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ORIGINAL ARTICLES

Survival of sharp-tailed grouse *Tympanuchus phasianellus* chicks and hens in a fragmented prairie landscape

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We studied survival and probable causes of mortality for plains sharp-tailed grouse *Tympanuchus phasianellus jamesi* chicks up to 30 days of age, and for hens during the reproductive period in Alberta, Canada, during 1999-2001. We used the Kaplan-Meier function for estimating survival for > 1 radio-marked chick in the same brood and a bootstrapping technique to calculate standard errors while accounting for censored data. Chick survival was 47% over two years (95% CI: 29-64%) with 81% of mortalities occurring during the first 15 days. Predation accounted for 72% of chick mortalities with mammals taking the largest portion. Chick survival was similar when compared between landscapes with < 35% vs \geq 35% crop and sparsely covered grassland (8 km²). Hen survival was 53% (95% CI: 44-63%) during the reproductive period over three years. Most hen mortalities were from predation (96%), with mammals accounting for the largest portion followed by raptors. Hen survival was similar in landscapes (8 km²) with < 35% crop and sparsely covered grasslands compared with those in areas with \geq 35%. Our study helps clarify values of two critical vital rates, i.e. early chick survival and hen survival over the reproductive period.

Key words: chick, hen, Kaplan-Meier, landscape, mortality, predation, sharp-tailed grouse, survival

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Sharp-tailed grouse *Tympanuchus phasianellus* have declined in portions of their range over the past century (Connelly et al. 1998). Reasons for these declines are uncertain. However, lower breeding success for ground nesting birds has been associated with increases in cropland (Greenwood et al. 1995) and heavy livestock grazing (Baines 1996, Calladine et al. 2002, Kirsch et al. 1973, Kirsch et al. 1978). Habitat loss or degradation is often implicated as the ultimate cause for declines in grassland birds (Schroeder & Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999), but predation is the proximate cause of mortality for most individuals (Schroeder & Baydack 2001). Indeed, predation is an important limiting factor for many bird species (Newton 1993), and increasing predator density has been associated with increasing proportions of crop and pasture land at landscape extents (Andr n 1992, Kurki et al. 1998, Manzer & Hannon 2005).

The initial weeks after hatching are a vulnerable time for grouse (Aldridge & Brigham 2002), but chick survival rates and factors associated with mortality are not well known (Lindstr m 1994, Connelly et al. 1998). Predation, along with exposure and low food availability, are common explanations of mortality for precocial young (Criddle 1930, Marcstr m et al. 1988, Johnson & Boyce 1990, Korschgen et al. 1996a, Riley et al. 1998, Park et al. 2001). However, empirical evidence of the causes of mortality for prairie grouse is lacking (Lindstr m 1994, Connelly et al. 1998, Schroeder et al. 1999) and difficult to obtain because kill events are rarely observed.

The reproductive period can be a risky period for hens as well. Hens invest considerable physical energy in egg laying and rearing a brood (Erikstad 1986), and can experience heightened risk of predation during this period (Flint & Grand 1997, Hannon et al. 2003). High rates of hen mortality occur over the reproductive period for some species of waterfowl (Miller et al. 1995, Flint & Grand 1997), but information is lacking for sharp-tailed grouse (Lindstr m 1994, Connelly et al. 1998). Consequently, our objectives were to: 1) measure survival of sharp-tailed grouse chicks from hatching to 30 days of age and for hens during the reproductive period, 2) identify the probable causes of mortality for chicks and hens, and 3) compare survival rates among areas with different levels of human-caused habitat disturbance at landscape extents.

Material and methods

Study area

We conducted our study in the Mixed Grass Prairie region of southeastern Alberta (51 45'N, 111 W) over an area of 1,392 km². We selected this area because it provided a gradient in the proportion of cropland across the grassland matrix. Topography was predominately flat with moderately rolling hills to the southeast. Prominent grasses were fescue *Festuca* spp. and needle and thread *Stipa comata*. Common shrubs included western snowberry *Symphoricarpos occidentalis*, rose *Rosa* spp. and willow *Salix* spp. Small patches of trembling aspen *Populus tremuloides* were common along north slopes, depressions and around homesteads, but wider encroachment was evident across the matrix. The primary land use was cattle ranching, followed by agricultural crops (wheat, canola and peas). Oil and gas extraction occurred in clusters across the region.

