0(t)X + \lambda_0(t)s(t)cXY - \mu Y - \gamma(t)Y \quad (5)$$

When learning parameters ( $\lambda_0(t)$  and  $s(t)$ ) are estimated from a sample of foragers, these estimates will not adequately capture the total accumulation of foragers described in equation 5. To remedy this mismatch, we also include a scaling factor,  $a$ , that translates NBDA estimates from a sample of the population into a final model of the total accumulation of foragers (see ‘Sensitivity analysis’ below for a test of this assumption using alternate learning and scaling parameter values and Figs. S1-S7):

$$\frac{dY}{dt} = a\lambda_0(t)X + a\lambda_0(t)s(t)cXY - \mu Y - \gamma(t)Y \quad (6)$$

### Simulation algorithm

When simulating the number of foragers, we started simulations on April 1, 2001 with an initial number of foragers,  $Y(0)$  (See SI Methods for parameter estimation). Because asocial learning allowed for accumulation of foragers in the absence of other foragers, we note that  $Y(0) \geq 0$ . For changes in the number of foragers week to week, we assumed an order of events within each week where new foragers arrived first, then were culled, and then were naturally removed, with all removals constrained so that the number of foragers was always greater than or equal to zero. Because return rates to Bonneville were relatively high (see Supporting Information) and all arrivals and departures occurred over a short time frame, we did not explicitly model the arrival and departure of foragers at Bonneville Dam. Rather seasonality in the accumulation of foragers was driven by fluctuations in the weekly count data that described the number of non-foragers,  $X(t)$ , capable of learning the behavior.

Lethal removals in the model began the week of April 16 in years during which lethal removals occurred, in line with the timing of actual removals (Stansell *et al.* 2014). A maximum of four individuals were removed each week to mimic actual culling efforts (Stansell *et al.* 2014) (i.e.,  $\gamma(t) = 4$ ) until the total number of allowed removals during that year was reached (Table S1). To look at alternate removal strategies, including removals during 2011 and removals occurring before 2008, we used the mean number of yearly removals that occurred in 2008-2010 and 2012-2014 as the number of removals occurring in any additional years (Table S1). Although there was a change in the learning process associated with the start of lethal removals (Table 1), we assumed that this change in parameter values always occurred in 2008 even when removals

began before. Thus, based on our finding that culling is associated with reduced learning rates, model predictions on the effect of culling are likely to be conservative. More research is needed to establish a causal link between culling and learning behavior, but this may suggest that fewer removals will be needed if social transmission rates decrease after culling is implemented.

### Weekly count data

To obtain weekly counts of the number of sea lions at the East Mooring Basin in Astoria, OR for all weeks of the year, we took the mean number of individuals observed on any day within a week. Because counts were not taken during all weeks, we fit a non-parametric smoothing function to the observed weekly counts using B-splines of order 6, with predicted counts constrained to be greater than zero (Fig. S9). This smoothed count data was used to force the number of non-foragers in Equation 1.

### Estimating epidemiological model parameters

#### *Learning parameters*

We used the parameter estimates presented in Table 1 and converted any rates to weekly rates (see Table S2 for this and alternate parameter values).

#### *Contact strength*

To estimate the average contact strength between any two individuals,  $c$ , we used the association matrix generated in the NBDA analysis, again using associations between any two individuals that were sighted at least twice (but for a test of this assumption see ‘Sensitivity analysis’ below and Table S2). However, because this matrix includes associations of zero for

individuals whose residencies at Astoria did not overlap, we only consider associations of individuals who overlapped temporally or who were observed within one year of each other (whether or not they were observed together). We then used the average association between these temporally overlapping individuals as our average contact strength,  $c$  (Table S2).

### *Natural removal rate*

To estimate the rate at which individuals are naturally removed from Bonneville Dam, (e.g. through death or finding alternate foraging grounds), we used the dates that foragers were first and last observed at Bonneville to estimate total observed foraging duration, the reciprocal of which gives us an estimate of the natural removal rate. For this estimation, we only required that an individual be observed more than once (but for a test of this assumption see ‘Sensitivity analysis’ below and Table S2). However, natural removals become confounded with human initiated lethal removals after 2008. In order to avoid this, we only consider foraging durations for individuals who were last observed before 2008 and not lethally removed in the estimate of the daily natural removal rate (Table S2).

An alternate estimation procedure yielded a similar estimate for the natural removal rate. Here, we used data on the observed probability of identifiable sea lions returning to Bonneville Dam each year from 2003-2014 (0.192, 0.512, 0.771, 0.657, 0.656, 0.692, 0.685, 0.354, 0.620, 0.676, 0.3, and 0.397, respectively (Stansell *et al.* 2014). The complement of these probabilities provides information on both the probability of death and the probability of not returning given survival. Taking the mean of the complement of these probabilities and converting to a weekly leaving rate (i.e.,  $-\log(0.543)/52$ ) yielded a similar estimate to the one used (0.0117 vs. 0.00784, Table S2).

### *Scaling parameter and initial number of foragers*

The scaling parameter,  $a$ , and the initial number of foragers,  $N$ , were estimated by fitting the model with the actual culling strategy to data. Because we did not explicitly model the arrival and departure of foragers at Bonneville Dam, we needed data on the total number of foragers through time that is not influenced by seasonal changes in abundance at the Dam. We used the maximum number of California sea lions counted on a single day during the spring at Bonneville Dam as representative of the total foraging population in each year (Stansell *et al.* 2014) (but for a test of this assumption see ‘Sensitivity analysis’ below and Fig. S8). To calculate a single likelihood for the model, we assumed that the observed maximum numbers of California sea lions each year were drawn from independent Poisson distributions with means determined by the predicted number of foragers in the model during the week of April 23, to match the observed late April timing of the count data. Maximum likelihood estimates for the scaling parameter and the initial number of foragers were found using the ‘optim’ function in R version 3.2.0(R Development 2014)(Table S2)

### Sensitivity analysis

To assess the robustness of our results to uncertainties in the modeling framework, we performed sensitivity analysis on data and parameter uncertainties.

### *Bias due to sighting thresholds*

When estimating the NBDA and other model parameters, we used any California sea lions that were sighted at least twice. To determine the robustness of our results to this assumption – and to provide an additional assessment of parameter uncertainty – we also conducted the NBDA analysis and estimated the average contact strength and natural removal rate of foragers using sighting thresholds of 10 and 20 (Table S2). We then assessed the timing of implementation of removal and target removal strategies using these alternate parameterizations (Figs. S1-S2). Although social learning rates were lower using these alternate sighting thresholds (Table S2), the qualitative result that earlier culling is more effective was similar (Figs. S1-S2). However, targeted culling strategies were higher when social learning rates were lower (Figs. S1-S2) indicating that accurate estimates of social learning rates will be needed to set management policies.

