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Ecological Management of Vertebrate Pests in Agricultural Systems

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ABSTRACT

Managing vertebrate pests has been a neglected topic of research in sustainable agriculture. Conventional approaches, often reactionary rather than preventative, have failed to provide sustainable solutions. Indeed, conventional control through density reduction often involves battling natural ecological processes. Agricultural practices may improve habitat quality for vertebrates that then become pests. Density reduction, but without a concomitant reduction in carrying capacity, may stimulate density-dependent reproduction and survival, rapid recolonization, or both; thus, vertebrate pests often show remarkable resilience in recovering from density reduction. Effective management of vertebrate pests in agricultural systems should incorporate knowledge of temporal and spatial dynamics of pest species.

We review several approaches for managing vertebrate pests that might be successful in sustainable agriculture. Habitat quality, and thus carrying capacity, for pests might be reduced by modifying cultural systems; repellent or diversionary crops also can be effective. Predators, either real or simulated, might reduce the density or alter the behaviour or distribution of pests. A variety of scaring devices may protect crops or commodities, although protection is usually temporary and is ineffective for some pest species. Chemical repellents, either synthetic or naturally-occurring, can discourage pests. Physical exclusionary devices can protect individual plants or entire fields, although expense often is high. Pest damage, especially from birds, can be reduced by relatively modest changes in crop phenology, and pest-resistant cultivars have been developed for several agricultural crops. Preventative pest management should employ forecasting, use a landscape approach, and incorporate cost-benefit analyses.

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INTRODUCTION

The sustainability of agricultural systems is increasingly an issue of international importance. A sustainable agricultural system provides: (1) sufficient quantity and quality of food and fiber for present and future human populations; (2) profitability to the grower; and (3) a conservative use of resources (modified from Geng *et al.*, 1990, and defined by 133 farmers *c.f.* in Grieshop & Raj, 1992). If any of these criteria are neglected, then agriculture will not be sustainable, whether at the scale of the farm or the agricultural landscape.

By not responding until a problem is recognized, conventional agriculture has relied on curative or reactionary solutions (Hill, 1990). Conventional agriculture has been based on the belief that modern technology can cure problems when they arise. Pests, defined as those species that cause significant economic damage, can be a major problem for agriculture (Putman, 1989). The rise of Integrated Pest Management (IPM) over the last two decades has revolutionized the curative approach by expanding the range of alternative strategies and methods. A variety of alternatives is imperative to the preventative solutions of sustainable agriculture (Hill, 1990), which are sought mainly through reduced production intensity: that is, reduced use of synthetic pesticides and fertilizers, water, fossil fuel energy, and tillage. Reduced production intensity is achieved with crop diversification and improved use of information.

In agriculture, information is the choices available for decision-making, and the set of perceived outcomes of the farming system. Information improves with research and monitoring, and increases the variety and reliability of management strategies and methods to prevent perceived threats, each method with a cost-benefit analysis. For example, practices of British farmers fall short of conservation potentials, not because of disinterest, but because of a lack of necessary information (Carr & Tait, 1991). Sustainability is promoted by a balance of production, profitability, and conservation, in response to the complexities of modern agricultural systems. The preventative method and IPM emphasize information about natural systems (Harmsen, 1990), particularly ecological interactions.

Because arthropods and weeds cause greater losses to agriculture than do vertebrates (Pimentel, 1986), management of vertebrate pests has been a neglected aspect of sustainable agricultural research. Nonetheless, vertebrate pests can devastate agricultural production and profits (Salmon, 1987). Conventional vertebrate pest control, which has emphasized density reduction (Howard, 1962; Putman, 1989), evidently has failed to provide sustainable solutions. For example, most agricultural and wildlife professionals surveyed in the United States felt that vertebrate damage has increased over the last three decades (Conover & Decker, 1991). Yet, recent research has produced

promising new approaches for managing vertebrate pests. Our purpose is to review recent literature on ecological approaches for managing vertebrate pests in sustainable agricultural systems. We begin by synthesizing relevant ecological concepts that have been de-emphasized in conventional methods, but which are integral to successful, sustainable solutions. We then summarize promising approaches to preventative management of vertebrate pests, emphasizing the need for forecasting, landscape management, and cost-benefit analyses.

ECOLOGICAL CONCEPTS

Habitat quality and agriculture

Habitat is defined as an area with the combination of resources, such as food and cover, and environmental conditions, such as temperature and absence of competitors, that promote occupancy by a given species (Morrison *et al.*, 1992a). High quality habitat provides resources and conditions that result in relatively high rates of survival and reproduction for long periods. In marginal habitat, resources and conditions may be adequate only for intermittent occupancy. Areas lacking essential resources or conditions are unsuitable for occupancy by a species (Hansson, 1977; Morrison *et al.*, 1992a).

