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COMMENTARY

Equivalence classification, learning by exclusion, and long-term memory in pinnipeds: cognitive mechanisms demonstrated through research with subjects under human care and in the field

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Abstract

Comparative cognition, as an interdisciplinary field, should utilize a holistic approach for studying cognitive mechanisms. We suggest that research with species of interest should employ both work with animals under human care and in the field. This complimentary approach allows for a better understanding of functional cognitive mechanisms themselves (i.e., comparative cognition regarding processes), and how these skill sets can relate to a particular species' ecological niche. We suggest that research evidence for equivalence classification, learning by exclusion, and long-term memory in pinnipeds can provide a foundation for discussion and implementation of a two-pronged methodological approach utilizing 'lab' and field' work. First, we describe evidence from research with pinnipeds under human care supporting each of these cognitive abilities, then follow this with evidence for implications of these mechanisms from complimentary field research. Lastly, we provide a brief discussion of implementation of a purposeful and two-pronged research approach as an understanding of pinnipeds' high levels of cognitive flexibility may underlie their success for navigating the ever-changing, and often human-altered, natural environment.

Keywords Pinniped · Comparative cognition · Marine mammals · Equivalence classification · Learning by exclusion · Long-term memory

Introduction

Comparative cognition is interdisciplinary by nature. As such, it includes diverse perspectives with researchers varying in expertise from areas such as biology, behavioral ecology, neuroscience, animal behavior, zoology, and psychology. Accounting for the intersections between these disciplines, the cognitive mechanisms underlying behavior in a species within its natural environment are best understood when the expertise of behavioral ecologists and comparative psychologists are considered together. Including life history characteristics and phylogenetic perspectives, one could also utilize information from species evolution to infer about cognitive mechanisms. Collectively, a more global development of theories, testing of hypotheses, and interpretation of results is possible (Bräuer et al. 2020; see also Shettleworth 1993, 2009). Individuals in these various areas should work together to increase communication across disciplines, and further utilize knowledge gained (see Shettleworth 2010).

It should therefore not be surprising that the research methods used in the discipline of comparative cognition can be as varied as the species studied and perspectives explored. In that vein, a holistic approach for studying complex cognitive mechanisms with a species of interest not only lends itself, but should require, utilizing methods of both field work and studies with animals under human care (i.e., in laboratories, zoos/aquaria, and rescue/rehabilitation centers). While this approach is becoming more common, historically 'field' and 'lab' studies have been in conflict. Studies with animals under human care can provide precise control over experimental variables, as well as a subject

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animal's past experiences and overall living and testing environment, whereas in field studies, the application of cognitive mechanisms in the natural environment regarding problems the animals face in the wild and their effect on natural behavior can be investigated and provide robust ecological validity (see Heyes and Dickenson 1990; Allen and Bekoff 1995; Bekoff et al. 2002; Allen 2004, 2014). We support the use of complimentary data from studies conducted with animals under human care and in the field. While studies with animals under human care may perceptually lack ecological validity, they can provide precise control over experimental variables, as well as a subject animal's past experiences and overall living and testing environment, which are aspects not often able to be controlled in field studies because of the difficulty of experimentally isolating variables in situ. Field studies investigate behaviors and the application of cognitive mechanisms in the natural environment and provide robust ecological validity as these mechanisms allow a species to solve problems that they face in the wild. As the strengths and weakness of these two approaches are complementary, it is beneficial to purposely integrate their methodologies in a precise and planned way so that the findings allow one to best provide a more complete representation of species cognition. For example, research with Clark's nutcrackers (*Nucifraga columbiana*) under human care demonstrated memory for cache sites longer than 285 days (Balda and Kamil 1992), while field research with Clark's nutcrackers has documented successful retrieval of seeds seven to nine months after they were cached (Shettleworth 1983). The former work supports the existence of the underlying mechanism (i.e., well-developed long-term memory capabilities) inferred in the field research. Similarly, echolocation in cetaceans has been supported by work under human care and in situ. For example, studies with dolphins under human care provide evidence for the direct perception of an object's shape through echolocation when vision is experimentally occluded (Norris et al. 1961; Pack and Herman 1995; Herman et al. 1998; Harley et al. 2003), while Atlantic spotted (*Stenella frontalis*) and bottlenose dolphins demonstrated the cetaceans' ability to detect prey fish in the sandy bottom where use of vision would not be possible (Rossbach and Herzing 1997; Herzing 2004; Hüttner et al. 2021). We suggest that future research should not only take these 'lab' and field studies into account post hoc, but rather to use a more purposeful, two-pronged, and a priori approach, in which research with animals under human care and in the field are conducted in tandem and with a planned feedback loop for data analysis and hypothesis testing.