#### *Uncertainty in learning, contact, and natural removal parameters*

The learning parameters estimated using NBDA showed some uncertainty that could also impact results (Table 1). We determined the importance of this uncertainty by considering all combinations of the maximum-likelihood estimates and the endpoints of the 95% confidence intervals (i.e., 4 variables with 3 values each for 81 parameter combinations, Figs. S3-S5; Table 1). For these combinations, we used the previously derived values for the average strength of contact and natural removal rate (Table S2) and re-fit the model to determine the scaling parameter and the initial number of foragers for each parameter combination. To assess the impact of uncertainty in the average strength of contact between individuals and the natural rate of removal of foragers from Bonneville on model results, we used a similar approach using the estimated values of the contact and natural removal parameters and values that were double and

half their actual estimates to characterize uncertainty (i.e., 2 variables with 3 values each for 9 parameter combinations, Fig. S6). For these combinations, we used the previously estimated learning parameters (Table 1), and re-fit the model to again determine the scaling parameter and the initial number of foragers for each parameter combination. For all parameter combinations, we then determined the total number of foragers that had ever been at Bonneville, the total number of animals culled, and the target yearly removals for each culling strategy. In general, parameter combinations that caused increases in the total number of foragers that had ever been at Bonneville Dam were associated with higher target yearly removals, no matter the culling strategy employed (Fig. S7).

#### *Imperfect detection of foragers*

We used the maximum daily number of sea lions observed at Bonneville as a proxy for the total number of individuals foraging. However, this assumes that there is near perfect detection of sea lions on any given day. To test the effect of this assumption, we assumed that each year's maximum daily count was drawn from a binomial distribution with a set probability of observation (i.e., 0.1, 0.25, 0.5, 0.75, or 0.9). Under this scenario, we calculated the expected total number of foragers in each year by dividing the observed data by the probability of observation. We then simulated 100 random time series of the total number of foragers present in each year from these binomial distributions (by taking random draws and recalculating the expected total number of foragers in each year). We re-fit the model to each of these time series and determined target removal strategies (Fig. S8).

## **SI Results**

## Sensitivity Results

To determine how robust our conclusions were to model assumptions and uncertainties, we conducted three sensitivity analyses.

### *Bias due to sighting thresholds*

Imperfect sampling of individuals at Astoria may impact observed association strengths between individuals and estimates of social learning as a result. To increase sample size, we only required individuals to be observed twice to be included in our analysis. Observation thresholds of ten and twenty yielded markedly lower estimates for social learning (Table S2). However, the lower social learning rates were compensated by higher asocial learning rates (Table S2). Despite these differences in parameter estimates, we found qualitatively similar results across observation thresholds indicating that estimates of social learning (Table S2) and the general need for early removals do not depend critically on the sampling regime for association strengths (Figs. S1-S2). These alternate parameterizations do, however, reveal that target yearly removal strategies will depend on the specific estimates of association strengths that determine learning rates (Figs. S1-S2). Specifically, lower social learning rates increased the target number of yearly removals, and for culling strategies that completely coincided with time periods where social learning was absent (i.e., post-2008 under the 10 and 20 observation threshold), there is no added benefit to culling beyond the removals themselves (Figs. S1-S2).

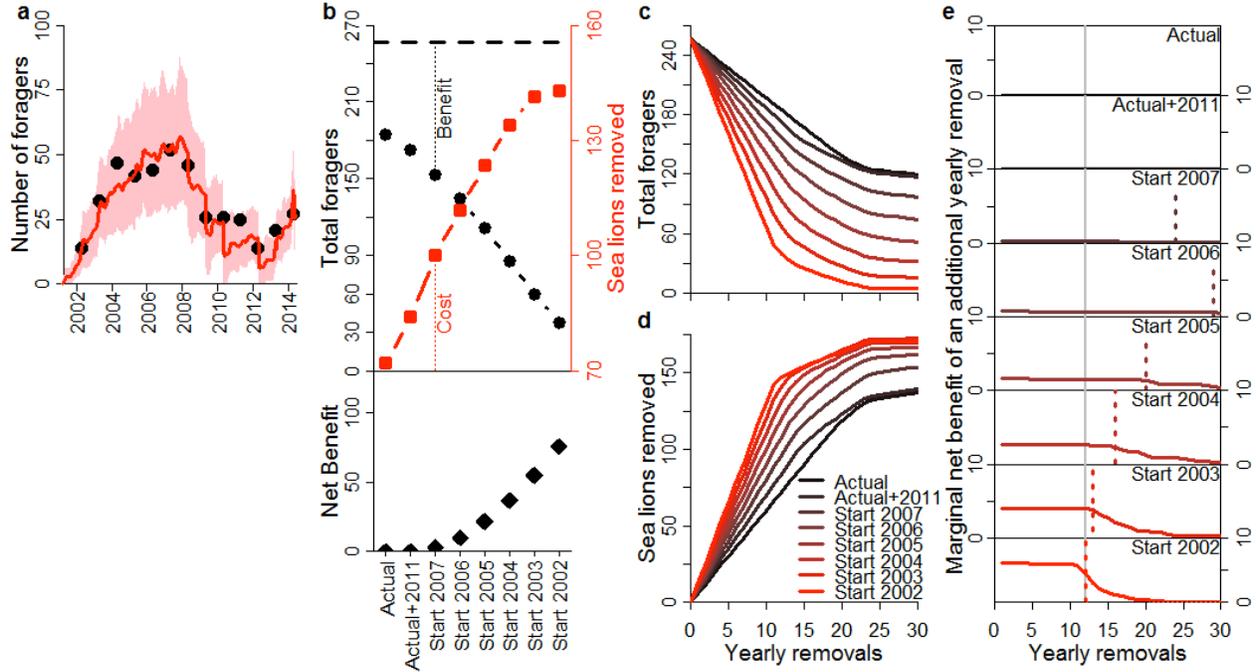
### *Uncertainty in learning, contact, and natural removal parameters*

Similarly, when assessing the impact of parameter uncertainty, we found that parameter combinations that generated greater numbers of foragers resulted in higher target numbers of yearly removals (Fig. S3-S7). This result highlights the importance of observation efforts to not only determine the total number of foragers present but to also ensure parameter estimates reflect the true learning process.

