ECOLOGICAL CONSIDERATIONS IN THE MANAGEMENT OF WILDLIFE DAMAGE

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Abstract: Strategies for managing wildlife damage may be divided into 3 broad categories: direct manipulation of populations, manipulation of behavioral or ecological traits of pest species, and manipulation of environmental features. For each of these categories, I review the importance of ecological considerations in determining the effectiveness of management strategies. Proper incorporation of ecological information is important to the success of management strategies in all 3 categories. I predict that future demands will increase for ecologically-based strategies that require minimal intervention, and for integration of management strategies that simultaneously address problems posed by both vertebrate and invertebrate pests. Several recent ecologically-based techniques are discussed, and pioneering efforts at comprehensive programs of integrated pest management are identified. Successful management of wildlife damage requires balancing ecological, sociological, and economic concerns. Attaining this balance in the future ultimately may depend upon our ability to develop new strategies of managing damage and to foster among the public an increased understanding of ecological processes pertaining to damage and its management.

Ecological considerations are of paramount importance to the wildlife professional in formulating strategies for managing wildlife populations. In fact, wildlife management in its simplest form may be defined as the application of ecological knowledge to vertebrate populations. My objectives are to provide an overview of how ecological considerations presently are or could be incorporated into strategies for management of wildlife damage and to identify some ecologically-based strategies which may prove useful in the future.

Effective strategies for reducing damage rely upon an understanding of the biological factors that lead to damage. Population size often is a principal determinant of the extent of damage. In addition, numerous behavioral and ecological attributes of individuals may influence the extent of damage, including foraging habits and food preferences, mobility, habitat requirements, and various aspects of behavior (Fig. 1). Three general approaches to managing damage can be identified within this framework. Damage may be reduced by: (1) direct manipulation of population levels; (2) indirectly, by manipulation of behavioral or autecological characteristics; or (3) indirectly, by manipulation of naturally occurring environmental features. I will summarize selected examples of these 3 approaches in the following sections.

DIRECT MANIPULATION OF POPULATIONS

The efficiency with which the abundance of a pest population can be reduced may be improved by basing management strategies on ecological and life history characteristics of the species. I use 2 examples to illustrate the potential impact of ecological factors on strategies designed to directly reduce population numbers.

Voles

Voles (Microtus) cause extensive damage to apple trees in orchards of eastern North America (Anthony and Fisher 1977, Ferguson 1980), typically by gnawing phloem and cambium tissue of the main stem and large lateral roots. Gnawing often reduces tree vigor and yield, and increases mortality of affected trees (Sullivan et al.1980, Richmond et al.1987). Various toxic baits commonly are used to reduce vole populations in orchards, including acute toxicants such as zinc phosphide and multipledose toxicants such as chlorophacinone and diphacinone.

Fig. 1. Some key components contributing to the type and extent of damage caused by a wildlife population. Although not shown in the diagram, ecological and behavioral characteristics of individuals may be altered by changes in population size.

Development and selection of effective rodenticides can be enhanced by considering several features associated with selection of food by voles. Like other rodents, voles presumably use sensory stimuli such as smell and taste to select their food, as well as associative learning (Garcia and Hankins 1975, Swihart 1990). Consequently, bait formulations that closely mimic a preferred taste presumably enhance the acceptability of a bait (Reidinger and Mason 1983). The degree to which

ingestion of a bait is associated with subsequent illness also can influence a compound's effectiveness. For instance, ingestion of a sublethal dose of zinc phosphide can result in subsequent bait shyness. And finally, many rodents are capable of generalizing learned aversions to similar-tasting foods (Nachman et a1.1977). Thus, in orchards where > 1 toxicant is applied, either baits with dissimilar taste features should be used, or in the case of sequential applications, a bait should be used that produces minimal bait shyness following consumption of a sublethal dose (Reidinger and Mason 1983).

