Ecological approaches to reduce predation on ground-nesting gamebirds and their nests

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Abstract In human-modified environments, high predation rates on ground-nesting birds and their eggs can be a serious problem. We reviewed the literature to determine the effectiveness of ecological approaches to improve recruitment of ground-nesting birds. Ecological approaches reduce predation rates by modifying natural interactions among predators, prey, and their habitats. These approaches include modification of the predator community, associational defense, use of alternative prey, and habitat or landscape manipulation. These techniques can be applied successfully only under limited conditions and for a specific array of species. Because of this, no management practice is uniformly better than another to increase avian recruitment; different techniques are complementary rather than exclusive. Managers need to select the best technique(s) based on the predator community, local topography, size of the area, the avian species in need of protection, and economics.

Key Words avian recruitment, ducks, ground-nesting birds, integrated pest management, predation, predator-prey interactions, wildlife damage management

High predation rates on ground-nesting birds and their eggs are a serious problem in many parts of North America. Predation may be greater today than historically owing to a decrease in the quality and quantity of nesting habitat (Cowardin et al. 1985, Wilcove 1985, Sargeant et al. 1993). Furthermore, densities of some nest predators—such as American crow (*Corvus brachyrhynchus*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*)—are high in human-modified environments.

Increased nest predation reduces avian recruitment, limits population growth, and can make some populations nonsustainable (Cowardin et al. 1985). In extreme cases, predation on breeding birds has resulted in extirpation of local populations, as documented by Bailey (1993) for the Aleutian Islands, where arctic fox (*Alopex lagopus*) and red fox were the main predators. More subtle effects are long-term population declines, such as those experienced by dabbling duck populations nesting in the Prairie Pothole region (Cowardin et al. 1985, Greenwood et al. 1995, Beauchamp et al. 1996*b*). In this region, low nest success because of intense predation on eggs has resulted in recruitment rates well below those needed to sustain dabbling duck populations (Klett et al. 1988, Johnson et al. 1989, Sargeant et al. 1993).

Wildlife managers use a variety of direct and indirect management techniques to increase avian recruitment, such as habitat improvements and predator control (Lokemoen 1984). However, many of these techniques are expensive, controversial, or inadequately tested (Clark and Nudds

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1991, Sargeant et al. 1995, Greenwood and Sovada 1996).

We reviewed the literature to examine the effectiveness of ecological approaches to improve recruitment of ground-nesting game birds. We define ecological approaches as those designed to reduce predation rates on avian nests by modifying the natural interaction among predators, prey, and their habitats.

Methods

We reviewed ecological methods that hold promise to reduce predation rates on upland-nesting birds. We searched the literature using indexes, including Agricola, Biological Abstracts, Wildlife Review, and Wildlife Worldwide. We also searched through back issues of all wildlife and ornithological journals written in English. We emphasized studies conducted in the Prairie Pothole region of North America because much of the research on nest predation has been conducted there.

Extrapolation of artificial nest studies to natural conditions has been criticized (Storaas 1988, Willebrand and Marcström 1988, Major and Kendal 1996). Although some authors have argued that these data are acceptable for comparative purposes (Wilson et al. 1998), we have excluded experiments using artificial nests except in a few rare cases where similar data were unavailable for natural nests.

Results

Modifying the predator community

Because of selective harvesting and local extirpation of larger predators (e.g., wolves *Canis lupus*, coyotes *C. latrans*), populations of medium-sized predators that are more efficient nest predators (e.g., red foxes, raccoons, skunks) may have increased in abundance and expanded their ranges (Robinson 1961, Sargeant et al. 1984). Changes in densities or species composition of predators in the Prairie Pothole region of North America are described by Sargeant et al. (1993) and in northern Europe by Angelstam (1986) and by Andrén and Angelstam (1988).

