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MANIPULATING HABITAT QUALITY TO MANAGE VERTEBRATE PESTS

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ABSTRACT: Wildlife damage management has often emphasized density reduction through lethal means. In addition to facing increasing regulatory and social restrictions, this approach also faces ecological problems; density reduction without a concomitant decrease in carrying capacity may only stimulate density-dependent responses that quickly return population densities to pre-control levels. Consequently, habitat manipulation, either to reduce pest density or to divert the pest away from the commodity, has been pursued as an alternative. Habitat manipulation has proven effective in some circumstances and appears promising in others, but the approach is limited by our ability to identify limiting resources or highly preferred foods that can be manipulated economically and with the desired effect. Further, habitat manipulation is not always a long-term solution, may have unwanted effects on non-target species, and may be ineffective if not viewed on a regional scale. Nonetheless, the approach is promising in certain situations. Further research is needed.

KEY WORDS: vertebrate pest management, habitat modification, habitat quality, carrying capacity, alternate foods

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INTRODUCTION

Wildlife damage management has often relied upon reduction of pest densities, chiefly through the use of toxicants, as a primary means of controlling damage. With increasing regulatory and social restrictions on lethal approaches, greater interest has been paid to manipulating habitat quality as an alternative means of reducing damage. In theory, habitat manipulation has decided advantages over lethal approaches; in practice, however, habitat manipulation has important limitations. The purpose of this paper is to outline the conceptual basis for habitat manipulation as a means of managing vertebrate pests, present examples of instances in which habitat manipulation has been applied or proposed, and assess the potential and limitations of the approach.

ECOLOGICAL CONCEPTS

Carrying Capacity and Density Dependence

Carrying capacity is the natural limit of the density of a population, set by availability of resources in a given habitat (Caughley and Sinclair 1994). Exactly which factors determine this limit is the subject of much debate (Pulliam and Haddad 1994), but habitat quality plays a key role.

Demographic processes such as reproduction and survival often vary according to population density and its relationship to carrying capacity. When density is well below carrying capacity, resource availability per individual is increased, thereby promoting higher survival and reproduction in remaining individuals.

Density reduction to control pest damage typically is implemented without a concomitant reduction in carrying capacity. A density-dependent increase in survival, reproduction, or both often results (Putman 1989); such responses may be dramatic (Knowlton 1972; Parkes 1984; Choquenot 1991). Consequently, density reduction to control pest damage may only stimulate density-dependent responses that quickly return population sizes to pre-control levels. Further, the presence of depopulated habitat may serve as a "dispersal sink" (Lidicker 1975; Dobson 1981) that attracts dispersers from elsewhere, further hastening the return to pre-control population levels (Sullivan 1987). Recovery of vertebrate populations following density reduction can occur remarkably quickly, and numbers may even exceed pre-control levels (reviewed in Van Vuren and Smallwood 1996). Thus, a program of long-term density reduction becomes, in effect, an attempt to drive a negative feedback loop in the wrong direction (Caughley and Sinclair 1994). In theory, manipulating habitat quality provides a long-term solution to this dilemma.

Habitat and Habitat Quality

Habitat is defined as an area with the combination of resources (such as food and cover) and environmental conditions (such as the absence of predators) that promote occupancy by a given species (Morrison et al. 1992). 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. Unsuitable habitat results when one or more essential resources or conditions are lacking (Hansson 1977; Morrison et al. 1992). Habitat provides four basic resources required by most vertebrates: food, cover for protection against predators and environmental extremes such as heat and cold, free water for drinking, and space. In addition, particular species may require more specialized resources such as perch or resting sites.

Habitat manipulation might reduce pest damage in either of two ways. First, carrying capacity, thus pest density, might be reduced by lowering habitat quality. Second, vertebrate pests might be lured away from a commodity by providing alternate, higher quality food resources.