Interspecific differences in ecological and life history traits may also affect the success of a strategy for controlling voles. Forinstance,both meadow voles (Microtuspennsylvanicus) and pine voles (M. pinetorum) inhabit eastern orchards. However, life history traits differ markedly between the species: meadow voles produce larger litters (meadow vole X = 5.0, pine vole x = 2.2; Keller 1985), reproduce at an earlier age (Reich 1981, Schadler and Butterstein 1979), and have a shorter gestation period than pine voles (Kirkpatrick and Valentine 1970, Reich 1981). Reproductive rates of meadow voles apparently are not density dependent, whereas reproduction of young female pine voles is pheromonally suppressed by adult females (Anonymous 1985). Overall, then, meadow voles have a greater biotic potential than pine voles. Meadow voles also move over more

voles (Miller and Getz 1969, FitzGerald and Madison 1983, Getz 1985, Swihart et al. 1988). Pine voles are primarily fossorial, whereas meadow voles travel along surface runways (Wolff 1985). In addition, meadow voles expand their movements under snow cover (Madison and McShea 1987). Coupled with their high biotic potential, these traits suggest that meadow voles are capable of recolonizing and repopulating treated orchards more rapidly than pine voles. From these data we can infer that: (1) similar reductions in populations of pine and meadow voles will have a longer-lasting effect on the former, and (2) a single application of toxic bait in autumn will be less effective at reducing vole problems in orchards where meadow *voles are abundant in* adjacent habitats, unless these habitats also ace treated

Differences in social structure and foraging *behavior* also can influence the effectiveness of a particular control strategy. Pine voles are monogamous and live in extended family units (FitzGerald and Madison 1983), whereas meadow voles are polygynous and females are territorial during the breeding season (Madison 1980, Boonstra and Rodd 1983). Moreover, pine voles have a strongly developed caching instinct (Byers et

al. 1976). Caching promotes repeated feeding on baits b members f f il

Woodchucks (Marmota monax) cause damage in agricultural areas by feeding on row crops and garden plantings, by gnawing on young fruit trees, and by constructing burrows that

are hazardous to farm machinery, livestock, and laborers. Gas cartridges placed in burrows often are used to reduce woodchuck populations in problem areas (Phillips et al. 1987).

The effectiveness of gas cartridges can be enhanced by taking into account several ecological and behavioral attributes of woodchucks. For instance, the temporal distribution of above ground activity of woodchucks is multimodal, with peaks in early morning, early-afternoon, and early-evening hours (Bronson 1962, Merriam 1966), although more lateevening activity (2100-2200 hr) than early-morning activity (0700-0800 hr) was noted by Merriam (1966). Clearly, selecting treatment periods when most woodchucks are below ground is advisable. Treatment of burrows during spring also can increase efficiency because burrows are not yet concealed by vegetation, and because juveniles have not yet dispersed from natal burrows.

Size of burrows also may influence success of a fumigation program. Woodchuck burrows can differ dramatically in size and number of entrances (Henderson and Gilbert 1978), and woodchucks are less susceptible to fumigation when occupying larger burrow systems with multiple entrances (Dolbeer et al. 1991). Hence, > 1 cartridge may be required for successful fumig'atio'n of largeburrows.

Finally, movements and habitat use of woodchucks may be influential in determining the long-term effectiveness of a management program relying primarily on gas cartridges. In addition to using burrows in cultivated fields, meadows, and orchards, woodchucks often use burrows in woods, along fencerows, and in other nonagricultural habitats adjacent to these sites (Grizzell 1955, Henderson and Gilbert 1978). For instance, females use burrows in woodland edges dispropor-tionately often as natal sites, and adults continue to use these areas heavily after the breeding season (Swihart 1992). Typi-cally, only 1 woodchuck occupies a burrow at any given time during the postbreeding season, but considerable time-sharing of *over* burrows occurs (swihart 1992) woodchucks also range

fairly large areas that usually encompass several habitat

types, and their ability to recolonize sites is quite good (Davis et al. 1964). Consequently, *the effectiveness of a fumigation* program is dependent upon treatmentofadjacentnonagriculturdl areas, monitoring of treated burrows, and the extent to which treated areas are embedded within a mosaic of untreated areas that serve as source populations from which recolonization can occur (de Vos and Merrill 1957, Davis et a1.1964, Byers 1980, Dolbeer et al. 1991).