Control of the medium-sized predators responsible for most of the nest predation in the North American prairies has been proposed by encouraging coyote reestablishment in areas where they are absent (Sargeant and Arnold 1984, Klett et al. 1988). Given their low densities and larger home ranges, coyotes pose less of a threat to breeding hens and their nests than red foxes (Greenwood et al. 1987, Sovada et al. 1995). By allowing coyotes to repopulate areas where fox populations have expanded, we may be able to enhance reproductive output of local birds, because coyotes do not tolerate red foxes and drive them out of their territories. In fact, one coyote pair can displace 5 pairs of red foxes (Sargeant et al. 1987). Allowing coyotes to establish territories can be used to increase nest success in ducks (Johnson et al. 1989, Ball et al. 1995). Correlational evidence from a study in the Prairie Pothole region supports this idea. Sovada et al. (1995) found that ducks had a 32% nesting success in areas with coyotes and no red foxes, but only 17% in areas with no coyotes but with foxes. A similar biological method has been proposed to control arctic foxes by releasing sterilized red foxes in the Aleutian Islands (Schmidt 1985, Bailey 1992). Hopefully, red foxes would exclude arctic foxes, but would be unable to reproduce.

[T]here are no panaceas for the problem of reducing predation on nesting birds.

Another example of competitive interaction among nest predators was described by Henry (1969) in Tennessee. He found that predation by foxes, dogs, and snakes on artificial nests of ruffed grouse (*Bonasa umbellus*) and turkey (*Meleagris gallopavo*) was less in areas with larger populations of hogs (*Sus scrofa*) than in areas with fewer hogs. Henry (1969) speculated that hogs, which are inefficient nest predators, may drive foxes and dogs away and prey on snakes.

The idea of selectively changing the predator community to improve nest success is appealing, but to our knowledge, no one has ever tested whether nest success can be improved by introducing alternative predators. In fact, we found only 3 studies that experimentally tested whether selective removal of a single predator species from an area would result in increased nest success; all showed discouraging results. Greenwood (1986) selectively removed striped skunks and Clark et al. (1995) and Parker (1984) removed crows, but nesting success improved little or not at all. The authors speculated that compensatory predation by other local predators may have occurred.

Protective umbrella or associational defense

Dyrcz et al. (1981) coined the term "protective umbrella" to describe the propensity of some species to nest close to a more pugnacious species that attacks or mobs predators. This behavior can increase reproductive output of species unable to protect themselves. In Europe, species using the "protective umbrella" strategy include waders and passerines gaining protection by lapwings (*Vanellus vanellus*) and godwits (*Limosa limosa*, Dyrcz et al. 1981, Elliot 1985), godwits (*Limosa lapponica*) protected by whimbrels (*Numenius phaeopus*, Larsen and Moldsvor 1992), and curlews (*Numenius arquata*) protected by kestrels (*Falco tinnunculus*, Norrdahl et al. 1995). In North America, species extending protective umbrellas include herring gulls (*Larus argentatus*) for savannah sparrows (*Passerculus sandwichensis*, Wheelwright et al. 1997), snowy owls (*Nyctea scandiace*) for brant (*Branta bernicla*, Underhill et al. 1993) and snow geese (*Chen caerulescens*, Tremblay et al. 1997), and common terns (*Sterna hirundo*) for pintails (*Anas acuta*) and lesser scaup (*Aythya affinis*, Vermeer 1968). This protective umbrella strategy, however, is not always successful. Vermeer (1968) documented >90% hatch success for waterfowl nesting with gulls (*Larus californicus*, *L. delawarensis*). However, gull predation on ducklings resulted in almost complete reproductive failure.

The protective umbrella behavior can be used as a nonlethal tool to improve recruitment of certain birds by favoring and protecting the aggressive species. Although not currently practiced in management, the strategy shows potential.

Table 1. Studies showing either a positive or a negative relationship between nesting success and availability of alternate prey.