HABITAT MANIPULATION TO REDUCE PEST DENSITY

Cultural practices may inadvertently enhance habitat quality for vertebrates that cause damage (e.g., Fitch

1948; Nicholson and Richmond 1984; Loeb 1990; Licht and Sanchez 1993). Consequently, cultural practices might be modified in ways that reduce habitat quality, and thus pest density. To do so, we must be able to identify habitat resouces or environmental conditions, such as food, cover, or absence of predators, that limit habitat quality for a particular species, then reduce or eliminate these resources or conditions. This approach, however, faces three major problems. First, some vertebrate pests have varied diets and generalized cover requirements, thus these species will be relatively unaffected by habitat modification. Second, our knowledge of habitat components that limit abundance is incomplete for some species. Third, modifications of cultural practices that reduce habitat quality for pests may also reduce the yield of the commodity being protected. An obvious example is where damage is caused by the pest feeding on the commodity; reducing food availability to the pest means reducing production. For this reason, habitat manipulation often targets habitat components besides food. Despite these limitations, habitat manipulation to reduce pest densities has shown promise for a variety of species.

Rodents and Rabbits

Voles (*Microtus* spp.) cause serious damage to a variety of crops, especially orchards. Voles require dense herbaceous vegetation both for food and for cover (Sullivan and Hogue 1987; Tobin and Richmond 1993; Edge et al. 1995). Thus, vole density or activity in orchards can be reduced substantially by decreasing the height of herbaceous vegetation through cultivation (Byers et al. 1976), mowing (Brooks and Struger 1985; Godfrey 1987; Edge et al. 1995), or the use of herbicides (Sullivan and Hogue 1987; Davies and Pepper 1989). The frequency of mowing can be reduced by applying growth retardants to mowed vegetation (Godfrey 1987). Cover is apparently more important to voles than food; voles preferred unmowed vegetation even though mowing resulted in higher quality forage (Brooks and Struger 1985). Voles also respond to vegetation density (Nicholson and Richmond 1984), so Tobin and Richmond (1993) proposed that vole activity might be reduced by planting erect, bunch-type plants that provide poor cover. Prunings, brush, and other debris may provide cover for voles and should be removed (Pagano and Madison 1982; Godfrey 1987).

Pocket gophers damage numerous crops. Like voles, gophers require herbaceous vegetation for food; unlike voles, however, gophers rely primarily on underground tunnels for cover. In situations such as orchards and regenerating forests in which the commodity at risk is not the primary food of gophers, gopher densities and damage can be reduced by removing hercaceous vegetation through the use of herbicides (Keith et al. 1959; Hull 1971; Sullivan and Hogue 1987; Engeman et al. 1995, 1997).

Ground-dwelling squirrels, such as ground squirrels (*Spermophilus* spp.), prairie dogs (*Cynomys* spp.), and woodchucks (*Marmota monax*), all require burrows for cover and feed primarily on herbaceous vegetation. Further, because squirrels often detect predators visually, some species appear to prefer areas with sparse, low-stature vegetation. Destruction of burrows can render habitat unsuitable for squirrels, but burrows must be damaged enough to prevent discovery and repair by immigrants (Klitz 1982; Salmon et al. 1987; Gilson and Salmon 1990). Attempts to reduce habitat quality by managing for dense, tall vegetation have had mixed results; this approach shows potential for black-tailed prairie dogs (*C. ludovicianus*) (Cable and Timm 1988; Licht and Sanchez 1993) but appears ineffective for California ground squirrels (*S. beecheyi*) (Fitzgerald and Marsh 1986). Similarly, the addition of hiding cover for predators had no effect on prairie dog activity (Knowles 1988). Swihart (1990) suggested that woodchuck densities in orchards might be reduced by planting herbaceous species that provide poor quality food for woodchucks.

Arboreal squirrels might be managed by manipulating the trees they depend on for habitat. Red squirrels (*Tamiasciurus hudsonicus*) cause damage to regenerating forests by feeding on the vascular tissues of young trees. Stand thinning in lodgepole pine (*Pinus contorta*) forests reduces red squirrel densities (Sullivan and Moses 1986a; Sullivan et al. 1996) and, if conducted on a sufficiently large scale, reduces feeding damage to young trees as well (Sullivan et al. 1996). Further, because damage is greatest in stands with a dense shrub understory, removing shrubs has the potential for reducing damage (Sullivan et al. 1994).

The canefield rat (*Rattus sordidus*) is a major pest in sugar cane in Australia. Damage can be reduced by leaving crop debris in the fields that inhibits growth of summer grasses, the favored food of cane rats, but only if done on a regional scale (Whisson 1996).

