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Abstract
Chemical repellents and other aversive strategies are the core of non-lethal wildlife management. These strategies typically depend on irritation (pain), conditioning, or fear for their effectiveness, and none is universally successful. Thus, conditioned food aversions deter browsing and foraging by deer (virginianus , O.hemionus)*, but are less useful with predators, because killing, not consumption, is the behavior of interest. Broadly speaking, the utility of non-lethal strategies is affected by number and density of wildlife species, availability of alternative foods, palatability and novelty of treated items, and intensity of pain, sickness, or fear used to establish avoidance. Some of the most promising areas for successful predation management are those involving a combination of strategies tailored to a specific problem. For example, behavioral-contingent auditory and visual stimuli coupled with presentations of electric shock or momentary vibration (via telemetry collars) could provide an effective and unambiguous cue for withdrawal. Non-lethal methods, however, are rarely stand-alone technologies. More often, integrated strategies, involving both lethal and non-lethal methods, are required for effective predation management.*

Predation Management

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*Chemical repellents and other aversive strategies are the core of non-lethal wildlife management. These strategies typically depend on irritation (pain), conditioning, or fear for their effectiveness, and none is universally successful. Thus, conditioned food aversions deter browsing and foraging by deer (*Odocoileus virginianus, O. hemionus*), but are less useful with predators, because killing, not consumption, is the behavior of interest. Broadly speaking, the utility of non-lethal strategies is affected by number and density of wildlife species, availability of alternative foods, palatability and novelty of treated items, and intensity of pain, sickness, or fear used to establish avoidance. Some of the most promising areas for successful predation management are those involving a combination of strategies tailored to a specific problem. For example, behavioral-contingent auditory and visual stimuli coupled with presentations of electric shock or momentary vibration (via telemetry collars) could provide an effective and unambiguous cue for withdrawal. Non-lethal methods, however, are rarely stand-alone technologies. More often, integrated strategies, involving both lethal and non-lethal methods, are required for effective predation management.*

Introduction
The survival or restoration of threatened and endangered species can depend on protection from predators (Witmer and Fall 1995; Witmer et al. 1996; Hecht and Nickerson 1999). Most of the relevant data for managing predation stem from research on the protection of livestock, crops, and commodities (Campbell et. al 1998; Fall and Jackson 1998). Deterring predators from prey is even more complex than protecting crops or other commodities because more is involved than food consumption (Fall 1990; Knowlton et al. 1999). Especially challenging is the development of non-lethal approaches. Demand for these strategies is increasing despite the fact that effective options remain virtually nonexistent. Repellents and other aversive techniques provide cases in point. If wildlife numbers are sufficiently high, or alternative foods are sufficiently scarce, repellents usually fail as a deterrent. Few demonstrably effective alternatives exist, and practical obstacles to the development of new materials are considerable. The present discussion will cover these topics by considering: mechanisms underlying the effectiveness of repellents and aversive agents, regulatory constraints that govern implementation of new methods, and the importance of employing multiple sensory modalities (i.e. visual and auditory cues, chemical and color cues) whenever non-lethal strategies are implemented.

Chemical repellents
Vertebrate chemical repellents are effective because they are irritating, cause sickness, or stimulate fear (Mason and Clark 1997). As a rule, these substances are most useful when they are applied directly to inert materials (e.g., prepared foods, fruits, grains, electrical wiring, irrigation hose; Werner et al. 1998). There is no good evidence that predators or other wildlife will avoid areas protected solely with border treatments. To illustrate the point, Renardine is commercially available for use with red fox (*Vulpes vulpes*) in the United Kingdom and

is being evaluated for use with coyotes (*Canis latrans*) in Canada (Martin and O'Brien 2000). (Mention of trade names and manufacturers is for identification only and does not imply endorsement by the authors or the U.S. Department of Agriculture.) The substance is bone tar oil dissolved in kerosene. The label advises that it should be applied liberally to pasture borders (on fence posts, etc.) to prevent predators from entering and attacking livestock. In testing with captive coyotes in the U.S., not only did Renardine fail to prevent entries into areas, but food adulterated with the material was eaten as rapidly as unadulterated food (Zemlicka and Mason 2000). This probably reflects the fact that sulfurous compounds in bone tar oil are attractive to coyotes (see **Fear** below).

