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Causes and Patterns of Mortality in Lesser Prairie-chickens Tympanuchus pallidicinctus and Implications for Management

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Causes and patterns of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management

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Life-history studies of prairie grouse have focused on reproductive ecology, habitat use, movement patterns and survivorship, with only cursory or anecdotal references to mortality causes, or they have been of insufficient duration or scale to infer mortality patterns. Because mortality causes and patterns affect other life-history traits, their determination adds to our overall understanding of grouse demographics. As part of a long-term study on lesser prairie-chicken *Tympanuchus pallidicinctus* natural history in Oklahoma and New Mexico, we recovered 322 carcasses of radio-tagged birds captured on leks. We were able to determine the cause of death for 260 of these birds. Predation by raptors accounted for the largest number of mortalities (91), followed by collisions with fences (86), predation by mammals (76), collisions with power lines (4), and collisions with automobiles (3). Mortality causes differed considerably between study sites and between sexes, with all collisions more frequent in Oklahoma than in New Mexico, in females than in males, and in older than in young females. Although predation is a major cause of mortality, we argue that predator control may not be effective for grouse conservation. Moreover, in cases where top predators reduce mesopredator population densities, for example those of red foxes *Vulpes vulpes*, indiscriminate removal of predators may hasten the decline of grouse populations. Land managers striving to conserve prairie-chickens and other grouse species should attempt to reduce or eliminate collision mortality risks in addition to efforts to improve nesting or brood-rearing habitat. Collision risks should also be evaluated for potential release sites of translocated or captive-reared grouse.

Key words: collisions, grouse management, lesser prairie-chicken, mortality, predation, survival, Tympanuchus pallidicinctus

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Like other species of North America's grassland grouse, the lesser prairie-chicken *Tympanuchus pallidicinctus* has declined sharply throughout its range, and it has suffered an associated range contraction (Taylor & Guthery 1980, Giesen & Hagen 2005). Declines and range contractions continue in Oklahoma (Horton 2000), resulting in non-contiguous populations within the state and even less continuity with populations in other states. The prairie-chicken's range has diminished considerably in New Mexico as well, but that population remains relatively stable, albeit localized (Bailey & Williams 2000).

In most areas, causes for the precipitous drop in population size have been largely mysterious. Likely culprits include changes in predator communities and abundance, as well as habitat loss, degradation and fragmentation, yet no single cause is obvious (Hagen et al. 2001, Silvy et al. 2001). A number of mammals and raptors prey upon prairie grouse (Schroeder & Baydack 2001, Giesen & Hagen 2005), but changes to predation rates have not been detected. An overlooked problem associated with fragmentation of prairie habitat is the effect of fences and power lines, which can lead to fatal collisions of various avian species (Borell 1939, Ligon 1951, Toepfer 1988, Allen & Ramirez 1990, Wolfe 1993).

In an effort to learn reasons for the decline of lesser prairie-chicken populations, we radio-tagged birds on spring and autumn gobbling grounds in northwestern Oklahoma and in southeastern New Mexico. A key objective was to discover factors affecting survivorship in this species. Accordingly, we analyzed recovered carcasses to determine cause of mortality with respect to age, sex and season. Our results allowed us to recommend measures to minimize mortality of lesser prairie-chickens. In doing so, we hope that lesser prairie-chicken survival can be restored to more natural levels, a goal that may allow populations to recover or stabilize.

Material and methods

Field data

From March 1999 through May 2004, we captured 719 adult and young (< 1 year old) lesser prairie-chickens on gobbling grounds in spring and autumn in Beaver, Ellis and Harper Counties in northwestern Oklahoma and in Roosevelt County in eastern New Mexico. Birds were captured using drift fences and modified walk-in traps (Schroeder & Braun 1991). All hens and most cocks were fitted with ≤ 15-g, bib-mounted, tuned-loop radio transmitters. Radio-tagged birds were usually located once or twice each week. Aerial searches (Gilmer et al. 1981), using strut-mounted antennas, were conducted 4-6 times annually at each study site to aid in relocating birds missing for > 3 weeks. All radio transmitters were equipped with a 12-hour delay mortality switch, which allowed detection and immediate recovery of dead birds.

Mortality cause was determined using criteria developed by Dumke & Pils (1973) and Small et al. (1991). Because many predators (and some rodents) scavenge carcasses, it can often be difficult to determine whether a bird was killed or merely scavenged. For example, Toepfer (1988) related an incident in which a greater prairie-chicken *Tympanuchus cupido pinnatus* collided fatally with a power line and was fed upon subsequently by a red-tailed hawk *Buteo jamaicensis* and a domestic dog *Canis familiaris*. For cases in which the transmitter had become separated from the carcass or was buried or had been dragged into a burrow, the exact cause of death was sometimes impossible to determine. For each carcass, we also recorded distance from the nearest fence, road and power lines, and carefully documented nearby tracks, scat and other clues. Each carcass was examined for sheared feathers (mammal consumption), stripped tendons (raptor consumption), bite marks on bones and/or the radio transmitter (mammal or raptor consumption), and abrasions, contusions or broken wings (collisions). We made no concerted effort to identify predators beyond mammalian or raptor. We inferred a collision with a fence or power line when a carcass was < 20 m from that obstacle or the carcass remained to show evidence of a collision. By using proximity alone, we may have underestimated collision rates given that several carcasses 25-50 m from fences or power lines were intact enough to determine that a collision had occurred. If prairie-chickens were being killed at random locations across the landscape, ~12% of the carcasses should be found < 50 m from a fence in the most densely fenced areas (¼-section pastures or 65 ha), and only ~6% would be found within that distance if fences were moderately dense (full-section pastures; i.e. 1 mile^2 or 259 ha).

