Review

Training Captive-Bred or Translocated Animals to Avoid Predators

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Abstract: *Animal reintroductions and translocations are potentially important interventions to save species from extinction, but most are unsuccessful. Mortality due to predation is a principal cause of failure. Animals that have been isolated from predators, either throughout their lifetime or over evolutionary time, may no longer express appropriate antipredator behavior. For this reason, conservation biologists are beginning to include antipredator training in pre-release preparation procedures. We describe the evolutionary and ontogenetic circumstances under which antipredator behavior may degenerate or be lost, and we use principles from learning theory to predict which elements can be enhanced or recovered by training. The empirical literature demonstrates that training can improve antipredator skills, but the effectiveness of such interventions is influenced by a number of constraints. We predict that it will be easier to teach animals to cope with predators if they have experienced ontogenetic isolation than if they have undergone evolutionary isolation. Similarly, animals should learn more easily if they have been evolutionarily isolated from some rather than all predators. Training to a novel predator may be more successful if a species has effective responses to similar predators. In contrast, it may be difficult to teach proper avoidance behavior, or to introduce specialized predator-specific responses, if appropriate motor patterns are not already present. We conclude that pre-release training has the potential to enhance the expression of preexisting antipredator behavior. Potential training techniques involve classical conditioning procedures in which animals learn that model predators are predictors of aversive events. However, wildlife managers should be aware that problems, such as the emergence of inappropriate responses, may arise during such training.*

Entrenamiento de Animales para Evitar Depredadores

Resumen: *Las reintroducciones y el desplazamiento de animales son intervenciones potencialmente importantes para salvar especies de la extinción, pero la mayoría no son exitosas. La mortalidad causada por la depredación es una de las principales causas de los fracasos. Los animales que han sido aislados de sus depredadores, ya sea a lo largo de su vida o a lo largo de un tiempo evolutivo, podrían dejar de expresar las conductas adecuadas contra los depredadores. Por esta razón, los biólogos conservacionistas están iniciando la inclusión de entrenamientos contra depredadores en los procedimientos de preparación previa a las liberaciones. Describimos las circunstancias evolutivas y ontogénicas bajo las cuales la conducta contra los depredadores puede degenerar o ser perdida y usamos los principios de la teoría del aprendizaje para predecir que elementos pueden ser reforzados o recuperados mediante un entrenamiento. La literatura empírica demuestra que el entrenamiento puede reforzar las aptitudes anti-depredadores, pero la efectividad de estas intervenciones es influenciada por un número de restricciones. Nosotros predecimos que será mejor enseñar a los animales a lidiar con los depredadores si han experimentado un aislamiento ontogénico a que si los animales han pasado por un aislamiento evolutivo. Similarmente, los animales deberían aprender más fácilmente si han sido aislados evolutivamente de algunos pero no de todos los depredadores. El entrenamiento*

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sobre un nuevo depredador sería más exitoso si una especie tiene respuestas efectivas contra depredadores similares. En contraste, puede ser difícil enseñar conductas adecuadas para evadir, o introducir respuestas especializadas específicas para un depredador, si los patrones motores adecuados no están presentes. Concluimos que el entrenamiento previo a las liberaciones tiene el potencial para mejorar la expresión de conductas anti-depredadoras preexistentes. Las técnicas potenciales de entrenamiento involucran procedimientos clásicos de acondicionamiento en ls cuales los animales aprenden que los modelos de los depredadores son pronósticos de eventos adversos. Los manejadores de vida silvestre deberán estar al tanto de problemas, como la potencial emergencia de respuestas inapropiadas durante estos entrenamientos.