Tastes, per se, are rarely effective feeding deterrents. While bitter and acidic substances can initially reduce the consumption of treated materials slightly (cf. Nolte et al.1994b), intake typically returns to baseline within a short period of time. Products that claim effectiveness solely because of a "bad" taste are doing so largely because humans find the taste repulsive. Some species of interest, including obligate carnivores such as the Felidae, have taste sensitivities that are greatly different than humans, including insensitivity to salt and sweet (Beauchamp and Mason 1991). In particular, products that contain denatonium derivatives (compounds very bitter to humans) are ineffective repellents, almost regardless of species (although bears, *Ursus horribilis* and *Ursus americanus*, may avoid denatonium in foods; G. Witmer, National Wildlife Research Center, personal communication) or method of application (e.g., topical spray, incorporated into products). Canids, in particular coyotes, are markedly insensitive to denatonium benzoate (Mason and McConnell 1997). Despite this lack of demonstrated utility, new veterinary and wildlife control products containing denatonium derivatives as the active ingredient are regularly offered for sale.

Irritation

Among the three types of chemical repellents, substances that cause sensory irritation or pain (the same neural receptors are involved) usually are most effective. This is because sensory pain leads to immediate withdrawal, independent of learning. Such avoidance does not habituate (diminish) for as long as the irritating stimulus is present. Moreover, taxonomic differences in irritant sensitivity between birds and mammals (Clark 1998a) permit the development of repellents with some degree of selectivity (e.g., Norman et al. 1992).

For mammals, strong irritants include capsaicin and capsicum oleo resins (i.e. the active ingredients in 'hot sauce' preparations; Norman et al. 1992), volatile chemicals like mustard oil (allyl isothiocyanate) and ammonia (Budavari et al. 1996), and non-volatile substances including astringent tannins such as quebracho (Swihart 1990). None of these substances repel birds (Mason and Clark 1997). Unfortunately, when irritant chemicals dissipate (e.g, by evaporation or photolysis), there is usually an immediate resumption of the unwanted behavior (Mason et al. 1985). A more important drawback is that intrataxonomic differences in irritant sensitivity are small. There are no known irritants that affect only some mammalian species but not others (e.g., coyotes but not sheep, *Ovis aries*, or humans).

This is not to say that irritants are completely ineffective deterrents to predation. Irritants can be effective when prey are completely infused. This strategy is relatively common among insects (e.g., Wickler 1968), amphibians, reptiles (e.g., Schmidt et al. 1989), and occasionally birds. One example is the Pitohui bird (*Pitohui dichrous*) that stores and uses toxicants from insects it ingests (Dumbacher et al. 1992). However, in the absence of complete infusion, repellency is easily circumvented. This explains the ineffectiveness of topically applied irritants as deterrents to predation. For example, sheep fitted with collars containing capsicum oleo resin were killed as readily as sheep without collars, despite the fact that attacking coyotes punctured collars and were exposed to high concentrations of the irritant (Burns and Mason 1996).

Fear

Sulfur compounds and volatile ammonium soaps of higher fatty acids induce what humans describe as fear in herbivores (Milunas et al. 1994). These substances underlie the effectiveness of predator urines and many commercial preparations used to repel browsing deer, rabbits (*Sylvilagus floridanus*), and rodents (Nolte et al. 1994a; Lewison et al. 1995; Mason et al. 1999). Typically, substances that frighten herbivores attract obligate carnivores and many omnivores (Kimball et al. 2000). There are no published data consistent with the belief that urine samples from one predator are actively avoided by other predators.

A disadvantage of fear-inducing chemicals is that animals readily habituate to their presence. The rate of habituation is largely dependent on the degree to which the chemical cue is associated with a risk of predation. When risk is low, habituation is rapid. Cues may even become attractive. For example, wolf (*Canis lupis*) urine applied as a repellent along roadways in winter can attract moose (*Alces

alces) and other ungulates that learn to associate the odor with the presence of road salt (T. Sullivan, personal communication).

Sickness (conditioned or learned avoidance)

When the ingestion of novel flavors or tastes by mammals or distinctively colored foods by birds is followed by sickness, a learned avoidance usually results (Beauchamp and Mason 1991). This effect is variously called conditioned (or learned) taste, food, or flavor avoidance (CA). CA can occur after a single aversive experience, particularly when the intensity of sickness is great and the taste, food, or flavor is new (Pelchat et al. 1983). As with other chemical repellents, substances that elicit CA are classified as pesticides by regulatory agencies, which typically require extensive data sets for registration prior to commercial use.

An extensive literature on theory, use and applications of CA is available (e.g., Riley and Tuck 1985). CA is the mechanism underlying the utility of commercial bird repellents containing methiocarb or anthraquinone (Conover 1982; Reidinger and Mason 1983), and commercial deer, rabbit, and rodent repellents containing thiram or ziram (Thomson 1995). CA using lithium chloride or estrogens to induce sickness has been investigated as a way to: reduce depredation by coyotes, resolve nuisance feeding by black bears (*Ursus americanus*; Ternent and Garshelis 1999), and curtail egg predation by raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), mongooses (*Herpestes nyula*), and ravens and crows (*Corvus spp.*; e.g., Nicolaus and Nellis 1987; Nicolaus et al. 1982, 1983; Semel and Nicolaus 1992). While evidence suggests that CA can be used to successfully manage nuisance complaints and egg depredation under some conditions, no lithium chloride- or estrogen-based method has been registered by the U.S. Environmental Protection Agency.