Potential avian predators for hens and chicks included red-tailed hawk *Buteo jamaicensis*, northern harrier *Circus cyaneus*, Swainson's hawk *Buteo swainsoni*, ferruginous hawk *Buteo regalis*, and great horned owl *Bubo virginianus*. Black-billed magpie *Pica hudsonia* and American crow *Corvus brachyrhynchos* were common in the region (Manzer & Hannon 2005). Coyotes *Canis latrans* were frequently observed in the area, and to a lesser extent red fox *Vulpes vulpes*, skunk *Mephitis mephitis*, and American badger *Taxidea taxus*.

Capture and radio-telemetry

Sharp-tailed grouse hens were captured annually in late April during 1999-2001, before nesting, using walk-in funnel traps (Toepfer et al. 1987). Captures occurred at a total of 16 leks, with no more than four hens taken from one lek in a given year. Hens were fitted with 14-g radio necklaces (Holohil Systems, Carp, Ontario, Canada), and located with a portable receiver and three-element yagi antenna once every 2-3 days during laying, and once every five days during nesting and brood rearing. Radios featured a sensor that changed pulse rate if a bird was inactive for > 12 hours, allowing us to document mortality.

Chicks were fitted with micro-transmitters to estimate survival and assess probable causes of mortality. We captured chicks on the day of hatching

to two days post-hatch, and randomly selected two chicks/brood and attached a 1.1 g transmitter (life expectancy 35 days, Holohil Systems, Carp, Ontario, Canada). The transmitter was placed along the midline of the chick's back, and attached to the skin using two sutures (Burkepile et al. 2002). A sterile needle was inserted through the skin perpendicular to the spine, leaving approximately 3-5 mm between the point of entry and exit. Suture material was fed through the interior of the needle, the needle was removed, and the suture fed through the holes in the posterior end of the transmitter and tied. The second suture was tied at the anterior end of the transmitter. One drop of Krazy Glue™ was placed on each knot and on the bottom side of the transmitter. We tied the sutures to allow for growth by leaving 2-4 mm of slack. Handling took approximately 20-30 minutes per brood, and <10 minutes per radio-marked chick. All captured chicks were returned to the hen simultaneously. We did not capture chicks on days with cool temperatures (<12-14°C), nor when precipitation was expected within 1-2 hours of handling activities. This procedure was approved by the University of Alberta, Animal Care Committee.

Every five days during brood rearing to 30 days post-hatch, chicks and hens with transmitters were located using triangulation from distances of approximately 30-50 m to avoid flushing chicks. We approached individual chicks to locate the carcass if the signal was not close to the hen (e.g. >100 m). In the pilot year (1999), we captured radio-marked chicks at each five-day interval to inspect the condition of the skin near the transmitter, and take body measurements. We discontinued this procedure in 2000 and 2001 to minimize the potentially negative influence of additional handling on survival. At 30 days post-hatch, we attempted to flush all chicks from each brood to estimate survival of chicks. Radio-marked chicks were recaptured on day 30 with a hand-held net and the transmitter removed by snipping the sutures. Hens were located at five-day intervals until 13 August annually. We searched for missing hens and chicks with a fixed-wing aircraft intermittently during the reproductive period (April-August).

Probable causes of mortality

Dead chicks and hens were recovered as quickly as possible and categorized by the probable cause of mortality into six classes: avian predation, mammalian predation, unknown predation, farm mor-

talities (trampled by cattle, machinery), exposure and investigator handling. We based predator identification on trauma to the transmitter and carcass and, in some cases, on the location of the recovery site (i.e. coyote den, fox earth or raptor nest site). Bite or beak marks on the transmitter, consumed body parts, faecal spray and pulled vs chewed feathers were used to assign predator type to either mammal or avian (Korschgen et al. 1996a, Riley et al. 1998). Death was classified as exposure if no trauma was found on the carcass or transmitter. This category may be underestimated if chicks were scavenged post-death but before we discovered the carcass (Bumann & Stauffer 2002). Chicks presumed to experience heightened mortality risk due to handling were not included in estimates of survival, nor probable causes of natural mortality.

