



Predation and the management of prairie grouse

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Abstract This paper examines the importance of predation in the life cycles of sage grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*), greater prairie-chicken (*T. cupido*), and lesser prairie-chicken (*T. pallidicinctus*). Most individual prairie grouse eventually succumb to predation, with substantial effects on nest success, juvenile survival, and adult survival. Predator control has occasionally been used as a management tool with the belief that reducing predator numbers can enhance viability of game populations in general and prairie grouse in particular. Although some experimental research has shown that direct reduction of predator numbers can increase grouse recruitment, most current management plans recommend indirect management of the grouse-predator relationship by manipulating habitats. However, as habitats become more fragmented and altered and populations of prairie grouse become more threatened and endangered, it is important to reconsider predator control as a management option and to evaluate its viability through experimentation.

Key Words *Centrocercus urophasianus*, greater prairie-chicken, grouse management, lesser prairie-chicken, population regulation, predator-prey relationships, sage grouse, sharp-tailed grouse, *Tympanuchus cupido*, *Tympanuchus phasianellus*, *Tympanuchus pallidicinctus*

Life histories of sage grouse, sharp-tailed grouse, greater prairie-chicken, and lesser prairie-chicken have been studied throughout their ranges. Despite variation in behavior, habitat, and status, populations of prairie grouse are similar regarding extent, timing, and significance of mortality from predation (Schroeder and Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999). The consequences of predation on the population dynamics of prairie grouse are often considered to be substantial enough that the effective management of prairie grouse requires the direct and indirect manipulation of predation pressure (Batterson and Morse 1948, Hamerstrom et al. 1957, Lawrence 1982, Riley et al. 1992).

We review available information on the importance of predation in the life cycles of prairie grouse and place that information into a management context. Because predation pressure can be manipulated directly by controlling predator numbers (Batterson and Morse 1948) and indirectly by manipulating habitats (Hamerstrom et al. 1957), an additional objective of this paper was to evaluate the viability of alternative strategies.

Description of prairie grouse predation

Sage grouse

Average clutch size for sage grouse varies from 6.6 to

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9.1 eggs, and the nest success rate varies from 15 to 86% (Wallestad and Pyrah 1974, Connelly et al. 1993, Gregg et al. 1994, Schroeder 1997). Nest predators include ground squirrel (*Spermophilus* spp.), badger (*Taxidea taxus*), coyote (*Canis latrans*), and common raven (*Corvus corax*, Batterson and Morse 1948, Patterson 1952, DeLong et al. 1995). Nest success is positively correlated with the presence of big sagebrush (*Artemisia tridentata*) and relatively thick grass and forb cover (Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998). Consequently, improper management of habitat has often been implicated in declines in nest success (Trueblood 1954, Klebenow 1969, Braun et al. 1977, Fischer et al. 1996).

Primary predators of sage grouse include golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*B. swainsoni*), ferruginous hawk (*B. regalis*), northern harrier (*Circus cyaneus*), common raven, weasel (*Mustela* spp.), and coyote (Rasmussen and Griner 1938, Scott 1942, Patterson 1952, Dunkle 1977). Mortality for juveniles has been estimated to be 63% during the first few weeks after hatch (Wallestad 1975). Habitat alteration associated with grazing, drought, and wildfire may increase the rate of predation on juveniles, but the relationships are not clear (Batterson and Morse 1948, Klebenow 1972).

Annual mortality of breeding-age sage grouse varies from 55 to 75% for females and 38 to 60% for males; mortality appears to be greater in hunted populations (June 1963, Zablan 1993, Connelly et al. 1994). Relatively little mortality is caused by fire, weather, and collisions with wires, fences, and vehicles (Patterson 1952, Dalke et al. 1963, Schroeder et al. 1999). Predation appears to be particularly important for females during the incubation and brood-rearing seasons and for males during the breeding season (Patterson 1952, Schroeder et al. 1999). Predation rate on breeding-age birds may not be influenced by harvest rate or habitat (Braun 1998).