Gustavson (1974) conducted the first studies of CA as a management strategy with coyotes. His initial data were promising, generating considerable interest in the approach. Some investigators have reported success in preventing predation (Gustavson et al.1974; Ellins and Martin 1981; Gustavson et al. 1982; Forthman-Quick et al. 1985a, 1985b), while others have reported failure (Conover et al. 1977; Burns 1980; Burns and Connolly 1980; Bourne and Dorrance 1982; Burns 1983). Two large field trials conducted in Canada generated opposite results (Bourne and Dorrance 1982; Gustavson et al. 1982). Ten years after the most extensive field trial (Gustavson et al. 1982; Jelinski et al. 1983), survey responses of 52 participating ranchers indicated that while 54% initially considered lithium-chloride baiting "successful" or "somewhat successful," only one participant continued to use it (Conover and Kessler 1994). While no explanation for differences among studies is completely accepted, most arguments have focused on methods and experimental design (Bekoff 1975; Gustavson et al. 1975; Sterner and Shumake 1978; Horn 1983; Forthman-Quick et al.1985b; Conover 1997). Although CA may be a useful tool in some situations, its utility in predation management appears quite limited. Gustavson acknowledged that coyotes often resumed killing sheep shortly after conditioning, and ". . .once a coyote becomes a confirmed sheep-killer, perhaps it will be necessary to remove it from the population" (Gustavson et al. 1978). This could reflect the possibility that while CA may affect consumption of prey, the generalization of learning from consumption to killing is weak. There are no data on the use of CA to protect big game from predators, but considerable data relating to attempts at livestock protection provide little promise of potential utility.

Mechanical and electronic devices

There are many parallels between chemical repellents and mechanical or electronic devices that provoke fear or deliver painful or irritating stimulation. Scarecrows and their modern analogues have been widely examined with both birds and mammals. Studies typically report rapid habituation and variability among species and settings (Koehler et al. 1990; Bomford and O'Brien 1990). Nevertheless, at least for depredation management, there are promising results in certain situations. For example, Linhart et al. (1984) found that combinations of battery-operated strobe lights, sirens, and high frequency horns, placed on the edges of sheep pastures or bedgrounds and activated for short irregular intervals during night and early morning, stopped predation for 27 to 136 nights. Coyotes apparently remained active around the peripheries of the test pastures, but habituation to the devices was delayed by the irregular patterns of activation. More recently, using animal-activated or demand-performance frightening devices (Stevens et al. 2000), Shivik and Martin (in press) showed that motion-activated sirens were more effective than random sirens in delaying habituation by captive coyotes. Limited field trials of behavior-contingent, multistimulus (light and sound), systems to deter wolf predation are ongoing and appear promising (Shivik and Martin in press). Devices are activated when radio-collared wolves approach livestock production areas.

Application of a brief, non-lethal electric current has been widely studied as a means of deterring predators (Linhart et al. 1982; Sargeant and Arnold 1984). Linhart et al. (1976) found that coyotes fitted with collars that provided a contingent electric shock stopped attacks on rabbits for several months. More recently, commercial electronic dog training collars that deliver a mild static electrical discharge have been successfully tested as a deterrent to captive coyotes attacking sheep (Andelt et al. 1999). Manual activation of collars stopped attacks in progress and greatly reduced the probability of subsequent attacks. After one to three training bouts, coyotes avoided or retreated from sheep in tests four months after initial sessions. Shivik and Martin (in press) are testing similar collars, triggered by radio signals, with wolves. Animals wearing modified radio telemetry collars self-activate the static discharge when they approach within biting distance of a calf, providing an unambiguous cue for withdrawal. Collars utilizing momentary vibration (a sensation humans perceive as similar to static discharge) are also commercially available for dog training and could have similar application. Shivik and Martin (in press) describe efforts to develop auto-attaching collaring systems that utilize breakaway snare technology, which, if successful, would substantially reduce the cost of the method.