Beavers (*Castor canadensis*) require water for cover, either rivers or ponds of a sufficient depth, or smaller streams that beavers impound by dam-building. Removing the aquatic resource renders a habitat unsuitable for beavers. Breaking a beaver dam, however, is ineffective because the sound of running water stimulates beavers to repair the break (Wood and Woodward 1992; Olson and Hubert 1994). The solution is to install a drain that either does not stimulate the repair response or is constructed so that beavers cannot plug it (Wood and Woodward 1992; Olson and Hubert 1994).

Mountain beavers (*Aplodontia rufa*) are burrowing rodents that cause problems for forest regeneration in the Pacific Northwest. Hacker and Coblentz (1993) found that mountain beavers prefer habitats with woody debris and suggested removal of such debris from reforested areas as a means of reducing habitat quality. Destruction of underground nests to prevent reinvasion, however, appears ineffective (Campbell and Evans 1988).

Species of rabbits and hares vary in their habitat requirements. Snowshoe hares (*Lepus americanus*) prefer habitats with dense vegetative cover, so removal of cover either mechanically or chemically will reduce hare densities (Sullivan and Moses 1986b) or damage (Borrecco 1976) in regenerating forests. The European rabbit (*Oryctolatus cuniculus*) is unusual in that it requires burrows for cover; consequently, burrow destruction is an effective means of making habitat unsuitable for rabbits (Burley 1986; Williams and Moore 1995). Jackrabbits

(*L. californicus*) prefer barley as food, but apparently avoid rye, thus a barley field can be protected from jackrabbit depredation by sowing a strip of rye around the perimeter (Lewis 1946). This approach, however, appears ineffective when jackrabbits are at high densities (Evans et al. 1970).

Large Mammals

Brush and Ehrenfeld (1991), noting that early seral stages of deciduous forests provide excellent habitat for white-tailed deer (*Odocoileus virginianus*), proposed that deer damage to a crop might be reduced by managing adjacent woodlands for late seral stages. Feeding damage to gardens can be reduced by planting species that provide poor quality forage for deer (Coey and Mayer undated). Black bears (*Ursus americanus*) cause serious damage to young conifers by stripping off the bark and consuming the cambium tissue beneath (Giusti 1990; Ziegltrum 1994). Because bears select trees of a specific size and damage often occurs soon after a stand is thinned, altering thinning practices has been proposed as a means of reducing damage (Giusti and Schmidt 1988; Guisti 1990).

Birds

Sunflowers and other crops are damaged by a variety of blackbirds. Depredating blackbirds use cattail vegetation in adjacent marshes for roosting, so damage might be reduced by using herbicides to remove cattails (Linz et al. 1992, 1995, 1996). Homan et al. (1994) suggested that plowing sunflower fields soon after harvest will remove an important food source that could promote greater numbers of depredating blackbirds. In contrast, however, Mott (1975) noted that delaying plowing may protect unharvested crops by attracting birds to alternate food sources, such as grain stubble, in unplowed fields. Because blackbirds prefer ears of corn infested with insects, control of insect populations has the potential for making cornfields less attractive to blackbirds (Woronecki et al. 1981; Okurut-Akol et al. 1990). Blackbirds also are a nuisance when they roost in large numbers in urban areas; tree trimming or stand thinning is effective in reducing roost quality, thereby inducing birds to move elsewhere (Good and Johnson 1976; Lyon and Caccamise 1981; Erdman 1982).

Canada geese (*Branta canadensis*) grazing on lawns have caused problems for golf courses, parks, playing fields, and around homes and buildings. Conover (1991, 1992) suggested planting tough-leaf grass species that are poor quality food for geese, or replacing grass turf with unpalatable ground cover, as a means of reducing habitat quality for geese. Additionally, planting shrubs and hedges around smaller lawns may discourage use because geese prefer to feed in areas free of hiding cover for predators (Conover 1992).