Sharp-tailed grouse

Average clutch size for sharp-tailed grouse varies from 10.9 to 12.3 eggs and nest success rate from 50 to 72% (Hamerstrom 1939, Hart et al. 1950, Ammann 1957, Meints 1991). Nest predators include coyote, striped skunk (*Mephitis mephitis*), ground squirrel, common

raven, and American crow (*Corvus brachyrhynchos*). Because nest success is positively correlated with the presence of relatively thick grass cover, activities such as grazing or haying may negatively impact nest success (Kohn 1976, Kirsch et al. 1978, Marks and Marks 1987, Giesen and Connelly 1993).

Primary predators of sharp-tailed grouse include coyote, northern goshawk (*Accipiter gentilis*), gyrfalcon (*Falco rusticolus*), rough-legged hawk (*Buteo lagopus*),

Predator controls are rarely recommended for North American prairie grouse, even for increasingly threatened and endangered populations living in altered, isolated, or fragmented habitats. This is due to...factors including the lack of information about the long-term consequences of predator control, the relatively high cost of predator control, the protected status of many potential predators, and concerns about public attitudes toward predator control...

northern harrier, red-tailed hawk, and great horned owl (*Bubo virginianus*, Lano 1912, Gross 1930, Marshall and Jensen 1937, Blus 1967). Although mortality of juveniles is poorly documented, it appears to be substantially greater than for breeding-age birds (Ammann 1957, Hillman and Jackson 1973, Connelly et al. 1998). Annual mortality of breeding-age sharp-tailed grouse varies from 17 to 55% (Robel et al. 1972, Moyles and Boag 1981, Giesen 1987, McDonald 1998). Predation appears to be particularly important for breeding-age birds during the breeding season (Bergerud 1988, McDonald 1998). Predation also may be substantial during severe winters, particularly from avian predators (Ulliman 1995, Connelly et al. 1998).

Greater prairie-chicken

Average clutch size for greater prairie-chickens varies from 8.2 to 12.9 eggs and nest success rate from 22 to 65% (Yeatter 1943, Ammann 1957, Vance and Westemeier 1979, Peterson and Silvy 1996). Nest predators include ground squirrel, badger, striped skunk, opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), coyote, American crow, and fire ants (*Solenopsis* spp., Gross 1930, Lehmann 1941, Bowen et al. 1976, Svedarsky 1988). Nest success is greater in areas with relatively thick grass and forb cover (Yeatter 1963, Bowen et al. 1976, Buhnerkempe et al. 1984, Lutz et al. 1994). Management of habitat that results in loss of residual vegetation may result in reduced nest success (Lehmann 1941, Arthaud 1970, Kirsch et al. 1973).



Greater prairie-chicken nest in northeastern Colorado. Research on prairie grouse has demonstrated a relationship between nest success and habitat quality.

Primary predators of greater prairie-chickens include red-tailed hawk, northern goshawk, rough-legged hawk, broad-winged hawk (*Buteo platypterus*), northern harrier, great horned owl, and coyote (Yeatter 1943, Berger et al. 1963, Hamerstrom et al. 1965, Sparling and Svedarsky 1978). Juvenile mortality appears to be greater than for breeding-age birds, particularly during the first few weeks after hatch (Bowman and Robel 1977, Peterson and Silvy 1996). Annual mortality of breeding-age greater prairie-chickens is estimated to be 45% for males and 49% for females; mortality tends to be greater in hunted populations (Hamerstrom and Hamerstrom 1973). Relatively small amounts of mortality are caused by fire, weather, and collisions with wires, fences, and vehicles (Gross 1930, Hamerstrom 1939, Lehmann 1941, Ammann 1957, Svedarsky 1988). There is little information on the annual distribution of predation pressure (Schroeder and Robb 1993).