While there are various reasons taxa or specific species may be used as research subjects (e.g., evolutionary history, Bolker 2019; e.g., genetic similarity, Simmons 2008), the use of marine mammals as a model for studying cognition has already proven a fruitful line of research, and we suggest an increased focus on the use of pinnipeds. Pinnipeds are an amphibious group of marine mammals consisting of the phocids (true seals), otariids (eared seals: fur seals and sea lions) and obodenids (walrus), of which knowledge gained is comparatively applicable to both marine and terrestrial species since pinnipeds solve complex problems in their environment both in water and on land. They have successfully served as research models, but empirical studies are less frequent than perhaps they should or could be (Schusterman and Kastak 1995) as they offer an exciting opportunity for a complimentary, two-pronged, research approach. Their natural history, both within and between species of pinnipeds, provides a foundation for a variety of research questions and the testing of differing hypotheses in areas such as breeding and foraging behaviors (see Reidman 1990; Boness and Bowden 1996; Biolsi 2017) and sensory adaptations for perception on both land and underwater (Renouf 1991a; Wartzok and Ketten 1999; Hanke et al. 2021). For example, one can investigate concept learning in differing contexts (e.g., using multiple sensory modalities of stimuli) within a single species as well as between multiple species differing in habitats (e.g., tropical vs arctic species). Pinnipeds can be found living in all climates, ranging from Arctic/Antarctic to tropical which allows for wide array of investigations into problem solving based on behavioral strategies of thermoregulation (Boness and Francis 1991), foraging (Villegas-Amtmann et al. 2008), predator avoidance (Nordstrom 2002), mating and pupping (Le Boeuf 1991), with past research indicating high-level cognitive abilities such as utilizing logic and reasoning skills (Samuelson 2017; Cook et al. 2021). Furthermore, different species of pinnipeds vary in levels of their dependence on land, water, and ice. For example, elephant seals breed on land while harbor seals breed in the water (Sullivan 1981; Le Boeuf 1991). Some rely on ice (both flows and fast ice) for breeding/pupping (e.g., harp seals, *Phoca groenlandica*; Le Boeuf 1991; Lydersen and Kovacs 1999) while others require the warmth of the tropics (e.g., Hawaiian monk seals, *Monachus schauinslandi*; Alava 2017). Species are also exposed to varying degrees of human activities. For example, while historically some pinnipeds may be hunted by indigenous groups (McKechnie and Wigen 2011; Radde 2021) there is currently an increase in clashes with recreational and commercial fisheries (David and Wickens 2003; Kemper et al. 2003; Wilkinson et al. 2003; Ramos et al. 2020) as well as government sanctioned cullings (Bowen and Lidgard 2013). Additionally, researchers can gain relatively easy access to them as model species both in the wild and under human care. Unlike some marine mammals, such as cetaceans and sirenians, pinnipeds spend a significant portion of their lives on land and ice, which often allows for more direct observation of critical life and social functions, such as breeding and pupping. Pinniped species can thrive under human care

(Small and Demaster 1995; Clegg and Butterworth 2017; Delfour and Aviva 2021) thereby making research labs, rehabilitation facilities, zoos and aquaria ideal locations for researchers to access a species of interest.

In this paper, we demonstrate the balance of these differing research approaches between 'lab' and field as it relates to three specific areas of cognitive research with pinnipeds: equivalence classification, learning by exclusion, and long-term memory. First, we describe evidence from research with pinnipeds under human care to demonstrate, under precisely controlled experimental conditions, that these cognitive mechanisms are found in at least some pinniped species. We then follow these examples with complimentary field research demonstrating the potential application of each of these mechanisms in the natural environment. Lastly, we provide a brief discussion of implementation of a purposeful and two-pronged research approach in this vein.

Equivalence classification

Research under human care

Equivalence classification is defined as a group of perceptually dissimilar stimuli whose relations to each other emerge due to them sharing a spatiotemporal or functional contingency (Schusterman et al. 2003). According to Sidman (2000), it is demonstrated when an untrained relationship emerges among disparate stimuli. Whether any non-humans were capable of this complex categorization has been debated as equivalence classification was previously thought to be dependent on human language (e.g., see Horne and Lowe 1996). We argue instead that stimulus equivalence is not dependent on language and is a more general cognitive process found in at least some non-human animals and that it can serve as a mechanism by which pinnipeds may accomplish many social interactions. Here, we discuss the data from studies with animals under human care that provide evidence for equivalence classification in pinnipeds.

One of the most complex examples of equivalence classification in a non-human animal comes from Schusterman and Krieger (1984), who were able to train two California sea lions (*Zalophus californianus*) to understand a gestural artificial sign language consisting of different signs that could make up over 7000 different instructional combinations. Specifically, equivalence was thought to underlie the results of gestural language studies (Schusterman and Keriger 1984; Schusterman and Gisiner 1988, 1989), and it was argued that the California sea lions were not performing a linguistic task comparable to human language, but rather that they were using equivalence categorization of gestures to classify the meaning of these as objects, actions, and modifiers, thus enabling language-like behaviors. In addition, Schusterman and Kastak (1993) successfully demonstrated equivalence classification in controlled laboratory conditions with a California sea lion, named Rio. Rio was taught 30, three-member classes (e.g., 'A'—'B'—'C' stimuli) of arbitrary visual stimuli using a matching-to-sample procedure (MTS). The results showed that Rio was able to demonstrate the formal experimental requirements of equivalence—the directional relationships of reflexivity (e.g., A→A), symmetry (e.g., B→A) and transitivity (A→C) within an MTS paradigm. She was also able to spontaneously demonstrate the equivalence relationship (C→A) (Schusterman and Kastak 1993). To this day Schusterman and Kastak's (1993) work provides the strongest evidence for equivalence relations in a non-human animal. Later, additional tests using a variant of this MTS procedure demonstrated that Rio and another California sea lion Rocky were able to form equivalence relations under different experimental methodologies, which provided even stronger evidence for these animals' abilities to form complex associations (Reichmuth-Kastak et al. 2001).

