



Learning and Conservation

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Introduction: History and Definitions

A rat scuffles along a track in the undergrowth and comes across a food source it has not encountered previously. Next day, heading out to feed, it goes straight to that location to forage once again. A hummingbird lands on a pink flower and discovers a rich source of nectar. On subsequent foraging trips, it chooses to land preferentially on pink flowers. A young calf narrowly escapes an attack by a crocodile while drinking at a riverbank. Next time it approaches the river, it does so more cautiously and remains more vigilant while it drinks. In all these examples, animals change their behavior as a consequence of experience. This ability, referred to as 'learning,' is taxonomically widespread and is critical to survival and reproduction.

The study of learning has a long and rich history. Early interest in the phenomenon can be traced back to the great biologist, Charles Darwin, who conducted extensive empirical work to explore whether earthworms learn where to build holes. The study of learning emerged as a modern academic discipline in the nineteenth century when Russian scientist, Ivan Pavlov, began his well-known work on associative learning in dogs. Continuing in Pavlov's tracks, other psychologists, such as Edward Thorndike and Burrhus Skinner, undertook to determine the laws that govern how, when, and under which conditions learning occurs – a field of widespread research even today. For psychologists, the primary motivation has been, and still is, to formulate so-called universal laws that are assumed to govern learning across all species and all situations, an approach known as 'the General Process approach' to the study of learning. Consequently, their highly controlled empirical work has employed only a handful of convenient model laboratory species, such as rats and pigeons, a surprising approach given the motivation to establish general laws of learning, and has focused on asking how these animals learn about arbitrary stimuli with little ecological significance (e.g., single tones). In the 1960s, however, findings from the emerging field of

ethology brought with them the awareness that learning occurs in a broad range of contexts outside the laboratory and plays an essential role in the survival of most animal species. Subsequently, zoologists and behavioral ecologists embraced the study of learning, successfully combining experimental control with ecological significance. A particular focus of this work has been on the mechanisms and functions of social learning. Involvement of this scientific community in the study of learning brought with it an increase in taxonomic breadth.

An awareness of how important learning is to conservation emerged in the early 1990s when the number of captive-breeding programs increased dramatically as conservation biologists began to attempt to stall the impending global species extinction crisis. Motivated by the initially poor success rates of wildlife reintroductions, reintroduction biologists began to pay more attention to the role of learning in captive-breeding programs in particular. Although the role of learning has been considered mostly within the captive-breeding context, learning needs to be considered in any wildlife management strategy that isolates an individual from the habitat in which it will ultimately have to survive. Translocation of animals to predator-free islands to increase population numbers with the ultimate aim of returning future generations to their original environment is one such example.

Types of Learning

To understand how animal learning affects conservation, it is necessary to briefly introduce the reader to two classes of learning phenomena, as well as their mechanisms and functions. Of most importance to conservation have been two types of associative learning traditionally known as 'classical' (a.k.a. Pavlovian) conditioning and 'instrumental' (a.k.a. operant) conditioning. The principles that describe when and under which conditions classical and instrumental conditioning occur are well established. Some attention to the huge body of empirical data on

associative learning is important for conservation work because it provides the basis for understanding how experience shapes behavior and for designing conservation interventions that produce animals well suited to the postrelease environment.

In classical conditioning, an initially neutral stimulus (conditioned stimulus, CS; e.g., a light) is presented repeatedly together with a biologically significant event, which evokes a spontaneous response (unconditioned stimulus, US; e.g., food). As a result, animals learn an association between the CS and US. Learning of the association is reflected in that the CS acquires the ability to evoke a response that is related to the response evoked by the US (e.g., foraging behavior). It is generally accepted that learning occurs when appearance of the CS predicts, or signals, the subsequent occurrence of the US. Hence, the function, or adaptive significance, of classical conditioning is to allow organisms to prepare themselves for biologically significant events. For instance, young white-tailed ptarmigan chicks (*Lagopus leucurus*) learn to forage on foods high in protein (CS), which they have associated with their mother's food calls (US). In trials designed to reduce egg depredation in endangered species, American crows (*Corvus brachyrhynchos*) learn to avoid green-painted eggs after ingesting similar colored eggs (CS) injected with a chemical that made them ill (US). Crows acquire aggressive responses to humans (CS) who have netted them (US).