Human activities, particularly agriculture, have resulted in wholesale alteration of plant communities that wild vertebrates depend upon for habitat. These activities typically result in the conversion of relatively stable, climax plant communities to unstable, early successional communities. Vertebrate species vary in their responses to habitat alteration, depending on how habitat quality is affected (Leopold, 1966). Many species are adapted to climax plant communities and have declined, some to extinction. Others are adapted to early successional communities and have thrived; some of these are considered pests.

Thus, agriculture often has improved habitat quality for those species that are causing damage. For example, grazing by cattle may alter grassland communities in ways that improve habitat quality for the California ground squirrel (*Spermophilus beecheyi* Richardson, Rodentia: Sciuridae) (Fitch, 1948), which is considered a competitor of cattle (Howard *et al.*, 1959). Irrigation improves yields in alfalfa fields, but an unwanted result is a nearly threefold increase in reproduction of gophers (*Thomomys bottae* Eyraud & Gervais, Rodentia: Geomyiidae), which are thought to cause damage to alfalfa (Loeb, 1990).

Carrying capacity and density dependence

Carrying capacity is defined as the natural limit of the density of a population, set by availability of resources in a particular habitat (Caughley & Sinclair, 1994). Exactly which factors determine this limit is a matter of considerable debate (Pulliam & Haddad, 1994), but habitat quality plays a fundamental role. Carrying capacity for a given species may vary greatly, both spatially and temporally, according to local conditions. For example, in temperate latitudes, carrying capacity for most vertebrates varies seasonally and is highest during spring and summer, when most agricultural production occurs.

Among vertebrates, demographic processes such as reproduction and survival often vary according to population density in relation to carrying capacity. When density is reduced below carrying capacity, the quantity of resources per individual increases, thereby promoting higher survival and reproduction in remaining individuals. Conventional approaches to managing vertebrate pests usually involve density reduction, but without a concomitant reduction in carrying capacity; a density-dependent increase in survival, reproduction, or both often results (Putman, 1989). For example, intensive control programs resulted in a doubling of litter sizes of coyotes (*Canis latrans* Say, Carnivora: Canidae) (Knowlton, 1972), a 77% increase in productivity of feral goats (*Capra hircus* L., Artiodactyla: Bovidae) (Parkes, 1984), and a two-fold increase in juvenile survival in feral donkeys (*Equus asinus* L., Perissodactyla: Equidae) (Choquenot, 1991). Density reduction to reduce or prevent damage may only stimulate density-dependent responses that quickly return population sizes to pre-control levels. A program of long-term density reduction becomes, in effect, an attempt to drive a negative feedback loop in the wrong direction (Caughley & Sinclair, 1994).

Dispersal and recolonization

Dispersal, the one-way movement of an animal away from its home range (Lidicker, 1975), is a common phenomenon among vertebrates. Because of the apparent dangers of movement through unfamiliar habitat, survival of dispersers is believed to be low (Anderson, 1989). Recent research, however, has shown that many dispersers may survive and establish a new home range (Nelson & Mech, 1991; Harrison, 1992; Van Vuren & Armitage, 1994). Thus, over time a substantial number of individuals will emigrate from a population in search of vacant, suitable habitat, and may cover long distances in their searches.

The means by which dispersers locate vacant habitat vary according to spatial scale. Some dispersers detect a vacancy adjacent to their home range and disperse through a local shift in home range (Rood, 1987; Boutin *et al.*,

1993). Others discover vacancies beyond their home range through 'exploratory excursions', round-trip forays that allow assessment of opportunities elsewhere before eventual dispersal (Johnson, 1989; Van Vuren, 1990; Larsen & Boutin, 1994). Many dispersers, however, discover vacant habitat by chance encounter during one-way movements through previously unknown areas; such movements often are abrupt, rapid, and may cover long distances (Wiggett *et al.*, 1989; Van Vuren, 1990; Harrison, 1992). Dispersers often move along habitat corridors, but some will cross large areas of inhospitable terrain (Wiggett *et al.*, 1989; Van Vuren, 1990).

Thus, a control program that locally reduces or eradicates a pest species, but without a concomitant decrease in carrying capacity, will create an artificial 'dispersal sink' (Lidicker, 1975; Dobson, 1981) that may be rapidly recolonized by dispersers from elsewhere (Morris, 1970; Stroud, 1982). Indeed, local density reduction may produce a 'vacuum effect' (Gaines *et al.*, 1979); residents of nearby populations may be encouraged to disperse into the area when they detect vacant habitat, either because their home ranges are adjacent or as a result of exploratory excursions.

