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August 1995

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Michael R. Conover

Utah State University, Logan, UT

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Behavioral Principles Governing Conditioned Food Aversions Based on Deception

Michael R. Conover, Jack Berryman Institute and Department of Fisheries and Wildlife,
Utah State University, Logan, UT 84322-5210

ABSTRACT

We often are unable to reduce wildlife damage because of our inability to apply a repellent directly to the plant, animal, or item that needs protection. Conditioned food aversions based on deception (CFABD) is one method that can be used to extend protection to these items (hereafter called models). In CFABD, the model is not treated; instead mimics of the model are created and then treated with a chemical that will sicken, but not kill, the animal consuming them. This approach is a reverse form of Batesian mimicry; normally the models are poisonous and the mimics are innocuous. Yet, the behavioral and ecological principles governing Batesian mimicry should also apply to CFABD. For instance, in both Batesian mimicry and CFABD, models and mimics must be indistinguishable to the predator before it will generalize an aversion from poisonous to palatable prey. Unfortunately, mimics have not been similar to models in many attempts to use CFABD, and, not surprisingly, the results have been negative. Based on our knowledge of Batesian mimicry, I hypothesize that if mimics and models are indistinguishable, animals will stop consuming models when the costs (in terms of illness) of making a mistake and consuming a poisonous mimic outweigh the nutritional benefits of consuming a model. This implies that key variables affecting the success of CFABD include illness severity, nutritional value of the model, ratio of mimics to models, and alternate sources of nutrients.

KEY WORDS

aversive conditioning, Batesian mimicry, Canis latrans, conditioned food aversions, coyote, lithium chloride, mimicry, predation, sheep predation, taste aversion, wildlife damage management

INTRODUCTION

Chemical repellents have been used for hundreds of years to protect food, crops, or other resources from wildlife damage. In these applications, repellents are applied directly to the vulnerable item and ingested with consumption of the food. Successful applications include reduction of wildlife damage to germinating seeds (Stickley and Guarino 1972), ripening small

fruit (Guarino et al. 1974, Stone et al. 1974, Conover 1985a) and lawns (Conover 1985b) and have led to the development of several repellents.

Apart from these successes, there are a plethora of problems caused by foraging wildlife for which we lack the technology to apply a chemical repellent in such a manner as to protect the item from predation without having a detrimental effect on the item itself. For instance, protecting pecans from squirrels is not an easy task. Attempts to spray pecans with a repellent have failed because squirrels do not eat the shell, but rather crack it open and eat the seed. To be effective, a way must be found to place the chemical in the seed itself. Furthermore, because the seed is intended for human consumption, the repellent has to be effective against squirrels but innocuous to humans. Lastly of course, approval must be obtained for the use of the chemical on human foods.

As another example, consider the problem of trying to protect a duck nest from predation. Spraying eggs with a repellent is ineffective because most predators do not eat the egg shells, but only the contents. Injecting a repellent into an egg would solve this problem, but we lack the technology to do so without killing the embryo. Even if this problem were overcome, there would still be the logistical task of finding duck nests so that we could spray them. Nest searches also are counterproductive; nests visited by humans are more likely to be depredated than unvisited nests, because predators often follow human trails.

There are many other examples, but the above should suffice to illustrate problems caused by wildlife predation or herbivory where the item needing protection cannot be directly treated with a repellent. Aversive conditioning can still be used to protect these items (hereafter called models), using a technique called conditioned food aversions based on deception (CFABD). With this approach, the model is left untreated. Rather, the aversive conditioning chemical (hereafter referred to as the chemical) is applied to a bait that mimics the model. CFABD work when the depredating animal finds the mimic, consumes it along with the aversive conditioning chemical, becomes ill, develops an aversion to the mimic, and finally generalizes its aversion to the model. In the last 2 decades, there have been several attempts to use CFABD to solve wildlife problems. This study examines these attempts and seeks broad behavioral principles that can explain why some attempts have succeeded while others have failed. This study also may prove useful as a guide for future research on CFABD.

BACKGROUND

CFABD were first used to teach coyotes not to kill sheep (Gustavson et al. 1974). They hypothesized that by distributing sheep carcasses and bait packages laced with the emetic agent, lithium chloride (LiCl), coyotes would consume them, become ill, develop an aversion to the taste of mutton, and stop killing live sheep and lambs. While some initial tests yielded positive results (Gustavson et al. 1974, 1976; Ellins et al. 1977), other tests did not (Conover et al. 1977, 1979; Griffiths et al. 1978; Burns 1980, 1983a,b; Burns and Connolly 1980; Conover 1982). The two large-scale field tests involving replicated samples also produced mixed results (Bourne and Dorrance 1982, Gustavson et al. 1982, Jelinski et al. 1983, Conover and Kessler 1994). Because of these conflicting results, this subject has become controversial (Burns and Connolly 1985, Ellins 1985, Forthman Quick et al. 1985a, 1985b; Lehner and Horn 1985, Wade 1985).