MANIPULATION OF BEHAVIORAL OR ECOLOGICAL CHARACTERISTICS

Most damage problems are associated with wildlife feeding on domesticated plants or animals. Crops prone to *damage*

typically are highly palatable, abundant, and easily accessible to wildlife. Nonetheless, wildlife species generally also feed upon a wide array of naturally occurring foods. Efficient foraging thus entails maximization of nutritional and/or caloric

benefits derived from foods relative to costs of foraging and ingestion that might lower the value of a type of food by lowering an individual's probability of survival (Stephens and Krebs 1986, Howe and Westley 1988).

One strategy for reducing crop damage relies upon manipulation of behavioral or ecological characteristics so that the actual or perceived benefit:cost ratio of feeding on a crop is reduced. At least 3 general variations of this strategy exist (Table 1; cf. Conover 1981). In the first, access to a crop is prevented or delayed using a physical barrier. A second variation involves application of chemicals that reduce the value of a food either by reducing its palatability (repellents) or by producing postingestional illness that is subsequently associated with the food item (aversive conditioning). A third variation increases the perceived cost of obtaining a food item by using fear-evoking stimuli. Examples of the latter 2 approaches are presented below.

Chemical Repellents and Aversive-Conditioning Compounds

Numerous chemical repellents are available commercially, and several have been tested for their ability to reduce feeding damage by wildlife (Table 1). Mostrepellents reduce palatability of treated crops by making them either distasteful or malodorous, although the sensory modality through which repellency is effected is difficult to determine (Garcia and Rusiniak 1980). For large herbivores such as deer *(Odocoileus),* consistent reductions in browsing damage to woody plants have been achieved usingputrescent egg solids (e.g., Big GameRepellentR) or eggs (Palmer et a1.1983, Conover 1987a, DeYoe and Schaap 1987, Swihart and Conover 1990, Andelt et al. 1991). Consumption of corn seed and apple twigs by small mammals also can be reduced by using repellents such as thiram or methiocarb (Luke and Snetsinger 1975, Zurcheret a1.1983, Swihart 1990).

At least 2 problems are associated with chemical repellents. First, repellents may lower the palatability of a food item without reducing its actual nutritional value. Consequently, a repellent's effectiveness may vary as a function of the density of a pest population, the presence of alternate foods, and the innate palatability of the target crop (Swihart and Conover 1988, 1990). Second, costs of applying repellents may be prohibitive on all but the most highly-valued crops. For instance, costs of commercial formulations of putrescent egg solids probably limit their use as deer repellents (Andelt et al. 1991). Because of cost considerations, moderately effective and inexpensive deer repellents such as HinderR may be more practicable (Conover 1984, Andelt et al. 1991), particularly if used in conjunction with other management strategies.

Several aversive conditioning agents have been identified, including lithium chloride (Gustavson et a1.1974), methiocarb (Stickley and Guarino 1972, Guarino et al. 1974), and emetine dihydrochloride (Conover 1989). The major attraction of aversive conditioning agents is their potential to protect an untreated crop. An aversion is achieved by conditioning

wildlife to associate the crop with gastrointestinal illness produced by prior ingestion of the compound while feeding on a treated portion of the crop.

Table 1. Examples of 3 general approaches to manipulation of ecological and behavioral characteristics as a means of reduc ing damage caused by wildlife.

Approach Example	Target Group	Reference
Physical *Barriers*		
Fences	Marsupialia' Lagomorpha Rodentia Artiodactyla	McICillop and Sibly (1988); Mayer and Ryan (1991)
Tree guards	Deer, Elk Voles	Schaap and DeYoe (1986); O'Brien (1983)
Bags, tape, netting	Raccoons Birds	Conover (1987b) Foster (1979)
***Reducing Food* Quality Via Chemicals**		
Repellents	Voles Ground squirrels Deer mice Deer Starlings	Swihart (1990); Zurcher et al. (1983); Holm et al. (1988); Conover (1984) Clark and Shah *(1991)*
Aversive agents Crows	Canada geese Coyotes Raccoons Woodchucks	Conover *(1985, 1990);* Nicolaus et al. *(1983);* Gustavson et al. *(1974);* Swihart and Conover *(1990)*
Increasing Costs Via Fear-Evoking Agents		
Livestock-guarding dogs	Coyotes	Green et al. *(1984)*
Auditory devices	Birds	Booth *(1983)*
Predator odors	Small mammals Snowshoe pares Woodchucks Deer	Sullivan et al. *(1985a,b, 1988a);* Swihart *(1991)* Swihart et al. *(1991)*