Ecological and behavioral consequences

At issue is effective adaptation of agricultural methods to endangered species protection, while avoiding negative ecological consequences (e.g., affecting wildlife other than target species) often associated with pest control efforts. Much attention has focused in the past on unintended consequences on non-target species of broad-spectrum pesticide use. However, all proposed methods of pest control, including those presumed to be non-lethal, must be carefully examined for effectiveness in specific situations, selectivity, and potential environmental and behavioral effects. For example, fences placed to exclude a predatory species may interrupt movement patterns or block migration routes of another. Selectivity for particular problem species, or individual animals causing predation, and avoidance of problems with primary or secondary effects on non-target animals are desirable features for all animal control tactics, especially those involving chemical applications. Classic examples of past successes in agriculture in finding such alternative approaches include: (1) replacing dynamiting of vampire bat (*Diphylla ecaudata*) caves to control paralytic cattle rabies with vampire bat-selective toxicant treatments (Mitchell 1986; Lewin 1986); and (2) replacing poisoned carcass bait stations as a method of coyote predation control with selective methods, such as Livestock Protection Collars (Connolly et al. 1978; Connolly 1993), den hunting (Till and Knowlton 1983), and aerial hunting (Connolly and O'Gara 1988; Wagner and Conover 1999; and Mason et al. in press).

Similarly, control programs aimed at protecting endangered species from predation must be planned strategically for specific areas to assure they achieve desired objectives. For example, Conner et al. (1998) found no relationship between annual coyote removal and levels of coyote predation on sheep on a California agricultural experiment station where non-lethal methods and non-selective coyote removal had not achieved desired reductions in predation after several years of effort. Sacks et al. (1999) found that adult territorial coyotes responsible for sheep killing in the area were less vulnerable to these control tactics than coyotes not involved in livestock predation. Ultimately, removal of specific depredating individuals by shooting and Livestock Protection Collars greatly reduced predation (Blejwas et al. in press). Livestock Protection Collars, however, have recently been banned in California by a ballot initiative, creating a need for development of effective alternative methods. In another situation, probably common in both agriculture and conservation predation management applications, feral cat (*Felis catus*) control efforts had to be implemented following a highly successful rodent control effort to protect nesting Dark-rumped petrels (*Pterodroma phaeopygia*) from predation in the Galapagos Islands (Cruz and Cruz 1987). When black rats (*Rattus rattus*) were removed as the primary predator, cats, which had been subsisting on rats, switched prey, diminishing initial increases in nesting success achieved by the rat control program. Although non-lethal tactics, if they become available, would be expected to be more benign and specific in such situations, both legal and ethical considerations require their careful assessment before implementation takes place.

Regulatory constraints

Obstacles to development of new materials and methods are considerable. These include a variety of constraints imposed by regulatory agencies. Even when new repellent technologies are uncovered, the path to commercial availability is long and can be very expensive (Fagerstone and Schafer 1998). For example, methyl anthranilate is one of two new bird repellents to become commercially available in the United States during the past 25 years. This natural substance is GRAS-listed (generally recognized as safe) with the U.S. Food and Drug Administration and it has been widely used as a grape flavoring in human and animal feeds since the turn of the century. Despite these facts, registration efforts to permit spraying of methyl anthranilate on turf to deter grazing Canada geese (*Branta canadensis*) took five years and cost $5 million (P.J. Voigt, R. J. Advantage, Inc., personal communication). While research on non-lethal methods for agricultural applications has been relatively well-supported, support needed to develop and evaluate methods for endangered species applications has been more elusive, usually coming in the form of small grants that cannot cover long term costs of developmental research to meet regulatory requirements.

Combinations of stimuli

Beauchamp (1997), among others, has suggested that the most effective strategy in development of repellents may be use of combinations of stimuli. The evidence is consistent with this suggestion (Clark 1998b). Thus, a mixture of capsaicin (irritation), thiram (sickness-based conditioned avoidance), and Big Game Repellent (sulfur-based fear) is a more effective deterrent to browsing white-tailed deer (*Odocoileus virginianus*) than any of these substances alone (M. Richmond, U.S. Geological Survey, Cornell University, personnel communication). Likewise, mixtures of methiocarb (sickness-based conditioned avoidance) and methyl anthranilate (irritation) are more effective than either substance alone. Cinnamaldehyde (Crocker and Perry 1990) and d-pulegone (Mason 1990) are both broadly effective vertebrate (bird and mammal) repellents that have both irritant and sickness-inducing effects.

Conclusion

Development and application of ecologically sound and effective repellents is dependent upon a knowledge of the sensory *Umwelt* of the species in question (von Uexkull 1934). Even when aversive strategies can be successfully applied, their continued utility will likely depend on application of other techniques in a mosaic of management strategies designed to meet requirements of a specific location, time, and context. Indeed, selective removal of wildlife (either in terms of local population suppression or removal of specific individuals) may often be prerequisite for effective implementation of non-lethal alternatives. For this reason, integrated strategies that incorporate both lethal and non-lethal methods will often be the most logical course for effective predation management. The high cost of development and application of alternative technologies for endangered species applications and the highly specific minor-use markets for such products, which limit private industry interest in the problem, present challenges to the emergence of new technologies needed to help assure effective recovery of species threatened by predation.

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