Fish-eating birds cause depredations at fish farms. Suggestions for reducing habitat quality for birds include removal of structures used as perches or modification of pond borders to eliminate the shallow water preferred by wading birds (Parkhurst 1994). Some wading birds, however, apparently can adapt to feeding in deep water (Hoy et al. 1989). The use of fish stocks that are less vulnerable to predation has been suggested to reduce losses (Parkhurst 1994). Also, because fish are more difficult to see and capture in turbid water, increasing turbidity of ponds might reduce food availability for depredating birds. This approach, however, may interfere with fish production, thus it is not suitable for some types of commercial fish (Cezilly 1992). Feral pigeons (*Columba livia*) consume stored grain and are a nuisance in urban areas. Removing food sources such as spilled grain may be helpful in some situations (Williams and Corrigan 1994), but may have limited value because pigeons readily use a variety of foods (Fitzwater 1988). Preventing access to water sources, such as rooftop air conditioners, and rendering perch sites unsuitable or inaccessible are effective in reducing habitat quality for pigeons (Martin and Martin 1982; Fitzwater 1988; Williams and Corrigan 1994).

Ravens (*Corvus corax*) are considered a threat to the desert tortoise (*Gopherus agassizii*), a federally-protected species, because they may prey upon young tortoises (Boarman 1992). Efforts to lower habitat quality for ravens include reducing food resources by covering landfills and removing roadkills from highways, eliminating standing water, and denying ravens access to perch sites by installing spike-like devices on utility poles and fenceposts (Boarman 1992; Alice Karl pers. comm.).

Presence of Predators

The presence or absence of predators influences habitat quality for many species of vertebrates. For mammals, the application of predator odors to simulate predator presence alters local distribution, changes feeding behavior, or in some cases reduces damage caused by a variety of species including house mice (*Mus domesticus*) (Dickman 1992), voles (Sullivan et al. 1988a, 1988b; Jedrzejewski et al. 1993; Parsons and Bondrup-Nielsen 1996), gophers (Sullivan et al. 1988c), woodchucks (Swihart 1991), mountain beavers (Epple et al. 1993; Nolte et al. 1993), hares (Sullivan 1986; Sullivan and Crump 1984, 1986), and mule deer (*Odocoileus hemionus*) (Melchiors and Leslie 1985; Andelt et al. 1991). A response to predator odors, however, is not always observed (Wolff and Davis-Born 1997; Thorson et al. 1998).

For birds, simulation of predator presence through visual models (Conover 1982, 1984, 1985; Hothem and DeHaven 1982) or even a trained falcon (Erickson et al. 1990) has proven effective in reducing damage in certain situations. Some studies employed a kite with the image of a hawk that was flown suspended from a helium balloon (Conover 1982, 1984; Hothem and DeHaven 1982), while others used full-size, realistic models (Conover 1979, 1985). For both the kite and the model, motion is important for eliciting a response from birds (Conover 1979, 1985; Marsh et al. 1992). Efficacy of predator models, however, is limited because birds habituate rather quickly (Conover 1979), and they are ineffective for some species (Conover 1979, 1982).

HABITAT MANIPULATION TO DIVERT PESTS

Much damage by vertebrate pests is caused by the pest feeding on a commodity. Damage might be reduced by providing more desirable food resources that alter foraging behavior, thereby diverting the pest away from the commodity. Decisions made by vertebrates during

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foraging are affected by factors such as the ease with which a food is acquired or eaten, as well as palatability or nutritional content of the food (Krebs and Davies 1993). This approach, however, relies upon the pest discovering and preferring the alternate food, and these processes are not well understood (Perry and Pianka 1997). Further, food may be a limiting resource (e.g., Sullivan 1990); consequently food enhancement, if carried out long enough, might increase carrying capacity for the pest, ultimately leading to an increase in pest density. Nonetheless, short-term enhancement of appropriate food resources has the potential for reducing damage. Two approaches have be proposed: managing for increased availability of natural foods, and provisioning of introduced foods.