Introduction

The global extinction crisis has led to more active population management. Reintroduction, which moves captive-born animals into their natural historical range (Beck et al. 1994), and translocation, which moves wild-caught animals from one natural location to another (Kleiman 1989), will become increasingly important tools for population and species management (Griffith et al. 1989; Magin et al. 1994). A high proportion of translocations and reintroductions have not been successful in establishing viable populations (Kleiman 1989; Griffith et al. 1989; MacMillan 1990; Beck et al. 1994; Wolf et al. 1996), and mortality caused by predation has been implicated in some cases (Beck et al. 1991; Short et al. 1992; Miller et al. 1994). There are several ways to address this problem—moving animals to predator-free areas, building predator-proof fences, and eradicating predators—all of which reduce contact with predators but none of which offers a long-term solution.

Recently, interest has grown in training naive animals to recognize predators. Preliminary results have been encouraging (Miller et al. 1994; Maloney & McLean 1995; McLean et al. 1996, 1999, 2001; Richards 1998). Nevertheless, the idea of teaching animals about predators is viewed skeptically by wildlife managers. Antipredator behavior must be expressed properly the first time it is required, so such responses are often thought to develop without experience. Yet a substantial empirical literature demonstrates that animals that initially show no fear can be conditioned to respond to live and model predators (e.g., for fish: Dill 1974; Magurran 1989; Chivers & Smith 1994*a*; for birds: Ellis et al. 1977; Curio 1988; Maloney & McLean 1995; for mammals: Mineka & Cook 1988). Training has also been used to enhance initially low-level antipredator responses (Miller et al. 1990; McLean et al. 1996).

We critically evaluate the usefulness of training animals to cope with predators as part of reintroduction and translocation programs, and we present a theoretical framework to help decision makers evaluate the likelihood of success. We also suggest potential antipredator training methods and highlight possible drawbacks of training procedures.

General Principles of Learning

Assessing the feasibility of training animals to cope with predators and designing effective methodologies requires some knowledge of basic learning mechanisms. Learning is defined as "an enduring change in the mechanisms of behavior that results from experience with environmental events" (Domjan & Burkhard 1986:12). Such changes often underpin adaptive responses to environmental variation. Over 90 years of research has demonstrated that learning is a widespread phenomenon: many species, from insects to primates, store environmental information and consequently alter their behavior (Dukas 1998).

Types of Learning

Psychologists have defined several classes of learning (Mackintosh 1983), and the principles that determine whether or not learning will occur are well established (Mackintosh 1974). Here, we are principally concerned with two types of associative learning traditionally referred to as classical conditioning (Pavlov 1927) and instrumental conditioning (Thorndike 1911), rather than with simpler processes such as habituation.

In classical conditioning, a biologically insignificant event, such as a light or a noise, that initially elicits no response (the conditioned stimulus, CS) is paired with a biologically significant event, such as food or an electric shock (the unconditioned stimulus, UCS). The UCS elicits an unlearned reflexive response, for instance salivating or eye blinking. After several paired presentations, the CS presented alone elicits the same response as the UCS.

Instrumental conditioning is a procedure in which the frequency of a response (R) is either increased by pairing its performance with a reinforcer or decreased by pairing its performance with a punishment. For example, the frequency with which a rat presses a lever increases if this action is immediately followed by the delivery of food.

Information Acquired

Despite considerable historical debate (Shettleworth 1998), it is now believed that animals learn to respond to a previously neutral stimulus (the CS) because it elicits a representation of a biologically meaningful event (the UCS; e.g., Holland 1990). Animals learn this association because the CS signals, or predicts, the occurrence of the UCS (Wagner et al. 1968). Similarly, in instrumental conditioning, animals learn an association between their behavior and its consequences (Dickinson 1994).

A further development in animal learning theory was initiated by the behavioral system approach (Hogan 1988). There is empirical evidence that behavior is "preorganized" into units that group actions with similar functions (such as sexual or feeding behavior) (Fanselow 1994; Timberlake 1994). The CS engages such preexisting behavioral units once it has been learned. For instance, if the CS predicts an aversive event, it will engage an animal's repertoire of defensive behaviors (Bolles 1970).

Finally, recent research has demonstrated that learning is not restricted to a CS-UCS association. Animals can learn a network of other predictive relationships. In particular, animals can learn the conditions under which the CS occurs. When animals learn about predictors of the CS, this is termed second-order learning.