Even so, scavengers can move carcasses in excess of 50 m (Bumann & Stauffer 2002), and livestock trails along fence lines complicate the situation because we suspect that coyotes *Canis latrans* and other mammals make regular use of such trails, thereby encountering fence kills more often than they would in a homogenous landscape. For example, Bradley &

Fagre (1988) reported that both coyotes and bobcats *Felis rufa* used fence lines and roads as travel lanes more often than expected by chance. Similarly, Way et al. (2002) reported that coyotes traveled extensively along power lines, golf courses, railroad tracks, dirt roads and trails. Indeed, there is the reasonable possibility that scavengers learn to follow fence lines because they are rewarded by finding carcasses of prairie-chickens and other species. In any case, we made every effort to assign the proper cause of death to all birds, but in ambiguous cases we left the cause as 'unknown'.

Statistical analyses

Because all radio-tagged birds were being tracked regularly, the probability of locating carcasses resulting from collisions was assumed to be the same as for other mortality causes. We therefore did not employ a cause-specific mortality model with differing probabilities of carcass recovery (e.g. Schaub & Pradel 2004). Instead, we performed simpler survival analyses and associated contingency table analyses, including those for cause-specific mortality (e.g. Conner 2001). We treated the day of first capture as the day on which a bird entered the study. Although this means that birds of different ages were being tracked, our sample size and capture methodology should have removed any systematic bias. We calculated the 'life span' of a bird from the capture date to the carcass recovery date. We constructed comparative Kaplan-Meier survival curves by gender and study site (see Patten et al. 2005b), as well as by age at death (adult or young) and cause of death (collision, raptor or mammal). We also examined various interactions of these categories (e.g. sex*cause). We judged survival curves to differ statistically on the basis of a log-rank χ^2-test (Pyke & Thompson 1986). We used contingency table analyses of frequencies to detect associations between cause of death and gender, age or study site (Sokal & Rohlf 1995).
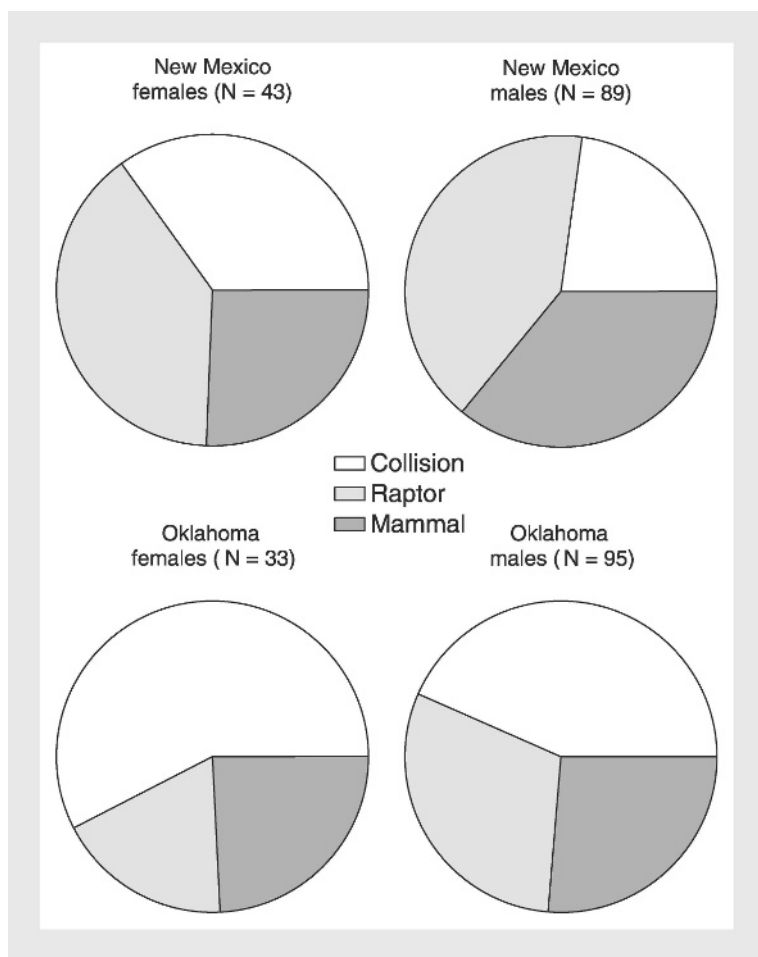