Other applications of CFABD, however, have been more successful and less controversial (Table 1). For instance, Conover (1989, 1990) taught raccoons (*Procyon lotor*) to stop eating untreated eggs by first giving them treated ones; Nicolaus et al. (1983) had similar success with American crows (*Corvus brachyrhynchos*). Woodchucks (*Marmota monax*) generalized an aversion from treated to untreated tomatoes (Swihart and Conover 1991), and livestock were taught not to graze certain plant species (Burritt and Provenza 1989, 1990; Lane et al. 1990).

BEHAVIORAL PRINCIPLES GOVERNING DECEPTION-BASED AVERSIVE CONDITIONING

Many animals, especially insects and amphibians, which have evolved chemical defenses against predation, also have conspicuous color patterns or behaviors that enhances the predator's ability to learn to avoid them (Jarvi et al. 1981, Sillen-Tullberg et al. 1982, Wiklund and Jarvi 1982). Other species, which lack these chemical defenses, have evolved color patterns and behaviors that mimic poisonous ones, a phenomenon known as Batesian mimicry (Brower 1969, Brower and Moffitt 1974, Fink and Brower 1981). One important assumption of the theory of Batesian mimicry is that these palatable prey obtain some degree of protection from predation by their mimicry, at least from those predators having experienced poisonous models. Several studies have supported this assumption (e.g., Brower 1958*a,b,c*; Duncan and Sheppard 1965; Morell and Turner 1970).

CFABD can be viewed as a reverse form of Batesian mimicry because in CFABD the models are innocuous and the mimics (chemically-treated baits) are poisonous. Nevertheless, the general ecological and behavioral principles that apply to Batesian mimicry should also apply to CFABD. Each of these principles will be discussed separately.

Precision of Mimicry

Some Batesian mimics are preyed upon because predators learn to detect subtle differences between them and the poisonous models (Sillen-Tullberg et al. 1982, Brower and Fink 1985). CFABD, too, are based on the premise that the depredating animal (or subject) cannot distinguish between those items which have been chemically treated (mimics) and those needing protection (models). Hence, an important assumption of CFABD are that the subject will generalize the aversion to both mimics and models. In cases where attempts to use CFABD have failed, there has not been a close match between models and mimics (Table 1). In this regard, using CFABD to teach coyotes not to kill sheep is difficult to accomplish because we lack the technology to make chemically-treated mimics that are similar to a live animal. Instead, sheep mimics were made by injecting chemicals into mutton baits wrapped in sheep fur or into sheep carcasses. Fortunately, a closer mimicry is possible for other wildlife damage management problems. For instance, a beehive can be easily mimicked, as can food handouts from humans, garbage cans, or nests (Table 1). Precise mimics of vegetable crops (Swihart and Conover 1991) or seeded fields (Avery 1989) can be created by treating part of a field while leaving the rest untreated.

For mimics to be indistinguishable from models, the chemical used to treat the mimic must be undetectable (Conover 1982). Otherwise, animals will avert from the treated mimics but not

Table 1. Wildlife Damage Management Problems for Which Deception-Based Aversive Conditioning Has Been Tested