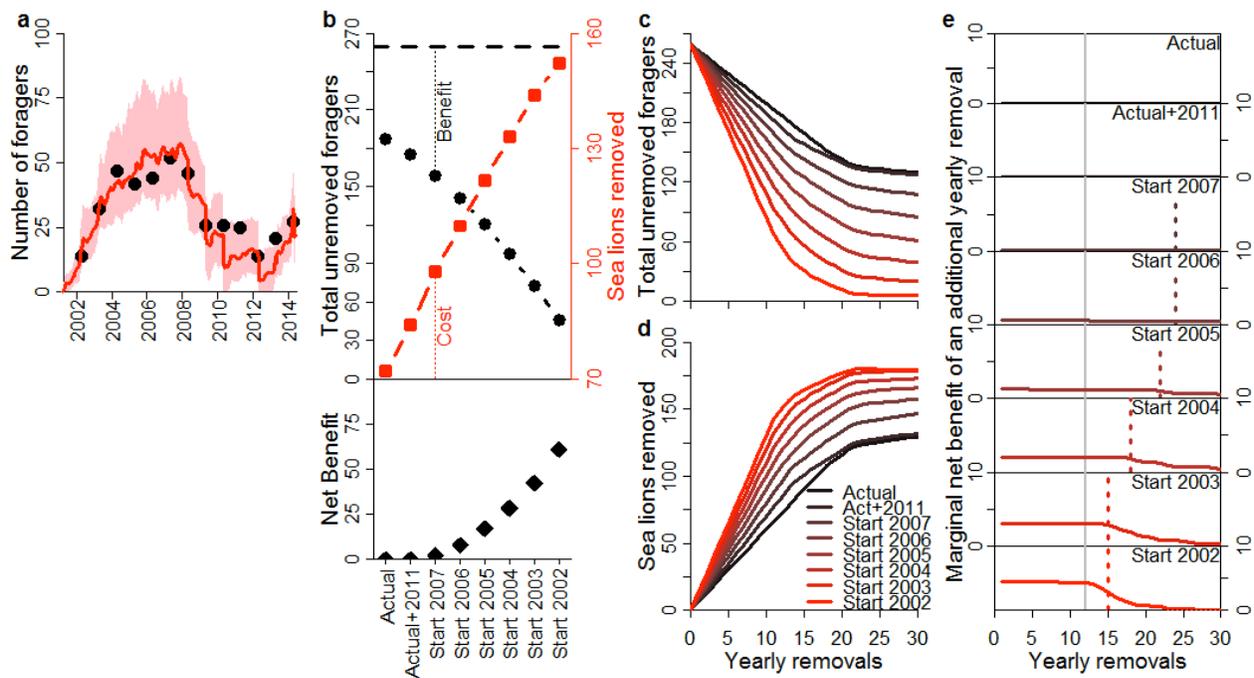
### *Imperfect detection of foragers*

Imperfect detection of sea lion foragers at Bonneville Dam is likely to underestimate the number of removals necessary to curb the spread of the behavior. However, in simulation-based sensitivity analyses, target strategies changed little as long as more than half of foragers were observed (Fig. S8). Under this threshold, the qualitative pattern still held generally, although the target number of yearly removals increased to compensate for the greater number of foragers (Fig. S8). Thus, target strategies can be set with relative confidence if it is apparent that observation efforts are capable of detecting more than half of all foragers present at Bonneville.

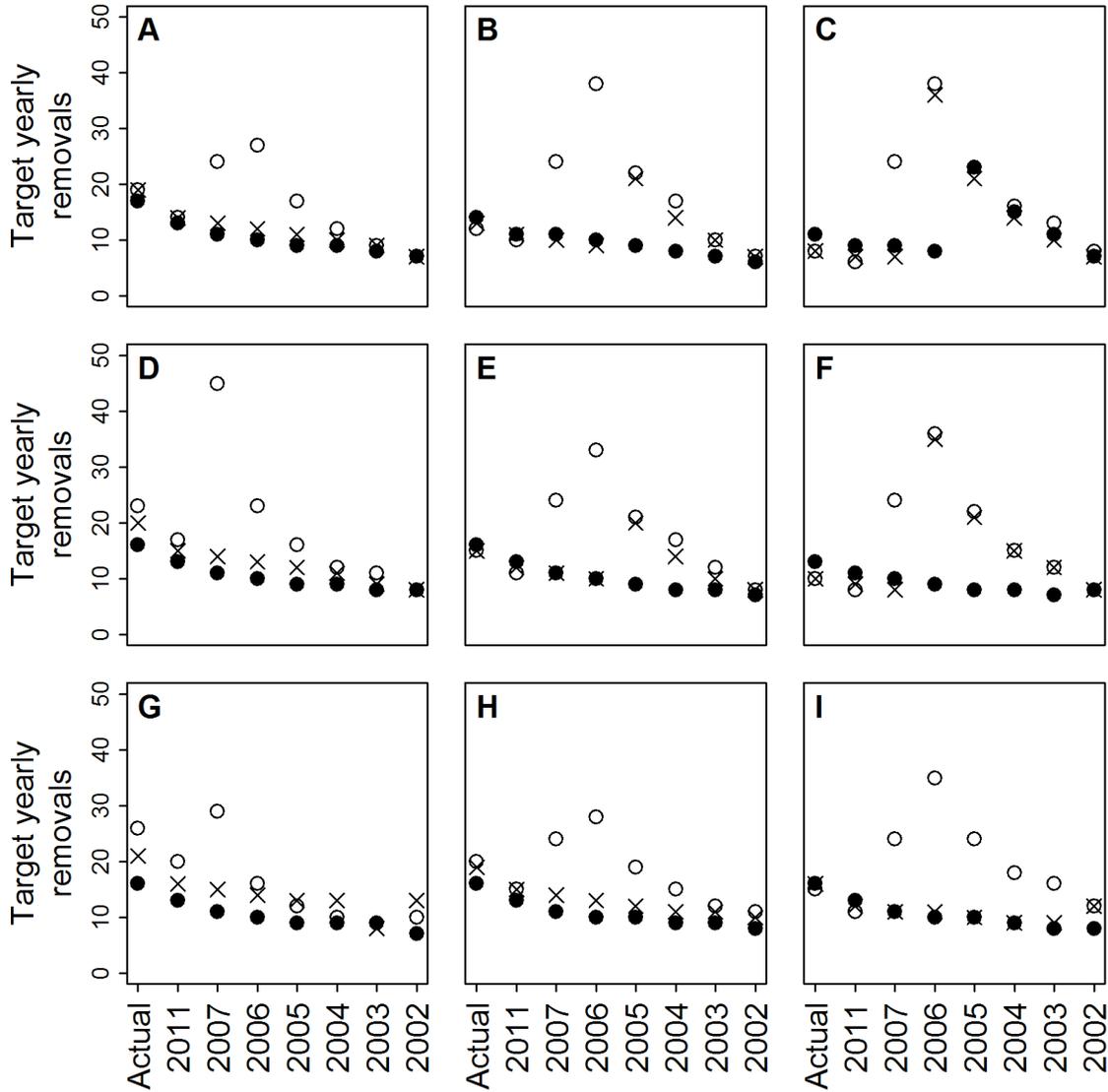
## SI Figures



**Fig. S1: Output on with parameters estimated using a 10 sighting observation threshold for sea lions.** (A) and (B) are similar to panels in Figure 2, and (C)-(E) are similar to panels in Figure 3. These results indicate that qualitative conclusions hold, but reducing parameter uncertainty is crucial to derive robust, quantitative conclusions on the target number of yearly removals.