Nesting bird	Alternate prey	Nature of relationship	Source
Tetraonids	Microtinae	Positive	Marcström et al. (1988)
Black grouse (*Tetrao tetrix*)	Microtinae	Positive	Angelstam et al. (1984)
Ruffed grouse	Small mammals	Positive	Darrow (1945)
Quail	Small mammals	Negative	Komarek (1937)
Northern bobwhite (*Colinus virginianus*)	Small mammals	Positive	Scott and Klimstra (1955)
Northern bobwhite	*Microtus ochrogaster*	Negative	Klimstra and Roseberry 1975)
Eastern meadowlark (*Sturnella magna*)	*Microtus ochrogaster*	Negative	Roseberry and Klimstra (1970)
Blue-winged teal	Small mammals	Positive	Byers (1974) Weller (1979)
Oldsquaw (*Clangula hyemalis*)	Microtinae	Positive	Phersson (1986)
Brant	*Microtus oeconomus*	Positive	Anthony et al. (1991)
Brant	*Lemmus sibiricus*, *Dicrostonyx torquatus*	Positive	Ebbinge (1989)
Wading birds	Microtinae	Positive	Beintema and Müskens (1987)
Brant and wading birds	*Lemmus sibiricus*, *Dicrostonyx torquatus*	Positive	Summers and Underhill (1987)
Brant and wading birds	*Lemmus sibiricus*, *Dicrostonyx torquatus*	Positive	Underhill et al. (1993)

Providing alternative prey for predators

Most nest predators are opportunistic species that eat a variety of food items. It has been hypothesized that alternative prey can buffer the effect of predators on nests. Predators may respond to alternative prey by changing their search image for food, altering their prey selection (i.e., dietary shift or functional response), shifting foraging locations, or increasing their numbers in the area of abundant prey (i.e., numerical response) through immigration or increased reproduction.

Information on effects of alternative prey on bird recruitment is mainly anecdotal and based on correlations between nest success and abundance of alternative prey. Most studies have reported a positive relationship between nesting success and abundance of alternate prey (Table 1). Presumably in these cases, availability of alternative prey draws the attention of predators away from nests. This relationship is particularly evident in the Arctic region and boreal forests, where nesting success of birds increases during years when there are high populations of lemmings and voles (Microtinae). In more temperate regions, the relationship between nest success and abundance of alternate prey is less clear and can be negative (Table 1). In these cases, the interpretation is that availability of the alternate prey attracted predators to the same area where the birds were nesting and predators, once there, find nests while foraging for the alternate prey (Roseberry and Klimstra 1970, Klimstra and Roseberry 1975).

Only 2 studies experimentally tested the effect of alternative prey on nesting success of ground-nesting birds (Crabtree and Wolfe 1988, Greenwood et al. 1998). Crabtree and Wolfe (1988) mimicked increased alternative prey by providing carp (*Cyprinus carpio*) and pet food in a Utah wetland. They found an increased nest success of gadwalls during June, but not in July. Apparently, predators other than skunks did not respond to the treatment. However, this study lacked replication. Similar approaches were used for nesting waterfowl in North Dakota by providing a mixture of seeds and fish offal (Greenwood et al. 1998) or chicken eggs (King et al., unpublished data) as alternative prey for predators.

However, Greenwood et al. (1998) and King et al. (unpublished data) did not detect changes in nest success in their experimental areas.

Wildlife managers choosing to manipulate the prey base for predators to enhance birds' nesting success can do so by either providing alternative prey or by manipulating the habitat to favor alternative prey. Our findings indicate that supplemental feeding apparently does not decrease nest predation effectively. It also may not be cost-effective. Furthermore, numerical responses of predators might counteract the benefits over short (through immigration into the food-rich area) or longer time periods (through reproduction, Phersson 1986, Crabtree and Wolfe 1988, Ebbinge 1989). Alternatively, wildlife managers can increase the prey base for predators by manipulating the vegetation cover or plant species composition. However, nesting birds and predators respond themselves to type and quality of cover, and this may lessen any benefits provided by habitat manipulation (see below).

Removing mammalian den sites and perch sites for avian predators

Fleskes and Klaas (1991) and Herkert (1994) have contended that abundance and composition of a local predator community can be changed by removing den sites (e.g., abandoned farm buildings, rock piles, and hollow trees) and nesting and perching structures (i.e., trees). In addition to protecting large tracts of grasslands, Greenwood et al. (1995) have suggested removing brush in areas where nest predation is high.

Improving cover

Cover for breeding birds provides crucial shelter from climatic conditions and concealment for the hen and nest. Many studies have reported greater waterfowl nest success in taller and denser cover (Milonski 1958, Kirsch et al. 1978, Livezey 1981, Kantrud 1993, Gregg et al. 1994). The dependence of breeding birds on concealment also is supported by increased duck recruitment (Schranck 1972, Greenwood et al. 1995, Beauchamp et al. 1996*a*) and greater pheasant (*Phasianus colchicus*) nesting success (Chesness et al. 1968) as cover grows during the nesting season.