' See reference for complete list of species managed within each order.

Aversive conditioning agents apparently perform better with some species than with others. For instance, methiocarb creates a conditioned aversion by Canada geese *(Branta canadensis) to* grass (Conover 1985), yet deer mice (Peromyscus maniculatus) fed seeds of corn and meadow voles fed apple twigs failed to generalize aversions subsequent to ingestion of food treated with methiocarb (Holm et al. 1988, Swihart 1990). Intraspecific variability in performance also occurs. Studies of lithium chloride-inducedaversiveconditioningofcoyotes(Cams latrans) have produced both positive and negative results (Gustavson et al. 1974, Conover et al. 1977, Bums 1980).

In field trials, raccoons (Procyon lotor) avoided untreated eggs if they previously had ingested eggs treated with emetine dihydrochloride (Conover 1990). Thus, waterfowl eggs could be protected from predation by raccoons, but only if sufficient numbers of treated eggs are ingested to induce an aversion before the onset of laying. Such a conditioning program does not entail reductions in predator populations. However, costs will be proportional to the abundance of predators because more treated eggs (and hence more labor) will be required to avert the same proportion of the population. Consequently, the cost-effectiveness of an aversive conditioning program will be lower than a program of predator control (Conover 1990).

Fear-Evoking Stimuli

Increasing the actual or perceived risk associated with feeding in the vicinity of a crop can reduce a pest species' activity in an area, and hence reduce the amount of damage. Livestock-guarding dogs are an example of increasing actual risk; they can reduce or eliminate sheep predation by coyotes (Green et al. 1984).

Pest species also may respond aversively to the presence of predator odors. Mammalian prey species readily recognize and avoid odors of sympatric predators (Fink 1972, Stoddart 1980). Experiments have demonstrated that predator odors reduce damage caused by several species of mammalian herbivores, including snowshoe bares *(Lepus americanus)* (Sullivan et al. 1985a, Sullivan 19S6), voles (Sullivan et al. 1988a), pocket gophers (Thomomys *talpoides)* (Sullivan et al. 1988b), woodchucks (Swihart 1991), and deer (Melchiors and Leslie 1985, Sullivan et al. 1985b, Swihart et al. 1991). Nearly all of these studies examined feeding responses of prey on woody plants. Few studies have examined the effectiveness of predator odors in reducing consumption of herbaceous plants or other food types (Muller-Schwarte 1972).

The degree to which a pest species responds aversively to a predator's scent probably is dependent upon the length of the evolutionary association between the 2 species as well as the intensity of the predator-prey relationship during the species' association (Swihartetal.1991). Cultural transmissionbyprey of aversive responses to predator odors also may be important.

Habituation to predator odors may limit the long-term effectiveness of this technique. However, minimal habituation of prey to predator odors has been demonstrated thus far. Innate responses to fear-evoking stimuli should not habituate (MullerSchwarze 1974), and available evidence indicates that aversive responses in some species apparently have a genetic *component* (Muller-Schwarze 1972, Gorman 1984). Nonetheless, occasional reinforcement would seem desirable, especially in areas where suitable alternative foods are in short supply.

sive than Big Game RepellentR or thiram (Andelt et al. 1991) The cost-effectiveness of predator odors could possibly bi enhanced if the repellent components of urine, feces, or glaa dular secretions could be identified and synthesized. In the lash decade, work has focused primarily on identification of repellent components of red fox *(Vulpes vulpes)* urine and mustelid *(Mustela spp.)* anal gland secretions (Sullivan and Crump 1984, 1986), and some preliminary work on bobcat (Lynx rufus) urine (Mattina et a1.1991).