Rodents

Rodents cause damage in regenerating forests by eating conifer seeds and seedlings and by consuming cambium tissue. Conifer seed survival can be increased dramatically by distributing alternate foods, especially sunflower seeds, which are highly preferred by seed-eating rodents (Sullivan 1978, 1979; Sullivan and Sullivan 1982). Similarly, distribution of sunflower seeds reduces bark damage by squirrels to conifers (Sullivan 1992; Sullivan and Klenner 1993). Because Douglas fir (*Pseudotsuga menziesii*) seedlings are not the preferred food of mountain beavers, Hacker and Coblentz (1993) proposed that damage to fir seedlings might be reduced by managing for preferred foods such as sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*). Voles show a preference for soybean oil; accordingly, provisioning of artificial "logs" treated with soybean oil has the potential to reduce damage by voles to trees in orchards (Sullivan and Sullivan 1988).

Large Mammals

Consumption of conifer seedlings by black-tailed deer (*Odocoileus hemionus columbianus*) can be reduced substantially by prompt establishment of native forbs that are preferred by deer (Campbell and Evans 1978). Long (1988) proposed that elk (*Cervus elaphus*), which cause feeding damage to private rangelands, might be drawn away by improving habitat quality on public rangelands through the application of herbicides and fertilizer. Bison (*Bison bison*) in Alaska began feeding in barley fields after wildfire suppression caused a reduction in quality of their winter range; thus, Gipson and McKendrick (1982) suggested that resumption of natural burning might draw bison back to adjacent wildlands. Black bear damage to conifers can be reduced by increasing the availability of alternate foods; provisioning of sugarized wood chips has proven effective (Ziegltrum 1994), and planting of highly palatable forbs has been proposed (Giusti and Schmidt 1988).

Birds

Many wildlife refuges plant crops that provide high quality food in order to attract waterfowl away from surrounding agricultural fields (Cowan 1970). A related approach is the lure crop, where depredating birds are allowed to feed unmolested on a crop purchased from a private landowner, thereby reducing depredations on surrounding fields (Gustad 1979; Fairaizl and Pfeifer 1988). If the lure crop is entirely consumed, grain may be provisioned to hold the birds for a time longer (Gustad 1979). Distribution of whole corn softened in water has been proposed as a means of diverting crows (*Corvus brachyrhynchos*) from consuming corn seedlings in recently planted fields (Johnson 1994). Galah (*Cacatua roseicapilla*) depredation on wheat in Australia was reduced by providing an alternative, more preferred food source nearby (Jarman and McKenzie 1983). Batcheller et al. (1984) proposed that depredation by blue jays (*Cyanocitta cristata*) in pecans might be reduced by managing adjacent forests for mature oaks (*Quercus* spp.) that produce large quantities of acorns, a preferred food of blue jays. Establishing buffer populations of frogs, non-commercial fish, or other alternate foods around fish farms has been suggested to divert fish-eating birds away from aquaculture stocks (Parkhurst 1994; Mott and Boyd 1995).

DISCUSSION

The appeal of habitat manipulation as a means of wildlife damage management is that it is nonlethal, works with rather than against ecological processes, and may provide durable and cost-effective solutions. The approach, however, has limitations. Habitat manipulation to reduce pest density will work only for species for which limiting habitat resources have been identified and that can be modified economically. Habitat manipulation to divert the pest from the commodity relies on identification of a more highly preferred food that can be economically enhanced or provisioned and that reliably attracts the pest. Further, long-term food enhancement could lead to increased pest density.

In addition, habitat manipulation faces limitations that extend beyond the interaction between the pest and its habitat. Habitat manipulation is not always a long-term solution because plant populations that have been altered chemically or mechanically may show the same ability for rapid recovery as do some vertebrate populations. In such cases, habitat treatments will require repeated application. Food enhancement, especially when forage species are seeded, must be done judiciously to preclude the introduction or spread of exotic plants. Because a given habitat supports numerous species besides the pest, habitat manipulation may have unwanted consequences for nontarget species (Howard 1967; Borrecco 1976). For example, destruction of ground squirrel burrows may harm rare species that require these burrows for habitat (Loredo et al. 1996). Finally, habitat manipulation relies on inducing the pest to live or feed elsewhere; consequently, the approach should be viewed on a scale larger than that of the individual farm, golf course, or forest stand (Conover 1992; Sullivan et al. 1996; Whisson 1996).

Despite these limitations, studies have shown that both approaches to habitat manipulation, either reducing pest density or diverting the pest away from the commodity, are promising for reducing damage in certain situations. Further research is needed.

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