Figure 1. Cause-specific mortality of the lesser prairie-chicken by gender and study site. The overall proportion of collisions was significantly higher in Oklahoma than in New Mexico ($\chi^2 = 120.0$, df = 1, P < 0.001). Moreover, females had lower overall survivorship than males (see Fig. 2), largely as a result of their increased mortality from collisions (Patten et al. 2005b).
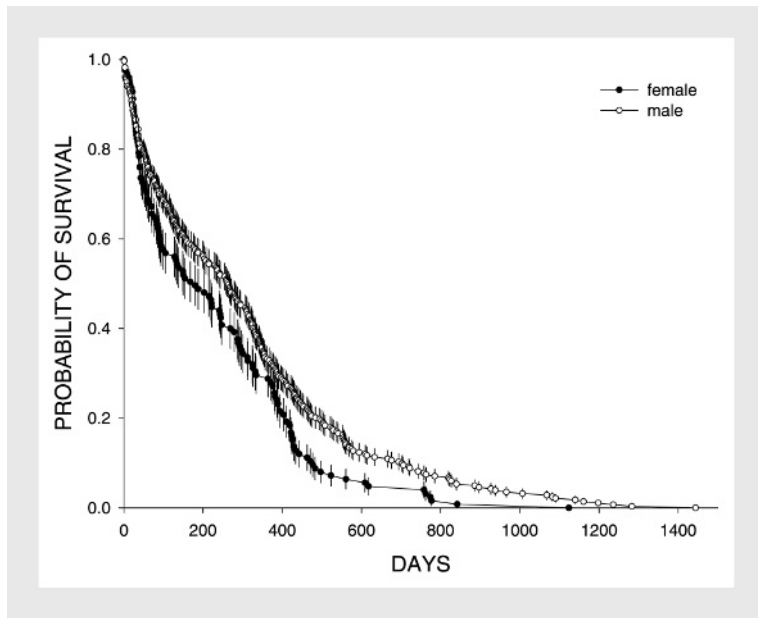
Figure 2. Relative survivorship of the lesser prairie-chicken by gender for New Mexico and Oklahoma combined. Females had significantly lower survivorship (log-rank: $\chi^2 = 7.02$, df = 1, P < 0.01). Bars on the Kaplan-Meier curves are standard errors.

Results

Between April 1999 and September 2004, we recovered 322 carcasses of radio-tagged lesser prairie-chickens. We were able to assign cause of death to 128 carcasses from Oklahoma and 132 carcasses from New Mexico (Fig. 1). There was not enough evidence to assign cause for the remaining 62 carcasses. Of 59 collisions from Oklahoma, 51 (86.4%) were the result of fence strikes, the remainder being the result of

power line or vehicle collisions. In contrast, all of the fewer collisions in New Mexico resulted from fence strikes. Overall, among recovered birds, females had lower survivorship than males (Fig. 2), the difference being significant in Oklahoma, but not in New Mexico (Fig. 3).

We found evidence that some prairie-chickens survived the initial impact of a collision only to die later from the injury or to be taken by a predator. We twice found females dead on the nest with obvious

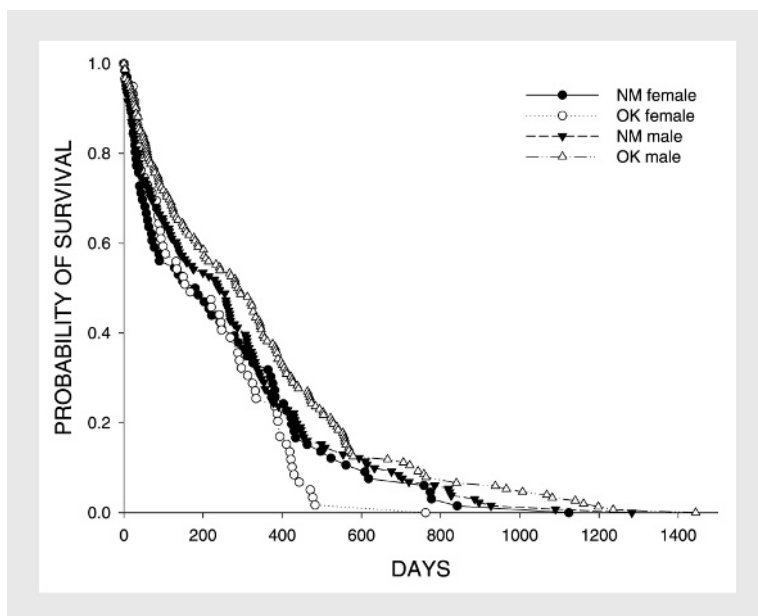Figure 3. Relative survivorship of the lesser prairie-chicken by gender and study site for males and females in New Mexico (NM) and Oklahoma (OK). Oklahoma females had significantly lower survivorship than their male counterparts (log-rank: $\chi^2 = 12.01$, df = 3, P < 0.01), presumably owing to being much more prone to fence collisions (see Fig. 1). Survivorship did not differ between the sexes in New Mexico.
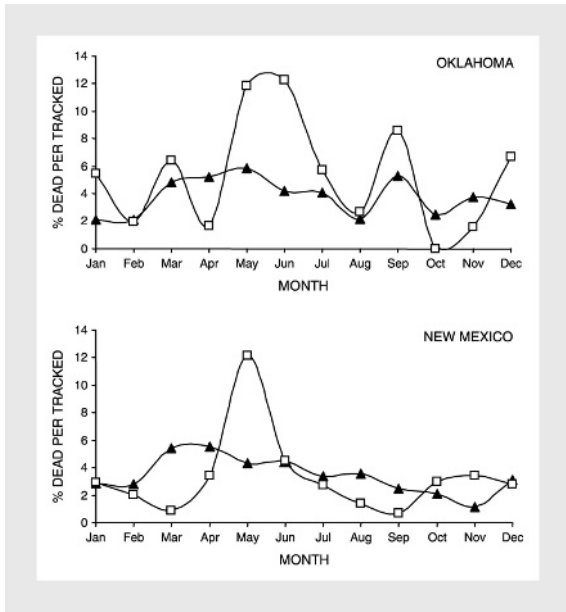
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Figure 4. Percentages of male (▲) and female (□) lesser prairie-chickens found dead per total tracked in each month.
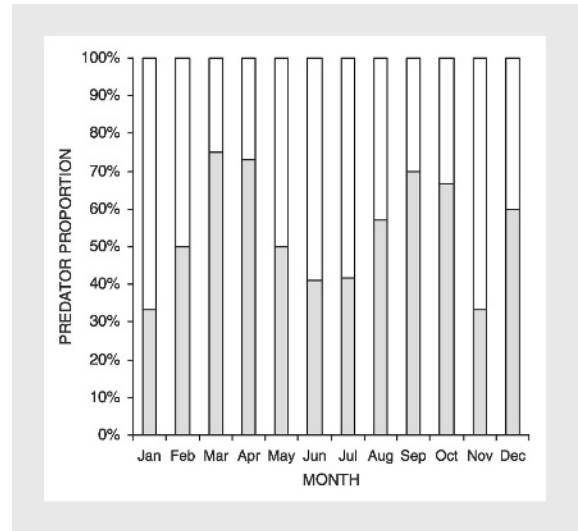