Population resiliency

Because of density-dependent responses, rapid recolonization, or both, populations of vertebrate pests have shown remarkable 'resiliency' (Holling, 1973) in recovering from density reductions (Sullivan, 1987). For example, a population of deer mice (*Peromyscus maniculatus* Wagner, Rodentia: Cricetidae) that was eliminated by poisoning recovered to pre-treatment numbers in 5 to 7 months; the first immigrants appeared within 19 days, and reproduction began soon thereafter (Gashwiler, 1969). Eradication of ground squirrels showed similar consequences; immigration fully restored populations of Richardson's ground squirrels (*Spermophilus richardsonii* Sabine, Rodentia: Sciuridae) in 20 days (Alsager, 1972) and California ground squirrels in 4 months (Stroud, 1982). Experimental depopulation of several species of small mammals stimulated immigration at rates of 6% to 48% of the original population size, per week (Gaines & McClenaghan, 1980). Through reproduction alone, a feral goat population reduced by 80% can recover to 90% of its former size in just 4 years (Rudge & Smit, 1970).

Density reduction may even result in recovery to numbers higher than those before control. In forest clear-cuts that were experimentally depopulated of gophers (*Thomomys* spp.), rapid recolonization resulted in densities that within 12 months were at least twice as large as those in control plots (Smallwood, in preparation). After populations of the meadow vole (*Microtus pennsylvanicus* Ord, Rodentia: Arvicolidae) were reduced by poisoning, increased rates of survival and immigration stimulated rapid recovery.

Densities eventually reached levels that substantially exceeded pre-control levels, apparently because abrupt density reduction had disrupted the social structure (Morris, 1970, 1972).

Temporal and spatial dynamics

Demographic attributes of vertebrates, such as density, reproduction, and dispersal, vary though time on several scales, and the impacts of vertebrate pests on agriculture often vary accordingly. Thus, control programs should incorporate information on temporal variation in pest populations (Gurnell, 1989; Hansson, 1992). For example, most vertebrates show an annual increase in density because of seasonal reproduction. Rate of dispersal also may vary seasonally. On a multi-annual scale, some vertebrates, especially those influenced by weather conditions such as rainfall, exhibit an irregular 'boom-bust' variation in density. Population increases may be so spectacular they are labelled 'outbreaks' (Pearson, 1963; Newsome, 1969; Ryszkowski & Myllymäki, 1975). Other vertebrates exhibit predictable cycles of abundance on a 4-year or 10-year periodicity (Hansson & Andersson, 1975); peaks in the cycle are often characterized by dramatic increases in density and rates of dispersal, followed by equally dramatic crashes. Cycles are sufficiently predictable that the timing of peak numbers can be forecast (Myllymäki, 1975).

Vertebrate populations vary spatially as well. On a local scale, individuals of a species may occupy home ranges that are substantially larger than the locality where damage is occurring; thus, the spatial scale of pest management should be expanded accordingly (Pagano & Madison, 1982; Richards & Buckle, 1987; Gurnell, 1989). On a landscape scale, spatial heterogeneity in habitat quality can have a major influence on population dynamics of a pest species (Hansson, 1977). For example, dispersers will move from high quality habitats to marginal habitats (Hansson, 1977). Thus, a pest population subjected to persistent density reduction, but without coordinated density reduction in surrounding populations, may be maintained by equally persistent recolonization. The result would be a 'source-sink' relationship, in which there is a continued dispersal of individuals from areas where reproduction exceeds mortality, to areas where mortality exceeds reproduction (Pulliam, 1988).

Attempts at density reduction often vary in effectiveness in both time and space. For example, farmers in a given region may differ in the amounts of financial or other resources that they have available for pest control, and they may differ in their decisions about when those resources should be applied. Thus, depopulation of a given pest species within a region may occur at different localities and at different times. Such temporal and spatial variation may create a 'metapopulation' (Levins, 1969; Stenseth, 1977), in which a pest

species is resistant to regional extirpation because local depopulation is balanced by recolonization from intact populations nearby. For effective control, pest species should be considered in a landscape context (Stenseth, 1981a), and control efforts should be coordinated in time and space (Levins, 1969; Stenseth, 1977, 1981b). Ironically, the concept of the metapopulation, which was first developed to promote local extirpation of pest species, has since been advocated as a model for preventing extinction of rare species (Harrison, 1994).