Learning in Nature

Animals are predisposed both to learn things about their environment that are particularly relevant to their survival and to respond in adaptive ways. These distinct capabilities are the result of the interplay between natural selection operating over evolutionary time and the accumulation of experiences during individual lifetimes (Domjan & Galef 1983).

For example, learned taste aversion involves the relative avoidance of food that has previously generated gastrointestinal distress; the association is between food flavor or odor and illness. Food avoidance does not develop if smell or flavor is paired with electric shock (Garcia & Koelling 1966). Similarly, in instrumental conditioning, the phenomenon of autoshaping is characterized by the spontaneous appearance of behavior that is specifically related to the nature of the reinforcement (Jenkins & Moore 1973). If the UCS is an aversive event, such as an electric shock, animals exhibit species-specific defense reactions (SSDRs) (Bolles 1970), such as freezing.

Taste aversion and autoshaping demonstrate that animals have predispositions to learn preferentially some types of information. Furthermore, the nature of their responses is influenced by reinforcer characteristics. Training protocols may be more effective if they are designed to engage such natural predispositions to learn.

Learning about Predators

Antipredator behavior often must be functional when a predator is first encountered, but animals can improve their responses with experience. The majority of the evidence for such learning has been obtained with fish, but additional data have been collected in birds and mammals.

Many species of fish display unlearned fear responses when exposed to alarm substances released from the damaged skin of conspecifics. If the alarm substance is experimentally paired with the presentation of a neutral stimulus, individuals acquire an alarm response. For instance, Magurran (1989) demonstrated that naive European minnows (*Phoxinus phoxinus*) learned to respond fearfully to the odor of northern pike (*Esox lucius*) if they experienced it in the presence of minnow alarm substance. Similar results have been obtained with fathead minnows (*Pimephales promelas*; Chivers & Smith 1994*b*) and brook sticklebacks (*Culaea inconstans*; Chivers et al. 1995). Magurran (1989) showed that the learned response was greatest when the fish were conditioned to respond to a predator rather than to a nonpredator, indicating that the fish were predisposed to learn about chemical cues from predators. Field experiments show that such learning also occurs as a consequence of natural encounters, even when prey initially are predator-naive (Chivers & Smith 1995).

Similar data demonstrating that animals can learn to perceive a novel stimulus as dangerous have been obtained in birds. European Blackbirds (*Turdus merula*) display mobbing responses to a model Australian Honeyeater (*Philemon corniculatus*), a nonpredatory bird that initially elicited no response, once they have seen conspecifics mobbing it (Curio 1988). Qualitatively similar results were obtained when the model bird was replaced with an arbitrary object, but the magnitude of the conditioned mobbing was considerably weaker, suggesting that the birds were predisposed to learn about predator-like stimuli. Recent studies by McLean et al. (1999) have demonstrated that New Zealand Robins (*Petroica australis*) also learned to respond fearfully to a model predator when they viewed a model conspecific in an aggressive mobbing posture beside the predator and when they were chased by the model.

Mammals too can learn fear responses to novel objects. Juvenile rhesus monkeys (*Macaca mulatta*) became fearful of snakes after watching video recordings of their mothers reacting fearfully to them (Mineka & Cook 1988). In contrast, juveniles did not learn to fear a plastic flower when it was paired with antipredator behavior in the same way. Conditioned fear responses to model predators have also been obtained in infant squirrel monkeys (*Saimiri sciureus*) by presenting the models simultaneously with adult alarm calls (Herzog & Hopf 1984).

Learning about predators does not have to involve the acquisition of a fear response to an initially neutral stimulus, as in the above examples. It can simply involve quantitatively improving the efficiency of responses as a result of experience. For instance, Walther (1969) observed that Thomson's gazelles (*Gazella thomsoni*) increased flight distance (the distance at which they first moved away from an approaching predator) in areas where they were hunted. Similarly, Dill (1974) observed that zebra danios (*Brachydanio rerio*) increased flight distance after experience with a model predator. Animals also adjust their levels of vigilance in areas where predation pressure is high (Hunter & Skinner 1998).