Habitat

Habitat composition was estimated with the GIS program Arcview 3.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) using a Landsat 7 image taken in 1999 at 30 × 30 m resolution. Data were classified using the program PCI Geomatica 8.2 (PCI Geomatics, Richmond Hill, Ontario, Canada). Aerial photos (1:30,000) and stratified ground truthing (Jensen 1996) were used to improve the accuracy of classification. Accuracy ranged within 80-94.8% for each class with an overall rating of 85.6% (K_{hat}). Cover class accuracy was conducted using stratified random ground truthing with ≥ 60 points to verify each class.

Habitat across the study area was categorized into six classes: dense grassland (39%), sparse grassland (27%), crop (26%), trees (4%), wetland (2%) and water (2%). Dense grassland included areas with perennial grasses and shrub cover. Sparse grassland included areas with perennial grass and shrub, but had more bare ground reflectance than dense grassland. We used random ground-surveyed points (N=128) to calibrate the classification for sparse grassland based on Daubenmire (1959) readings with > 25% bare ground. Bare ground was averaged over three measurements along a 100-m transect running east to west using a 20 × 50 cm plot. Sparse grasslands were affected by soil type and potentially by heavy live stock grazing over a period of years. Evidence for the relative influence of grazing was anecdotal based on personal communication with landowners and the regional range manager. Crop included cultivated land, hay land and anthropogenic disturbance (i.e. homesteads and country

Table 1. Range in proportion (%) of habitat composition within 1600 m of sharp-tailed grouse leks classed as less disturbed (< 35% crop and sparse grassland, N = 6) vs more disturbed (\geq 35% crop and sparse grassland, N = 10) in Alberta during 1999-2001.

Habitat type	Less disturbed	More disturbed
Trees	2-24	1-9
Crop	<1-18	<1-41
Sparse grassland	17-31	5-51
Dense grassland	55-70	26-50
Wetland	<1-6	<1-9
Water	<1-3	<1-4
Crop + sparse grassland	21-34	43-70

roads). The amount of crop and sparse grassland (< 35% vs \geq 35%) was evaluated within a 1,600-m radius ($\sim 8 \text{ km}^2$) around the nearest lek (Table 1). We categorized habitat in this manner because reproductive success and predator densities were both linked to these categories. Nests were more likely to succeed in landscapes with < 35% crop and sparse grassland (Manzer & Hannon 2005), and raptor density was associated with landscapes having more sparse grassland at this scale (Manzer 2004). We refer to landscapes as more disturbed or less disturbed to differentiate between areas with more or less crop and sparse grassland (< 35% vs \geq 35%).

Survival

We used the Kaplan-Meier (K-M) function to estimate survival for radio-marked chicks to 30 days post-hatch (Kaplan & Meier 1958, Pollock et al. 1989). Flint et al. (1995a) expanded the K-M approach for cases where survival estimates are desired for > 1 individual in the same brood. They used a bootstrapping technique to deliver an unbiased estimate of the standard error (SE) to meet the assumption that individuals in the same brood have independent survival. We applied their technique and used radio-marked chicks as individual sample units. We estimated SE by treating broods as clusters to avoid inflating degrees of freedom through pseudoreplication (Flint et al. 1995a). Standard error was derived from 1,000 runs by resampling chicks from broods with replacement using bootstrapping until the number of broods in the original sample was drawn.

