Chapter 18
The California Sea Lion: Thriving in a Human-Dominated World

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Abstract  California sea lions offer an important case study of a species that has successfully adapted and thrived in a human-dominated world. The recovery of California sea lion populations over the past four decades is a conservation success story. Unfortunately, their recovery has put them in direct conflict with human activities resulting in new management challenges in the regions where they occur. Here, we review the role of learning in California sea lions and their capacity to tolerate and successfully capture prey from commercial or recreational fishing lines or salmon at dams. Learning underlies tolerance to novel human-related stimuli, locating novel foraging resources, and responding to environmental change. According to modern animal learning theory, there are basic mechanisms, or types of experiences underlying animal learning. The simplest learning process of habituation is non-associative because it involves an individual’s experience with a single stimulus, whereas complex associative learning mechanisms elicit changes in behavior as a result of experience with two stimuli or stimulus and response. We focus on these fundamental associative and non-associative learning mechanisms in California sea lions which could be used to manage wildlife-human conflicts involving otariids. For instance, understanding what kinds of stimuli California sea lions respond to and learn from, or how social factors influence learning processes, are all important parameters that can be used by managers for modifying animal behavior. Lessons from both human-tolerant species and those in conflict could inform best practices for ensuring human-wildlife coexistence in a human-dominated environment will be enhanced with lessons from both human-tolerant species as well as those that do not do well with humans.
18.1 Introduction

Relationships among otariids and humans have been intertwined for centuries. Interactions include exploitation through historical hunting of sea lions, competition over prey (Chap. 24 by Crespo; Betts et al. 2009; Braje and DeLong 2009; Lyman 2003; Hildebrandt and Jones 1992; Gerber and Hilborn 2001) and space for haulouts (Schakner et al. 2019). Most otariid populations experienced intense hunting in the nineteenth and twentieth centuries, which dramatically reduced population sizes. Protective management measures have led to the recovery of some, but not all populations (Chap. 24 by Crespo; Gerber and Hilborn 2001). As humans develop our coastal areas, new threats and challenges have arisen from species being forced to live in a human-dominated land and seascape. Human-induced rapid environmental change (HIREC; Sih 2013; Sih et al. 2016) shifts prey concentrations (exacerbated by intense fishing effort), creates novel stimuli from vessel traffic and reduces habitat on land from coastal development (see also Chap. 21 by Giardino et al.).

As aquatic mammals that forage at sea but rest, socialize, and pup on land, sea lions are exposed to urbanization, intense competition from fishing, shipping noise, and coastal development. Human-induced disturbances range from adverse exposure to stimuli such as vessel noise, reduction of natural food availability, to the creation of resources around fishing gear/pens or at dams. A fundamental question within conservation behavior is how some species respond adaptively to HIREC, yet others do not (Geffroy et al. 2015).

California sea lions (*Zalophus californianus*) in particular illustrate one of the most successful recoveries in the modern conservation era (Chap. 28 by Elorriaga et al.; Fig. 18.1; NOAA). California sea lion populations have grown considerably since the inception of the United States’ Marine Mammal Protection Act of 1972 (MMPA 1972; Laake et al. 2018). The MMPA offers robust protections for marine mammals in US waters. The law has brought species back from the brink of extinction, and many populations have fully recovered since it was enacted.

For California sea lions, the capacity for learning, including learning from human trainers, which makes them popular in zoos, circuses, and aquaria, seemingly predisposes them to tolerate humans. This behavioral flexibility, and their capacity to behaviorally innovate and learn in a human-dominated land and seascape likely contributed to their success. In a rapidly changing environment, California sea lions have learned to exploit novel concentrations of prey, novel habitats, and even capitalize on human fishing effort. As an unintended consequence of their recovery, there are increasing competitive interactions between sea lions and humans. Along the west coast of the United States, expanding sea lion populations create management conflicts of consumption of endangered salmonid species, interactions with
fisheries, and damage to docks and personal vessels (Jeffries and Scordino 1997; Marshall et al. 2015).

California sea lions thus offer an important case study into a species that has successfully adapted to living in a human-dominated world. Yet, California sea lion’s success is in stark contrast with other USA west coast otariids such as some stocks of Steller sea lions (Eumetopias jubatus) which remain endangered (Atkinson et al. 2008; Chap. 23 by Trites). This is potentially because of the formers’ ability to learn rapidly and socially transmit this knowledge, as well as being particularly behaviorally plastic with respect to habitat and diet. Such traits lead to the rapid tolerance of humans and human infrastructure.