More evidence that with experience animals can fine-tune their responses to predators comes from attempts to prepare captive-bred animals for reintroduction. Ellis et al. (1977) exposed juvenile Masked Bobwhites (*Colinus virginianus ridgwayi*) to dogs (*Canis familiaris*) and found that the birds rapidly learned when to hide, when to freeze, and when to flush. Similarly, Miller et al. (1990) showed that young Siberian polecats (*Mustela eversmanni*) took refuge in their burrows more quickly and increased the time spent hiding after viewing a model badger and simultaneously experiencing a mildly aversive stimulus (being shot at with elastic bands). Finally, rufous hare-wallabies (*Lagorchestes hirsutus*) increased their vigilance and hid more from a model fox (*Vulpes vulpes*) or cat (*Felis catus*) after the models were paired with either wallaby alarm signals or water squirts (McLean et al. 1996).

In summary, there is good evidence that many species can acquire fear responses to previously neutral stimuli. The consistent pattern from studies involving a wide taxonomic range (fish, birds, and mammals) is that cues from conspecifics trigger learning about predators and that adaptive biases guide this process. Animals can also improve quantitatively the efficiency of their responses as a result of experience with predators. These results provide strong support for the idea that training procedures may be successful if they are designed to take advantage of a species' natural mechanisms and predispositions to learn.

Components of Antipredator Behavior

Antipredator behavior reduces the probability of an individual or its kin being killed. It can be divided into two broad categories (Lima & Dill 1990): avoidance behaviors reduce the probability of encounters with predators, and response behaviors operate once a potential predator has been detected and function to avoid attack.

Avoiding predators requires potential prey to assess their environment and adjust behavior in both space and time as a function of predation risk (Lima & Dill 1990). This process involves the use of cues that indirectly predict the presence of predators. An animal that increases its vigilance in open areas (Cowlishaw 1997), preferentially feeds near cover (Brown 1988), or reduces its foraging on bright moonlit nights (Lockard & Owings 1974) behaves as though it "recognizes" that these environmental factors are associated with increased predation risk.

Responses are triggered once an animal detects a predator. These range from multipurpose behaviors, such as running, to sophisticated and specialized responses, such as alarm calling (Evans 1997). Specialized antipredator behavior is often displayed to a specific class of predators, such as raptors or carnivores (Macedonia & Evans 1993). When faced with a particular class of predator, animals must make a rapid decision and select the most effective response in their repertoire. Adequate responses imply the presence of recognition processes (Curio 1993).

The Evolution and Loss of Antipredator Behavior

Antipredator behavior can be viewed as falling along a continuum of "innateness." At one extreme, some defense behaviors are expressed fully on first encounter. The response of noctuid moths to bats provides a good example of such "hard-wired" antipredator behavior (Roeder & Treat 1961). Responses of this type are characteristically inflexible: they are elicited whenever the auditory nerve is stimulated by sounds of the appropriate frequency and amplitude. Most other antipredator behaviors to some extent depend on experience.

Responses to predators are often costly because they must be traded off with other activities, such as feeding, resting, or looking for mates (Lima & Dill 1990). For this reason, one effect of isolating prey from predators is the loss of formerly adaptive antipredator behavior (Berger 1998). Such changes may be partial (Coss 1999) and occur either over evolutionary time (i.e., over generations; Foster 1999; but see Coss 1999) or ontogenetic time (i.e., during an animal's life).

Teaching Antipredator Behavior

Isolation Type

The feasibility of antipredator training depends on the type of isolation (evolutionary or ontogenetic) and the specific components of antipredator behavior (avoidance, recognition, response) that have been lost (Fig. 1). We use the term *key predator* to identify the predator for which training is attempted.