These first studies on equivalence in California sea lions only investigated performances within the visual modality; therefore, it was important to investigate these same performances across the sensory modalities especially as field work provides evidence of cognitive ability across the senses (i.e., visual, olfactory, and vocal recognition). Lindeman-Biolsi and Reichmuth (2013) trained the California sea loin subject, Rio, on auditory-visual (A-V) discriminations and then tested for the emergence of transitive relations across modalities. The results of this work show that Rio was able to immediately solve novel transfer problems. New transitive relations emerged between the acoustic and visual stimuli that were separately related to a common visual mediating stimulus.

Following Lindemann-Biolsi and Reichmuth's (2013) demonstration of A-V transitivity with a sea lion they investigated A-V symmetry (another aspect of equivalence classes) with the same subject (Lindemann 2007; Lindemann-Biolsi et al. 2009; Lindemann-Biolsi and Reichmuth, unpublished data). The subject was presented with the 'symmetrical' relationship consisting of a visual sample and auditory comparison choice. The sea lion subject performed above chance levels ($p < 0.001$) on her first trials in an A-V symmetry test (Lindemann Biolsi, unpublished data; see also Lindemann-Biolsi et al. 2009). This is, to our knowledge, the only demonstration of A-V symmetry in a non-human species. The sea lion subject did perform successfully on her first exposures to a novel A-V symmetrical relationship in a similar manner to her A-V transitivity tests and her V-V equivalence relationships.

Research in the field

For pinnipeds, important social interactions seem to rely on recognition of conspecifics, which may utilize the mechanism of equivalence. For example, for pups to recognize their mothers they may form an equivalence class that consists of the mother's attraction call, visual sight of the female, and the mother's smell. These auditory, visual and olfactory cues may represent the many attributes that go along with the mother–pup relationship (Partan and Marler 1999; Wierucka et al. 2018a, 2018b). The pup can hear the mother's call without seeing or smelling her yet respond appropriately by vocalizing back. Therefore, the call or smell or sight of the mother does not simply represent a sound of another seal, an olfactory sensation, or the visual presence of another, but rather evokes responses that are enveloped in what it is to be with the mother and all of its affordances.

Perhaps successful classification of multi-modal stimuli for mother–pup reunions (e.g., Charrier 2020, 2022), mate selection (e.g., Gisiner 1985), and some male–male interactions such as competition during the breeding season (e.g., Casey et al. 2015) are accomplished through an ability to form relations using "if-then" rules among environmental stimuli, creating categories in which the class members may become interchangeable, such as in an equivalence class. In fact, individual recognition has been well documented in the field (e.g., see Dodson and Jouventin, 2003; Insley et al. 2003; Charrier and Harcourt 2006; Charrier 2020). Otariids have a lactation period that lasts approximately four months to three years during which time the female will alternate bouts of foraging with bouts of nursing (Reidman 1990; Renouf 1991b; Boness and Bowden 1996; Biolsi 2017). Mother–pup pairs have evolved a mechanism by which they can survive these separations through an ability to reunite following a female's foraging bout. If this reunion is not successful the pup will not survive, making it critical for the mother to recognize her own pup and vice versa (Royle et al. 2012). For the female, nursing the wrong pup could mean not having enough milk for her own pup to survive. For the pup, allosuckling or fostering, is rare and it is dangerous to approach the wrong female as it could mean injury or death since females have been known to behave aggressively to non-filial pups (Harcourt 1992; Phillips 2003).

Due to the critical nature of successful reunions, there is a strong rationale for the process to be multimodal (Hepper 1991). In fact, redundancy of important cues is not uncommon in signaling (Partan and Marler 2005). That said, these cues may not be equally relied upon or hold equal significance during reunions (see Weirucka et al. 2018a), but they can each be successfully utilized to 'represent' the individual and accurately convey identity information. We suggest that pinnipeds can use these differing modal stimuli (smell, sight, and sound of conspecifics) interchangeably (though probably not equally), much in the same manner that stimuli in an equivalence class are interchangeable in representing a common item or object. Some pinniped studies have focused on either an olfactory cue at the level of the individual (e.g., Pitcher et al. 2011; Stoffel 2015; Weirucka et al. 2019) or visual cues at the age-class level (e.g., Wierucka et al. 2017, 2018b) but the majority have investigated auditory cues via vocal recognition (see Insley et al. 2003; Charrier 2022).

Trillmich (1981) showed that female Galapagos fur seals (*Arctocephalus galapagoensis*) differentially responded to their own pups' calls indicating vocal recognition. Similar evidence was found in auditory playback studies with Northern fur seals (*Callorhinus ursinus*; e.g., Insley 2000), Subantarctic fur seals (*A. tropicalis*; e.g., Charrier et. al., 2003a), and Australian sea lions (e.g., Pitcher et. al., 2010a). Maternal care in odobenids also predicts individual recognition as walrus (*Odobenus rosmarus*) have a longer period of maternal care than otariids (Reidman 1990). Young walrus are found to stay with their mothers for up to three years and are therefore around their mothers after being weaned (Reidman 1990). As would be predicted by this relationship, Charrier et al. (2010) demonstrated differential responding of female Atlantic walrus (*O. rosmarus rosmarus*) to their own calf's calls compared to novel calves calls in playback studies with this species. It can also be noted that in addition to the abundant evidence of vocal recognition of pups by females, there is also strong evidence for pups' recognition of their mothers (see Charrier 2020 and Charrier 2021 for review).