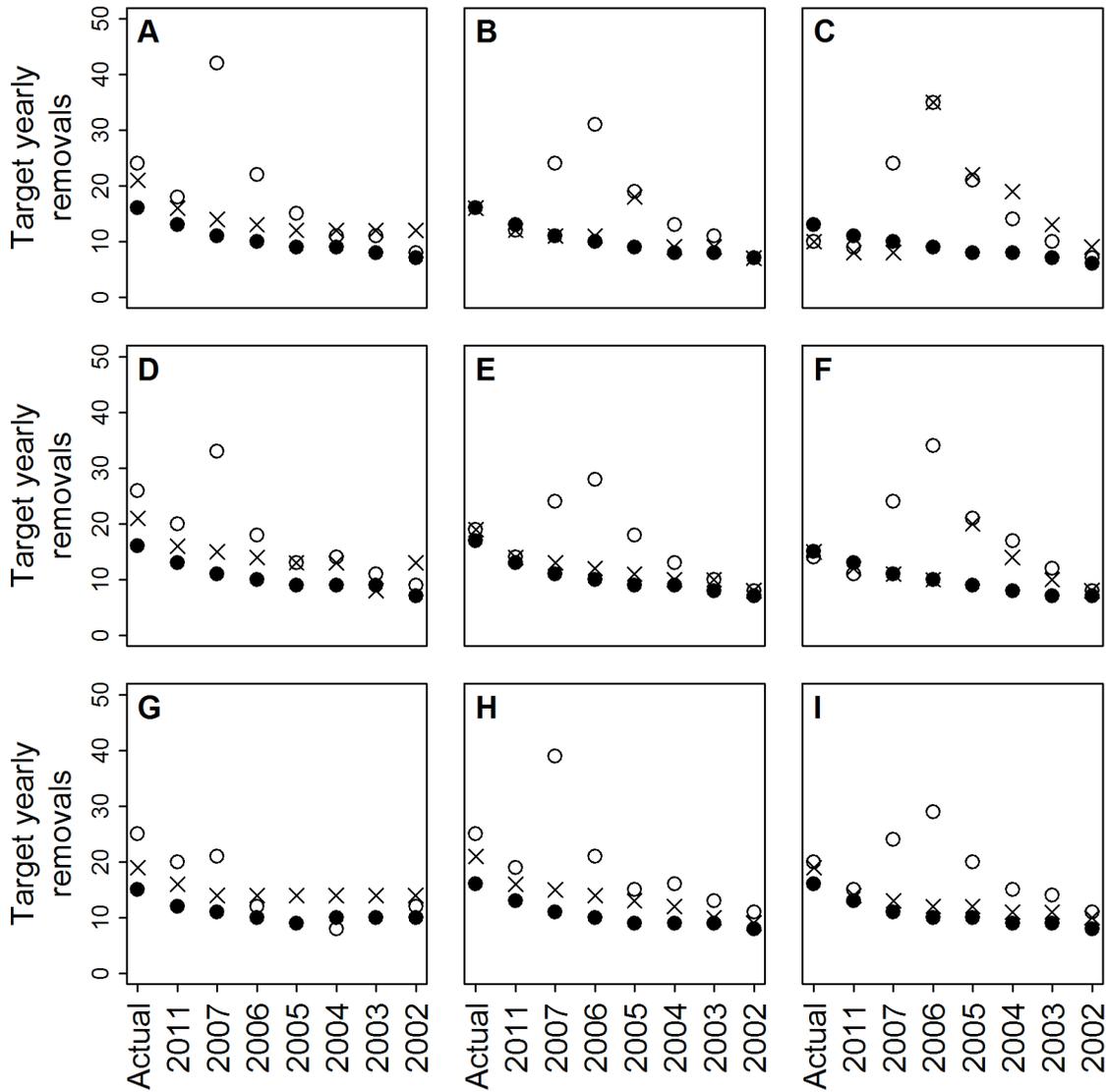


**Fig. S2: Output on with parameters estimated using a 20 sighting observation threshold for sea lions.** (A) and (B) are similar to panels in Figure 2, and (C)-(E) are similar to panels in Figure 3. These results indicate that qualitative conclusions hold, but reducing parameter uncertainty is crucial to derive robust, quantitative conclusions on the target number of yearly removals.



**Figure S3: Sensitivity of target yearly removals to uncertainty in social and asocial learning rates when the post-2008 asocial learning rate is at the lower-bound of its 95% confidence interval (i.e.,  $1.42 \times 10^{-5}$ ).** Gives the number of yearly removals needed to maximize the marginal benefit of each culling strategy (e.g., actual strategy vs. starting in 2002) when the pre-2008 social learning coefficient is at the upper-bound of its 95% CI (19.02; A-C), estimated value (11.23; D-F), or lower-bound of its 95% CI (3.96; G-I) and when the pre-2008 asocial learning rate is at the upper-bound of its 95% CI ( $2.42 \times 10^{-5}$ ; C, F, and I), estimated value (1.22