PREVENTATIVE PEST MANAGEMENT

Conventional, intensive agricultural practices often conflict with the criteria for sustainable agriculture. Conventional vertebrate pest control often not only fails to prevent future damage, but also may harm the very non-target species that can serve as predators or competitors of the pests. These methods are increasingly unacceptable, partly because of public outcry over the application of lethal measures to highly visible vertebrates, and partly because of increasingly strict governmental regulation of toxicants and their use (Kendall, 1992). Thus, the range of tools available to farmers and forest managers is steadily decreasing, and agriculture cannot be sustainable without a range of alternatives.

Several management approaches show promise for reducing damage by vertebrate pests. Some involve manipulating ecological variables that in turn reduce pest density or damage, some employ negative stimuli to alter pest distribution or behaviour, some use physical exclusion to prevent damage, and some focus on modifying cultural systems to reduce the vulnerability of commodities. Underlying all is the need for forecasting, a landscape approach, and an analysis of costs and benefits.

Reduce habitat quality

Habitat quality for vertebrates is determined, in part, by availability of necessary resources, especially food and cover (Hansson, 1977; Morrison *et al.*, 1992a). Cultural practices may inadvertently enhance these resources for vertebrate pests, thereby improving habitat quality. For example, raking hay into windrows provides meadow voles with cover from raptor predation (Baker & Brooks, 1982), and removal of vegetation provides ground squirrels with the habitat openness that they require for visual detection of predators (Leger *et al.*, 1983).

Consequently, relatively modest modifications of cultural practices may substantially reduce habitat quality, and thus carrying capacity as well, for

vertebrate pests. For example, habitat quality for various ground-dwelling squirrels might be reduced by removal of nearby stumps and brushpiles (Flint, 1985) or by managing for increased height of herbaceous vegetation (Klitz, 1982; Cable & Timm, 1988). Planting tall, dense vegetation, however, failed to reduce numbers of California ground squirrels (Fitzgerald & Marsh, 1986). Cattle graze and trample the vegetation around point attractants, such as watering tanks and supplemental feeding sites, thereby creating disturbed habitats that are preferred by black-tailed prairie dogs (*Cynomys ludovicianus* Ord, Rodentia: Sciuridae). Thus, moving point attractants periodically should reduce habitat quality for prairie dogs (Licht & Sanchez, 1993). Burrow destruction can reduce habitat quality for several species of rodents and rabbits (Parker *et al.*, 1976; Klitz, 1982; Kingery *et al.*, 1987; Gilson & Salmon, 1990), but burrows must be damaged enough to prevent discovery and repair by immigrants (Salmon *et al.*, 1987). Damage by voles (*Microtus* spp.) and gophers to orchards was reduced by removing or reducing herbaceous vegetation around trees (Keith *et al.*, 1959; Hull, 1971; Godfrey, 1987; Sullivan & Hogue, 1987; Davies & Pepper, 1989). Reduction in habitat quality for voles also can be achieved by planting short-stature herbaceous vegetation that has an erect, bunch-type growth form (Tobin & Richmond, 1993). Because early seral stages of deciduous forests provide excellent habitat for white-tailed deer (*Odocoileus virginianus* Zimmerman, Artiodactyla: Cervidae), deer damage might be reduced by managing adjacent woodlands for late seral stages (Brush & Ehrenfeld, 1991).

Repellent crops may be planted to discourage pests from attacking a vulnerable commodity. Occurrence of woodchucks (*Marmota monax* L., Rodentia: Sciuridae) in orchards might be reduced by planting relatively unpalatable forage species such as orchard grass (*Dactylis glomerata* L., Poaceae) for ground cover (Swihart, 1990). Barley, a highly preferred food of jackrabbits (*Lepus californicus* Gray, Lagomorpha: Leporidae), was protected from depredation by sowing the perimeter of the field with cereal rye, a crop that is avoided by jackrabbits (Lewis, 1946).