Animals that have been isolated from predators for many generations will likely show modified antipredator behavior, although the rate of change and the types of behavior lost depend upon their cost and the degree to which the underlying perceptual and cognitive processes are shared with other behavioral traits (Coss 1999). Consequently, the degree of loss is unlikely to be simply proportional to the number of generations since isolation. We consider first the worst case, in which all components of antipredator behavior have been lost and there are no remaining species-specific defense reaction

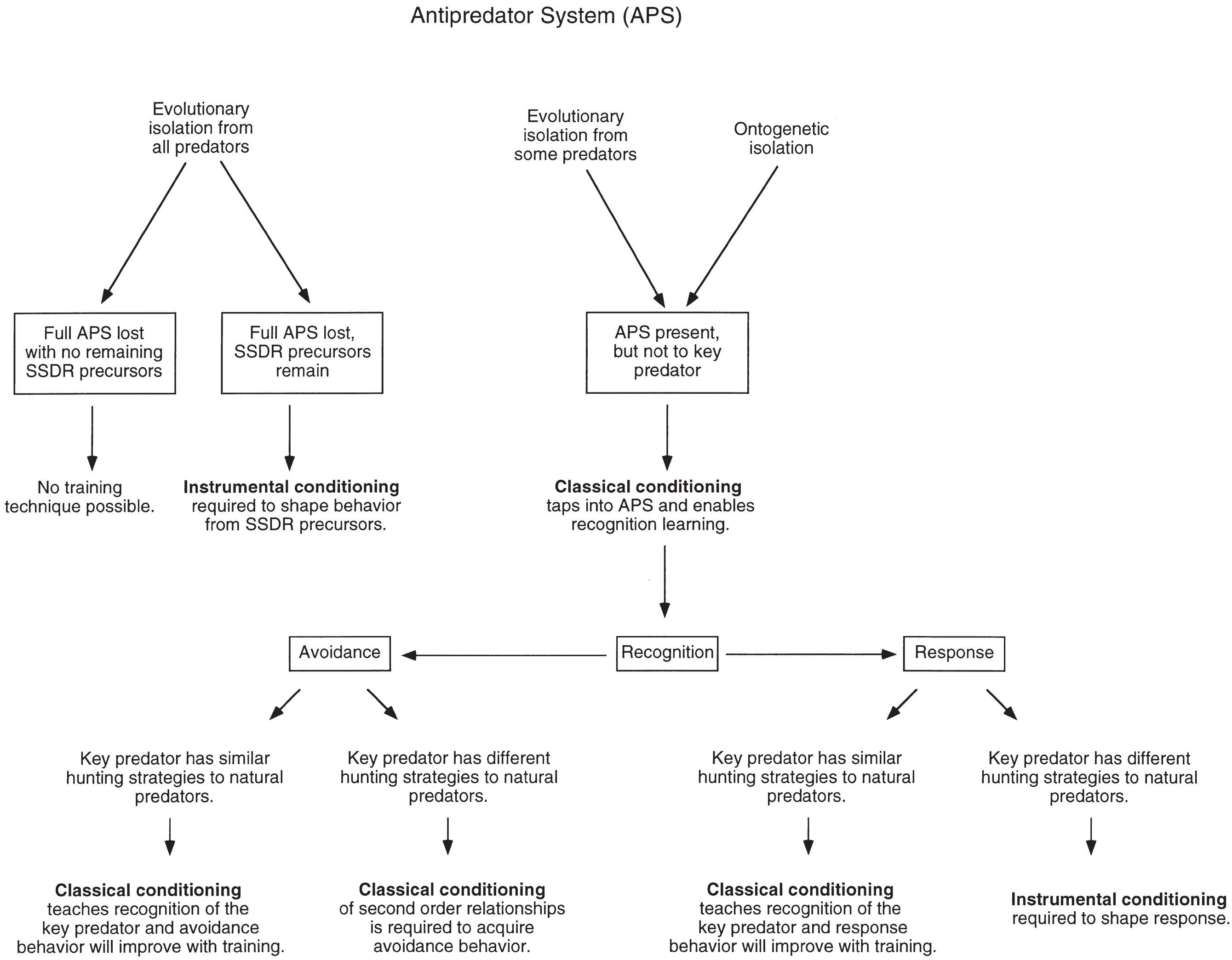

Figure 1. A theoretical framework for determining the likelihood of successful antipredator training. The degree to which animals have been isolated from predators influences the extent to which antipredator behavior is lost (top part). This in turn determines which training technique should be applied. Although instrumental conditioning to shape behaviors may be impractical, classical conditioning techniques are likely to be successful (see text for details). Species-specific defense reactions (SSDR) are innate defense behaviors, such as freezing and fleeing, that function to avoid events or situations that may decrease survival (after Bolles 1970).

(SSDR) precursors. We anticipate that it will not be possible to correct these deficits because neither classical nor instrumental training techniques can inculcate completely arbitrary and novel behaviors. In contrast, if some SSDR precursors are present, then instrumental conditioning techniques could, in principle, be used to generate adequate antipredator behavior by selectively reinforcing specific components. This technique underlies the training of circus animals. We suggest, however, that antipredator training will be impracticable in this case because instrumental conditioning is a time-consuming and labor-intensive training technique.

Animals that have been isolated from only some types of predation threat will likely show effective responses to extant predators, but not to the key predator. Similarly, animals that have been ontogenetically isolated (e.g., bred in captivity) may have the capacity to express competent antipredator behavior, but this might not occur without specific experience. These behavioral deficits should be easily rectified by classical conditioning because this technique engages existing behavioral systems.

Predator Recognition

For the purpose of illustration, we consider the problem of teaching prey to recognize a predator by sight. Our predictions, however, are not modality-specific: the same considerations apply to inducing animals to learn about olfactory or auditory information. Teaching or improving visual recognition skills is equivalent to teaching animals the visual features of a conditioned stimulus. It is well established that animals can learn the visual characteristics of both artificial and biologically significant stimuli, including simulated predators (Mineka & Cook 1988; Curio 1993), through classical conditioning procedures.