Model	Wildlife Species	Test	Chemical	Results	References
Sheep & lambs	Canids	Both	LiCl	Mixed	References appear in the text
	Coyotes	Field	LiCl	Negative	Bourne and Dorrance (1982)
		Field	LiCl	Positive	Gustavson et al. (1982), Jelinski et al. (1983)
		Field	LiCl	Negative	Conover and Kessler (1994)
Chickens	Raccoons	Field	LiCl	Positive	Nicolaus et al. (1982)
Adult gulls & eggs	Foxes	Field	LiCl	Negative	Hanners and Southern (1980)
Eggs					
Odd color & taste	Crows	Field	Trimethacarb	Positive	Nicolaus et al. (1983)
		Field	Landrin	Positive	Dimmick and Nicolaus (1990)
	Mongoose	Both	Carbachol	Positive	Nicolaus and Nellis (1987)
Avian	Raccoons	Lab	Many	Mixed	Conover (1989)
		Lab	Emetine	Mixed	Conover (1990)
		Field	Estrogen	Positive	Semel and Nicolaus (1992)
	Mammalian predators	Field	LiCl	Negative	Sheaffer and Drobney (1986)
		Field	LiCl	Negative	Nicolaus et al. (1989b)
		Field	Estrogen	Positive	Nicolaus et al. (1989b)
		Lab	Several	Mixed	Avery and Decker (1994)
	Predator guild	Field	Trimethacarb	Positive	Nicolaus (1987)
Turtle	Raccoons	Both	LiCl	Negative	Hopkins and Murphy (1982)
Honey & apiaries	Bears	Lab	LiCl	Positive	Colvin (1975)
		Field	LiCl	Positive	Gilbert and Roy (1977)
		Field	Thiabendazole	Positive	Polson (1983)
Food handouts	Coyotes	Field	LiCl	Positive	Cornell and Cornely (1979)
Rice seed	Blackbirds & cowbirds	Lab	Methiocarb	Positive	Avery (1989)
Vegetables	Woodchucks	Lab	Emetine	Positive	Swihart and Conover (1991)
	Raccoons	Both	Emetine	Mixed	Conover (unpubl. data)
Plants					
Palatable shrubs	Lambs	Lab	LiCl	Positive	Burritt and Provenza (1989, 1990)
Grain & feed	Horses	Lab	Apomorphine	Mixed	Haupt et al. (1990)
	Ruminants	Lab	Apomorphine	Positive	Zahorik et al. (1990)
Larkspur	Cattle	Both	LiCl	Positive	Olsen et al. (1989), Lane et al. (1990)

from the models. For instance, Nicolaus et al. (1989c) reported that free-ranging predators learned to discriminate between salty-tasting eggs containing LiCl and untreated eggs, depredating 29% of the former and 86% of the latter. When the taste of LiCl was partially disguised by microencapsulating it or by substituting it for NaCl on normally salty food, aversions were more likely to be generalized to untreated sources of the same food (Conover 1982, 1984). Likewise, raccoons were more likely to generalize an aversion to the model when the chemicals used to treat the mimic were harder to detect (Conover 1989). Burns and Connolly (1980) and Nicolaus and Nellis (1987) have found that stronger aversions were established using lower dose rates than higher ones, either because the chemical was less detectable or more of the chemical was absorbed at the lower dose rate. Unfortunately, most poisons or emetic chemicals are detectable by taste or odor. Such is not surprising because evolution will favor poisonous prey that can convey information about their toxicity to a predator before they are consumed or injured (Wiklund and Sillen-Tullberg 1985). Likewise, evolution will also favor those predators that are able to detect a poison over those that cannot. For instance, some grosbeaks and orioles forage in the huge wintering aggregations of monarch butterflies by giving each captured monarch a taste test and only consuming those that are not poisonous (Fink and Brower 1981) or by consuming only those body parts that contain low levels of toxin (Brower and Fink 1985).

Searches for undetectable aversive conditioning agents which can be employed in CFABD have not been totally successful, although some chemicals have been identified which are harder to detect than those used previously (Conover 1989, Nicholas et al. 1989a). Still, CFABD cannot live up to their potential until truly undetectable chemicals are discovered.

Deception Discovery Rates

With Batesian mimicry, palatable mimics may be afforded some protection although they are not identical to the poisonous models, owing to the time a predator takes to learn to distinguish between models and mimics (Brower and Fink 1985). For the same reason, CFABD may be able to help solve wildlife damage problems, even without an exact match between mimic and model, if the problems are of short duration. Examples include protecting fields of ripening vegetables, the eggs of birds that are synchronous layers (such as gulls and terns), and the spawning runs of salmon.

The best candidate problems for CFABD are those caused by species that are solitary foragers. These species likely will take longer to learn the deception than those, such as red-winged blackbirds (*Agelaius phoeniceus*), that feed in groups and can learn foraging knowledge through social facilitation (Mason and Reidinger 1981, 1982; Mason et al. 1984). In the latter, knowledge of the deception will quickly spread through the group once one has learned the deception and starts to consume models. For instance, heifers conditioned to avoid larkspur (*Delphinium barbeyi*) lost their aversion after foraging with nonaverted heifers (Lane et al. 1990). Conover (1990) found that raccoons generalized an aversion from treated eggs to untreated eggs when they were presented sequentially but not when presented simultaneously. One explanation is that when models and mimics were presented simultaneously, raccoons made immediate comparisons between them and identified their subtle differences. Consequently, the raccoons averted from mimics but not models. Mongooses (*Herpestes auropunctatus*) also were able to pick out subtle taste differences between carbachol-treated and untreated eggs when both were distributed

simultaneously (Nicholas and Nellis 1987). These findings suggest that until we find undetectable chemicals, CFABD will be more likely to succeed if mimics are placed out before the models. This requires, of course, the ability to predict when and where problems will occur and respond proactively rather than trying to use CFABD in a reactive mode.