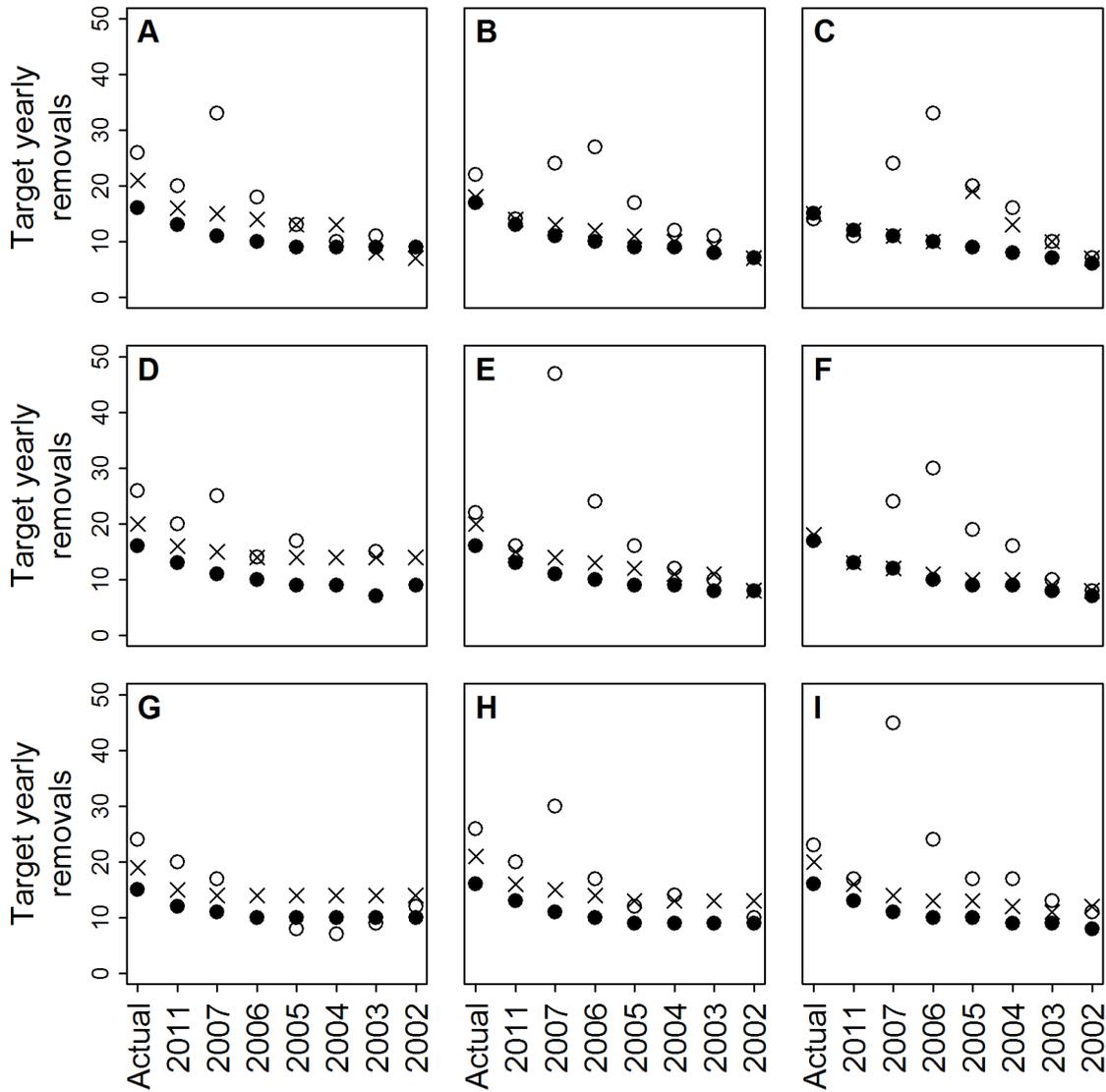
$\times 10^{-5}$ ; B, E, and H), or lower-bound of its 95% CI ( $4.07 \times 10^{-6}$ ; A, D, and G). Within each panel, uncertainty in the post-2008 social learning coefficient is represented by different symbols – upper-bound of its 95% CI (3.67; filled circles), estimated value (1.05; x's), or lower-bound of its 95% CI ( $6.66 \times 10^{-5}$ ; open circles). Culling strategies are arranged from the actual culling strategy used on the left to culling beginning in 2002 on the right. Taken together, this shows that uncertainty in social and asocial learning rates has less effect on the determination of a target removal strategy when removal is begun early.



**Figure S4: Sensitivity of target yearly removals to uncertainty in social and asocial learning rates when the post-2008 asocial learning rate is at its estimated value (i.e.,  $2.57 \times 10^{-5}$ ).**

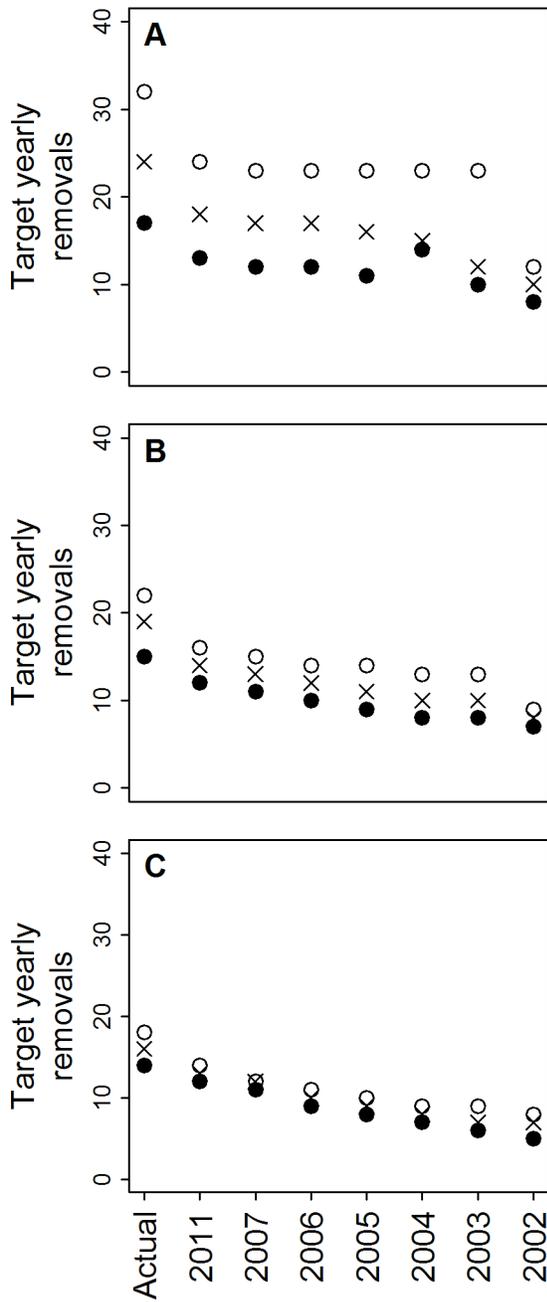
Gives the number of yearly removals needed to maximize the marginal benefit of each culling strategy (e.g., actual strategy vs. starting in 2002) when the pre-2008 social learning coefficient is at the upper-bound of its 95% CI (19.02; A-C), estimated value (11.23; D-F), or lower-bound of its 95% CI (3.96; G-I) and when the pre-2008 asocial learning rate is at the upper-bound of its 95% CI ( $2.42 \times 10^{-5}$ ; C, F, and I), estimated value ( $1.22 \times 10^{-5}$ ; B, E, and H), or lower-bound of

its 95% CI ( $4.07 \times 10^{-6}$ ; A, D, and G). Within each panel, uncertainty in the post-2008 social learning coefficient is represented by different symbols – upper-bound of its 95% CI (3.67; filled circles), estimated value (1.05; x's), or lower-bound of its 95% CI ( $6.66 \times 10^{-5}$ ; open circles). Culling strategies are arranged from the actual culling strategy used on the left to culling beginning in 2002 on the right. Taken together, this shows that uncertainty in social and asocial learning rates has less effect on the determination of a target removal strategy when removal is begun early.