18.2 Learning in a Changing World

Learning is a key aspect of behavior that may greatly enhance the survival of animals, especially in a dynamic environment. We and others have reviewed learning mechanisms elsewhere (Chap. 17 by Cook et al.; Greggor et al. 2019, Schakner et al. 2016), but believe it is worth focusing on fundamental mechanisms given the extensive comparative and experimental psychology literature. According to modern animal learning theory, there are three basic mechanisms, or types of experiences underlying animal learning. The simplest learning process, habituation, is non-associative because it involves an individual’s experience with a single
stimulus, whereas more complicated, associative learning mechanisms elicits behavioral change as a result of experience with two stimuli or stimulus and response. We believe that applying insights from the psychology literature provides mechanistic insights for a variety of human-wildlife conflict management interventions. For instance, understanding what kinds of stimuli animals respond to and learn from, as well as the reinforcement schedules necessary to sustain such learning, are all important parameters that can be used by managers for modifying animal behavior. We review these fundamental mechanisms derived from animal learning theory, and then discuss how these mechanisms facilitate California sea lion survival on the USA west coast, and then discuss how understanding these mechanisms may be applied to sea lion management issues.

18.3 Single Stimulus Learning: Habituation and Sensitization in a Changing World

Anthropogenic human disturbance provokes fear responses because many animals respond to humans as predators (Frid and Dill 2002; Lima and Dill 1990). This ecology of fear has wide-ranging negative effects on individual, population, species and ecosystem scales. However, some species are able to detect, recognize and learn to tolerate humans while some species do not (Blumstein 2014). Habituation, the simplest learning process, is the fundamental mechanism by which animals reduce their response to non-threatening stimuli.

Habituation is non-associative single-stimulus learning. It involves diminishing of behavioral responses after repeated exposure to stimuli (Groves and Thompson 1970; Schakner and Blumstein 2016a, b). In a human-dominated world, learning to ignore novel yet non-threatening cues via habituation versus overreacting to these cues via sensitization (the opposite of habituation) can determine which species can adapt to HIREC (Sih et al. 2016). Habituation involves stimulus specificity. That is to say, if the stimulus is changed in intensity or a novel stimulus is introduced after habituation has occurred, responsiveness is restored (Rankin et al. 2009). This stimulus specificity suggests that habituation filters innocuous stimuli from novel or significant stimuli (Rankin et al. 2009) by modulating responsiveness. In contrast to habituation, heightened/increasing responsiveness after repeated exposure is termed sensitization. The dual process theory suggests that the observed behavior after repeat exposure to a stimulus is the summation of two underlying processes habituation and sensitization (Groves and Thompson 1970; Schakner and Blumstein 2016a).

We expect that human disturbance is likely to impose the greatest fitness costs under two contexts; feeding and reproduction. California sea lions habituate to humans and anthropogenic disturbance in both contexts. This is evidenced by their use of human docks and buoys as haul-out sites and their generalized tolerance to being in close proximity to humans or fishing vessels. Even more, they are
remarkably tolerant of human disturbance at breeding grounds (Gerber and Hilborn 2001), and captive experiments have shown that even pregnant female sea lions habituate to the presence of human visitors (de Vere 2018). In some locations, California sea lions have begun breeding on human structures. For example, the Morro Bay breakwater was constructed by the Los Angeles District of the U.S. Army Corps of Engineers in the 1940s. Recently increasing numbers of California sea lions use it as a breeding ground and some even occupy it year round (Fig. 18.2). California sea lions illustrate the adaptive value in learning to adapt to a human-dominated environment (For an interesting parallel please also see the southern sea lion male haulouts described in Chap. 21 by Giardino.

In captivity, California sea lions rapidly habituate to humans (de Vere 2018), fishing stimuli (Bowles 2012), and novel sounds (Kastak and Schusterman 1983); and subsequent tolerance to novelty has been well documented for decades (Kastak and Schusterman 1983; Table 18.1). Perhaps most tellingly, this habituation response pathway is often in sharp contrast to other species of pinnipeds. For instance, in a series of individual playback experiments, California sea lions rapidly habituated to a novel, pulsed acoustic stimulus, whereas northern elephant seals (Mirounga leonina) had the opposite reaction, sensitization, subsequently hauling out away from and avoiding the playback pool altogether (Kastak and Schusterman 1983). These studies demonstrate important species-specific constraints on habituation to novel stimuli in pinnipeds.