Antipredator Responses and Avoidance

Animals are predisposed to act in particular ways in response to certain situations. An aversive unconditioned stimulus always produces an SSDR. If the animal has several SSDRs in its repertoire, the one which is selected depends on the degree of threat perceived by the animal (Fanselow & Lester 1988). In this instance, the training difficulty depends on whether existing antipredator behavior is also an effective response to the key predator.

If the key predator's hunting strategies are similar to those of natural predators, than the selected SSDR will likely work. Furthermore, acquisition of a fear response to the key predator via training should produce quantitative changes in escape behaviors which improve their effectiveness, such as increased flight distance or decreased reaction time. Such changes rely on rapid identification of the predator. Similarly, avoidance behaviors for extant predators are likely to be effective for the key predator and training should further improve their effectiveness.

In contrast, where the key predator's hunting strategies are different from those of the natural predators, existing SSDRs and avoidance behaviors are unlikely to be effective. Response training would require the use of instrumental conditioning techniques to shape novel, complex behaviors from existing antipredator responses. We suggest that this approach is unlikely to be practical.

Similarly, for an animal to acquire efficient avoidance behavior, training would have to teach the cues that predict the appearance of the key predator (i.e., second-order relationships). Although such second-order conditioning is possible, we suggest it would be difficult to produce conditions in the training context that would adequately resemble those that predict the appearance of predators in a natural situation.

Cultural Transmission of Trained Antipredator Behavior

We conclude that antipredator training will be easier in some cases than in others, but before ruling out antipredator training as too difficult, wildlife managers should take into account another consideration. When trained animals are reintroduced into the wild, they potentially serve as models for predator-naive individuals, including their offspring and other adults, which may then acquire antipredator behavior. Cultural transmission of acquired antipredator behavior can amplify substantially the effects of the initial investment in pre-release training, ensuring that the intervention benefits a much larger number of animals over the short term and that its effects are apparent for generations. In species for which training individuals may be difficult and the manager is hesitant to undertake the task, the enhanced benefits of social transmission may outweigh the costs. Social transmission of acquired antipredator behavior is most likely to occur in species that produce altricial young and in all social species that exhibit delayed reproduction.