Lesser prairie-chicken

Average clutch size for lesser prairie-chickens is 10.4 eggs and nest success rate varies from 0 to 67% (Copelin 1963, Sutton 1968, Donaldson 1969, Riley 1978, Merchant 1982, Haukos 1988, Giesen 1998). Nest predators include Chihuahuan raven (*Corvus cryptoleucus*), coyote, badger, striped skunk, ground squirrel, and bull snake (*Pituaphis melanoleucus*, Davis et al. 1979, Haukos 1988, Haukos and Broda 1989, Giesen 1998). Nest success is positively correlated with the presence of relatively thick grass cover (Riley 1978, Wisdom 1980, Riley et al. 1992). Consequently, drought and grazing by livestock can reduce nest success (Riley 1978, Wisdom 1980, Merchant 1982, Haukos and Smith 1989).

Primary predators of lesser prairie-chickens include

red-tailed hawk, rough-legged hawk, ferruginous hawk, prairie falcon (*Falco mexicanus*), great horned owl, golden eagle, and northern harrier (Campbell 1950, Copelin 1963, Merchant 1982, Haukos 1988, Giesen 1998). Juvenile mortality appears to be substantial during the first few weeks after hatch (Giesen 1998). Annual mortality of adult male lesser prairie-chickens ranges between 35 and 45% (Campbell 1972). Relatively small amounts of mortality are caused by drowning and collisions with wires, fences, and vehicles (Campbell 1972, Sell 1979, Merchant 1982). There is little information on the annual distribution of predation pressure (Giesen 1998).

Predation and life history

Most prairie grouse are eventually killed by predators (Bergerud 1988). Predation has the potential to affect the annual life cycle in 3 primary ways: 1) success of nests, 2) survival of juveniles during the first few weeks after hatch, and 3) annual survival of breeding-age birds. The relative importance of predation on population viability remains largely unstudied (Peterson and Silvy 1996).

Nest success

Nest success, which is the proportion of nests where ≥ 1 egg hatches, is usually considered the most significant feature influencing the population dynamics of prairie grouse (Angelstam 1986, Bergerud 1988, Peterson and Silvy 1996). This is primarily due to the fact that nest success is extremely variable and differences in nest success can be attributed to variation in habitat characteristics or predation pressure associated with year, area, population density, or management strategy (Peterson and Silvy 1994, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999). Although prairie grouse may respond to high rates of nest predation by renesting within the same breeding season (Svedarsky 1988, Schroeder 1997, Connelly et al. 1998, Giesen 1998), predation pressure on nests also can be mitigated by providing habitat in sufficient quality and quantity (Hamerstrom et al. 1957, Kirsch 1974, Connelly et al. 1991, Riley et al. 1992).

Juvenile survival

Survival of juveniles has been difficult to assess because of problems in obtaining accurate information about their fate, particularly during the first 2 weeks after hatch (Ammann 1957, Christenson 1970, Hillman and Jackson 1973, Bowman and Robel 1977). Nevertheless, juvenile survival has the potential to dramatically affect population viability (Peterson and Silvy 1996). Because variation in juvenile survival may be correlated with

variation in habitat characteristics, increased attention has been directed toward managing habitat to increase survival of juveniles (Peterson and Silvy 1996, Edelman et al. 1998).

Survival of breeding-age birds

Annual survival of breeding-age birds usually is not variable enough to permit comparisons among different habitats or among areas with different densities of predators (Schroeder and Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999). Consequently, adult survival usually is considered to be a relatively unmanageable period of the life cycle. The primary exception to this consideration has been with manipulation of harvest. For example, survival of female sage grouse was estimated as 67% in a harvested population in Wyoming (June 1963), 55% in a harvested population in Colorado (Zablan 1993), and 75% in an unharvested population in Idaho (Connelly et al. 1994). Although harvest may have significant effects on local populations (Ammann 1963, Taylor and Guthery 1980, Crawford and Lutz 1985, Marks and Marks 1987), harvest rates generally are considered to be small when compared with predation rates (Dalke et al. 1963, Hamerstrom and Hamerstrom 1973, Hillman and Jackson 1973, Johnson and Braun 1999).