Pests might be attracted away from a commodity by planting diversionary crops or by providing higher quality habitat or habitat resources. Control of wildfires in Alaska has reduced winter range quality for bison (*Bison bison* L., Artiodactyla: Bovidae), which shifted to barley fields for winter range (Gipson & McKendrick, 1982); resumption of natural burning might draw bison back to adjacent wildlands. Prompt establishment of catsear (*Hypochaeris radicata* L., Asteraceae), fleabane (*Erigeron strigosus* Muhlenberg, Asteraceae), phacelia (*Phacelia nemoralis* Greene, Hydrophyllaceae), and hawkbeard (*Crepis capillaris* L., Asteraceae), forbs that are preferred by mule deer (*Odocoileus hemionus* Rafinesque, Artiodactyla: Cervidae), reduced deer damage to conifer seedlings (Campbell & Evans, 1978). Conifer seed survival was increased dramatically by distributing sunflower seeds, a highly preferred

food of seed-eating rodents (Sullivan, 1979; Sullivan & Sullivan, 1982). Similarly, distribution of sunflower seeds reduced damage by rodents to trees in a managed conifer forest (Sullivan & Klenner, 1993). Plywood sticks soaked in soybean oil showed promise as a preferred food for reducing damage to apple trees by voles (Sullivan & Sullivan, 1988). Depredation by blue jays (*Cyanocitta cristata* L., Passeriformes: Corvidae) on pecans might be reduced by managing adjacent forests for mature oaks (*Quercus* spp. L., Fagaceae) that produce large quantities of acorns, a preferred food of blue jays (Batcheller *et al.*, 1984). Oaks may not produce acorns every year, though, so jays still may cause damage in some years.

Juxtaposition of crops and adjacent wildlands also can have an important effect on crop vulnerability. Mule deer in Idaho rely on broken terrain and juniper (*Juniperus* spp. L., Cupressaceae) stands for cover; winter wheat or pasture planted more than 300 m distant was grazed less by deer than were fields closer to cover (Thomas & Irby, 1991).

Predation

Although dynamics of vertebrate prey and their predators are incompletely understood, predators do have an impact on prey species (Pearson, 1971; Skogland, 1991; Lindström *et al.*, 1994). In the context of pest control, predators can affect vertebrate pests in two ways. First, predators may reduce prey densities directly through predation. A substantial body of evidence, primarily from Australia and New Zealand, shows that once pest densities have been reduced by other means such as severe weather, predation can keep densities low (Newsome, 1990; Pech *et al.*, 1992).

Second, the threat of predation may alter prey behaviour or distribution. For example, flock size of house sparrows (*Passer domesticus* L., Passeriformes: Passeridae) was smaller when merlins (*Falco columbarius* L., Falconiformes: Falconidae) were nearby (Sodhi, 1991), and house mice (*Mus domesticus* Rutt, Rodentia: Muridae) shifted to dense vegetation when mammalian predators were present (Dickman, 1992).

Predator presence might be encouraged by improving habitat quality for predators. Providing hiding cover for mammalian predators showed promise as a means of reducing use of an area by black-tailed prairie dogs (Knowles, 1988). Raptor presence can be promoted through the installation of perches (Craighead & Craighead, 1956; Askham, 1990; Smallwood *et al.*, 1996) or by leaving crop debris after harvest to support prey populations (Smallwood *et al.*, 1996). Several species of raptors were observed hunting from artificial perches soon after the perches were erected in alfalfa fields (Hall *et al.*, 1981). Raptors can be attracted to agricultural fields where non-production vegetation has been removed, thereby exposing pest species to predation (Baker *et al.*, 1976; Baker & Brooks, 1982).

Vertebrate predators, particularly birds and mammals, often shift their hunting efforts readily from one prey to another. For example, gophers are a preferred prey of coyotes in some areas; when gophers are scarce, coyotes switch to alternate prey (Van Vuren, 1991). Alternate prey can sustain predator numbers while a scarce, preferred prey is further depleted (Pearson, 1971). Thus, predation on pests might be promoted by managing for alternate, non-pest prey or by providing supplemental food for predators (Stenseth, 1977).

The threat of predation can be simulated. A visual model of a raptor (Conover, 1982) or even a trained falcon (Erickson *et al.*, 1990) may prove useful in reducing depredation by birds. In the absence of a visual image, presence of predators may be communicated olfactorily; odors from predators changed the distribution of bank voles (*Clethrionomys glareolus* Schreber, Rodentia: Arvicolidae) (Jedrzejewski *et al.*, 1993) and reduced damage to crops and commodities by rodents, rabbits, and deer (Sullivan *et al.*, 1988a, 1988b, 1988c; Andelt *et al.*, 1991; Swihart, 1991; Nolte *et al.*, 1993).