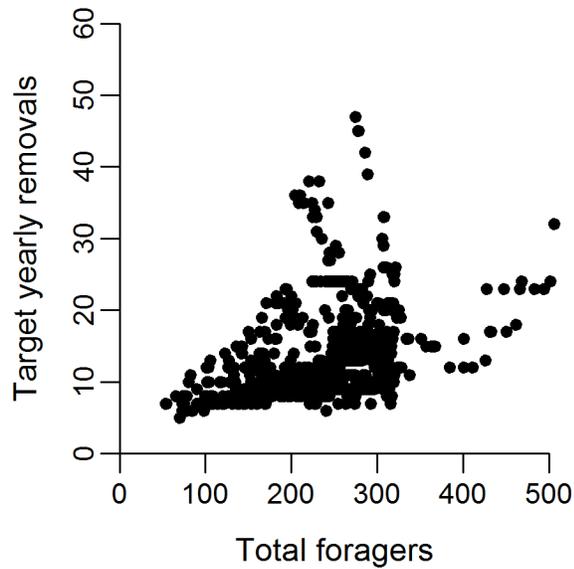
**Figure S5: Sensitivity of target yearly removals to uncertainty in social and asocial learning rates when the post-2008 asocial learning rate is at the upper-bound of its 95% confidence interval (i.e.,  $3.98 \times 10^{-5}$ ).** Gives the number of yearly removals needed to maximize the marginal benefit of each culling strategy (e.g., actual strategy vs. starting in 2002) when the pre-2008 social learning coefficient is at the upper-bound of its 95% CI (19.02; A-C), estimated value (11.23; D-F), or lower-bound of its 95% CI (3.96; G-I) and when the pre-2008 asocial learning rate is at the upper-bound of its 95% CI ( $2.42 \times 10^{-5}$ ; C, F, and I), estimated value (1.22

$\times 10^{-5}$ ; B, E, and H), or lower-bound of its 95% CI ( $4.07 \times 10^{-6}$ ; A, D, and G). Within each panel, uncertainty in the post-2008 social learning coefficient is represented by different symbols – upper-bound of its 95% CI (3.67; filled circles), estimated value (1.05; x's), or lower-bound of its 95% CI ( $6.66 \times 10^{-5}$ ; open circles). Culling strategies are arranged from the actual culling strategy used on the left to culling beginning in 2002 on the right. Taken together, this shows that uncertainty in social and asocial learning rates has less effect on the determination of a target removal strategy when removal is begun early. Delayed implementation requires more knowledge of learning parameters.

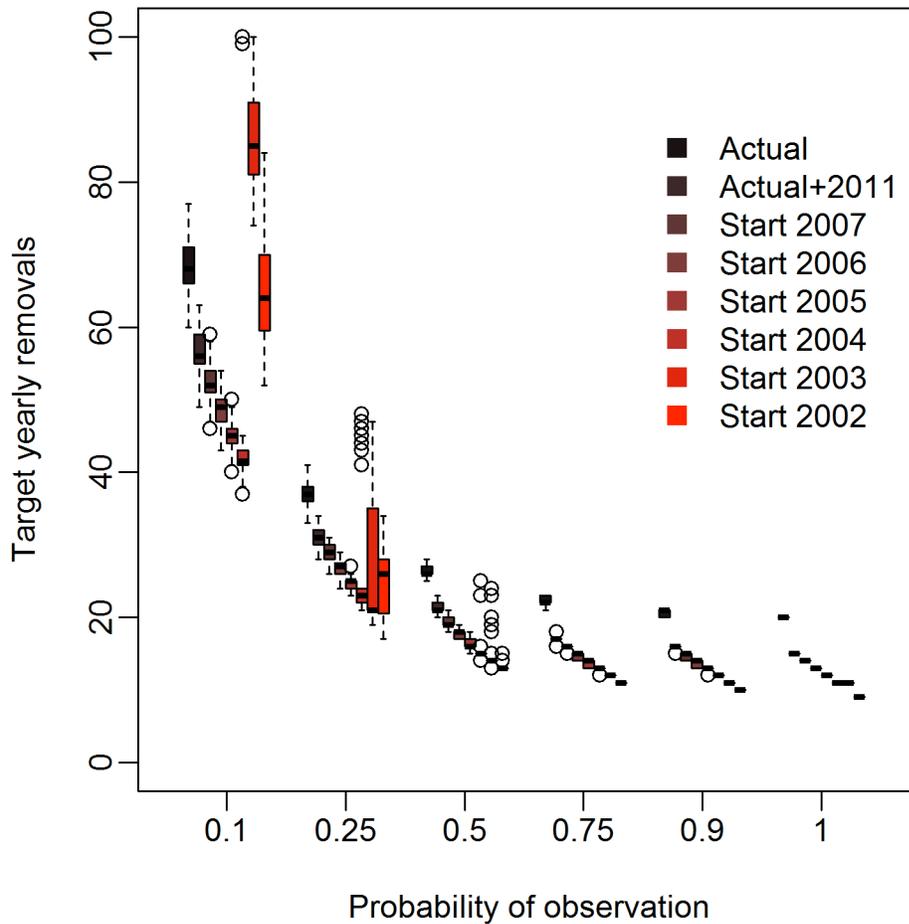


**Figure S6: Sensitivity of target yearly removals to uncertainty in the rate at which viable social learning opportunities occur between California sea lions and in the rate at which foragers are naturally removed (e.g., death, moving to alternate feeding locations).** Gives the number of yearly removals needed to maximize the marginal benefit of each culling strategy (e.g., actual strategy vs. starting in 2002) when natural removal rate is twice its estimated value

(0.0023; A), its estimated value (0.00115; B), or half its estimated value (0.00058; C). Within each panel, uncertainty in the contact rate is represented by different symbols – twice its estimated value (0.0244; filled circles), its estimated value (0.0122; x's), or half its estimated value (0.0061; open circles). Culling strategies are arranged from the actual culling strategy used on the left to culling beginning in 2002 on the right. Taken together, this shows that uncertainty in contact and natural removal rates had little impact on the observation that earlier implementation of culling would require a lower target number of removals. As the natural removal rate increased, however, specific target strategies across all alternate implementations were scaled relatively evenly according to the contact rate.