Despite decades of laboratory experiments focused on the parameters influencing the underlying process of habituation in organisms such as humans, rats, and pigeons, less is known about the evolutionary ecology of habituation (Blumstein 2014, 2016). Among otariids, early observations of the differences in habituation go

Fig. 18.2 A growing California sea lion rookery on a man-made structure in California
back several decades. Schusterman suggested different responses to humans among 
a range of different pinnipeds including the same species at different locations, 
noting that “...all of these observations suggest that to some extent startle or flight 
reactions habituate at different rates in different species and in different populations 
as a function of age, sex, season, and time of day” (Schusterman 1981: 134).

There is extensive literature on the parameters that influence habituation in the 
laboratory, such as complexity or intensity of the stimulus, timing of stimulus 
presentation, etc. However, the parameters that influence habituation/sensitization 
in the wild are not well known, nor are the factors that determine habituation versus 
sensitization responses. Individual variation in habituation/sensitization is likely 
influenced by a variety of factors, including previous experience, sex, and person-
ality (i.e., bold - shy continuum; Ellenberg et al. 2009, 2013; Fig. 18.3, see Chap. 19 
by DeRango and Schwarz). Across populations, variation in habituation can be 
based upon a population’s level of human disturbance or a sorting process by 
which sensitizers flee (Bejder et al. 2009; Fig. 18.3). Even less is known about the 
specific factors that underlie variations in species-specific habitation (Fig. 18.3), but 
there are likely selective advantages to sensitization or habituation depending on a 
species’ life history.

A relatively new theory of habituation, Behavioral Homeostasis Theory (BHT), 
suggests that the primary determinants of an individual’s response to a stimulus (i.e., 
sensitize or habituate) will involve signal detection and state/responsiveness (Eisen-
stein and Eisenstein 2006, 2012; Fig. 18.4). Whether habituation or sensitization 
occurs in response to repeated exposures is primarily a function of the individual’s 
state of overall ‘alertness/vigilance’ at the time of the initial exposure. Behavioral 
homeostasis theory operates on the perspective that habituation/sensitization function 
as a mechanism for filtering novel stimuli. An alert individual will more rapidly detect, 
assess and recognize the novel stimulus, and thus respond with habituation. In contrast, 
an individual at a low level of alertness will respond with sensitization in order to 
increase responsivity and thus rapidly increase detection/assessment. According to the 
theory, how individuals respond is indicative of the stimulus significance to the 
organism at that point in time (Eisenstein and Eisenstein 2006, 2012).

Table 18.1 Early descriptions of otariid tolerance toward humans based upon experiments on 
captive animals

| Species                  | Tameness a | Trainability b |
|--------------------------|------------|----------------|
| California sea lion      | Excellent  | Excellent      |
| Steller sea lion         | Poor       | Good           |
| Southern sea lion        | Poor       | Good           |
| Northern fur seal        | Fair       | Good           |
| South African fur seal   | Excellent  | Excellent      |
| Antarctic fur seal       | Excellent  | Unknown        |

Recreated from the original publication in Schusterman (1981)

aTameness refers to an animal reliably accepting approach by strangers and handling by familiar 
trainers

bTrainability refers to the ease with which an animal can be brought under stimulus control by 
operant and Pavlovian procedures
Fig. 18.3 Factors influencing habituation

Fig. 18.4 Behavioral homeostasis theory (BHT) The state of individual at the moment of initial exposure influences habituation or sensitization. For California sea lions, state may be influenced by proximity to human or conspecifics.
Behavioral homeostasis theory emphasizes the role at which an animal’s state is prior at the moment of initial exposure to a stimulus (Fig. 18.4). For most habituation studies in the wild, there is a minimal description of the initial state, and this shortcoming limits our ability to understand habituation in nature. For otariids and other pinnipeds that overlap with humans, individuals may be more often in a heightened state of awareness. This must be costly and according to BHT, the initial response to experiencing a novel stimuli will more often lead to habituation, because it helps the individual to return to baseline levels. Conversely, for those species that are less disturbed and thus less vigilant, the cost-effective response may be to be sensitized to novel stimuli. This view offers testable hypotheses for comparing the relative responsiveness among disturbed versus undisturbed populations, as well as furthers exploration into variation in individual responsiveness.