Figure 5. Relative monthly mammal (□) and raptor (■) predation on the lesser prairie-chicken in eastern New Mexico and western Oklahoma during 1999-2004. Spring and autumn peaks in relative predation by raptors coincided with raptor migration peaks.

fence collision wounds on the breast. We also recovered two intact carcasses with breast injuries > 200 m from a fence, and one had neck injuries, the other a broken wing, consistent with fence or power line collisions. In 2001, we captured a male with primaries 6-10 on his left wing cut in a straight line, as if sheared by a fence. This bird was incapable of flight and was found dead five days later as a result of mammal predation. In 2004, another male showed similar damage to primaries 8-10 on his right wing; he was found dead a day later as a result of raptor predation. Although we categorized both mortalities as (indirectly) resulting from fence collisions, cause of death would have been misinterpreted had we not documented the injuries only days earlier. The ability to survive for a time after sustaining injuries was further demonstrated in 2001 when we found a male carcass in a typical roosting posture at a location where he had roosted previously. Whereas the cause of death was not apparent immediately, post-mortem examination revealed extensive internal hemorrhaging and a crushed cranium, both of which appeared to result from a vehicle collision, even though the closest road was > 400 m away. Had a scavenger found this carcass prior to our recovery, we would have misclassified the cause of death.

The percentage of deaths resulting from fence collisions was significantly higher in Oklahoma than in New Mexico (39.8 vs 26.5%; $\chi^2 = 5.22$, df = 1, P < 0.025). Females were more susceptible than males to collisions (including power line and automobile collisions; 57.6 vs 43.4% in Oklahoma, 34.9 vs 22.8% in New Mexico; see Figs. 1 and 3). As a result, the median age at death of an Oklahoma female was significantly lower than that of an Oklahoma male (median two-sample test: Z = -1.64, P ≈ 0.05). Brood mortality rates for the lesser prairie-chicken are high (e.g. Fields et al. 2006), but among birds that grew to full size, the vast majority of mortalities were of birds that had reached adulthood (191 adult vs 40 young). As a whole, even though a much smaller percentage of young birds (17.1%) collided with fences relative to adults (30.4%), age at time of death was not related to mortality cause ($\chi^2 = 3.88$, df = 2, P > 0.10). However, there was a significant effect of age for females ($\chi^2 = 16.05$, df = 2, P < 0.0005). Adults (41.5%) were much more likely to die from collisions than were young birds (13.3%), whereas young birds were much more likely to be killed by a mammal (66.7%) than were adults (15.1%).

For both sexes, but especially for females, mortality rates peaked in spring and early summer (Patten et al. 2005b; Fig. 4). More than half (51%) of males were found dead between March and June, chiefly from predation. Raptor predation occurred in two seasonal peaks (Fig. 5).

Discussion

Differences in mortality causes between our study sites, especially fence, power line and vehicle collisions, are likely a result of the greater level of fragmentation in Oklahoma (Patten et al. 2005b), which is composed largely of 1-mile^2 (259 ha) sections, usually with county roads separating adjacent sections, and often fenced in ¼-section (65 ha) pastures or row crops. By contrast, New Mexico has much larger pastures, upwards of 4 mile^2 (1,036 ha), with scattered irrigated crop circles. Thus, the Oklahoma site was considerably more fragmented and included a higher density of fences, roads and power lines (Patten et al. 2005b). Indeed, with collisions removed, predation patterns were virtually identical between study sites: 52.9% raptor and 47.1% mammal in Oklahoma and 55.7% raptor and 44.3% mammal in New Mexico.

Male mortality

Peak mortality of male lesser prairie-chickens coincides with peak lekking activity in spring (see Fig. 4). We suggest that (a) males are more conspicuous at this time and (b) various predators focus on lekking activity. If a male intends to breed, it is essential for him to be on the lek nearly every day from March through May. He is thus dependable and conspicuous. Even outside of the 1-3 hours of daily displays, many males remain on or near the gobbling ground through the day and night, perhaps making them easier to locate, even when the conspicuous displaying is not occurring.

Spring lekking also entails an energetic cost. Our capture data showed that male lesser prairie-chickens weighed an average of 778 g in New Mexico and 789 g in Oklahoma in March (regardless of age) but 691 g and 714 g, respectively, by May. Although this ≈10% reduction in body weight may be in part an adaptation to warming weather, it also is likely a result of extreme energy expenditure during the intense lekking period, perhaps even to the exclusion of foraging. Vehrencamp et al. (1989) noted a similar relationship in male greater sage-grouse *Centrocercus urophasianus* during spring lekking. Accordingly, male prairie-chickens may be in poorer condition by the later parts of the spring lekking season, making them more vulnerable to predators.