Costs–Benefits Ratio

If we can develop the technology to create mimics that are identical to models so that animals cannot distinguish between the two, depredating animals will be placed in a dilemma. Consider for instance, an attempt to protect turtle eggs from raccoons by placing out treated mimics. If a raccoon finds a nest and eats the eggs, it runs the risk that the eggs are mimics and that sickness will ensue. If it does not eat any, it runs the risk of missing a nutritious meal. Which decision the animal makes will depend upon three variables: the severity of the illness, the nutrient value of the model, the animal's nutritional needs, and the ratio of mimics to models. Each will be discussed individually.

Severity of Illness

If the risk of making an error and eating a treated mimic is low, the animal probably will take that risk. However, if the illness caused by eating a mimic is severe and long-lasting, the animal is less likely to take the chance of getting ill. Predation rates on the monarch butterfly (*Danaus plexippus*) populations, for example, vary with their toxicity (Calvert et al. 1979, Brower and Fink 1985). Aversive conditioning chemicals also vary in the severity of the illness they produce. For instance, Nicolaus and Nellis (1987) reported that 9 of 32 mongooses fed carbachol-treated eggs were killed by the drug; the survivors averted from eggs. In contrast, consumption of LiCl is rarely fatal and most predators appear well in a few hours; not surprisingly, most attempts to avert predators for consuming eggs using this chemical have failed (Hanners and Southern 1980, Hopkins and Murphy 1982, Sheaffer and Drobney 1986, Conover 1989).

Nutrient Value of the Model Versus the Nutritional Needs of the Animal

Animals are more likely to consume a novel food and risk becoming ill when they are nutritionally deficit and the food contains the needed nutrients. For instance, birds forage on toxic monarch butterflies and their Batesian mimics in the winter when they are easier to catch and alternate food supplies are lacking, but not in the summer (Fink and Brower 1981, Brower 1985). Houpt et al. (1990) reported that when illness followed ingestion, horses had more difficulty learning to avoid highly-palatable feeds than less palatable ones. If the nutrients in the model are irreplaceable, CFABD cannot be expected to change the animals' behavior. For instance, raccoons generalized an aversion from treated food to untreated sources of the same food as long as alternate foods were available, but did not do so when alternate foods were unavailable (Conover 1989). Thus, CFABD might be a viable option for those wildlife problems where alternate food supplies are abundant. Hence, I hypothesize that CFABD would be more likely to succeed for problems that occur during the growing season than during winter when alternate sources of food are scarce.

Ratio of Mimics to Models

In Batesian mimicry, the ratio of mimics to models is important (Brower and Fink 1985). Likewise, this ratio should be important in CFABD, because it influences the probability of an animal making either of two types of errors: passing up a nutritious meal or becoming sick. For instance, Conover (1989) was successful in teaching raccoons not to eat eggs only when mimics were placed out first, followed by models. In contrast, raccoons continued to consume both models and mimics when they were placed out simultaneously in equal ratio. In contrast, Avery (1989) found that an equal ratio of methiocarb-treated and untreated rice seed was as effective in reducing seed consumption as when all seeds were treated.

MANAGEMENT IMPLICATIONS

In summary, CFABD hold promise to help alleviate several wildlife damage problems. This approach has the advantage that the actual item that needs protection (the model) is not itself treated with a chemical; rather mimics of the model are created and distributed. It is these mimics that are chemically treated so that whenever a mimic is consumed, the animal gets sick. However, despite 20 years of research on CFABD, I am unaware of any wildlife damage problem where CFABD are commonly used to help alleviate the damage.

Perhaps some of the first uses of CFABD will be a partial repellent treatment of agricultural fields to protect them from birds (Avery 1989) or to teach livestock which plants to avoid (Burritt and Provenza 1989, 1990; Olsen et al. 1989; Houpt et al. 1990; Lane et al. 1990). For this latter problem, we have the advantage that the animals to be treated are captive and can easily be given either a drug injection or an orally administered drug. There are two applications for which it would be beneficial to teach livestock not to eat certain plants. First, in many parts of the United States, cattle are turned out on the range in the summer and have to forage by themselves. Such animals run the risk of becoming ill or dying from overeating poisonous plants before they have had an opportunity to learn of their toxic nature from postingestional feedback. To lessen this risk, a rancher could feed small amounts of the poisonous plant to the livestock while they are still penned up and follow that with an injection of LiCl, apomorphine, or other emetic agent.

The second application involves employing livestock in forest regeneration by having them consume competing vegetation in plots where young trees have already been planted. CFABD could be used to teach the livestock not to consume the planted trees by feeding them some of these trees followed by an injection of an emetic agent prior to their release.

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