Predation and population viability

Predation of prairie grouse is often considered to be a ramification of habitat quality and distribution, population pressure and density, or predator behavior and dynamics (Christisen 1969, Miller and Graul 1980, Taylor and Guthery 1980, Braun 1998). Inadequate quality of habitat may increase the predation risk for birds attempting to locate escape cover (Svedarsky 1988, Connelly et al. 1991, Riley et al. 1992, Gregg et al. 1994). Habitat degradation that alters visibility at lek sites may increase the risk of predation to displaying males (Hartzler 1974, Baydack and Hein 1987, Berger and Baydack 1993). The lack of adequate feeding areas may increase predation by forcing birds to feed longer, to feed in riskier habitats, or to travel farther to feeding areas (Gregg et al. 1993, Fischer et al. 1996, Pyle and Crawford 1996). Fragmentation of habitat may increase predation pressure by forcing nesting birds into marginal habitats, by increasing travel time through unacceptable habitats, and by increasing the diversity and density of predators (as shown for European grouse; Andr n et al. 1985, Andr n and Angelstam 1988, Bernard-Laurent and Magnani 1994, Kurki et al. 1997).

Population pressure is often considered to be a density-dependent mechanism controlling the size and growth of



Displaying male sage grouse on lek in north-central Colorado. Male prairie grouse may be vulnerable to predation during the breeding season. Photo by R. E. Bennetts.

a population (Hannon 1986). Increases in population density may increase the likelihood of dispersal and, conversely, may reduce the opportunities for recruitment (Keppie 1979). Subordinate male greater prairie-chickens and lesser prairie-chickens, which are less likely to establish territories, may have greater rates of predation (Robel 1970, Campbell 1972). Subordinate female greater prairie-chickens may be inhibited by dominant females from mating, resulting in delays in nesting with associated declines in productivity (Robel 1970, Robel and Ballard 1974). Increased densities of sharp-tailed grouse nests may result in an increased risk of predation (Apa et al. 1997).

The dynamics of predator populations are determined typically by the abundance of their primary prey species, which usually are rodents or lagomorphs rather than grouse (Bump et al. 1947, Angelstam 1986, Marcstr m et al. 1988, Myrberget 1988). In situations where populations of the primary prey species fluctuate, grouse numbers can be influenced by the changing densities of predators and the effects that prey densities have on the predator's foraging behavior. For example, when predators are forced to search for relatively scarce prey, they are more likely to encounter grouse and grouse nests (Angelstam 1983).

Predator management

Habitat quality, prairie grouse density, and predator numbers are all manageable to a certain extent. For example, prairie grouse density can be reduced by harvest, which has the potential to reduce the predation rate on the remaining birds (Ellison 1991). However, because the goal of predator management usually is to increase the numbers of the target species, reducing prairie grouse density is not a viable management option to manipulate predator populations. In contrast, manipulation of habitat quality or predator numbers has the potential to decrease predation rate and ultimately to increase grouse populations (Hamerstrom et al. 1957).

Most direct efforts to control predator populations have been regional in nature and not motivated by a desire to increase numbers of prairie grouse (Willis et al. 1993). Consequently, there are few examples of predator controls in which populations of prairie grouse were monitored. Batterson and Morse (1948) removed common ravens on one sage grouse area in Oregon and left another area as a control. They found a 3% nest success rate in the untreated area and 35% in the treated area. Mammalian predators (striped skunk, opossum, raccoon) were controlled on an experimental area in the range of the Attwater's prairie-chicken (*T. c. attwateri*, Lawrence 1982). The subsequent rate of success for artificial nests was 82% on the removal area and 33% on the area where predators were not controlled. Unfortunately, the small number of predator control experiments has left a substantial void in the information necessary to evaluate the viability of predator control as a management tool. For example, there is essentially no information on the long-term impacts of predator controls on the behavior, genetics, and abundance of prairie grouse.



Badger in southwestern Wyoming. Badgers are common nest predators in portions of the ranges of all prairie grouse.