MANIPULATION OF NATURALLY OCCURRING ENVIRONMENTAL FEATURES

Alteration of a pest species' physical or biotic environment provides another ecologically-based means by which damage may be reduced (Table 2). Alteration of vegetation may reduce damage by reducing a habitat's attractiveness or suitability for the pest species, or by providing alternative sources of food In certain situations, enhancement of predator numbers also may reduce the damage caused by a prey species (Sullivan et al. 1988c). The following examples focus on vegetative manipulation because vegetation is more commonly manipulated than other features of the environment.

Nuisance Canada Geese

Nonmigratory populations of Canada geese often eat grass growing in parks, and on lawns, golf courses, and playing fields. Geese frequently become nuisances in these areas because their feces accumulate there (Conover and Chasko 1985). Many nuisance sites occur in urban or suburban settings, and hunting at these sites often is prohibited by local ordinances (Conover and Chasko 1985). Methiocarb effectively repels geese from grazing sites (Conover 1985), but it is no longer registered for this use in the United States. Consequently, the feasibility of manipulating vegetation as a means of reducing nuisance goose problems recently was examined (Conover 1991, Conover and kania 1991).

Canada geese avoid eating ground cover plants such as common periwinkle *(Vinca minor),* Japanese pachysandra *(Pachysandra terminalis),* and English *ivy (Hedera helix).* Among grass species, feeding preferences were negatively correlated with the toughness of grass blades (Conover 1991). Thus, selecting unpalatable plants as ground cover may reduce goose numbers at a site. The practicality of ground cover management depends in part on landowner preferences for turf and on the severity of the goose problem. In many instances, landowners would be unwilling to replace bluegrass *(Poa pratensis)* with a coarser, less-palatable grass such as tall fescue *(Festuca arundinaceae).* However, water company managers or others with severe goose problems may be less hesitant to switch to a less-attractive, but unpalatable, ground cover (Conover 1991).

The economic practicality of predator odors has received Other vegetative modifications can also make a site less little attention. Coyote urine was more expensive, on a volu- suitable for geese. For instance, geese prefer sites with open, metric basis, than HinderR or eggs, although it was less expen- relatively unobstructed views where predators can easily be

detected (Conover and Kania 1991). Thus, planting bushes and hedges around a lawn may limit the view of geese sufficiently to discourage them from using the site.

Table 2. Examples of approaches to reducing wildlife damage that require manipulation of naturally occurring environments features.

Approach	Target Group	Reference
Cultural		
Using unpal-stable plants	Voles Deer Canada geese	Lewis et al. (1983); Conover and Kania (1988); Conover (1991;
Management of peripheral habitat	Voles Woodchucks Waterfowl	Cummins et al. (1984) Swihart (1992) Conover and Kania (1991)
Genetically resistant plants	Voles Deer Snowshoe bares Birds	Cummins et al. (1983) Dimock et al. (1976) Bullard (1988)
Alternative Foods	Deer mice Blackbirds	Sullivan and Sullivan (1982b) Cummings et al. (1987)
Enhancement of Predation	Voles	Sullivan et al. (1988c)

Seed Predation by Deer Mice

Seed predation by deer mice *(Peromyscus maniculatus)* and other small mammals can hamper reforestation projects on cutover lands (Radwan 1970, Sullivan 1979x). Deer mice apparently use olfaction to detect seeds (Howard and Cole 1967), and greater densities of deer mice result in reduced survival of seeds (Sullivan and Sullivan 1982x). Toxicants are of limited utility because deer mice quickly recolonize depopulated areas (Sullivan 1979x).