### 18.4 Management Implications of Habituation/Sensitization

The goal of reducing habituation while simultaneously eliciting sensitization is the objective of many deterrents designed to reduce pinniped fishery interactions (Table 18.2, Götz and Janik 2013; Schakner et al. 2016a). In southern California, California sea lions haul out on and forage at bait receiver pens. In an attempt to deter individuals to reduce their interactions, we tested the responses of wild California sea lions to a variety of potentially aversive acoustic stimuli, including biologically relevant signals such as predator vocalizations, bee swarms, or dog barks. We found clear evidence of habituation to the biologically relevant signals as demonstrated by decreasing responsiveness to repeated exposures of the sounds (Fig. 18.5). However, responses to an acoustic startle device (Götz and Janik 2011; Schakner and Blumstein 2016b, Schakner et al. 2017a) were the opposite; sea lions sensitized to the sounds, as evidenced by increasing responsiveness. Signals that elicit sensitization may show some promise because they rapidly arouse the individual to a responsive state (Götz and Janik 2011).

| Table 18.2 | Direct versus indirect interactions |
|-------------|-------------------------------------|
| Direct      | Depredation: removal of fish from gear |
|             | Examples: California sea lion and sport fishery in California, South American Sea lion and bottom trawl fisheries, seal salmon farm predation |
|             | Entanglement/bycatch: pinnipeds unintentionally captured |
|             | Example: Endangered New Zealand entanglement in Sub-Antarctic trawl fisheries, |
| Indirect    | Competition for prey, displacement or broader ecosystem scale effects |
|             | Example: Alaska Steller Sea lion decline in part from overlap with fisheries, Northern Fur seal declining population at Pribilof Islands |
Habituation, Haul Outs and Humans  California sea lion capacity to tolerate anthropogenic disturbances through habituation may enhance their survival in a human dominated environment, but this tolerance is a double-edged sword. Tolerating anthropogenic disturbance means that animals share spaces with humans, and for California sea lions this creates management issues. California sea lions haul out on almost any human structures and cause damage to docks and private vessels which create negative perceptions towards the animals and sometimes retaliatory actions (Scordino 2010). In addition, close proximity to humans increases the likelihood that sea lions may chase or bite humans, and these incidents are dangerous and may be reported widely in the news and social media (Schakner et al. 2019). Resolving conflicts over space is difficult and these conflicts are a lose-lose situation for all parties involved. Typically, most management actions occur after the animal has learned to associate humans with a favorable resource (haul-out space). Preventing the association from forming is ideal (Schakner et al. 2016), but we recognize that this is not always feasible. An understanding of associative learning processes is necessary to disrupt learning in the first place.

18.5  Associative Learning via Pavlovian and Instrumental Conditioning

Broadly, associative learning involves learning the relationship between stimuli and/or responses (Domjan 2005). The capacity to learn about the relationship between stimuli and/or responses is functional because it guides how an animal...
can adaptively respond to exogenous stimuli as well as anticipate future events (Domjan 2005; Shettleworth 2010). Individuals use associative learning to track environmental variation in a variety of contexts. In a variable world, individuals use associative learning to decide where to forage, what to forage on or where to avoid (Shettleworth 2010). Examples include associating sounds or context with the presence of a predator, taste cues associated with edible food, or honing a new extractive foraging technique to yield more prey.

California sea lions interact with nearly every commercial and recreational fishery on the west coast of the United States (Scordino 2010). Fishing or aquaculture creates novel concentrations of prey at a reduced cost by trapping fish in lines, nets or chumming. How individuals learn to remove fish from fisheries, referred to as ‘depredation’, is an open question, but likely involves a combination of Pavlovian and instrumental conditioning (Rescorla and Solomon 1967). Sounds associated with fishing vessels likely provide cues for individuals to locate the vessel. This Pavlovian conditioning process termed the ‘dinner bell effect’ has been observed in long term analysis of gillnet fishery, where pingers (sound emitters designed to deter porpoises) on gear appear to actually attract California sea lions (Carretta and Barlow 2011). In another putative example of the dinner-bell effect, sea lions may be able to cue in on sounds emitted on acoustic tags that are placed on salmonids to track their migration and this increases sea lion predation success (Bowles 2012; Cunningham et al. 2014). While plausible given the potential overlap of sea lion hearing thresholds and frequencies emitted from pingers, this dinner-bell effect requires more in situ observations and testing to determine whether sea lions are tracking tagged salmon.