Scaring devices

Vertebrates often respond to sudden stimuli that simulate a predator or other source of danger. Thus, numerous devices and techniques have been tested for frightening pests away from vulnerable commodities. The stimulus might be visual, such as scarecrows, balloons, flashing lights, white plastic flags, or reflectors (Mott, 1985; Bruggers *et al.*, 1986; Cummings *et al.*, 1986; Dolbeer *et al.*, 1986; Avery *et al.*, 1988; Koehler *et al.*, 1990; Mason *et al.*, 1993), or auditory, such as distress calls or loud noises (Long, 1982; Cummings *et al.*, 1986; Mott & Timbrook, 1988; Bomford & O'Brien, 1990; Koehler *et al.*, 1990; Gorenzel & Salmon, 1993). Some frightening devices appear ineffective for certain pests (Wilson & McKillop, 1986; Avery *et al.*, 1988; Tobin *et al.*, 1988; Conover & Dolbeer, 1989; Bomford, 1990); further, the effect usually is only temporary because the target species becomes accustomed to the stimulus (Bomford & O'Brien, 1990). Nonetheless, the approach still can be effective if selectively applied in a program that emphasizes phenology and the window of commodity vulnerability (Cummings *et al.*, 1989). Suppliers of various scaring devices, as well as other products for managing vertebrate pests, are listed in Hygnstrom *et al.* (1994).

Chemical repellents

Synthetic chemicals such as methiocarb, DMA, methyl anthranilate, ortho-aminoacetophenone, imidacloprid, and thiram are distasteful or otherwise

offensive and, when applied to crops and stored commodities, can discourage depredation by a variety of birds and mammals (Johnson *et al.*, 1985; Mechan, 1988; Mason *et al.*, 1989; Mason *et al.*, 1991a; Avery *et al.*, 1993; Clark & Mason, 1993; Rangen *et al.*, 1993). Naturally-occurring chemicals recently have shown promise for repelling vertebrates; phenylpropanoids (Jakubas *et al.*, 1992) and cinnamic acid derivatives (Avery & Decker, 1992; Crocker *et al.*, 1993a, 1993b; Crocker & Reid, 1993) found in plants, and hydrochromes and diketones found in the defensive secretions of the azalea lace bug (*Stephanitis pyrioides* Scott, Hemiptera: Tingidae) (Mason *et al.*, 1991b) have bird-repellent properties. Capsaicin, the chemical responsible for the strong taste of hot peppers, can reduce feeding on commodities by deer (*Odocoileus* spp.) and elk (*Cervus elaphus* L., Artiodactyla: Cervidae) (Andelt *et al.*, 1992, 1994). Pheromones in the urine of male rabbits inhibited feeding by European rabbits (*Oryctolagus cuniculus* L., Lagomorpha: Leporidae) on previously attractive food items (Bell, 1987). The bio-dynamic technique, however, which involves use of incinerated tissues of the pest species as a repellent, is ineffective (Eason & Hickling, 1992). Effectiveness of repellents may be species-specific (Conover, 1982) and may be influenced by the hunger level of the pest (Andelt *et al.*, 1991).

Learning may play a role in chemical repellents. A conditioned taste aversion can be developed in vertebrate pests by offering samples of the commodity treated with a synthetic or natural chemical, such as emetine dihydrochloride, lithium chloride, methiocarb, Landrin, or estrogen, that sickens the pest. The pest learns to associate sickness with consumption of the commodity (Conover, 1982, 1990; Burns, 1983; Dimmick & Nicolaus, 1990; Semel & Nicolaus, 1992).

Exclusion

A great variety of physical exclusionary devices has been in use for years, ranging from physical protection of individual plants or plant parts to fencing or other barriers to exclude pests over larger areas. Plant parts, such as fruits and ripening ears of corn, might be protected by wrapping or bagging (Conover, 1987; Marsh *et al.*, 1990). Trunks of trees can be wrapped with commercially available protectors (Marsh *et al.*, 1990; Adams & Weitkamp, 1992). Metal flashing attached to the trunk will prevent rodents from climbing trees to reach fruits and nuts (Marsh *et al.*, 1990). Terminal buds of trees can be protected with devices made of paper, polyester, plastic, or wire mesh (DeYoe & Schaap, 1984). Above-ground portions of seedlings may be enclosed with cylinders, cones, or domes made of wire-mesh or plastic (Davies & Pepper, 1989; Marsh *et al.*, 1990). Natural materials, such as thorns, briars,

or dense brush, may help exclude vertebrates from seeds and seedlings (Marsh *et al.*, 1990).