Several authors have emphasized the importance of residual vegetation from previous growing seasons for nesting birds. Fields with little residual cover had lesser nest densities and lesser nest success than fields with denser residual cover (Martz 1967, Chesness et al. 1968, Kantrud and Higgins 1992, Gregg et al. 1994). Early nesting species, such as northern pintails (*Anas acuta*), prefer stubble fields for nesting. Litter depth appears important for blue-winged teal (*Anas discors*) and some passerines (Byers 1974, Igl and Johnson 1995).

Clark and Nudds (1991) found that the importance of cover varied with predator species. Dense cover conceals nests from visually oriented predators such as magpies (*Pica pica*), herring gulls (*Larus argentatus*), and crows (Jones and Hungerford 1972, Brouwer and Spaans 1994). The same visual concealment that protects nests from avian predators may not protect them against predators that rely on olfaction, such as skunks, foxes, or snakes (Crabtree and Wolfe 1988, Fleskes and Klaas 1991, Sargeant et al. 1993, Zimmerman 1984).

Contrary to Clark and Nudds' (1991) conclusions that cover protected nests against avian, but not mammalian, predators, Erikstad et al. (1982) found that crows robbed well-concealed willow ptarmigan (*Lagopus lagopus*) nests at greater rates than poorly concealed nests. They claimed that crows located nests by watching hen movements to and from the nests. The same behavior was described by Kalmbach (1938), Hammond and Forward (1956), and Preston (1957) for crows preying on duck nests located in dense cover and by Preston (1957) for red grouse (*Lagopus scoticus*) nests.

One way that cover reduces predation on nests is by providing structural heterogeneity around the nest, which can decrease the foraging efficiency of a predator (Bowman and Harris 1980). Heterogeneity increases searching time of predators and reduces the number of clutches found. Local habitat heterogeneity can be more important than visual concealment for protecting nests (Bowman and Harris 1980, Mankin and Warner 1992). However, Zimmerman (1984) found greater nest predation by snakes in more heterogeneous habitats. Also, dense cover did not seem to act as an olfactory barrier for skunks (Crabtree et al. 1989). Other studies reported no relationship between nest success and cover (Byers 1974, Trevor 1989, Fleskes and Klaas 1991). This lack of pattern has not been explained fully, but may be the result of incidental encounters of nests by predators (Livezey 1981, Angelstam 1986).

A main paradigm in managing breeding grounds for upland-nesting waterfowl has been that dense nesting cover improves nesting success (United States Fish and Wildlife Service 1986) by deterring predators and decreasing their feeding efficiency (Duebbert 1969, Schranck 1972, Redmond et al. 1982). Although accepted widely, this hypothesis remains untested. In fact, isolated patches of dense nesting cover may act as ecological traps (Ratti and Reese 1988, Pasitschniak-Arts and Messier 1995) by attracting and concentrating nesting hens (Duebbert and Lokemoen 1980, Fleskes and Klaas 1991) and mammalian predators (Milonski 1958, Schranck 1972, Choromanski-Norris et al. 1989, Greenwood and Sovada 1996), with the result of high rates of nest predation (Labisky 1957, Hines and Mitchell 1983, Clark and Nudds 1991). Similarly, efforts in New Zealand to manage vegetation to deter predators produced the opposite results; the changes attracted predators and thus increased depredations on nesting birds (Alterio et al. 1998).

Pheasant nesting studies along linear patches and rights-of-way (Chesness et al. 1968, Haensly et al. 1987, Mankin and Warner 1992) support the ecological trap hypothesis, which argues that small habitat patches attract nesting birds, but their nests suffer greater predation than nests in larger patches (Ratti and Reese 1988, but see Joselyn et al. 1968). Instead of being sources for recruitment, small patches of dense nesting cover might serve as sinks for nesting birds (Clark and Diamond 1993). Because concentrations of nesting birds and dense cover attract predators, it may be necessary to increase the area of dense nesting cover to disperse the nests (Duebbert and Lokemoen 1976, Kantrud 1993).