In contrast to research on North American prairie grouse, predator control research has been relatively common for the management of European grouse, including black grouse (*Tetrao tetrix*), capercaillie (*T. urogallus*), hazel grouse (*Bonasa bonasia*), and willow ptarmigan (*Lagopus lagopus*). Most predator controls in Europe have been shown to increase nest success, juvenile survival, and population size (Parker 1984, Marcström et al. 1988, Baines 1990, Moss 1994), with rare exceptions (Korsch 1984). European management plans for grouse consistently include references to predator control (Hudson and Rands 1988; Bergmann and Klaus 1994; Klaus and Bergmann 1994a). This is in contrast to North American management plans for prairie grouse, even endangered species, which rarely include references to predator control (Taylor and Guthery 1980, Morrow 1986, Giesen and Connelly 1993, Westemeier and Gough 1999).

There are fundamental reasons for the differences in grouse management in Europe and North America. First, the small and isolated nature of remaining habitat in Europe is used as a justification for intervention in the predator-prey relationship (Korsch 1984, Andrén and Angelstam 1988, Hudson and Dobson 1995). Second, grouse restoration efforts in Europe usually depend on birds raised in captivity that are extremely susceptible to predation (Schroth 1991, Starling 1991, Mäkinen et al. 1997, Merker 1997). Third, the financial benefits of grouse hunting in Europe for the landowners increase the pressure to use predator control to increase the number of birds available for harvest (Jenkins et al. 1964, Jensen 1970, Hudson and Rands 1988, Moss 1994).

Predator controls are rarely recommended for North American prairie grouse, even for increasingly threatened and endangered populations living in altered, isolated, or fragmented habitats. This is due to numerous factors including the lack of information about the long-term consequences of predator control, the relatively high cost of predator control, the protected status of many potential predators, and concerns about public attitudes toward predator control (Messmer et al. 1999). Predator management for North American prairie grouse generally has been addressed by manipulating habitat, because it is believed to be the most economical, efficient, and viable long-term strategy to enhance populations of prairie grouse (Hamerstrom et al. 1957, Dalke et al. 1963, Giesen and Connelly 1993, Edelman et al. 1998).

All 4 species of prairie grouse in North America have populations or subspecies that are either federally listed or being considered for federal listing as threatened or endangered (Connelly and Braun 1997, Connelly et al. 1998, Giesen 1998, Silvy et al. 1999, Westemeier and



Remains of sharp-tailed grouse killed and partially eaten by northern goshawk in north-central Washington. Northern goshawks are predators of grouse wherever their ranges overlap.

Gough 1999). Because concerns for the conservation of prairie grouse are likely to increase, future management and recovery plans probably will need to consider all options for population recovery, including predator management. Whether predator management includes only the manipulation of habitat or both the manipulation of habitat and the direct control of predator numbers is a question that needs to be addressed in future research.

Conclusions and recommendations

Primary predators for prairie grouse include a combination of raptors, corvids, and mammals that substantially influence nest success, juvenile survival, and adult survival. Predator management has been conducted with the direct control of predator numbers and the indirect control of the grouse–predator relationship through the manipulation of habitat. Although predator control has not been used extensively for prairie grouse management in North America, it has been used extensively for grouse management in Europe. Habitat management has been a dominant tool to manage effects of predators on populations of prairie grouse in North America, with documented success. Determination and provision of key habitat components to meet seasonal requirements for local populations of individual species has been shown to be an effective and efficient management strategy. However, as populations of prairie grouse become smaller in size and more threatened in status, additional options for the management of the prairie grouse–predator relationship will probably need to be considered, including the direct control of predator numbers.

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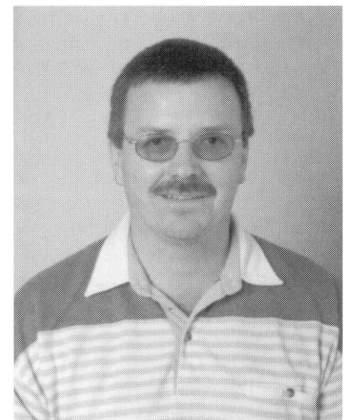
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