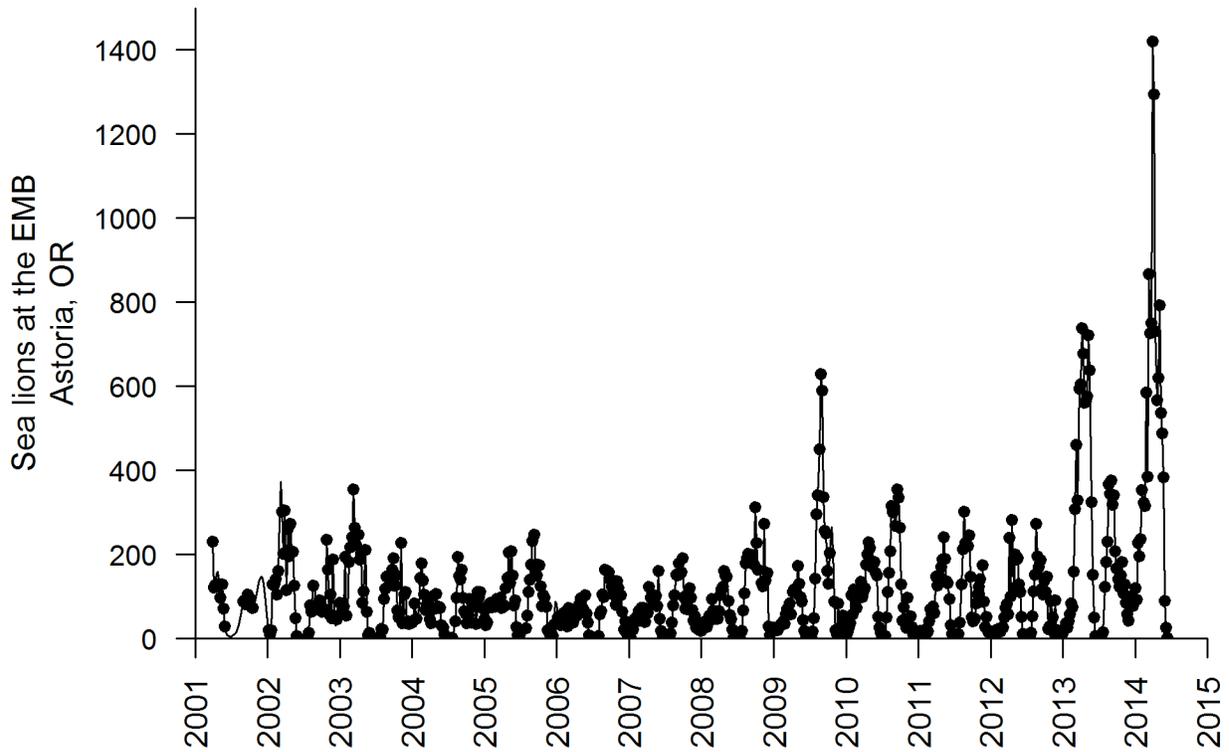


**Fig. S7: Relationship between the targeted yearly removal strategy and the total number of foragers predicted by the model.** Points show the targeted yearly removals for all parameter combinations (Figs. S3-S6) and all culling regimes (Table S1) as a function of the total number of foragers at Bonneville Dam predicted by the model for that parameter and culling regime combination. Generally, higher predicted numbers of foragers led to higher target levels of yearly culling, highlighting the need for accurate count data on forager numbers.

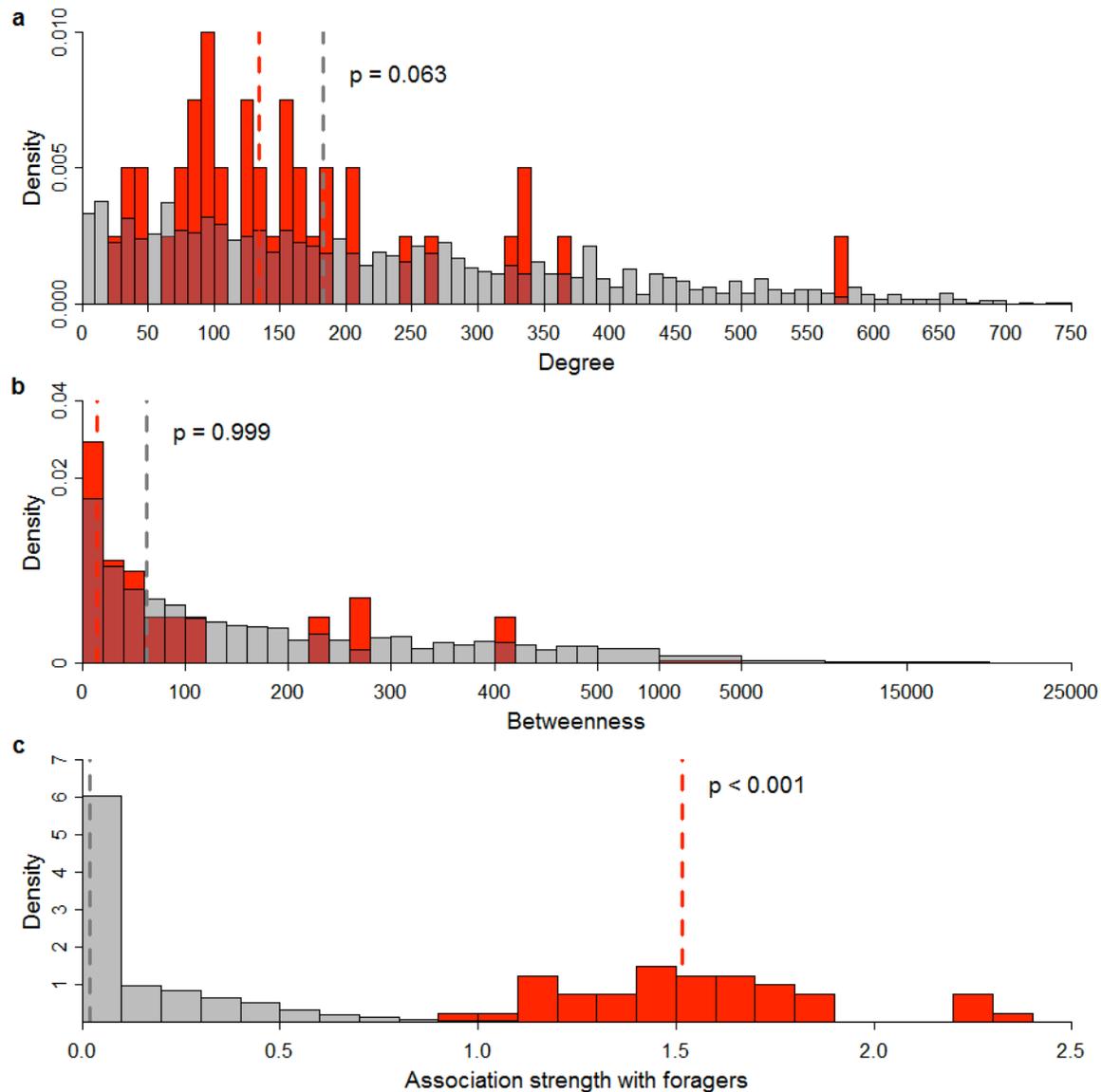


**Fig. S8: Sensitivity of target yearly removals to forager detection.** Gives the target number of yearly removals for each culling strategy (e.g. actual strategy vs. starting in 2002) as a function of the probability of observing a forager at Bonneville Dam. One-hundred random time-series of the number of foragers at Bonneville Dam were generated by assuming that the observed maximum daily numbers of foragers within a year were drawn from a binomial distribution with the specified probability of observation and total number of individuals given by the expected max daily number of foragers (i.e., observed number divided by probability of observation). Boxplots depict the target yearly removals for each of the 100 time-series, with boxes representing the interquartile range, whiskers extending to 1.5 times the interquartile range, and points represent outliers. Culling strategies are arranged within each level of observation

probability from the actual culling strategy used on the left in black to culling beginning in 2002 on the right in red. If the probability of observing a forager is greater than 50%, we can see that target removal strategies are relatively consistent, although not exactly equal, in both the quantitative number of removals and the qualitative pattern that earlier implementation of culling requires fewer yearly removals. Below this threshold, the number of yearly removals begins to increase sharply with earlier implementation generally, but not always, minimizing the target number of yearly removals.