Larger areas such as fields, orchards, and commodity storage facilities can be protected by enclosure with nets, wire fences, or electrified fencing. Bird-exclusion netting is a cost-effective means of reducing damage to commercial vineyards (Fuller-Perrine & Tobin, 1993). Polypropylene nets (Martin & Hagar, 1990) might reduce depredations by fish-eating birds at fish farms. Wire fences have successfully excluded mammals such as gophers (Keith, 1961), European rabbits (McKnight, 1969), and large artiodactyls (Antilocapridae, Cervidae) (Schneidmiller, 1988) from crops and stored commodities. Electrified fences have reduced damage by European rabbits (McKillop & Wilson, 1987), deer (Porter, 1983; Hygnstrom & Craven, 1988), and various other large mammals, including both herbivores and carnivores (Steger, 1988; Mayer & Ryan, 1991). Electrified fences employ a negative stimulus to exclude vertebrates from a commodity; thus, efficacy may be improved by baiting the pest to the fence to encourage the development of a conditioned aversion (Porter, 1983).

Barriers need not physically prevent access to be effective. A visual barrier slowed expansion of a prairie dog colony (Franklin & Garrett, 1989), and widely spaced lines or wires were effective in discouraging access to commodities by birds (Pochoy *et al.*, 1990; Andelt & Burnham, 1993).

Exclusionary methods usually are very effective, but they can be expensive in terms of materials and labour, especially when large areas are to be protected.

Crop phenology

Vertebrate pests are less likely than arthropods, weeds, or pathogens to be affected by manipulation of crop phenology. Vertebrates are generally longer-lived and able to persist through periods of harsh environmental conditions and lack of resources. Modest changes in crop phenology, however, can effectively reduce vertebrate damage, particularly from birds. Depredation by blue jays on pecans can be reduced by harvesting the crop before migration brings an increase in jay numbers (Batcheller *et al.*, 1984), and consumption of sprouting rice by blackbirds (Passeriformes: Icteridae) might be alleviated by delaying planting until after migrants have passed through (Wilson *et al.*, 1989; Brugger *et al.*, 1992). Similarly, bison depredation on grain fields in Alaska can be reduced by harvesting before the bison migration begins (Gipson & McKendrick, 1982). Gopher damage to forest regeneration may be reduced by planting immediately after timber harvest, so that seedlings can mature enough to avoid damage before gophers immigrate into the area from surrounding clearcuts and meadows (Crouch, 1982).

Cultivar resistance

A potentially rewarding area of research in reducing vertebrate damage, particularly to grain sorghum, corn, rice, and sunflower, is the development of plant strains that possess morphological or biochemical resistance to vertebrate pests (Bullard, 1988). Bird depredation was less on corn cultivars that produced husks that were difficult for birds to remove (Bernhardt & Seamans, 1990). Certain sunflower cultivars have morphological characteristics that may reduce damage by birds. Heads with a concave shape are resistant because perched birds have difficulty reaching seeds, inward-pointing bracts hinder access to seeds, and fibrous hulls are more difficult for birds to remove (Mah & Nuechterlein, 1991). The effectiveness of morphological resistance has been exploited by artificially coating rice seeds with clay; germination rate remained satisfactory, but the clay coating increased handling time by blackbirds, thus reducing rate of depredation (Daneke & Decker, 1988). Some varieties of spring barley suffered less grazing damage by European rabbits than did other varieties; reasons were unclear, but plant height probably played a role (Bell & Watson, 1993). Morphological resistance to damage obtains because vertebrates find resistant crops more difficult to acquire than other foods; thus, effectiveness is reduced when alternate foods are not available (Bullard, 1988).

Some plant cultivars are biochemically resistant to damage. Varieties of conifers and fruit trees may possess relatively high concentrations of phenolics or terpenes that discourage feeding by mammals (Radwan *et al.*, 1982; Hansson, 1988). Alkaloids and other natural toxins in certain varieties of grasses and forbs grown as forage may reduce depredation by herbivorous mammals (Hansson, 1988). Because some birds lack the enzyme to digest sucrose or are inefficient at sucrose digestion (Malcarney *et al.*, 1994), high-sucrose cultivars of commercial fruit trees might be resistant to damage by birds (Brugger, 1992; Brugger *et al.*, 1993; Clark & Mason, 1993).

Genetically-based differences in phenology may affect vulnerability to damage; late-ripening cultivars of cherries sustained less damage from birds than early-ripening cultivars (Virgo, 1971; Tobin *et al.*, 1991). Vulnerability of early-ripening cherries may have derived because such trees were relatively few in number (Tobin *et al.*, 1991), suggesting that late-ripening trees were less vulnerable because of abundance rather than phenology *per se*. Yet, cultivar differences in time of ripening may prove useful in a system that emphasizes crop phenology as a means of reducing depredation.