In instrumental conditioning, the animal learns a relationship between operant behavior and the consequence of that behavior, and behavioral frequencies are adjusted accordingly (Thorndike and Bruce 1911; Domjan and Burkhard 1986). While Pavlovian conditioning through the dinner bell effect is likely involved in the localization of prey, instrumental conditioning is used to hone an individual’s foraging technique to optimize foraging behaviors. Instrumental conditioning appears to underlie individual learning to extract prey from the fishing lines, nets, and aquaculture pens. In a series of experiments using underwater cameras attached to fishing lines from salmon trolling vessels, Woolery and Harvey (2005) tested whether the presence of captured fish increased sea lion interactions with salmon troll fishery. Interestingly, sea lions appeared to travel from line to line, irrespective of whether the line had hooked a salmon. It appears, therefore, that individuals iteratively visit all lines in the area to check for hooked prey.

18.6 Management Implications of Associative Learning

From first principles, we may not expect tactile or acoustic deterrents to work in a foraging context, but they are likely to work in terms of habitat selection. Garcia et al. (1955) showed that learning may be biased in such a way that it is easier for rats
to learn to associate nausea with food avoidance and shock with location avoidance. If similar biases exist in California sea lions, harassment may work, but not by animals learning to avoid specific food items (e.g., salmon), but rather by learning specific locations. Conditioned taste aversion (CTA) was briefly tested on California sea lions in captive settings as well as predating salmon at Ballard Locks in Seattle, Washington USA. In captive settings, CSL that were nauseated from Lithium Chloride laced salmonids avoided those specific species, but not other salmonids. In the wild, emetic laced salmon were given to several individual CSL on fishing lines at Ballard. The individuals became nauseated from the laced fish (Gearin et al. 1988) but nevertheless continued to forage at similar rates as prior to getting sick. Interestingly, the individuals would not take laced fish on fishing lines from the researchers. Therefore, we predict that emetics are useful for specific foraging contexts, such as removal of fish from fishing lines or removal of baitfish from bait docks.

Our goal is to not distill animal behavior down to Pavlovian or instrumental conditioning, but instead, focus on these learning mechanisms given how much is known from decades of comparative psychological experimentation. We believe these underlying mechanisms give us tools to manipulate behavior, and to potentially reduce conflicts with otariids. It is our perspective that well-meaning managers (not necessarily well-equipped with a modern understanding of animal behaviors) can apply mechanistic understanding to minimize human/pinniped conflicts.

18.7 A Learning-Based Approach to Deterrents

Our acoustic deterrent work on California sea lions suggests that any single deterrent is unlikely to mitigate conflicts (Schakner et al. 2017a, b). We suggest that a more comprehensive approach to deterrence is necessary. We hope that by demonstrating the underlying learning processes that elicit responsiveness, or lack thereof, we can change the conversation from a one deterrent fits all approach/perspective, to a more comprehensive approach to deterrence.

We know of only one case of implementation of a deterrence program that successfully solved the conflict between sea lions and humans in the mid to long term. In Gold Beach, Oregon, the local port association and fishing community came together to fund a comprehensive approach to deter sea lions. The program consisted of a single full-time hazing vessel that used tactile deterrents, corresponding port activities to prevent sea lions from hauling out on docks, and banning the disposal of salmon carcasses into the water at docks (feeding attraction). The Port Authority installed pipe barricades and sprinklers with motion detectors on docks to discourage sea lions from hauling out. The full-time hazing vessel used seal bombs, cracker shells, rubber buckshot, and vessel pursuit on individuals in the area during peak sport fishing effort (Lottis 2007a, b, 2009). Such interventions may or may not be acceptable to local communities in other places. Once the sea lions fled outside the entrance bar at the mouth of the bay, the vessel used cracker shells and/or rubber
buckshot to drive sea lions beyond the harbor jetties. This vessel operated daily
during the fishery which covered a relatively small area and any sea lion observed
was immediately targeted for hazing. This Gold Beach example highlights the
necessity for community buy-in and demonstrates how a comprehensive approach
can enhance mitigation of California sea lion port/fishery interactions.