The equations described by Flint et al. (1995a: 449) do not explicitly state how to account for right-censored individuals in the K-M estimate (those removed from the sample due to loss or radio-failure). We clarified their equations to account for

censoring by calculating the number of individuals at risk (r) in each time interval (t) for each brood (i), rather than using the number of chicks per brood at each life stage ($n_{t,i}$). We subtracted the number of right censored chicks ($c_{t,i}$) from the number of radio-marked chicks per brood to get the number of chicks at risk ($r_{t,i}$) in each life stage such that,

$$r_{t+1,i} = n_{t,i} - c_{t+1,i} \quad (1).$$

We substituted $r_{t,i}$ for $n_{t,i}$ in the equations of Flint et al. (1995a: 449) such that the survival ($\hat{S}_{t,i}$) for brood i at time t was

$$\hat{S}_{t,i} = r_{t+1,i}/r_{t,i} \quad (2).$$

The weighted survival estimate (\hat{S}_t) at time t was calculated as

$$\hat{S}_t = \sum_{i=1}^{M_t} r_{t+1,i} / \sum_{i=1}^{M_t} r_{t,i}, \quad (3)$$

and

$$SE(\hat{S}_t) = \sqrt{\sum_{i=1}^{M_t} r_{t,i}^2 (\hat{S}_{t,i} - \hat{S}_t)^2 / M_t \bar{r}_t^2 (M_t - 1)} \quad (4)$$

where

$$\bar{r}_t = \sum_{i=1}^{M_t} r_{t,i} / M_t$$

and M_t refers to the number of marked hens at time t . The K-M function was then used to estimate survival for the period of interest

$$\hat{S}(t) = \prod_{j=1}^t \hat{S}_j \quad (5).$$

We estimated hen survival using the K-M function (Pollock et al. 1989). Survival over the reproductive period was measured from 1 May to 13 August annually based on five-day intervals. If individuals survived more than one year, we randomly selected one year to include in survival estimates. Individuals were right-censored if their signal could not be located due to loss or failure. Winter survival was not the focus of this study nor did we monitor hens during the winter months. However, we searched for hens in April of the following year and used the return count as the measure of survival. Over-winter survival was based on those at risk from 14 August (t_0) to 30 April of the following year ($t+1$) using the K-M function. We used the estimate of over-winter survival to assist in calculating the portion of

annual mortality that occurs during the reproductive period.

We examined whether transmitters increased the mortality of chicks by comparing survival to 30 days for radio-marked vs non-radio-marked chicks. We used flush counts on broods with radio-marked chicks, so all broods received similar handling. We located the radioed hen, and then conducted flush counts on foot by searching systematically in a grid pattern over a 100-m radius of the suspected brood location. We assumed radio-marked and non-radio-marked chicks had equal likelihood of being flushed, and that no brood mixing had occurred. We calculated the K-M estimate of survival for non-radio-marked chicks using the number of chicks hatched at time zero (N_{t0}), less the number of radio-marked chicks, and compared this value to the number of chicks from all broods flushed at 30 days post-hatch (N_{t+1}), less radio-marked chicks. The total number of chicks hatched was derived by summing the number of eggs hatched per clutch for all the broods in the sample.

Survival rates were compared between habitats, years and marked vs non-marked chicks using χ^2 (Sauer & Williams 1989) and Z-test (Pollock et al. 1989) methods. Alpha levels were set to 0.10 to guard against type II errors. Means are reported with standard errors. Analyses were modeled in Microsoft Excel with the Pop Tools extension (version 2.7.1).

Results

Chick survival and mortality

We placed radios on 72 chicks from 36 broods over three years, but report survival only in the years 2000 and 2001 (59 chicks from 31 broods). In 1999 (pilot year), radios were placed on 11 chicks only and we assume this small sample inadequate to estimate survival in that year. We excluded two additional chicks that were presumed to have died as result of handling in 2000 (brood released prior to flash rainstorm) from our analysis.

Chick survival was 0.47 ± 0.09 ($N = 59$, 95% CI: 29-64%) to 30 days post-hatch. Most mortality (81%) occurred during the initial 15 days (Fig. 1). Survival was statistically similar among years (2000 = 0.40 ± 0.18 , $N = 29$; 2001 = 0.53 ± 0.12 , $N = 30$; $Z = 0.43$, $P = 0.33$), and between less and more disturbed landscapes (0.50 ± 0.15 , $N = 36$, and 0.31 ± 0.13 , $N = 23$, respectively; $Z = 0.69$, $P =$