Forecasting

Forecasting is integral to preventative pest management. Agricultural commodities are produced heterogeneously in time and space, with consequent influences on the dynamics of vertebrate pest populations. Therefore, preventative solutions involving changes in cultural practices and landscape management rely on an understanding of ecological interactions between vertebrate pests and the agricultural system. These interactions can be described functionally in ways that allow predictions about where and when vertebrate pests will pose a risk to agriculture. Further, knowledge of historical patterns of distribution and damage permits the forecasting of problems and the development of protocols for research and management of potential pests (Smallwood & Salmon, 1992).

For example, forecasting the likelihood of invasion or recolonization of a field by a vertebrate pest is an important component of a preventative solution. Research in this area initially focused on distance to source populations and areas of patches or islands (MacArthur & Wilson, 1967). More recently, the emphasis has shifted to corridors for dispersal and movement in the landscape, particularly linear, directional features such as field edges, roads, canals, and fencelines (Paoletti *et al.*, 1989; Duelli *et al.*, 1990). This emphasis has emerged from the sub-discipline of landscape ecology, the study of interactions and exchanges between patches and corridors in the landscape (Forman, 1982; Turner, 1989). The forecasting of vertebrate species distributions and abundances in agriculture, and their potential damage or benefit to specific crops, will likely be improved by applying the principles and methods of landscape ecology (Smallwood & Geng, 1994; Smallwood *et al.*, 1996).

Landscape management

Knowledge about how pests use the landscape should be incorporated into a management strategy. Conventional vertebrate control has been applied at spatial and temporal scales that are smaller than those in which the pest population functions (Smallwood & Geng, 1994). Landscape management strategies have yet to be developed, probably because little scientific investigation and planning has gone on beyond the local spatial scales that are more familiar to human society (Karr, 1994). Landscape strategies might involve incentive programmes and cooperation among many growers across the landscape.

One strategy may involve land-use decision making. For example, irrigated pasture is a typical source of dispersing gophers, so planting a gopher-vulnerable crop in an area with large acreages of irrigated pasture might be

imprudent. Another landscape strategy may involve promoting predator populations and their ability to hunt vertebrate pests (Smallwood *et al.*, 1996). Mammalian carnivores often require cover for movement along linear elements of the landscape, and raptors reproduce at nest sites and often hunt from perches. Thus, predators of vertebrate pests might be encouraged by providing these habitat resources throughout the landscape.

Cost-benefit analysis

Conventional programmes to control vertebrate pests seldom are based on scientific quantification of damage. In most cases, control is justified by only a suspicion or anecdotal evidence of damage. Damage often is assessed by questionnaires returned by growers, but reliability is unknown (Morrison *et al.*, 1992b). Visual evidence that a vertebrate species is feeding on a crop may be meaningless in determining whether yield has been affected (Putman, 1989). For example, ryegrass farmers in Oregon complained of depredations by Canada geese (*Branta canadensis* L., Anseriformes: Anatidae), but research showed that grazing by geese either had no effect on yield or even promoted increased yield (Clark & Jarvis, 1978). Similarly, the widespread belief of farmers in Colorado that grazing and trampling by pronghorn (*Antilocapra americana* Ord, Artiodactyla: Antilocapridae) reduces yield of winter wheat was disproven through research (Torbit *et al.*, 1993). California ground squirrels, long thought to compete with cattle for forage (Howard *et al.*, 1959), may consume less than 0.6% of available forage (Schitoskey & Woodmansee, 1978). In Iowa, a survey revealed that 64% of landowners with wild turkeys (*Meleagris gallopavo* L., Galliformes: Meleagrididae) in their fields felt that the turkeys were causing damage to crops, yet concurrent research discovered that turkey feeding reduced yields by less than 1% (Gabrey *et al.*, 1993). Browsing by mule deer in juvenile orchards during winter, a concern of landowners in Utah, had no effect on tree growth or fruit production (Austin & Urness, 1992).

Research has shown that vertebrates can cause significant economic loss to growers (e.g., Luce *et al.*, 1981; Palmer *et al.*, 1982; O'Gara *et al.*, 1983; Flegler *et al.*, 1987; Borrecco & Black, 1990; Swihart & Picone, 1994). Yet, evidence of significant damage is alone not sufficient to justify a control programme; the cost of damage must exceed the cost of control. Few cost-benefit analyses have been done, and some of these have suggested that the cost of control may exceed the cost of damage (Dolbeer, 1981; Gorenzel *et al.*, 1986; Miller *et al.*, 1990). Further, a control programme will entail non-economic costs, such as sociological consequences and ecological effects, that are difficult to quantify (Morrison *et al.*, 1992b). We suspect that in many cases, a full accounting of costs and benefits will

reveal that control is unjustified; agriculture will have to coexist with vertebrate pests.

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