That mortality did not differ with respect to age implies that even young males occupy leks and therefore are equally vulnerable to predation. Indeed, we caught a sizeable number of young males on spring leks, meaning that they potentially breed when < 1 year old.

Female mortality

The tendency for female lesser prairie-chickens to select a mate at a particular lek and to nest near a different lek (Giesen & Hagen 2005) yields higher mobility in females than in males. In Oklahoma a lek averaged 3.77 km from the next nearest lek, whereas in New Mexico the average distance was only 1.51 km. Similarly, the average distance from lek of capture to nest was 3.71 km in Oklahoma and 1.31 km in New Mexico. As a result, Oklahoma females moved further both among leks and from lek to nest site. Given the higher density of fences in Oklahoma and the greater mobility of females, we suggest that females in the Oklahoma population are exposed to an elevated risk of collision.

Unlike young males, it is possible that young females are less likely to attempt to breed. If so, then they may not move nearly as much as do adult females, meaning that they would not experience the associated risk of collision, which would explain the effect of age. The higher proportion of mammal predation of young females may be associated with behaviour as well, because young females may visit fewer leks, thus creating a movement pattern more like that of males.

As in the males, seasonality of mortality in females can be explained in terms of behaviour. In April, females often visit multiple leks to search among displaying males for a suitable mate. After mating, females disperse in search of a suitable nest site. Thus, one might predict that collisions would peak from late April through June (the latter accounting for multiple nest attempts), which corresponds to the pattern seen (see Fig. 4). We attribute the sharp reduction in collisions after June to hens rearing broods, when successful females, out of necessity, fly little.

Predation

Two peaks of raptor predation, the first in March and April, the second in September and October (see Fig. 5), coincide with peaks in spring and autumn lekking activity. On several occasions we found plucked feathers or raptor-consumed prairie-chicken carcasses on leks, yet we never witnessed predation by raptors. Berger et al. (1963) reported only three successful predation events by raptors, resulting from 1,379 raptor 'encounters' in 4,745 mornings of observing greater prairie-chicken booming grounds in Wisconsin. In northeastern and north-central New

Mexico, at latitudes roughly equidistant between our study sites, 80% of autumn migrant raptors were observed between 11 September and 16 October, and 80% of spring migrant raptors were observed between 17 March and 28 April (Smith 2005a,b), windows that seem to match observed peaks in raptor predation (see Fig. 5).

We have no reason to believe that lesser prairie-chicken populations are being impacted severely by predation. Many studies have made an effort to determine the primary predators of grouse, although often only during the nesting season. Our data imply differences in the types of predators throughout the year, meaning researchers should exercise caution when interpreting predator types during short-duration studies. Studies of diets of mammalian predators in the southern Great Plains and southwestern North America (Murie 1951, Kilgore 1969, Windberg & Mitchell 1990, Sovada et al. 2001, Henke 2002) determined that lagomorphs and rodents were the mainstays. What few bird remains were found in faeces or stomach contents were likely the result of scavenging rather than predation. Moreover, large carnivores may benefit ground-dwelling birds by reducing the number of mesopredators (e.g. striped skunks *Mephitis mephitis* and red foxes *Vulpes vulpes*) and by enhancing ground cover through the reduction of herbivores (Howard et al. 1959, Currie & Goodwin 1966, Guthery & Beasom 1977, Henke & Bryant 1999). Adequate brush cover and reduction of raptor perches such as trees, power poles and fence posts may lower predation more than conventional predator removal methods. For example, Patten et al. (2005a) demonstrated that adult lesser prairie-chicken survival was correlated positively with higher shrub cover, primarily of shinnery oak *Quercus havardii* and sand sagebrush *Artemisia filifolia*.

Fence collisions

Fences, power lines or other wire structures are an unnatural threat to many birds, yet they are seldom perceived as threats. Our data indicate that collisions with fences may significantly reduce lesser prairie-chicken survival, but collisions may have an even greater effect than what we detected. For example, we captured several birds with partially healed wounds from strikes and recovered carcasses with such wounds > 200 m from a fence. These non-lethal injuries may make these birds more susceptible to subsequent predation.

Neither Allen & Ramirez (1990) nor Wolfe (1993) reported grouse in their compilations of bird kills from fence collisions in North America. Grouse are likely underrepresented because they are rarely found impaled or entangled in fences and are more prone to fly or tumble some distance after impact, and their cryptic colouration tends to conceal carcasses in dense vegetation. The few fence collisions noted are typically anecdotal observations in obscure reports rather than in the mainstream of scientific literature. In North America, most documentation of collisions in grouse has regarded the ruffed grouse *Bonasa umbellus*, sage-grouse or prairie-chickens (e.g. Borell 1939, Bump et al. 1947, Ligon 1951, Krapu 1974, Danvir 2002, Toepfer & Septon 2003), yet both fence and power line collisions by grouse have been well documented in Europe (e.g. Bevanger 1995, Moss 2001). For instance, studies conducted in Scotland (Petty 1995, Baines & Summers 1997) or Norway (Bevanger & Brøseth 2000, 2004) of fence or power line collisions reported that 80-93% of kills were of various species of grouse *Lagopus* spp. and *Tetrao* spp., suggesting that this group of birds is particularly prone to collisions.