Also of importance to conservation is instrumental conditioning. Here, rather than an association between two stimuli, animals learn an association between a behavior and its consequences. Behaviors followed by successful outcomes increase in frequency, while those followed by adverse outcomes decrease in frequency. In many predator species, mothers bring live prey to their offspring, thus creating opportunities for them to practice their capturing and killing techniques. The adaptive value of instrumental conditioning is that it provides a mechanism by which animals increase the effectiveness of their behavior.

Ontogenetic Isolation and Its Effects on Behavior

Captive breeding isolates animals from the environment in which they will ultimately have to survive when they are released into the wild. Comparisons between behavior of captive-reared and wild-born individuals have shown that captive rearing can lead to substantial changes in behavior, and that these changes can affect postrelease survival. Captive-reared northern bobwhites (*Colinus virginianus*) have deficient antipredator skills and as a consequence undergo far greater postrelease predation than wild-born individuals. Juvenile black-tailed prairie dogs (*Cynomys leucurus*) bred in captivity are less vigilant and alarm call less to predators than age-matched wild

individuals, and suffer higher rates of mortality. Captive-bred Attwater's prairie chickens (*Tympanuchus cupido attwateri*) tolerate closer approach by humans and dogs than wild prairie chickens, and suffer high rates of postrelease predation. Captive-bred golden lion tamarins (*Leontopithecus rosalia*) are deficient in their locomotor and foraging skills when compared to their wild-born offspring, and these deficiencies persist several years after release.

There are exceptions, however, to the general rule that captivity has detrimental effects on behavior. For instance, survival rates of captive-reared takahe (*Porphyrio mantelli*) do not differ significantly from those of wild-born takahe. But, in many instances, equivalent survival requires implementing postrelease measures to reduce the impact of deficient behavior. For example, captive bred black and white ruffed lemurs (*Varecia variegata*) survive equally well as their wild counterparts, as do scarlet macaws (*Ara macao*) raised with wild mates, as long as they receive postrelease supplemental feeding.

Captivity-associated alterations in behavior have two sources. First, captive-bred animals do not have the opportunity to acquire lifetime experience with their natural environment. Both individual learning through direct experience with the environment, and social learning through interactions with more experienced individuals (e.g., a parent) are compromised. Taking this process one step further, animals may even adjust their behavior to suit life in captivity in ways that are detrimental to survival in the wild. Captive-held river otters (*Lontra canadensis*) are more prone to predation and accidents with traps than wild otters, perhaps reflecting habituation to captivity.

A second effect that may occur when animals are bred in isolation from their natural habitat over several successive generations is evolutionary loss of behavior. Loss may occur either because behavior well suited to survival in the wild is selected against in captivity, or alternatively because once beneficial behavior is lost under the effects of genetic drift. High numbers of captive-bred Saudi Arabian houbara bustards (*Chlamydotis macqueenii*) die from trauma-related deaths, usually involving collisions with cages by frightened birds. Such mortality can result in selection for individuals whose behavior is more suited to life in cages, but whose predator escape responses are inadequate. Indeed, pen-reared Attwater's prairie chickens fly significantly less far in response to an approaching human or dog than wild greater prairie chickens (*T. cupido*).

Evolutionary loss of behavior is complicated by the fact that genetic predispositions focusing attention on stimuli that are particularly relevant to survival often guide learning. Although this phenomenon has not been studied in the conservation context, several examples can be found in the literature on mechanisms of learning. Snake-naïve rhesus monkeys (*Macaca mulatta*) learn to associate snakes, but not flowers, with fear responses of

social companions. Male quail associate an object with quail-like features with copulation and feeding opportunities more quickly than an arbitrary object. Guided learning is also evident when young chicks learn the features of their mother, although the emergence of such preferences is itself dependent upon nonspecific visual experience shortly after birth. Learning predispositions ensure that animals learn quickly and effectively about ecologically significant events. Consequently, reintroduction biologists need to be aware that evolutionary isolation may lead not only to the loss of behavior, but also potentially, and for the same reasons, the loss of learning predispositions. By impacting both the experiential and the genetic underpinnings of learning, captive breeding has the potential to reduce substantially the ability of animals to survive once released into the wild.

To address this problem, a huge effort has been made to design captive-breeding environments that provide animals with enriched learning opportunities. In addition, numerous prerelease preparation programs are implemented to train individuals in the survival skills they lack. These conservation interventions target a diverse range of animal behaviors, three of which are discussed in the following sections.