The relationship between protective vegetation cover and predation is complex. Management of cover alone may not improve nest success (Trevor 1989, Fleskes and Klaas 1991). Greater knowledge of predators' searching behaviors is necessary (Erikstad et al. 1982, Greenwood et al. 1995). The dynamic composition of predator communities is a significant obstacle in gaining this understanding (Sargeant et al. 1993). Clark et al. (1995) suggested establishing vigorous stands of natural vegetation only where avian predation occurs. However, Sullivan and Dinsmore (1990) claimed that this practice may not be effective against predation by crows. Therefore, fields of dense nesting cover should be managed according to the predators present (Millenbach et al. 1996).

Landscape and patch manipulation

The effects of habitat loss on breeding birds and their interactions with nest predators and nest parasites in forested systems and grasslands have been reported extensively in Europe (Andrén and Angelstam 1988, Storch 1991) and North America (Greenwood et al. 1995, Donovan et al. 1997). In Canada, waterfowl nest success was correlated to amount of grassland habitat available and decreased with an increase in amount of cropland (Greenwood et al. 1987, 1995). Similar results were found by Ball (1996) in the Prairie Pothole region and by Andrén (1992) in Sweden.

In grassland ecosystems, habitat fragmentation is considered the primary factor in the decline of many bird populations (Johnson and Temple 1986, 1990). However, few studies have examined avian reproductive responses to grassland fragmentation. As summarized by Clark and Nudds (1991), the evidence for the relationship between nest success and patch size is inconclusive. There are studies that show positive relationships (Johnson and Temple 1986, Greenwood et al. 1987, Kantrud 1993), no relationships (Duebbert and Lokemoen 1976, see Martz 1967 for pair use and Storch 1991), or negative relationships (Livezey 1981). Clark and Nudds (1991) suggest that other factors (e.g., effect of concealment and predator species) confound results. Experimental research in parallel with management is needed (Clark and Diamond 1993).

Another consideration is the matrix nature of the landscape. The shape and spatial arrangement of cover patches also affect bird recruitment. In linear patches, such as fence rows and rights-of-way, even the most concealed pheasant nests were destroyed (Chesness et al. 1968) and waterfowl nests in these areas had low nest success rates (Klett et al. 1988, Cowardin et al. 1985, Greenwood et al. 1987). Opposite results were found by Warner et al. (1987, 1992) for pheasants and for waterfowl by Oetting and Cassel (1971) and Page and Cassel (1971). Local predator abundance and species composition, as well as abundance of alternative prey, possibly accounted for the differences.

Clark and Diamond (1993) outlined management practices at the landscape level that included increasing the size and density of habitat patches and reducing patch isolation. However, the limited availability of large patches and the large spatial scale and time frames are difficult management problems to solve. Instead of site-specific efforts, Betake and Nudds (1995) and Beauchamp et al. (1996*a*) recommend directing efforts toward encouraging extensive management, including the recovery of marginal farmland (Fleskes and Klaas 1991) and alternative farming practices (Warner and Etter 1985). Low-quality agricultural lands are used intensively by many wildlife species (Clark and Diamond 1993).

Conclusions

Productivity of ground-nesting birds may be increased through several nonlethal management techniques such as modifying the predator community, associational defense, improving cover, and landscape manipulation. Our review indicates a wide range in the success of different methods and the spatio-temporal applicability of the techniques.

Our review also showed that there are no panaceas for the problem of reducing predation on nesting birds. Techniques may be successful only under limited conditions and for a specific array of species. Because of this, no management practice is uniformly better than another to increase bird recruitment. In fact, it appears that the different techniques are complementary rather than exclusive. Managers need to select the best technique(s) based on the predator community, local topography, size of the area, the avian species that needs protection, and other management goals and constraints. The decisions also should be based on cost–benefit analyses involving the costs to produce an additional young (Lokemoen 1984). Hence, it is surprising that few studies provide such economical analysis because this is ultimately the common currency that wildlife managers must use when selecting among competing techniques. We believe that with more research, ecological techniques can be used to increase the nest success of a broad range of avian species.

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