**Fig. S9: Sea lion count data at the East Mooring Basin in Astoria, OR.** Points give the mean counts of all observation days within a week. The line is the fit of a non-parametric smoothing function to the observed weekly counts using B-splines of order 6, with predicted counts constrained to be greater than zero.



**Fig. S10: Network analyses of sea lion association data at East Mooring Basin, Astoria, OR.**

Networks were constructed using all association data from 1997-2014. Edges are weighted by the simple-ratio association index between two individuals. Distributions are shown for (A) total number of connections to other individuals (i.e., unweighted degree), (B) betweenness centrality, and (C) total association strength to foragers (i.e., the sum of association strengths, or the total weighted degree) for foraging (red) and non-foraging (grey) sea lions. Dashed lines indicate the median of each distribution, and the p-value is the result of a permutation test for a difference in

medians between foraging and non-foraging individuals. The distributions show that network structure, here given by degree and betweenness centrality, are not predictive of an animal learning to forage at Bonneville. Only association with other foragers is predictive of learning to forage at Bonneville supportive of a random mixing model.

## SI Tables

**Table S1:** Yearly removals allowed for the actual culling employed as well as for strategies that removed the hiatus in 2011 and started before 2008.

Year	Culling strategy							
	Actual	2011	2007	2006	2005	2004	2003	2002
2002	0	0	0	0	0	0	0	12
2003	0	0	0	0	0	0	12	12
2004	0	0	0	0	0	12	12	12
2005	0	0	0	0	12	12	12	12
2006	0	0	0	12	12	12	12	12
2007	0	0	12	12	12	12	12	12
2008	11	11	11	11	11	11	11	11
2009	15	15	15	15	15	15	15	15
2010	14	14	14	14	14	14	14	14
2011	1 <sup>†</sup>	12	12	12	12	12	12	12
2012	13	13	13	13	13	13	13	13
2013	4	4	4	4	4	4	4	4
2014	15	15	15	15	15	15	15	15

<sup>†</sup>This one individual was removed after culling resumed the week of May 17<sup>34</sup>.

**Table S2:** Estimated parameters used in the epidemiological model. Parameters were estimated using observation thresholds of sea lions of 2, 10, and 20 sightings. All rates are weekly rates.

Parameter	Description	Estimate using a 2 sight threshold	Estimate using a 10 sight threshold	Estimate using a 20 sight threshold
$\lambda_o(t)<2008$	Asocial learning rate before culling started in 2008	$8.54 \times 10^{-5}$	$2.59 \times 10^{-4}$	$3.54 \times 10^{-4}$
$\lambda_o(t)>2008$	Asocial learning rate after culling started in 2008	$1.80 \times 10^{-4}$	$2.35 \times 10^{-4}$	$2.33 \times 10^{-4}$
$s(t)<2008$	Social learning coefficient before culling started in 2008	11.23	2.62	1.49
$s(t)>2008$	Social learning coefficient after culling started in 2008	1.05	0	0
$c$	Average association strength between two individuals	0.0122	0.0151	0.0175
$\mu$	Natural removal rate of foragers from Bonneville	0.0081	0.0077	0.0078
$\alpha$	Scaling factor	9.90	8.57	7.93
$X(0)$	Initial number of foragers	12	0	0

## References

- Aplin, L. M. *et al.* 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541
- Bergstrom, B. J. *et al.* 2014. License to kill: Reforming Federal wildlife control to restore biodiversity and ecosystem function. *Conserv Lett* **7**,131–142
- Bettencourt, L. M. A., Cintrón-Arias, A., Kaiser, D. I., Castillo-Chávez, C. 2006. The power of a good idea: quantitative modeling of the spread of ideas from epidemiological models. *Physica A*. **364**,513–536
- Buhnerkempe, M. G. *et al.* 2014. The impact of movements and animal density on continental scale cattle disease outbreaks in the United States. *PLoS ONE* **9**, e91724
- Chiyo, P. I., Moss, C. J., Alberts, S. C. 2012. The influence of life history milestones and association networks on crop-raiding behavior in male African elephants. *PLoS ONE* **7**:e31382
- Christakis, N. A., Fowler, J. H. 2007. The spread of obesity in a large social network over 32 Years. *N Engl J Med* **357**, 370–379
- Cooper, B. S., Pitman, R. J., Edmunds, W. J., Gay, N. J. 2006. Delaying the international spread of pandemic influenza. *PLoS Med* **3**, e212
- Franks, D. W., Ruxton, G. D., James, R. 2010. Sampling animal association networks with the gambit of the group. *Behav Ecol Sociobiol* **64**, 493–503
- Hill, A. L., Rand, D. G., Nowak, M. A., Christakis, N. A. .2010. Infectious disease modeling of social contagion in networks. *PLoS Comput Biol* **6**, e1000968
- Hoppitt, W., Boogert, N. J., Laland, K. N. 2010. Detecting social transmission in networks. *J Theor Biol* **263**, 544–555

*Humane Society vs Locke*. 2010. No 08-36038 DC, No 3 08-cv- 00357-MO, Opinion. 23 Nov 2010.

Madden, F. 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. *Hum Dimens Wildl* **9**, 247–257

Marshall, K. N., Stier, A. C., Samhuri, J. F., *et al.* 2015. Conservation challenges of predator recovery. *Conserv Lett*. doi: 10.1111/conl.12186.

NMFS. *Endangered Species Act Section 7(a)(2)* 2014. *Supplemental Biological Opinion: Consultation on Remand for Operation of the Federal Columbia River Power System*. NOAA, Seattle, WA.

Schakner, Z. A., Lunsford, C., Straley, J., *et al.* 2014. Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. *PLoS ONE* **9**, e109079

Stansell, R. J., Gibbons, K. M., Nagy, W. T. *Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2008-2010*. (US Army Corps of Engineers, Bonneville Lock and Dam, 2010).

Whitehead, H. 2009. SOCPROG programs: analyzing animal social structures. *Behav Ecol Sociobiol* **63**, 765–778

Wright, B. E., Tennis, M. J., Brown, R. F. 2010. Movements of male California sea lions captured in the Columbia River. *Northwest Sci* **84**, 60–72