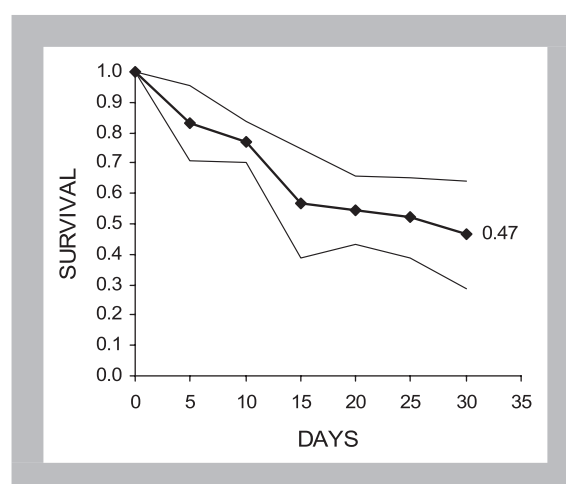


Figure 1. Kaplan-Meier survival function (thick-line) with 95% CI (fine-line) for 59 radio-marked sharp-tailed grouse chicks from 31 broods in Alberta during 2000-2001.

0.25). Survival for 287 ($N = 31$ broods) non-radio-marked chicks to 30 days post hatch (0.28 ± 0.04) appears lower than that for radio-marked chicks (0.47 ± 0.09 , $Z = 1.51$, $P = 0.07$).

Predation accounted for most chick deaths (72%), followed by exposure and farm activity (Table 2). Mammals killed more chicks than avian predators. Three broods had >1 radio-marked chick killed during the same five-day interval; chicks from two of these broods were killed by predators (of which three were mammalian and one could not be identified) and those in the third brood were trampled by cattle.

Hen survival and mortality

We monitored 111 hens during the reproductive period with an overall survival of 0.53 ± 0.05 (95% CI: 44-63%; Fig. 2) during 1999-2001. Survival was not different among years (1999 = 0.58 ± 0.10 , $N = 26$; 2000 = 0.52 ± 0.09 , $N = 38$; 2001 = 0.53 ± 0.08 , $N = 47$; $\chi^2 < 0.01$, $df = 2$, $P > 0.95$). Predation accounted for 96% of hen mortalities. Mammals

Table 2. Probable causes of mortality for radio-marked chicks and hens during the reproductive period for sharp-tailed grouse in Alberta during 1999-2001.

	Chick	%	Hen	%
Mammal	14	39	19	39
Avian	4	11	13	27
Exposure	5	14	1	2
Cattle/machine	5	14	1	2
Unknown predator	8	22	15	31

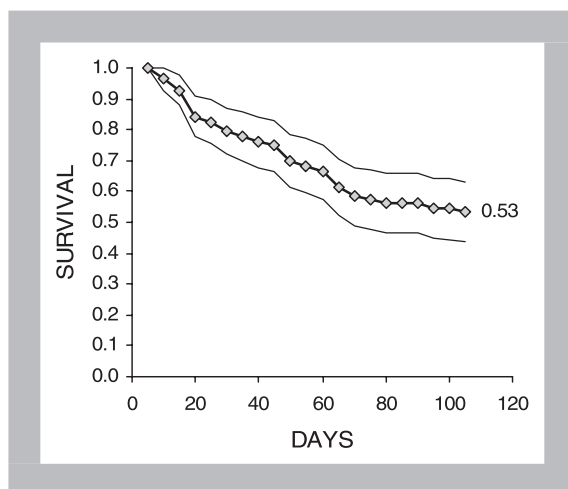


Figure 2. Kaplan-Meier survival function (thick-line) and 95% CI (fine-line) for 111 sharp-tailed grouse hens during the reproductive period in Alberta during 1999-2001.

were responsible for more deaths than raptors, but 31% of predator kills could not be assigned to a specific predator type (see Table 2). Over-winter survival was 0.81 ± 0.01 (95% CI: 79-82%, $N = 52$), over three years. Survival was similar for hens in more disturbed landscapes (0.45 ± 0.07 , $N = 65$), compared with those in less disturbed habitat (0.62 ± 0.07 , $N = 46$; $Z = 1.22$, $P = 0.11$).