Accordingly, the negative effect of fence collisions cannot be understated. For example, Moss et al. (2000) implied that if collisions could be eliminated then capercaillie *Tetrao urogallus* populations in Scotland would increase or stabilize. When modeling estimated future capercaillie population size, Moss (2001) projected that with present fence collision risks, the entire Scotland population would consist of only about 40 females by 2014, but without collisions females would instead number 1,300 by 2014. If mortality from fence collisions is additive, then together with mortality from 'natural' causes it will affect survivorship adversely. Although increased mortality may lead to compensatory response in other life history traits (Patten et al. 2005b), even these responses may not be sufficient to save a population from extirpation.

Management implications

"*Fortunately, fences and roads are human constructions capable of being changed if people agree to do so.*" (Freilich et al. 2003)

Throughout the occupied range of the lesser prairie-chicken, old, dilapidated fences are common, primarily because the cost of removal outweighs any benefit of removal. Obviously, efforts to remove unnecessary fences would reduce collision risks. Marking existing fences, especially in high-use areas such as

near leks, nesting habitat or foraging areas to allow improved visibility, may also benefit populations (Summers & Dugan 2001, Baines & Andrew 2003). Marking of existing fences with strips of barrier fence to increase visibility resulted in a 71% overall reduction in grouse collisions in Scotland (Baines & Andrew 2003). However, barrier fence has a life expectancy of < 2 years (Summers & Dugan 2001); as it deteriorates it becomes even more unattractive to humans and requires regular extensive maintenance or replacement. Barrier fence adds considerable weight and wind resistance and could allow build up of vegetation (e.g. Russian thistle (tumbleweed) *Salsola tragus*), snow and/or ice, perhaps leading to collapse.

New marking methods being used in Europe show greater promise economically and aesthetically, while being easy to apply, having a long life, and not adding significant weight or wind resistance to fences. In some locales, placards (called anti-bird-strike tabs) of white or black plastic (10 × 10 cm or 10 × 19 cm) have been attached to fences (Summers & Dugan 2001), in others strips of sheet metal have been connected to the top wire or two of livestock fences (Game Conservancy Fund 2002, http://www.blackgrouse. info/recovery/northpenn/stockfence.pdf). Continued research is needed to develop marking methods that are effective, inexpensive and easy to install and will not affect the integrity of fences or pose hazards to livestock or wildlife. Several types of generally effective power line markers (e.g. Morkill & Anderson 1991, Brown & Drewien 1995) perhaps could be adapted for use on fences.

In many parts of North America's Great Plains, ranchers practice high-intensity, short-duration livestock grazing. Ironically, cross fencing and rotational grazing systems often have been recommended as management tools to improve nesting cover for prairie-chickens (e.g. Applegate & Riley 1998, Mote et al. 1999). In the most intensive rotational systems, large pastures have been subdivided into 8, 10 or 12 paddocks (cell system) with water located centrally. Livestock are moved frequently (often weekly) between paddocks. Given a pasture size of 259 ha, a prairie-chicken flying across the landscape would, on average, encounter a fence every 1.6 km. In an 8-paddock cell system the same bird would encounter a fence every 0.4 km, a 4-fold increase in encounter rate. We suggest that, when possible, alternative methods of controlling grazing pressure be employed, such as patch burning (see Fuhlendorf & Engle 2001) or by placement of minerals. Where cross fencing remains necessary, fences should be of as low a height as pos-

sible. If controlling grazing within a management unit is the primary purpose of cross fencing, the typical height used for perimeter fences (107-122 cm) may be unnecessary. We recommend reducing fence height by 10% or more (i.e. 96-110 cm). We further recommend that all fences < 1 km from active gobbling grounds be marked in some manner to increase their visibility.

Collisions with power lines are much less common in our study areas, but we nonetheless recommend that, when possible, electrical transmission and distribution lines be buried rather than strung overhead. Moreover, although predation may be of less biological importance than collisions with fences, reduction in fences results in the reduction of movement corridors for mammals and perches for raptors. We thus recommend that removal of all non-essential fences to improve nesting or brood rearing habitat, as removal will reduce both collision risk and, perhaps, predation risk.

Rarely have predator removal efforts in North America met expectations, largely because such efforts fail to consider complex ecological webs. Gross (1928) summarized the problem when speaking of the now-extinct heath hen *Tympanuchus c. cupido*: "The problem of saving the heath hen is not the simple one of providing protection against Hawks and cats and supplying food when needed but is much more complex". An important consideration recognized only relatively recently is the notion of 'mesopredator release', i.e. the idea that removal of large carnivores will allow mid-size carnivores to flourish (Crooks & Soulé 1999). The concept of mesopredator release likely explains why removal of large carnivores has failed to help various grouse populations (e.g. Bump et al. 1947, Lawrence & Silvy 1995, Hewitt et al. 2001, Lyons 2002, Slater 2003). We therefore cannot recommend predator control (*cf*. Schroeder & Baydack 2001); instead, management should focus on fence collisions and other anthropogenic mortality factors.

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References

Allen, G.T. & Ramirez, P. 1990: A review of bird deaths on barbed-wire fences. - Wilson Bulletin 102: 553-558.

Applegate, R.D. & Riley, T.Z. 1998: Lesser prairie-chicken management. - Rangelands 20(4): 13-15.

Bailey, J.A. & Williams, S.O. III. 2000: Status of the lesser prairie-chicken in New Mexico, 1999. - Prairie Naturalist 32: 157-168.

Baines, D. & Andrew, M. 2003: Marking of deer fences to reduce frequency of collisions by woodland grouse. - Biological Conservation 110: 169-176.

Baines, D. & Summers, R.W. 1997: Assessment of bird collisions with deer fences in Scottish forests. - Journal of Applied Ecology 34: 941-948.