In addition to otariids and odobenids, some phocids have demonstrated individual recognition. McCulloch and Boness (2000) recorded gray seal pup *(Halichoerus grypus)* vocalizations and played them back to females in the rookery. They found that females responded differentially to the calls of their own pups indicating recognition (McCulloch and Boness 2000). In harbor seals (*Phoca vitulina*), Sauve et al. (2015) found evidence that females can recognize their pups calls relative to non-filial pups as seen in playback experiments. Linossier et al. (2021) found similar evidence of mother–pup recognition in Northern elephant seals (*Mirounga angustirostris*). This is surprising when using maternal care as a predictor for recognition abilities, as phocids have relatively short lactation periods (approximately 4 weeks to 3 years), little-to-no separations between mothers and pups (Schultz and Bowden 2005), and higher rates of allosuckling (Boness et al. 1992; Arso Civil et al. 2021). However, they have various interactions with conspecifics throughout their life history (e.g., breeding; Hayes et al. 2004; Casey et al. 2015) therefore, evidence for individual recognition in phocids provides support that pinnipeds may have the ability to form equivalence classes and that these cognitive abilities are not strictly connected to maternal care and dependency, and rather that they may underly multiple social behaviors. This indicates equivalence classification as a more general cognitive mechanism that is not domain specific. For example, evidence has been found for recognition among young, weaned gray seals, who often stay together in ‘weaner pods’ post lactation and prior to venturing off their natal beach (Robinson et al. 2015).

Additional research with phocids further shows that maternal care is only one predictor of individual recognition as social species have critical interactions with conspecifics in various contexts. Hayes et al. (2004) demonstrated that harbor seal vocalizations are important outside of the mother–pup dyad as male harbor seals make loud underwater ‘roar’ vocalizations during the breeding season (Hanggi and Schusterman 1994; Van Parijs et al. 1997). While much is unknown about the harbor seal breeding system as much of it takes place underwater, this work demonstrated that females did not seem to attend to the playback of male calls, indicating that the calls are not to attract females but rather to signal to other males (Hayes et al. 2004). Northern elephant seals recognize individuals by their vocalizations (Casey et al. 2015, 2020; Mathevon et al. 2017). They have a polygamous breeding system in which male–male competition may have served as an environmental pressure for the evolution of this ability. During the breeding season, the males compete with one another for dominance and thus access to females (Leboeuf 1972; Sandergren 1976). The males are large, and their interactions can be quite violent, even ending in severe injury or possibly death. Therefore, it would be advantageous to be able to recognize other males and their position in the dominance hierarchy, allowing one to avoid unnecessary aggressive interactions. Perhaps these seals are able to do this through the mechanism of equivalence relationships wherein they can learn dominance hierarchies. This information can then be used to infer their place in relation to conspecifics, thus enabling them to respond in ways most beneficial to themselves during male–male competitive interactions. In fact, field research has demonstrated via playbacks that males respond differentially based on the directionality and hierarchical level of the call heard (Holt et al. 2010).

The results of Holt et al. (2010) can potentially be explained by acoustic characteristics of calls that indicate an honest signal of size and strength. For example, a larger male may have different acoustic features in his call (e.g., spectral cues are correlated with body size) from a small male, and a ‘listener’ of the call could respond differentially to the larger versus smaller male’s vocalization without any knowledge of the dominance rank of the callers (i.e., responding based on call spectral cues alone). However, Casey et al. (2015) investigated male northern elephant seal call features and found that while there was a correlation between some acoustic features and body size (e.g., pulse rate and number of pulses), playback studies provided evidence that males did not use these features for recognition but rather recognized each other and their social status individually (Casey et al. 2015). This further supports the idea that the behaviors seen between males in the field are due to them recognizing individuals within the colony and responding in appropriate ways based on that information.

In social contexts, territorial male otariids also recognize each other by their calls. They are able to categorize conspecifics into groups of familiar ‘friends’ or novel ‘foes’ (Schusterman et al. 2000). This seems necessary for certain species such as Steller sea lions (*Eumetopias jubatus*), which must maintain control of a breeding territory for at least one season before successfully reproducing (Gisiner 1985). Observational studies have collated data regarding male–male interactions, the gaining and holding of territory by males, and mate selection by females over repeated breeding seasons. Data have shown that females are more likely to choose mates that have held the same territories for multiple consecutive years (Gisiner 1985 as discussed in Schusterman et al. 2003). Research with fur seals has also demonstrated male-male recognition during the breeding season. The ‘dear enemy’ effect was shown via neighbor-stranger vocal recognition as males showed a lower response to calls from their neighbors as compared to those from strangers, thus indicating recognition of individuals and their territories (Roux and Jouventin 1987; Tripovich et al. 2008).

The success of maintaining territories over subsequent years may be indicative of the benefits provided by utilizing individual recognition of conspecifics for successful decision making during social interactions. One consequence is to conserve energy by only fighting males that are unfamiliar (e.g., ‘foes’), providing an evolutionary advantage. Avoiding familiar males which one had previously lost to in a fight will save energy for competing with novel males and decreases risk of injury by avoiding high risk physical confrontations. Evidence that these males can recognize conspecifics over multiple seasons and the correlation between holding these territories and appropriate interactions with neighboring males for a successful outcome further supports this as a strategy (Gisiner 1985).