Specific Research Areas in Learning and Conservation

The Role of Learning in Predator Avoidance

The high incidence of postrelease predation on captive-bred individuals has been, and still is, one of the greatest challenges to wildlife reintroductions. Encouragingly, however, a large body of empirical work has demonstrated that a taxonomically wide range of species exhibit the ability to learn about novel predators. Learning can occur both through direct individual aversive experience with the predator stimulus, and through indirect (social) experience, for example by perceiving predator together with alarm responses of predator-experienced individuals. Both direct and indirect learning engage classical conditioning in which a novel predator plays the role of a CS and inherently aversive stimuli, such as being chased or bitten in direct learning, or social alarm signals in indirect learning, serve as the US. Furthermore, predator avoidance learning is guided by predispositions to learn about predator stimuli more readily than arbitrary (e.g., plastic bottle) or nonpredator stimuli (e.g., goat), and does not take long (one to three exposures to aversive associations are sufficient).

Building on this knowledge, reintroduction biologists have developed a range of predator avoidance training techniques for captive-bred animals. Broadly speaking, these methods all engage classical conditioning, in which opportunities are created for animals to associate novel

predator stimuli with aversive events. Both direct learning and indirect social learning training methods have been tested, with tentative evidence that social learning produces greater changes in behavior and greater improvements in survival. For example, several reintroduction programs (e.g., Attwater's prairie chickens, houbara bustards, takahe, bobwhite quail (*C. virginianus*), prairie dogs (*Cynomys ludovicianus*)) have used direct attack, or harassment, by a predator (e.g., fox (live or mounted); dog; stoat; human) to enhance antipredator responses. In bobwhite quail, training improves cover seeking and covey coordination and increases postrelease survival rates. In houbara bustards, harassment by a live fox, but not a fox mount, enhances postrelease survival rates. In prairie dogs, pairing predator stimuli with social alarm vocalizations or the opportunity to observe a predator-experienced prairie dog respond to the predator stimuli enhances antipredator vigilance, alarm call rates, and time in or near shelter. Social training increases postrelease survival to the point that trained prairie dogs survive as often as their wild counterparts.

Social learning can also be triggered by allowing predator-naïve individuals to watch the attack of a conspecific by a predator. For example, in an attempt to reduce postrelease predation of captive-bred Puerto Rican parrots (*Amazona vittata*) by red-tailed hawks (*Buteo jamaicensis*), captive-born individuals are given the opportunity to witness a staged attack of a nonendangered Hispaniolian parrot (*Amazona ventralis*) by the aerial predator. Similarly, takahe chicks watch a model stoat apparently attack and kill a takahe chick. In both cases, there is tentative evidence that such training increases postrelease survival.

It is important to note that firm conclusions about the effects of prerelease predator avoidance training on post-release mortality rates can really only be made if the content of learning is known. This is because training has the potential to cause general increases in stress, rather than to teach predator recognition or predator-specific antipredator responses, changes in behavior that are unlikely to improve postrelease survival. Consequently, measuring responses to the target predator both before and after training to ensure that learning has occurred, as well as to nontrained control stimuli to ensure that changes in behavior are predator-specific, is important.

The Role of Learning in Social Behavior

Just like antipredator behavior, social behavior is shaped by experience and is of prime importance to conservation. The learning phenomena that have received the most attention in this context are filial and sexual imprinting. During filial imprinting, the young individual learns soon after birth to recognize its mother (or its carer) and becomes socially attached to her. Such learning occurs

in precocial animals, such as ducks and guinea pigs, and is conceptualized as a form of classical conditioning in which learning of the carer's visual features (CS) is triggered by association with inherently salient stimuli (US), such as movement. Similar to predator avoidance learning, imprinting is guided by predispositions to learn about some stimuli more readily than others. For example, chicks imprint most readily on a hen-like stimulus. During sexual imprinting, individuals learn the visual attributes of potential mates. The critical experiences for sexual imprinting are different from those involved in filial imprinting and occur later in life.

Filial and sexual imprinting have serious implications for animals reared away from their natural social environment. For instance, widespread breeding techniques for endangered species, such as hand rearing and crossfostering to related species, can produce individuals maladapted to reproduction. While artificial rearing environments (e.g., brooder boxes; commercial incubators) can boost population growth at relatively low cost, benefits may be offset by problems associated with deficient social behavior. For example, from 1986 to 2000, 67% of unsuccessful releases of southern sea otter pups (*Enhydra lutris nereis*) reared using methods that rely heavily on human care were caused by failure of pups to integrate with wild populations and avoid interactions with humans.