Training Techniques

We present some guidelines for potential training techniques based upon the animal learning principles summarized above. Although much of what follows is necessarily hypothetical, we provide clear predictions that should be amenable to empirical test.

Choosing a CS and a UCS

We suggest the use of model predators as CSs and frightening stimuli as UCSs. Live predators have serious drawbacks as training stimuli (Table 1). Model predators offer many advantages (Table 1), although there is always a concern that subjects will be more likely to habituate to repeated presentations because most models do not reproduce natural variation in properties such as speed and gait (Shalter 1984). Habituation can be abolished, however, by small trial-to-trial variations in the presentation method—by changing stimulus location, for example (Shalter 1984).

For a UCS to be effective, it must elicit the same motivational state in the subject as a naturally occurring predatory event. There are several possibilities (Table 1). Mildly unpleasant stimuli do not mimic a predatory event. Frightening UCSs more closely resemble those present in natural predatory situations and are likely to be more effective than startling stimuli, which elicit only a transient orienting response. Painful stimuli are also effective for aversive conditioning, but they are unlikely to be associated with a natural experience that would be survived and hence provide the opportunity for learning.

Number of Training Episodes Required

Nothing is known about predator learning in the wild, but it would seem maladaptive for it to require many experiences. Most attempts to condition animals to recognize predators in controlled conditions show that learning occurs after only one or two exposures to the paired CS and UCS (Magurran 1989; Suboski et al. 1990; Chivers & Smith 1994*a*, 1994*b*; Chivers et al. 1995; Maloney & McLean 1995; McLean et al. 1999). Curio (1998) suggests that a single traumatic experience, such as being stared at, stalked, or chased at full speed, may be an effi-

Table 1. Advantages and disadvantages of conditioned and unconditioned stimuli for training animals to cope with predators.

Stimulus	*Advantages*	*Disadvantages*
Conditioned (CS)		
live predator	richer stimulus many reinforcers inherent to the stimulus more appropriate for generalization to occur	risk of attack raises ethical concerns disease logistics less control over eliciting stimuli
model predator	no possibility of attack more control over eliciting stimuli fewer ethical concerns disease less likely no logistical problems	stimulus activates fewer sensory modalities fewer reinforcers inherent to the stimulus
Unconditioned (UCS)		
unpleasant stimulus (e.g., water squirts)	technically straightforward	does not mimic a predatory event
frightening stimulus (e.g., being chased, loud noises, or looming object)	closely associated with predatory event	technically difficult if a standardized stimulus is required
natural signals (e.g., alarm calls)	closely associated with predatory event potential to exploit species-specific learning mechanisms	some options are technically difficult
painful stimulus* (e.g., electric shock)	highly salient	unlikely to be associated with a survivable predatory event raises ethical concerns

**The psychological literature generally treats electric shock as a stimulus that elicits fear, but we concentrate here on initial effects.*

cient way to learn about predators because it engages species-typical predispositions to learn.

It is difficult to predict how many trials conditioning may take, but a good rule is likely to be the fewer the better. Too many presentations may cause habituation, which would counteract the beneficial effects of associative learning. Short training regimes are also the most economical and practical.

Individual Versus Social Training

Social training seems most likely to work for group-living species and/or species with prolonged parental care or delayed maturation. Social learning about predators has been demonstrated in blackbirds (Curio 1988) and rhesus monkeys (Mineka & Cook 1988). Whether social learning is more effective than individual learning remains an open question. For a group-living species, predation upon a member of the group may well be an important source of information about predators (Magurran 1989; Chivers et al. 1995). In both group-living and solitary species, young may learn some degree of predator avoidance or recognition from their mothers, especially in species with a strong or long-lasting parent-young bond. Young may also learn to fine-tune their responses, thus increasing their effectiveness, during their association with their mothers. Parental care has been shown to promote the development of efficient antipredator behavior in three-spined sticklebacks (*Gasterosteus aculeatus*; Tulley & Huntingford 1987).