Learning by exclusion

Research under human care

A learning method for expanding upon existing equivalence categories is termed learning by exclusion, as opposed to trial-and-error learning. It can provide a high degree of cognitive economy, the least amount of trial-and-error learning, and highest chance of errorless learning. Exclusion allows one to take advantage of previously learned associations and can result in responding appropriately to novel stimuli in the environment on the first exposure. Perhaps it is a mechanism utilized by pinnipeds to increase the chances of desirable outcomes at times when rapid decisions must be made, such as when avoiding predation. If we are to infer that exclusion is a mechanism that is employed by pinnipeds in situ, then we must consider implications found through research with animals under human care.

Demonstration of learning by exclusion under controlled experimental conditions typically requires a training and testing phase in which the subject demonstrates exclusion by selecting a correct answer on the first exposure to a novel stimulus. As an example, consider a subject who has already learned that stimulus “A” is associated with stimulus “B”. How can we expect the subject to respond when now presented with a trial consisting of a novel stimulus “D” and asked to match it to one of two comparison choices, a novel choice (“E”) and a familiar choice (“B”)? In this example, a spontaneous exclusion performance would be demonstrated if the subject chose stimulus “E” since “B” is already defined by its association with “A”. Exclusion is therefore demonstrated when a subject, in the presence of an undefined sample (“D”), chooses an undefined comparison (“E”) as opposed to a familiar defined comparison (“B”) (Schusterman et al. 1993; Wilkinson et al. 1996). Note that these correct responses to the novel stimulus could occur through exclusion without the subject learning and retaining the connection between the two novel stimuli. Therefore, researchers can next present the subject with a test for a learning outcome. This test consists of trial types that cannot be solved by exclusion, in which two new stimuli presented in an exclusion, or training, phase are pitted against each other. Demonstration of successful learning outcomes has been variable, even in humans. Wilkinson et al. (1998) noted that this may depend on many factors such as the number of exclusion (i.e., training) trials presented to the subject, the nature of the stimuli, as well as the subject species. For example, in humans, nouns have been shown to be faster to map to the objects than verbs to the actions (Gleitman et al. 2005).

The question of whether a pinniped can use exclusion to solve novel problems has been investigated with California sea lions (Reichmuth-Kastak and Schusterman 2002a; Lindemann et al. 2006; Lindemann 2007; Lindemann-Biolsi and Reichmuth, unpublished data). Within the visual modality two sea lions, Rio and Rocky, demonstrated exclusion performances by choosing unfamiliar comparisons on the first exposure to novel samples, and successfully avoided selecting the familiar, non-matching comparison choices (Reichmuth-Kastak and Schusterman 2002a). The subjects also demonstrated successful learning outcomes by incorporating these new stimuli into previous existing classes through the associations formed during exclusion trials, similar to how a wild pinniped may incorporate a novel shark into a previously learned category of predators. In addition, researchers sought to expand on the modality of this exclusion research with one of the same sea lion subjects, Rio. Illustrated in both the field and under human care, many critical aspects of pinniped life history are multi-modal making a cognitive mechanism most beneficial if it can be utilized in more than one sensory modality. Therefore, Rio was taught new auditory-visual stimulus pairings to examine the possibility of cross-modal exclusion performances. She was presented with novel auditory stimuli and the familiar visual stimuli from the previously formed classes making this a cross-modal (A-V) task (Lindemann et al. 2006; Lindemann 2007; Lindemann-Biolsi and Reichmuth, unpublished data). The subject’s acquisition was assessed as well as her ability to demonstrate a spontaneous learning outcome. Surprisingly the sea lion did not demonstrate perfect trial one, or exclusion performances; however, her transfer, or learning outcome, performance was significantly higher than expected by chance and generally not different from performance on familiar trials. This finding illustrates that training associations with an auditory-visual exclusion procedure can lead to successful cross modal transfer performances. While formal trial-one exclusion performance was not seen, an advantage of speed of acquisition was demonstrated relative to trial-and-error learning using an exclusion technique (Lindemann et al. 2006; Lindemann 2007; Lindemann-Biolsi and Reichmiuth, unpublished data).

Research in the field

Individuals gain cognitive economy by using categories to organize information in meaningful ways. For example, if a pinniped has a category of ‘shark predators’, then it would be adaptive to survival if one could respond to a novel shark (e.g., avoid/hide) in the same manner as to a familiar shark whether it is a novel individual shark or a novel shark species. Without responding correctly on the first exposure to the predator, a pinniped may not survive the interaction to learn such an association by trial-and-error, as an error could be fatal in favor of the predatory shark. While the pinniped may have a pre-existing concept of predators that includes sharks, using the learning process of exclusion can increase one’s chances of responding appropriately in a critical decision making scenario. This is especially beneficial if one has a new or weak concept such is as a young animal with limited experience. The inclusion or exclusion of new stimuli in one’s environment shape the categories and concepts themselves and enables one to behave optimally in an ever-changing environment where the use of such logical inferences is beneficial. Adaptability to rapidly changing conditions is even more critical, as the world experiences significant environmental shifts and increased unpredictability due to climate change (Kovacs et al. 2011; Alava 2017;

Collins et al. 2019). The ability to learn though the process of exclusion can increase one's adaptability and behavioral flexibility by providing an opportunity for errorless learning in novel situations. While research specifically investigating the process of exclusion learning in the wild is limited at best, this cognitive ability can be inferred when observing various aspects of pinniped behavior. For example, pinnipeds often find themselves in interactions with both recreational and commercial fisheries (David and Wickens 2003; Kemper et al. 2003). The interactions can encompass a range of situations where one must make critical life or death decisions as pinnipeds can get caught in nets as bycatch and are even intentionally shot by fishermen (Kovacs et al. 2011). It could be speculated that pinnipeds may use exclusion to learn which configurations (e.g., boat/net type) offer high valued prey and/or easier escape, versus which configurations do not. Fisheries dynamics can also mean direct competition for pinnipeds by industry for prey fish as well as fisheries-induced changes to the ecosystem, which can shift predator–prey balance resulting in an increased rate of pinnipeds being prey (O'Shea and Odell 2008). Taken together, pinnipeds would benefit from the cognitive economy and flexibility in these critical decision-making scenarios that exclusion provides.