An increasing awareness of the interaction between early social environment and later reproductive behavior has triggered a number of strategies to expose animals to natural social contexts immediately after birth and during subsequent development. The Mississippi sandhill crane (*Grus Canadensis pulla*) reintroduction program has been at the forefront of such attempts. Here, extensive efforts are made to expose chicks immediately after hatching to adult cranes that can serve as imprinting models. Taxidermy mounts of adult cranes lying in brood posture are placed beneath the heat lamps and sandhill crane brood calls are played back by tape recorder, while mounts of crane heads are used to teach chicks to feed. Later on, chicks are housed in pens adjacent to adult cranes. Furthermore, during occasional interactions, humans are disguised in amorphous gray costumes. Chicks raised using these techniques survive at least as well as parent-reared birds, which are less wary of approach by humans and predators after release, a behavior attributed to their tendency to approach motor vehicles and uncostumed humans in captivity. Other reintroduction programs have followed in the steps of the sandhill crane reintroduction.

Social interactions between members of the same species can shape social behavior in subtle ways that extend beyond filial and sexual imprinting, however. Cultural transmission of mate choice in female Japanese quail (*Coturnix japonica*) is one example; they remember, and prefer to mate with, males whom they have previously

seen court and mate with another female. Social behavior of cowbirds (*Molotrus ater ater*) provides another. Here, females enhance the frequency of specific songs within the male song repertoire by using a wing stroke to indicate their song preferences, and these songs later evoke higher levels of female copulatory behavior. In addition, female cowbird behavior enhances male–male competition. Males that are involved in more male–male competition later receive more copulations, and aviaries containing more competitive males produce more eggs. Although such experiential effects have not been studied in a conservation context, these examples illustrate that learning associated with social interactions can have far-reaching consequences on the genetic composition of a population, on individual breeding success, and, as a result, on the long-term outcome of a reintroduction program.

The Role of Learning in Foraging Behavior

Finally, we turn to the effect of experience on foraging behavior. The fact that postrelease supplemental feeding is a widely recommended practice and so often increases postrelease survival rates provides indirect evidence that many animals reared away from their natural environment have deficient foraging behavior. Instrumental conditioning is critical to the development of adequate food handling techniques. In many predator species, such as cats, mothers bring live prey to their young, thus creating opportunities for inexperienced individuals to practice capturing and killing techniques. Similar opportunities can be created in captivity by exposing captive-reared animals to the foods they will later encounter in the wild. Captive-bred Puerto Rican parrots are fed a range of rainforest fruits, allowing them presumably not only to improve their handling skills, but also through classical conditioning, learn the colors and smells of edible foods. Such learning can start early. Rat pups exhibit preferences for foods, the flavor of which they have experienced through their mother's milk.

Animals also acquire foraging behavior from interacting with more experienced individuals. Ptarmigan chicks learn to forage on foods high in protein they have associated with their mothers' food calls. Southern sea otter pups reared by surrogate mother otters forage independently sooner and have higher survival rates than pups reared using methods that rely heavily on human care.

Individual and social learning shapes not only food preferences, but also food avoidances. Red-winged blackbirds (*Agelaius phoeniceus*) avoid a distinctively colored food after they have observed a conspecific eat the food and subsequently develop toxin-induced illness. Similarly, domestic chicks (*Gallus domesticus*) that peck at a colored bead dipped in a bitter-tasting chemical, or watch other chicks peck at the bead and express a disgust response, subsequently avoid pecking at beads of that color.

But learning about food is not restricted to acquiring handling techniques and recognizing edible and nonedible foods. Both temporal and spatial food-related information can be acquired through both individual and social experience, and can have far-reaching consequences on behavior of individuals after release. For example, young black bears (*Ursus americanus*) reared by mothers accustomed to feeding on anthropogenic food sources tend to maintain these preferences as adults, and are consequently more likely to venture close to humans. As a consequence, where, when, and on what an individual learns to forage early in its life can affect how it distributes its behavior in space and time as an adult, perhaps exposing it to greater risk of predation. Acquisition of food-related information can hence have consequences that extend far beyond the immediate problem of foraging skills and food recognition.