Discussion

Chick survival and mortality

Early survival and causes of mortality are not well known for prairie grouse chicks. Our estimate of 47% survival for 30 days post-hatch is similar to ring-necked pheasant *Phasianus colchicus* (hereafter pheasant) chicks in Iowa (Riley et al. 1998), which averaged 46 and 37%. Survival for ruffed grouse *Bonasa umbellus* chicks for ≥ 80 days over the brood rearing season was 29 and 32% over two years (Larson et al. 2001). However, in that study transmitters were placed on chicks between 5-10 days of age, which likely underestimated early mortality. Sharp-tailed grouse chicks were particularly vulnerable in the early stage of brood rearing, which is common for ground dwelling precocial young (waterfowl: Flint et al. 1995b, Korschgen et al. 1996a; galliformes: Zwickel & Bendell 1967, Riley et al. 1998).

Predation accounted for the majority of deaths with mammals perhaps taking more than avian predators (see Table 2). This is similar to other stud-

ies on precocial young in prairie systems. Mammals accounted for the majority of predation on ducklings in a prairie/forest ecotone (54%; Korschgen et al. 1996a), and pheasant chicks in a prairie biome (85%; Riley et al. 1998). In contrast, 78% of predator kills on ruffed grouse chicks in a forest matrix were from avian predators (Larson et al. 2001). Avian kills accounted for 27% of identified hen mortalities in our study compared with only 11% for chicks. We may have underestimated avian kills in the chick analysis because evidence was less distinctive than for mammals. If the majority of these 'unknown predator' chick deaths (i.e. five of eight; see Table 2) were from avian predators, the proportion of avian kills on chicks would be similar to that for hens ($9/38 = 24\%$).

Exposure probably accounts for some galliforme chick losses, but the evidence suggests the overall proportion of mortality from exposure is relatively low in most years (13% this study, 7% Riley et al. 1998). Death from exposure appears to be associated with periods of heavy precipitation (Korschgen et al. 1996a, Riley et al. 1998). For example, we found a dead hen with six dead chicks (not radio-marked) underneath her following three days of heavy rain in 1999. Carcasses were intact but sodden after the precipitation. Roersma (2001) reported a similar case with sharp-tailed grouse following severe weather in 1998. We speculate that heavy losses in a single year presumably could occur if a prolonged period of wet and cold weather persisted (2-3 days) through the early stages of chick growth before chicks are able to thermoregulate (Bousquet & Rotella 1998).

Assigning the cause of mortality for marked chicks or hens has subjective bias that is difficult to eliminate (Bumann & Stauffer 2002). Chicks dead from exposure were presumably available for scavenging before recovery and, therefore, we may have underestimated exposure kills. Moreover, secondary predation events can obscure evidence between predator types (Bumann & Stauffer 2002). We attempted to guard against bias in predator identification by recording kills as 'unknown predator' if evidence was contradictory or insufficient. Hence, 21 and 31% of events were classified as unknown predation for chicks and hens, respectively.

The effect of transmitters on survival has been studied in captive populations of ducklings (Korschgen et al. 1996b, Davis et al. 1999) and pheasant chicks (Ewing et al. 1994), with neither study reporting a significant difference between marked

and unmarked young. Our method of fitting transmitters with sutures was presumably less intrusive than the subcutaneous implant of transmitters in the pheasant study. Transmitter weight ranged within 6-8% of body weight when attached in our study compared with 7% for the pheasant chick study (Ewing et al. 1994).

In calculating survival, we assumed handling did not affect mortality. In reality, the process of capture, telemetry and wearing a transmitter probably does have an influence on mortality. We found that survival for non-marked chicks was statistically lower than for radio-marked chicks, but assume our approach may have missed non-marked chicks that did not flush. Flush counts on individuals without radios are likely biased low since individuals may not flush.