One may infer the use of exclusion learning under the context of predator avoidance, as this cognitive skill is most likely acted upon by evolutionary pressures, where errorless learning is strongly advantageous. In fact, past researchers studying birds suggested that the recognition of predators must be innate and not require learning (Tinbergen 1948). That said, there are benefits to predator detection being influenced by experience, as detection is plastic and based on variable temporal and conditional cues (Curio 1993; Martin and Hammerschlag 2012). Research investigating great white shark (*Carcharodon carcharias*) predation on pinnipeds indicates that the predator–prey dynamics consistently shift (Martin and Hammerschlag 2012). These shifts are rooted both in environmental aspects (e.g., time of year, water quality changes, topography of the environment) and in evolving behavioral changes due to unpredictable predator behavior in conjunction with unpredictable prey behavior (Curio 1993). Therefore, predicting outcomes of predator–prey interactions requires a multi-faceted approach and consideration of ever-changing variables such as predator hunting mode, anti-predator behavior, and habitat features (Martin and Hammerschlag 2012), thus further requiring frequent edits to categorical inclusion and exclusion of new stimuli in one's environment, as well as rapid decision making based on the combination of fluctuating variables.

In addition to humans and sharks, killer whales (*Orcinus orca*) can be a major threat as some of prey upon pinnipeds as a major food source. Interestingly, while pinnipeds are a stable source of prey all year in many areas, some groups of killer whales focus their hunting during the pupping seasons for both the harbor and gray seals (Ford and Ellis 1999; Weller 2018). The hunting of young inexperienced prey increases the likelihood of a catch as these seals do not have the experience of being hunted and therefore have limited strategies in the absence of opportunistic learning. An inference can then be made that it would be quite beneficial to learn by exclusion that animals in one's environment are predators, and the best strategies for avoidance of detection as well as evasive techniques once spotted by a predator. The ability to learn phenotypic characteristics of a predator (e.g., shape, speed, swim pattern, sound) and how best to respond are not interactions that would be evolutionarily advantageous to learn solely by trial-and-error. Thus, selection favors learning by exclusion when repeatability is demonstrated.

Further examination into the dynamic between pinnipeds and killer whales provides insight into benefits of learning by exclusion. Killer whales in British Columbia, Canada (BC) are generally categorized into two types: the resident type which preys on fish, and the transient type which preys on marine-mammals (Ford and Ellis 1999; Jourdain et al. 2017). In BC, significant pinniped mortality is caused by transient orcas (Deeke 2002). It would therefore be beneficial for seals to be able to discriminate between these two types as spending energy to avoid a resident, fish-eating, orca would be wasteful, but not fleeing from a transient, mammal-eating orca could result in death. Consequently, learning to recognize cues for identification of orca type and appropriate behavioral response choices, while remaining flexible and selective in responses to novel predatory threats is critical. Deeke (2002 investigated this with wild harbor seals in BC, utilizing the fact that orcas typically have underwater vocalizations that are distinct between types (Barrett-Lennard et al. 1996). Playbacks of three types of calls were projected to the seals and behavioral reactions were recorded. They were exposed to underwater vocalizations of familiar fish-eating orcas, familiar mammal-eating orcas, and unfamiliar fish-eating orcas. Unsurprisingly the seals reacted with a predator avoidance behavior (hauling out of the water) to the calls of familiar mammal-eating calls, and unfamiliar fish-eating calls (but remained in the water and ignored the familiar fish-eating calls). These results indicate that the seals reacted appropriately in a situation with a novel predator call, and that they alter their predator classification based on previous experience. Deeke (2002) suggested that these results demonstrated selective habituation of seals learning what not to fear while also acknowledging that the complexity of killer whale vocal communication makes simple discrimination learning of these calls incredibly challenging. While we do not disagree with the role of habituation, we suggest the inference that learning by exclusion may play a role in this behavior as well, since it would be best not to learn each call individually but to rely on exclusion to modify already established equivalence categories of predator calls.

It should be noted that exclusion is methodologically difficult to determine in situ due to the very nature of controls required to rule out other possible mechanisms. That said, it is a reasonable inference as the ability provides cognitive economy, errorless learning, and is shown to be present in studies conducted under human care. More research is needed to tease apart strategies utilized in the wild in varying contexts.