Regardless of its real-world applicability to other locations, there are some
lessons from Gold Beach for a comprehensive, learning-based deterrence scheme,
especially from confined areas like bays, or ports that have sea lion issues.

1. Identify primary attractants to sea lions in the area and restrict them. In most
cases, attractants can be food-related such as fishing discards or chum, open
spaces for haul out, or live bait from bait receivers. Example mitigation measures
include port activities to prevent hauling out on docks and eliminate the disposal
of fishing discards into the water or live bait leakage from receivers.

2. Physical hazing to deter and drive out ‘repeat offenders’. Once individuals have
learned that the association between humans and food reinforcers has formed,
management efforts rely on raising the cost to the individual depredator. For these
repeat offenders, the association is difficult to extinguish, management efforts
must rely on forming new negative associations or on decoupling the contingency
between humans and reward. Hazing with physical deterrents appears to be the
most effective at eliciting short term flight responses (Schakner et al. 2016).
Additionally, emetics may be useful to prevent specific foraging behaviors, like
removal of fish from fishing lines, bait docks, or specific salmonid species.

3. We predict that deterrent modalities should be tailored to the context. If the goal is
to deter novel individuals from colonizing new habitat such as docks, then we
recommend the use of acoustic deterrents or non-tactile efforts to repel novel
individuals from colonizing or learning the association between human resources
and the attractant. If the goal is to repel individuals from foraging contexts, we
recommend the use of emetics to create negative associations with the novel
foraging resources. New individuals are likely to be more neophobic since they
have not yet learned the association between humans and food reward (or open
space). We predict that they may be more likely to respond to conventional
deterrent methods.

18.8 Social Learning Mechanisms

Social learning occurs as a result of interactions or observations with other individ-
uals (conspecific or heterospecífics). There is evidence that asocial and social
learning relies on the same underlying associative and non-associative mechanisms
(Heyes 1994, 2012). From this perspective, Fig. 18.6 describes the overlap of
associative/non-associative mechanisms in social learning and asocial learning.
While the underlying asocial/social mechanism is similar, social learning has unique
management implications. Social learning can function as a force multiplier, rapidly
spreading behaviors or knowledge through populations, almost like a disease (Hill et al. 2010; Schakner et al. 2016).

Social species with a life history that involves early parental care and overlap at breeding grounds have the opportunity to learn from conspecifics. Otariid mothers remain with their pups only during the first week or so following parturition (Costa 1991). This overlap of young otariid pups and juveniles with mothers in early life creates an opportunity for some vertical social transmission of foraging tactics, but there is little evidence for social transmission of foraging (Fowler et al. 2007; Leung et al. 2014). While studies have largely focused on breeding aggregations around rookeries, adult and subadult male social relationships are not well described. Yet animals do haul out together and this provides an opportunity to learn from others. Indeed, we know that male sea lions learn where to forage from their peers (Schakner et al. 2017a, b).

Little is known about social interactions among male otariids. Unlike females and pups, adult and subadult males range further than females, typically to forage and gain the mass that is required to successfully compete for mates at breeding grounds. Adult and subadult male otariids are the demographic group that more frequently interact with fisheries (Kirkwood et al. 2006). California sea lions, for example, migrate from breeding grounds off California to higher latitude regions in Oregon, Washington, and Alaska. This demographic group frequently interacts with salmonid fisheries (Scordino 2010; Weise and Harvey 2005) and their predation on endangered salmonids creates multiple challenges for endangered salmonid recovery. Whether males actively form social bonds to migrate and cooperatively forage is
not known, but we identified the occurrence of social networks at well-known haul-out sites in the Pacific Northwest of the United States (Schakner et al. 2017a, b).