Berger, D.D., Hamerstrom, F. & Hamerstrom, F.N. 1963: The effect of raptors on prairie chickens on the booming grounds. - Journal of Wildlife Management 27: 778-791.

Bevanger, K. 1995: Estimates and population consequences of tetraonid mortality caused by collisions with high tension power lines in Norway. - Journal of Applied Ecology 32: 745-753.

Bevanger, K. & Brøseth, H. 2000: Reindeer Rangifer tarandus fences as a mortality factor for ptarmigan Lagopus spp. - Wildlife Biology 6: 121-127.

Bevanger, K. & Brøseth, H. 2004: Impact of power lines on bird mortality in a subalpine area. - Animal Biodiversity and Conservation 27(2): 67-77.

Borell, A.E. 1939: Telephone wires fatal to sage grouse. - Condor 41: 85-86.

Bradley, L.C. & Fagre, D.B. 1988: Coyote and bobcat responses to integrated ranch management practices in south Texas. - Journal of Range Management 41: 322-327.

Brown, W.M. & Drewien, R.C. 1995: Evaluation of two power line markers to reduce crane and waterfowl collision mortality. - Wildlife Society Bulletin 23: 217-227.

Bumann, G.B. & Stauffer, D.F. 2002: Scavenging of ruffed grouse in the Appalachians: influences and implications. - Wildlife Society Bulletin 30: 853-860.

Bump, G.R., Darrow, W., Edminster, F.C. & Crissey, W.F. 1947: The ruffed grouse: life history, propagation, mana-

gement. - New York State Conservation Department, Holling Press, Buffalo, NY, USA, 915 pp.

Conner, L.M. 2001: Survival and cause-specific mortality of adult fox squirrels in southwestern Georgia. - Journal of Wildlife Management 65: 200-204.

Crooks, K.R. & Soulé, M.E. 1999: Mesopredator release and avifaunal extinctions in a fragmented system. - Nature 400: 563-566.

Currie, P.O. & Goodwin, D.L. 1966: Consumption of forage by black-tailed jackrabbits on salt-desert ranges in Utah. - Journal of Wildlife Management 30: 304-311.

Danvir, R.F. 2002: Sage-grouse ecology and management in northern Utah sagebrush-steppe. - Deseret Land and Livestock Research Report, Woodroff, UT, USA, 39 pp.

Dumke, R.T. & Pils, C.M. 1973: Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. - Wisconsin Department of Natural Resources Technical Bulletin 72, Madison, WI, USA, 52 pp.

Fields, T.L., White, G.C., Gilbert, W.C. & Rodgers, R.D. 2006: Nest and brood survival of lesser prairie-chickens in west central Kansas. - Journal of Wildlife Management 70: 931-938.

Freilich, J.E., Emlen, J.M., Duda, J.J., Freeman, D.C. & Cafaro, P.J. 2003: Ecological effects of ranching: a six-point critique. - Bioscience 53: 759-765.

Fuhlendorf, S.D. & Engle, D.M. 2001: Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. - Bioscience 51: 625-632.

Giesen, K.M. & Hagen, C.A. 2005: The lesser prairie-chicken (Tympanuchus pallidicinctus), revised edition. - In: Poole, A. & Gill, F. (Eds.); The Birds of North America, No. 364. The Birds of North America, Inc., Philadelphia, PA, USA, 20 pp. (doi:10.2173/bna.364).

Gilmer, D.S., Cowardin, L.M., Duval, R.L., Mechlin, L.M., Shaiffer, C.W. & Kuechle, V.B. 1981: Procedures for the use of aircraft in wildlife biotelemetry studies. - U.S. Fish and Wildlife Service Resource Publication 140, Washington, DC, USA, 19 pp.

Gross, A.O. 1928: The heath hen. - Memoirs of the Boston Society of Natural History 6: 491-588.

Guthery, F.S. & Beasom, S.L. 1977: Responses of game and nongame wildlife to predator control in south Texas. - Journal of Range Management 30: 404-409.

Hagen, C.A., Jamison, B.E., Giesen, K.M. & Riley, T.Z. 2001: Guidelines for managing lesser prairie-chickens and their habitats. - Wildlife Society Bulletin 32: 69-82.

Henke, S.E. 2002: Coyotes: friend or foe of northern bobwhite in southern Texas. - In: DeMaso, S.J., Kuvlesky, W.P. Jr, Hernandez, F. & Berger, M.E. (Eds.); Quail V: Proceedings of the fifth national quail symposium. Texas Parks and Wildlife Department, Austin, TX, USA, pp. 57-60.

Henke, S.E. & Bryant, F.C. 1999: Effects of coyote removal on the faunal community in western Texas. - Journal of Wildlife Management 63: 1066-1081.

Hewitt, D.G., Keppie, D.M. & Stauffer, D.F. 2001: Predation effects on forest grouse recruitment. - Wildlife Society Bulletin 29: 16-23.

Horton, R.E. 2000: Distribution and abundance of lesser prairie-chicken in Oklahoma. - Prairie Naturalist 32: 189-195.

Howard, W.E., Wagnon, K.A. & Bentley, J.R. 1959: Competition between ground squirrels and cattle for range forage. - Journal of Range Management 12: 110-115.

Kilgore, D.L., Jr. 1969: An ecological study of the swift fox (Vulpes velox) in the Oklahoma Panhandle. - American Midland Naturalist 81: 512-534.

Krapu, G.L. 1974: Avian mortality from collisions with overhead wires in North Dakota. - Prairie Naturalist 6: 1-6.