Long-term memory

Research under human care

The ability to learn equivalence categories and to respond appropriately to novel stimuli in one's environment using exclusion techniques are both clearly beneficial to the survival of a social species, but neither of these skills would be very useful without a well-developed long-term memory (LTM) capability (for a review see Schusterman et al. 2002). Here, we discuss the relatively sparse research conducted with pinnipeds under human care. It should also be noted that there are varying ways to distinguish between working memory (WM) and LTM. In cognitive science, definitions of LTM often rely not solely on the amount of time between the presentation of a stimulus and the need to recall the information (i.e., retention interval), but rather on whether a distraction has occurred during the retention interval (Cowan 2008). Therefore, by this definition, delays of even a few seconds that include the insertion of a distractor stimulus to interrupt any potential mental rehearsal/cues are considered a test of LTM. The research with pinnipeds under human care used delays ranging from months to years, thus qualifying as evidence of extensive LTM. For instance, South African fur seals (*A. pusillus*) that learned an odor discrimination task demonstrated retention of these learned discriminations after both a 2-week and a 15-week retention interval (Laska et al. 2008). Additional evidence of LTM comes from a hand-reared California sea lion who was shown to recognize her human caregivers even though they had been separated for at least a month (Schusterman et al. 1992).

LTM of both categories and concepts with two California sea lion subjects (Rio and Rocky) was demonstrated by Reichmuth-Kastak and Schusterman (2002b). In this work, memory for equivalence categories (see Reichmuth et al. 2001) was retested after a retention interval of approximately one year with no decrement in classification performance. A relational concept (i.e., generalized identity matching; Kastak and Schusterman 1994) was retested after approximately 10 years and the sea lion immediately and reliably applied the identity concept to both familiar (therefore replicating past results) and novel stimuli (therefore using a concept to solve novel problems with new stimulus set) (Reichmuth-Kastak and Schusterman 2002b).

More recently, long-term memory was opportunistically studied in two California sea lion subjects, Bunker and Java. These subjects learned a simple discrimination task for a study on object recognition to a 95% criterion (see Lindemann-Biolsi and Paparo 2013). After an approximately 16-month interval with no exposure to the stimuli or the task/apparatus, both sea lions performed at 100% correct response levels. This was then replicated with the same two sea lions after a second, 18-month, interval without exposure to the stimuli or task, and once again, there was no decrement in task performance (Lindemann-Biolsi et al. 2016; Biolsi and Paparo, unpublished data).

Research in the field

While within a season, relationships may be modified with knowledge from newly observed social interactions, it benefits one to carry over a knowledgebase from year to year enabling one to avoid re-learning a significant amount of information therefore increasing the likelihood of desirable outcomes. For example, recognition of a conspecific as dominant to oneself, leading to a decision not to fight, which would save energy and avoid injury, is significantly more useful if that relationship is remembered not only within a breeding season, but across seasons from year to year.

The behavioral ecology of pinnipeds indicates that long-term retention of information is an important cognitive ability across domains. While mechanisms for navigation are an area of active investigation (Mauck et al. 2005; Matsumara et al. 2011; Hanke et al. 2012; Hanke and Dehnhardt 2018; Fuiman et al. 2020; Maaß and Hanke 2021) it is clear that pinnipeds can remember a goal state to navigate towards such as a foraging patch or a haul-out. Research from both radio and satellite tagged animals provide a significant amount of data on time, depth, location, and pattern of migratory and foraging routes (Condit and Le Boeuf 1984; Carter et al. 2016). For example, tagging data and research on foraging patterns indicate that female Antarctic fur seals show both a colony-level memory and an individual memory of foraging patches (Bonadonna et al. 2001; Call et al. 2008). Iorio-Merlo et al. (2022) collated 2-months of data from wild harbor seals and found that the animals repeatedly returned to productive foraging sites and utilized memory of prey availability to adjust their location movements. Ice seals, such as the Weddel seal (*Leptonychotes weddellii*) not only have to navigate for haul-out, breeding, and foraging, but must also attend to and recall breathing holes in fast ice in order to avoid drowning. Fuiman et al. (2020) relocated Weddell seals to unfamiliar locations to investigate navigation strategies using information from data loggers. While they focused on the environmental cues utilized by these seals, this study clearly demonstrates the ability of this pinniped species to remember its location of origin. Similarly, Oliver et al. (1998) translocated juvenile Northern elephant seals from their rookery to locations up to 100 km away and found that the seals not only were successful at navigating back to the rookery but that most followed a direct return path.

In addition, pinnipeds tend to return to their natal beach to breed each year (Reidman 1990); therefore, long-term recognition would be most useful if one could remember the individuals and their relationships to each other over long periods of time (e.g., beyond one breeding/pupping season). Recognizing kin/non-kin, as well as individuals with whom one has had affiliative exchanges (or not) can enable more successful social interactions. Hoffman and Forcada (2012) studied Antarctic fur seals and found that individual females not only returned to their natal beaches, but to within two meters of their location of birth on the beach. Observational studies have collated data regarding male–male interactions, the gaining and holding of territory by males, and mate selection by females over repeated breeding seasons. Data have shown that females are more likely to choose mates that have held the same territories for multiple consecutive years (Gisiner 1985 as discussed in Schusterman et al. 2003).

Field experiments with otariids support long-term recognition of conspecifics, and data supports that for at least some pinniped species with highly individualized calls, that the strategy is not solely kin recognition (see Charrier 2020). Insley (2000) conducted a field experiment in which he recorded mother and pup vocalizations of Northern fur seals and found that after four years between exposures to recorded vocalizations, mothers could recognize their pups' calls and the reverse was true as well. Therefore, mothers and adult pups recognize each other's signature vocalizations that are specific to mother–pup reunions during the lactation period. In other words, a mother's pup attraction call is distinct from other call types of her repertoire and only used in the context of mother–pup reunions, yet the adult 'pups' from the dyads tested were able to recognize their mother's call. Another study on LTM in the field with Australian sea lions had presented females with playbacks of their pups and non-pups at 2 months post-weaning and again after 2 years (Pitcher et al. 2010b). The females were able to distinguish both the earliest pup calls and the later ones which is important, as the calls change as the pup grows and matures. This indicates that females successfully recall differing versions of their own pups' vocalizations, while correctly discriminating against non-filial pup calls. While it is not surprising that females react to their pups within the lactation period, these studies demonstrating memory for the past pups' calls years later indicate a robust LTM system (Charrier et al 2003b; Mathevon et al. 2004).