Hen survival and mortality

The reproductive period is a high-risk time for ground dwelling females attending to nests and broods (Flint & Grand 1997). Survival was considerably lower for hens over this period than the rest of the year accounting for approximately 82% of their annual mortality. Mortality during the reproductive period is probably linked with high levels of parental investment (Hannon et al. 2003), including periodic travel to and from the nest during laying and incubation, increased movement and calling while rearing broods, as well as the risk associated with distracting predators away from chicks. Survival during this life stage appears to vary markedly among populations of prairie grouse. Our estimate of 53% was similar to that for greater prairie-chicken *T. cupido pinna-tus* hens in Minnesota (57%; Svedarsky 1988), more than Attwater's prairie-chicken *T. cupido attwateri* in Texas (36%; Lutz et al. 1994), but appears lower than for sharp-tailed grouse hens from southern Alberta ($\geq 75\%$; Roersma 2001). Roersma (2001) used similar radios and telemetry techniques as ours, suggesting that differences in survival rates may occur between study sites (> 300 km apart). Survival may vary markedly among years in some systems (Perkins et al. 1997), but does not appear to account for differences in 1999 between these two studies. Survival during the reproductive period appears greater (78%, $N = 18$) on the Milk River Ridge than in our area (56%, $N = 26$).

High proportions of mortality from predation are common among gallinaceous birds (Keith & Rusch 1989, Riley & Schultz 2001, Schroeder & Baydack 2001). Mammals are prominent predators

in many systems and accounted for the majority of hen and chick kills in this study followed by raptors. Svedarsky (1988) found a similar portion of mammalian vs avian kills on hen prairie-chickens in Minnesota. In contrast, raptors have a prominent role in the predation of grouse in other systems. For example, northern goshawks *Accipiter gentilis* were responsible for the majority of deaths for black grouse *Tetrao tetrix* hens in a forest matrix in Sweden (Angelstam 1984). In northern Finland, grouse are reported as the main diet of goshawks and accounted for 40% of the annual mortalities for black grouse and 35% for hazel grouse *Bonasa bonasia* (Tornberg 2001). Harriers may also have a major role in the predation of red grouse *Lagopus lagopus scoticus* in Scotland where mammalian predators are actively managed (Redpath 1991).

Survival and habitat

We caution the reader that our accounting of habitat was somewhat clumped having captured hens at 16 leks rather than one lek per hen. This shortfall of our design was made consciously as we balanced the need for independence among sample units with practical sampling limitations. As such, variance estimates may be understated in our landscape analysis for hens. However, we inflated the SE estimates with the bootstrapping approach for chicks and therefore assume that our analysis is less biased. Notwithstanding this limitation, survival was not statistically higher for hens in less disturbed landscapes compared with those in more disturbed areas. Patterns between measures of breeding success and habitat measured at landscape extents have been demonstrated (Andr n 1992, Kurki et al. 2000), but there is less evidence for associating survival with habitat (Riley et al. 1998). One possible explanation for lower survival in altered landscapes is an increase in the density of generalist mammalian predators as the proportion of agriculture increases within the landscape (Kurki et al. 1998, Gosselink et al. 2003). Hen survival over the reproductive period appears to be lower in our study area compared with that for sharp-tailed grouse on the Milk River Ridge (Roersma 2001), which suggests that the efficiency, density or community of predators may differ between the two areas. Our area was much larger (1,392 km²) accounting for a gradient of habitat conditions from less to more disturbed. In contrast, the Milk River Ridge study was conducted across a relatively small spatial extent (28 km²) of high quality continuous grassland, which may be too small to account for the

effects that landscape scale disturbance may have on predator density.

We predicted chick survival would be lower in more disturbed landscapes but this was not the case. Habitat features important for explaining sharp-tailed grouse nest and brood success include measures at smaller spatial extents than we account for here (50 and 583 m, respectively) as described in Manzer (2004), and Manzer & Hannon (2005). We speculate that habitat measured over smaller extents would be helpful for explaining chick survival, but more difficult to assess given the dynamic nature of precocial young over space and time.

Application and future work

Documenting survival of chicks and hens is important for understanding population trends for sharp-tailed grouse. To our knowledge, there are no individual estimates of early chick survival for sharp-tailed grouse and these data are an important contribution towards clarifying this parameter. Flush counts are a common approach for estimating early chick survival for gallinaceous birds, and can be applied with less effort, expense, and expertise than using micro-transmitters. We encourage the use of periodic flush counts, but recommend they be considered as minimum estimates. We suggest that flush counts be calibrated with survival estimates derived from radio-marked chicks to more accurately approximate mortality for this life stage.

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