Distribution of sunflower seeds during seeding of conifers on cutover lands can significantly increase survival of conifer seeds by providing deer mice with an alternative food. For instance, a 7:1 ratio of sunflower seeds:Douglas fir *(Pseudotsuga menziesii)* seeds increased survival of Douglas fir seeds at 2 weeks postseeding from 5% (no sunflower seeds) to 70% (Sullivan 1979b). In a similar experiment, 3-week survival of lodgepole pine *(Pines contorts)* seeds was increased from 1215% to 50-82% when mixed in a 2:1 pine seed: sunflower seed ratio (Sullivan and Sullivan 1982x). Conifer seed can germinate 2-4 weeks after seeding; thus, provision of alternate foods may significantly enhance efforts at direct seeding. Success of direct seeding programs also may be enhanced by seeding in

late winter to early spring when small mammal populations are low and soil moisture is adequate (Sullivan and Sullivan 1982b). Although alternate foods may exacerbate problems if they result in increased numbers of a pest species, numbers of deer mice in the preceding experiment never exceeded numbers found on control grids containing no sunflower seeds (Sullivan and Sullivan 1982x).

FUTURE DIRECTIONS

As illustrated by the examples above, aspects of ecology figure prominently in each of the 3 general approaches to managing wildlife damage. Nonetheless, considerable room exists for improvement and innovation. For instance, new strategies of reducing population levels via chemical contraception appear promising for reducing problems caused by some species in circumstances where current methods of control are not feasible (German 1985, Kirkpatrick et x1.1990, Bickle et x1.1991, Garrott 1991), and the utility of various methods of chemical contraception will depend in part on behavioral and ecological factors (Turner and Kirkpatrick 1991). Modification of prey behavior using semiochemicals also appears promising as a potential strategy for managing damage caused by herbivorous mammals. Advances have been made in the development of devices enabling a slow, controlled release of predator odors (Sullivan et al. 1990x, b), and predator odors also can be effective secondarily by attracting additional predators to an area (Sullivan et al. 1988c). Molecular modeling of chemicals shows promise as a means of developing more effective repellents (Clark and Shah 1991). Manipulation of vegetation may, in the future, incorporate newly acquired information regarding defenses found in woody and herbaceous plants. For example, chemical defenses of woody plants against herbivory vary with respect to historical browsing pressure (Bryant et x1.1989) and latitude (Swihart et x1.1990). Consequently, selection of nursery stock from areas with greater levels of chemical defense may reduce damage by resident herbivores.

A single method of control rarely is capable of eliminating a problem caused by a wildlife species. Moreover, most agricultural operations are beset with >1 pest, both invertebrates and vertebrates. Coordination of control programs to reduce pesticide use and increase efficiency makes sense from environmental and economic perspectives. Truly integrated pest management programs that include vertebrates as well as invertebrates currently arereceiving someattention, andfurther emphasis is deserved. Dolbeer (1990) stressed an integrated approach to reducing red-winged blackbird *(Agelaius phoeniceus)* damage to field corn that included use of birdresistant cultivars of corn, frightening devices, alternative feeding sites, and insect management in corn fields. A comprehensive management program relying on minimal pesticide use recently was shown to be a cost-effective means of controlling vertebrate and invertebrate pests in a small commercial apple orchard (Prokopy 1991). Vegetation management, repellents, and frightening devices were used to reduce problems caused by voles, deer, and birds, respectively.

ADDITIONAL CONSIDERATIONS

Consideration of nonecological factors forms an important component of the decision-making processregarding strategies of managing wildlife damage. A principal objective in the management of wildlife damage is to reduce damage to levels that are economically acceptable while simultaneously mini mizing adverse impacts on existing biotic systems (tiles 1980). As we have seen, the methods of obtaining such an objective are rooted in ecology. However, quantifying inherently subjective terms such as "tolerable" and "adverse impact" often is not entirely, or even primarily, based on ecological information. Rather, consideration of sociological and economic concerns fre-quently plays an important role in quantifying these terms (Pomerantz et a1.1986, Owens 1992, Timm 1992). In addition, an inadequate understanding of wildlife damage **and its man** agement contributes to public misperception of management strategies. Fortunately, education and open communication often are capable of correcting public misperceptions regarding management of wildlife damage (Timm and Schemnitz 1988, Johnson 1990). An enhanced understanding of the ecological basis of management strategies will enable decision-makers to balance moreequably social, economic, andecological concerns.

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