Lawrence, J.S. & Silvy, N.J. 1995: Effect of predator control on reproductive success and hen survival of Attwater's prairie-chicken. - Proceedings of the Southeastern Association of Fish and Wildlife Agencies 49: 275-282.

Ligon, J.S. 1951: Prairie chickens, highways, and powerlines. - New Mexico Magazine 29(5): 29.

Lyons, E.K. 2002: Effects of short-term predator control on nesting success and survival of northern bobwhites (Colinus virginianus). - M.Sc. thesis, Angelo State University, TX, USA, 60 pp.

Morkill, A.E. & Anderson, S.H. 1991: Effectiveness of marking powerlines to reduce sandhill crane collisions. - Wildlife Society Bulletin 19: 442-449.

Moss, R. 2001: Second extinction of capercaillie (Tetrao urogallus) in Scotland? - Biological Conservation 101: 255-257.

Moss, R., Picozzi, N., Summers, R.W. & Baines, D. 2000: Capercaillie Tetrao urogallus in Scotland - demography of a declining population. - Ibis 142: 259-267.

Mote, K.D., Applegate, R.D., Bailey, J.A., Giesen, K.M., Horton, R. & Sheppard, J.L. 1999: Assesment and conservation strategy for the lesser prairie-chicken (Tympanuchus pallidicinctus). Kansas Department of Wildlife and Parks, Emporia, KS, USA, 51 pp.

Murie, A. 1951: Coyote food habits on a southwestern cattle ranch. - Journal of Mammalogy 32: 291-295.

Patten, M.A., Wolfe, D.H., Shochat, E. & Sherrod, S.K. 2005a: Effects of microhabitat and microclimate on adult survivorship of the lesser prairie-chicken. - Journal of Wildlife Management 69: 1270-1278.

Patten, M.A., Wolfe, D.H., Shochat, E. & Sherrod, S.K. 2005b: Habitat fragmentation, rapid evolution, and population persistence. - Evolutionary Ecology Research 7: 235-249.

Petty, S.J. 1995: Assessment of fence collisions by grouse species in Scotland. - Forestry Commission Research Information Note 264, Edinburgh, Scotland, 9 pp.

Pyke, D.A. & Thompson, J.N. 1986: Statistical analysis of survival and removal rate experiments. - Ecology 67: 240-245.

Schaub, M. & Pradel, R. 2004: Assessing the relative importance of different sources of mortality from recovery of marked animals. - Ecology 85: 930-938.

Schroeder, M.A. & Baydack, R.K. 2001: Predation and the management of prairie grouse. - Wildlife Society Bulletin 29: 24-32.

Schroeder, M.A. & Braun, C.E. 1991: Walk-in traps for capturing greater prairie-chickens on leks. - Journal of Field Ornithology 62: 378-385.

Silvy, N.J., Peterson, M.J. & Lopez, R.L. 2001: The cause of the decline of pinnated grouse: the Texas example. - Wildlife Society Bulletin 31: 16-21.

Slater, S.J. 2003: Sage grouse (Centrocercus urophasianus) use of different-aged burns and the effects of coyote control in southwestern Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, WY, USA, 177 pp.

Small, R.J., Holzwart, J.C. & Rusch, D.H. 1991: Predation and hunting mortality of ruffed grouse in central Wisconsin. - Journal of Wildlife Management 55: 512-520.

Smith, J.P. 2005a: Fall 2004 raptor migration studies in the Manzano Mountains of central New Mexico. - HawkWatch International, Inc., Salt Lake City, UT, USA, 33 pp.

Smith, J.P. 2005b: Spring 2005 raptor migration studies in the Sandia Mountains of central New Mexico. - HawkWatch International, Inc., Salt Lake City, UT, USA, 28 pp.

Sokal, R.R. & Rohlf, F.J. 1995: Biometry. 3rd edition. - W.H. Freeman, New York, NY, USA, 887 pp.

Sovada, M.A., Roy, C.C. & Telesco, D.J. 2001: Seasonal food habits of swift fox (Vulpes velox) in cropland and rangeland landscapes in western Kansas. - American Midland Naturalist 145: 101-111.

Summers, R.W. & Dugan, D. 2001: An assessment of methods used to mark fences to reduce bird collisions in pinewoods. - Scottish Forestry 55: 23-29.

Taylor, M.A. & Guthery, F.S. 1980: Status, ecology, and management of the lesser prairie-chicken. - U.S. Forest Service General Technical Report RM-77, Fort Collins, CO, USA, 15 pp.

Toepfer, J.E. 1988: Ecology of the greater prairie-chicken as related to reintroduction. - PhD thesis, Montana State University, Bozeman, MT, USA, 536 pp.

Toepfer, J.E. & Septon, G. 2003: Prairie chickens and grasslands: 2000 and beyond. - Society of Tympanuchus Cupido Pinnatus, Ltd., Elm Grove, WI, USA, 69 pp.

Vehrencamp, S.L., Bradbury, J.W. & Gibson, R.M. 1989: The energetic cost of display in male sage grouse. - Animal Behaviour 38: 885-896.

Way, J.G., Ortega, I.M. & Auger, P.J. 2002: Eastern coyote home range, territoriality, and sociality on urbanized Cape Cod. - Northeast Wildlife 57: 1-18.

Windberg, L.A. & Mitchell, C.D. 1990: Winter diets of coyotes in relation to prey abundance in southern Texas. - Journal of Mammalogy 71: 439-447.

Wolfe, D.H. 1993: Sora impaled on barbed wire fence. - Bulletin of the Oklahoma Ornithological Society 26: 28-29.