Although a social learning training regime may be more effective for antipredator training in some species, it necessarily requires a trained individual who can act as a model for others. Wild-bred animals are a potential source of predator-experienced individuals, but bringing animals in from the wild to act as models is expensive and time-consuming. In the case of critically endangered species, it may be impossible. If models are unavailable, an individual training regime is the only option.

Training Age

Some types of learning can take place only during "sensitive periods." For instance, filial imprinting and song learning both occur early in life (Marler 1970; Bateson 1979). To our knowledge there have been no studies of whether learning about predators is restricted to a certain time in life, but it would seem maladaptive for animals to be capable of such learning only at specific developmental stages. There is evidence, however, that food preferences and predatory skills are learned during early development (Vargas & Anderson 1996, 1999). Consequently, juveniles may learn more easily about predators than adults do.

Ensuring that Animals Learn to Recognize the Attributes of the Key Predator

For training to enhance survival after release, animals must learn the general attributes of the key predator rather than specific things such as the location in which it is presented. Recognizing the key predator will also ensure that the animals do not generalize their responses to nonpredators that may share characteristics with the key predator (e.g., being a quadruped). Using several different models of the same key predator (e.g., in different body postures) and changing the presentation location between conditioning trials will ensure that the animals learn the characteristics of the key predator. This technique will also decrease the risk of habituation to the model.

Problems that May Occur with Training

Potential problems that may arise when animals are trained to cope with predators include a decrease in antipredator response over time, the learning of an inappropriate response, and the undetermined value of pre-release training.

An aversive stimulus that has acquired the power to elicit an antipredator response may lose its effect as a function of time. In nature, nothing is known about the maintenance of antipredator responses once they are learned because continued exposure to natural predators constantly reinforces the effects of earlier experience. In some experimental studies, animals have been shown to retain responses to learned stimuli for 2 (Chivers & Smith 1994*a*) to 3 months (Mineka & Cook 1988) after training. In other studies, animals no longer showed responses 30 days (Miller et al. 1990) to 8 months (McLean et al. 1996) after training. These particular studies dealt with the retention of antipredator behavior in the absence of the subsequent reinforcement that might occur naturally after release.

When animals are taught in captivity to recognize predators, housing facilities may provide inadequate conditions for appropriate responses to occur. For example, training animals in small enclosures may provide insufficient space for natural escape behavior and may inadvertently train the subjects to flee shorter distances (McLean 1997). For prey facing ambush predators, this may not be a problem because such predators typically give up pursuit as soon as they are detected (Hasson 1991). Ultimately, the appropriate antipredator response will be the behavior that gives the highest probability of survival when an animal is faced with a predator. It is difficult to predict what this behavior will be, although knowledge of the key predator's hunting strategies may provide some indications. If training can improve predator recognition, even partial responses may allow prey to survive their first encounters with a predator.

To our knowledge, only two studies have experimentally evaluated the effects of antipredator training on post-release survival. Ellis et al. (1977) found that pre-release training increased survival, whereas Miller et al. (1990) found no effect. Without more data from systematic studies, it is not possible to estimate the value of pre-release training with respect to survival.

Conclusions

Current pre-release preparation programs commonly train subjects to forage efficiently, move through complex spatial structures, and recognize appropriate shelter (Beck et al. 1991). We are optimistic that antipredator training will soon be an integral component of these programs.

Empirical evidence from both the psychological and ethological literature demonstrate that many animals not only improve the effectiveness of their antipredator behavior with experience but also learn about novel dangers. These results strongly support the idea that pre-release antipredator training programs should work. There is an urgent need for experimental antipredator training programs to evaluate the benefits of different training protocols and their effects on post-release survival. The challenge will be to design efficient training techniques that engage species-typical learning mechanisms and to identify and exploit the potential for cultural transmission.

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