The estuary of the Columbia River in the U.S. Pacific Northwest has several major California sea lion haul-out sites, with aggregations of tens to hundreds of migratory males during spring and summer months. We analyzed the haul-out patterns of males interacting at a large dock structure called the East Mooring Basin on the Columbia River. Social network analysis showed that social interactions were not patterned randomly; rather, individuals had preferential partners creating social structure. This social structure has implications for the transmission of knowledge of novel food sources/locations, which appears to be occurring at dams in the region. Foraging in the Columbia River estuary is not novel, but observations of sea lions foraging on bottlenecked salmon at upriver dams like Bonneville or Willamette (235 km upriver) from when (Bonneville was first built (in 1934 year) until the 1990s were rare. In an earlier study, we incorporated network-based diffusion analysis to demonstrate that knowledge of the novel food source is socially transmitted via California sea lion social networks (Schakner et al. 2017a, b). Not all individuals that haul out at the opening of the Columbia River estuary visit the dam, and not all the individuals that have discovered the dam are proficient foragers (Schakner et al. 2017a, b).

Increasingly, a sympatric otariid, the Steller sea lion (SSL), is hauling out at the East Mooring Basin and discovering bottlenecked salmon and steelhead at Bonneville or other upriver dams. The rapid, exponential increase (Fig. 18.7) in Steller sea lions at Bonneville suggests some form of social transmission because socially transmitted behaviors are expected to show accelerated diffusion through a population while traits acquired independently are not expected to spread as quickly (Smaldino et al. 2018, Rogers 1995; but see Hoppitt et al. 2010). The wave of
increasing numbers of Steller sea lions at Bonneville mirrors the increasing numbers of California sea lions, suggesting heterospecific social transmission may underlie their foraging upriver. Interspecific interactions among these two species at haulouts occur elsewhere (Edgell and Demarchi 2012). The haul-out patterns and interactions among these species provide the ability to formally test whether Steller sea lions use heterospecific cues for foraging.

## 18.9 Management Implications of Social Learning

Social learning has unique consequences for management. Compared to associative (individual) learning mechanisms, socially transmitted behaviors can rapidly sweep through populations much like a disease. Borrowing insights from epidemiology, we and others have argued that timing is critical to stem the spread of socially transmitted behaviors (Schakner et al. 2017a, b; Snijders et al. 2017). Understanding the structure of the underlying social network is crucial for predicting transmission patterns. Among otariids, adult and subadult males appear to form less cohesive social connections compared to females and their dependent young, and there is greater potential for behaviors to spread more quickly. In contrast, vertical transmission (from mothers to dependent young) leads to a more conserved transmission pattern.

Our case study at the Columbia River and Bonneville dams underscores the importance of having individuals marked or otherwise distinguishable from each other. Managers from state and federal agencies have been collecting individual identification branding and photographs for over a decade. This information enables the tracking of social networks, social transmission, and individual foraging success. All lethal and non-lethal management activities for reducing salmon predation aim to reduce the number of individual sea lions at the dam, but not all individuals are successful foragers and some individuals may be more prone to transmission than others. Therefore, data from individually discriminable animals along with social networks provide managers a predictive tool to focus efforts on particularly successful foragers (i.e., super-spreaders). Since management interventions such as lethal removal or hazing are involved, focusing efforts on specific individuals is not only more effective but is also more ethical.

## 18.10 Conclusions

While we have focused on the role of learning in adapting to HIREC in California sea lions, these issues are global, involving many species of otariids and the ideas and strategies should apply widely among other representative species. For instance, South American sea lions, *Otaria byronia*, increasingly are bycaught in or depredate numerous fisheries, including gillnets, purse seines and trawl fisheries (e.g., Crespo
et al. 1997; Sepúlveda et al. 2007). Additionally, conflicts have emerged when sea lions predate salmon farms in southern Chile, often resulting in retributive killings (Sepúlveda et al. 2015).

More generally, we view learning mechanisms as the levers that managers can use to adjust animal behavior and by modifying behavior, we have tools to solve human-wildlife conflicts. Decades of comparative psychology experimentation have described the underlying constraints of basic learning mechanisms. The parameters for learning and deterrents include stimulus intensity, presentation schedule, competing stimuli or state of organisms.

As humans rapidly change the environment, animals are challenged to behaviorally adapt through learning. California sea lions offer a glimpse into an organism that appears to not only adapt but succeeds along with human population expansion. Our ability to coexist with wildlife in an increasingly anthropogenically-driven world is enhanced with lessons from human-tolerant species and those that do not do well with humans. California sea lions offer a success story and with its successes come management challenges.

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