The Role of Learning in Adjusting to Urbanization

As urban environments expand and natural habitats retract, selection for species able to adjust to human-modified habitats intensifies. In recent years, there has been an increasing interest in understanding why some species, but not others, adjust to environmental change. One hypothesis is that environmental change is one of the factors that selects for increases in brain size. It is thought that larger brains afford greater innovation and learning capabilities (a.k.a. *behavioral flexibility*), which allow individuals to modify their behavior in adaptive ways and hence increase survival in modified habitats. Indeed, large-scale analyses of species-specific innovation rates, operationally defined as the number of anecdotal reports of feeding innovations in the wild (e.g., foraging on a novel food) and obtained by reviewing the field-based literature, have revealed a positive relationship in both mammals and birds between brain size and innovation rate once the effects of body size and phylogeny have been removed. Coupled with a small within-species experimental literature pointing to a positive relationship between innovation and learning, these analyses suggest that larger brains afford greater behavioral flexibility.

Furthermore, behavioral flexibility seems to increase survival in harsh, novel, or altered environments. Birds innovate more frequently in winter when resources are scarce. Species with larger brains and higher innovation rates are more likely to become established in novel environments than species with smaller brains, while long-term avian population trends in England indicate that large-brained species are fairing the best. In sum, relationships between brain size, behavioral flexibility, and environmental change point to a potential, but yet untested, relationship between behavioral flexibility and population expansion in disturbed environments.

It should be noted that the comparative correlational literature on brain size has its critics, who call for more experimental work to properly understand the function of large brains. It might also be helpful to properly identify the life history traits that support the evolution of big brains (e.g., extended parental care). Together, this information might allow us to predict whether large-brained species will be better able to adjust to large-scale environmental change, including rampant urbanization and climate change.

Future Research

Reintroduction programs are outcome-driven exercises that aim to restore species to their historical habitats. To date, much reintroduction research has been undertaken in an ad hoc manner, and knowledge regarding the parameters that favor reintroduction success has been gained using an opportunistic and/or a posteriori evaluation of management strategies. Development of methods to offset the effects of captivity is likely to benefit most from an experimental hypothesis-driven approach. Experimental protocols should measure behavior both before and after a controlled learning experience in both trained-experimental and nontrained-control animals to detect changes specifically attributable to the learning experience, use control stimuli to assess to what extent learning is specific to the trained stimulus, and include the release of nontrained animals to ascertain to what extent learning provides a survival benefit. Only in this way will we be sure that management practices provide a measurable benefit and are not simply a matter of faith. In this regard, the fundamental literature on animal learning, behavior, and developmental biology has much to offer in terms of procedures and theory, and should be used to inform reintroduction research. Integration of fundamental and applied research can only be achieved by providing reintroduction biologists with a thorough training in these scientific disciplines and/or through their close collaboration with behavioral scientists.

One of the greatest obstacles facing reintroduction biologists is that hypothesis-driven research designed to understand the effects of experience on behavior requires relatively large sample sizes, which are not always available when working with threatened species. One way to overcome this problem is to use surrogate species as models. For instance, the effects of puppet rearing have been evaluated using common ravens (*Corvus corax*) as a model for the endangered Hawaiian crow (*C. hawaiiensis*) and the Mariana crow (*C. kubaryi*). In Australia, tammar wallabies (*Macropus eugenii*) have been used as a model macropodid marsupial to develop predator avoidance training techniques and systematically assess their effect on behavior. Better planning and coordination of research

across reintroduction projects dealing with taxonomically related groups may also assist in this regard. For example, reintroduction programs involving precocial birds could work together to explore the effects of various rearing methods on social integration of wild populations.

Another possible approach is to use data from fundamental work in animal behavior to predict which interventions will be most successful. For example, Griffin and colleagues integrated an understanding of how ontogenetic and evolutionary isolation from predators modify antipredator responses with principles of associative learning to predict that predator avoidance training is likely to be more successful with animals that have undergone ontogenetic isolation from some, but not all, predators. This kind of predictive framework can assist decision makers in allocating limited resources to prerelease training.

In conclusion, it is proposed that integration of reintroduction research and fundamental work in animal behavior, coupled with an experimental hypothesis-driven methodology, will be the most fruitful way forward for research into learning and conservation.

See *also*: Memory, Learning, Hormones and Behavior; Ontogenetic Effects of Captive Breeding.

Further Reading

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