The above field research provides excellent evidence for LTM in wild pinnipeds as it demonstrates that natal sites, feeding areas, and individuals may be remembered over long periods of time. We suggest that the behaviors observed in the wild are based in this specific cognitive mechanism through demonstrations that pinnipeds can employ LTM capabilities in controlled experimental settings under human care.

Future directions

We propose that while much research of the kind discussed above may be considered and interpreted in light of research with animals under human care and in the field, the studies themselves are not carried out in tandem with the explicit goal of addressing a specific question with two complimentary approaches ('lab' and field). For example, as noted, research with animals in the wild demonstrate individual recognition (field work). We may want to infer from the field data that the pinnipeds use a mechanism of equivalence for this but we must test the hypotheses that this mechanism exists in, and is used by, pinnipeds (e.g., work with animals under human care). Taken together this approach can, and has, provided a foundation for the inference of equivalence being the mechanism used in natural behaviors. That said, these studies have been carried out independently in time, location, species, and by differing researchers. Our hope is that in addition to this past, and current style, future research will try and answer questions with a two-pronged approach consisting of dual a priori hypotheses and studies designed from the bottom-up to inherently include methodologies via the two avenues of 'lab' and field with explicit collaboration between researchers. As such, research would include testable hypotheses and methods for linked studies creating a data feedback loop carried out both with animals under human care and in the field by a team of researchers working in conjunction.

For example, the studies conducted demonstrating equivalence with pinnipeds under human care (e.g., Schusterman and Kastak 1993) used artificial stimuli to control for confounding variables which is required in cognition studies to demonstrate that performance is not based on perceptual aspects of the stimuli or evolved innate behavioral reactions elicited by specific natural stimuli. As also discussed, field data has investigated individual recognition in wild pinnipeds (e.g., see Charrier 2020, 2021). While these separate lines of research clearly lend themselves to informing inferences between the connection of the existence of a cognitive mechanism and its application in the wild, these types of studies are discussed in reference to each other post hoc. We suggest a situation in which data is collected with animals under human care, in a pre-planned way such that data is simultaneously collected in the field. Another example would be for the two groups to share raw data and conceptually design a study that incorporates data from the field into the 'lab'. For example, replication of the equivalence paradigm with naturalistic stimuli as decided purposefully through the field data and in conjunction with field researchers. This would provide elucidation as to the role of equivalence in decision making during encounters in the wild. It could also assist in fine tuning what we know about the perceptual stimuli themselves (e.g., what acoustic aspects are attended to; see e.g., Insley 1992). This approach is only truly complimentary if the two prongs of 'lab' and field are conducted in purposeful and pre-planned ways with a formal feedback loop between them.

To consider a broader example for conceptualizing this process one could look to research on predator/prey dynamics. This could be investigated in an aquarium setting with full access to the research subject(s), excellent above and underwater visibility for data collection, multiple subject viewing angles, clear audio and video recordings, and control over variables such as number of prey and prey type as well as habitat/location of the predator/prey interactions. Concurrently, data could be collected with wild pinnipeds on similar interactions in the field. These can be done on the same species, during the same times of year, in the same general geographic location and climate. Predictions and data from one could be used to inform the other in a timely, planned, and ongoing process. Based on field observations work under human care can be edited to design and tease apart the variables we are unable to control in the field and then provide a more direct feedback loop. In addition, researchers can make alterations in variables in the 'lab' and see if it models what is observed in the field. This more immediate back and forth would lead to more accurate and timely predictions with better communication and more purposeful and direct methodological planning between researchers working with pinnipeds under human care and in the field regardless of whether there is one researcher/research group conducting both research lines or separate research groups for each avenue working in a concurrent and strategically connected way.

Conclusion

Through a complimentary approach of research methodologies with pinnipeds under human care and in the field, a more holistic understanding of animal behavior and cognition can grow. Research provides evidence for the utilization of equivalence classification, learning by exclusion, and long-term memory with pinnipeds under human care and in wild pinnipeds. Using a purposeful approach to complimentary research can demonstrate that these cognitive abilities must underlie the complex behaviors these animals demonstrate in the wild such as individual recognition, navigation, foraging, and predator avoidance and provides both precisely controlled experimental conditions and ecological validity. In addition to more overall research focused on pinniped subjects, we also hope to support collaboration and conversations within and across research specializations and to highlight the value of a holistic and interdisciplinary approach. As comparative cognition benefits from differing research perspectives and methods of data collection allowing for improved scientific inferences to be made, purposefully connecting research with pinnipeds under human care and in the field can only add value. Taken together, researchers can learn what behaviors an animal exhibits, why it performs those behaviors, and how it accomplishes those behaviors. This is foundational in understanding the cognitive abilities of pinnipeds at the mechanistic level as well as how they are applied by these animals to survive and thrive in their natural environment.

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