Journal of Field Ornithology

J. Field Ornithol. 79(4):421–428, 2008 DOI: 10.1111/j.1557-9263.2008.00189.x

Predators of Greater Sage-Grouse nests identified by video monitoring

Peter S. Coates,[1,3] John W. Connelly,[2] and David J. Delehanty[1]

[1]*Idaho State University, Department of Biological Sciences, Pocatello, Idaho 83209-8007, USA*
[2]*Idaho Department of Fish and Game, 1345 Barton Road, Pocatello, Idaho 83204, USA*

Received 23 February 2008; accepted 25 August 2008

ABSTRACT. Nest predation is the primary cause of nest failure for Greater Sage-Grouse (*Centrocercus urophasianus*), but the identity of their nest predators is often uncertain. Confirming the identity of these predators may be useful in enhancing management strategies designed to increase nest success. From 2002 to 2005, we monitored 87 Greater Sage-Grouse nests (camera, $N = 55$; no camera, $N = 32$) in northeastern Nevada and south-central Idaho and identified predators at 17 nests, with Common Ravens (*Corvus corax*) preying on eggs at 10 nests and American badgers (*Taxidea taxis*) at seven. Rodents were frequently observed at grouse nests, but did not prey on grouse eggs. Because sign left by ravens and badgers was often indistinguishable following nest predation, identifying nest predators based on egg removal, the presence of egg shells, or other sign was not possible. Most predation occurred when females were on nests. Active nest defense by grouse was rare and always unsuccessful. Continuous video monitoring of Sage-Grouse nests permitted unambiguous identification of nest predators. Additional monitoring studies could help improve our understanding of the causes of Sage-Grouse nest failure in the face of land-use changes in the Intermountain West.

SINOPSIS. **Depredadores de nidos del *Centrocercus urophasianus* identificados durante monitoreos con cámaras de video**

La depredación de nidos es la principal causa del fracaso de las nidadas del Greater Sage-Grouse (*Centrocercus urophasianus*), pero la identidad de los predadores de los nidos es usualmente incierta. Confirmar la identidad de estos depredadores puede ser útil para el desarrollo de estrategias de manejo diseñadas para incrementar el éxito de las nidadas. Entre el 2002 y el 2005, monitoreamos 87 nidos del Greater Sage-Grouse (cámaras, $N = 55$; sin cámara, $N = 32$) en el noreste de Nevada y en el centro-sur de Idaho e identificamos predadores en 17 nidos, en donde el Raven común (*Corvus corax*) depredo las nidadas de 10 nidos y el American badgers (*Taxidea taxis*) las de siete nidos. Se observaron frecuentemente roedores en los nidos de grouse, pero no depredaron los huevos de grouse. Debido a que los rastros dejados por los ravens y los badgers fueron indistinguibles después de un evento de depredación, identificar los depredadores de nidos basado en la remoción de huevos, en la presencia de cascaras de huevos, u otro tipo de clave no fue posible. La mayoría de eventos de depredación ocurrieron cuando las hembras estaban en el nido. La activa defensa del nido por los grouse fue rara y siempre fue poco exitosa. El monitoreo continuo de nidos del sage-grouse mediante cámaras de video permito la identificación previamente ambigua de los depredadores de los nidos y comportamientos en el nido. Adicionalmente los estudios de monitoreo pueden ayudar a mejorar nuestro conocimiento sobre las causas del fracaso de los nidos del sage-grouse durante los cambios del uso de la tierra entre las montañas del oeste.

Key words: American badger, camera, *Centrocercus urophasianus*, Common Raven, Greater Sage-Grouse, ground squirrel, nest predation, Nevada, video monitoring

Greater Sage-Grouse (*Centrocercus urophasianus*) populations are declining in most portions of their range (Connelly and Braun 1997, Connelly et al. 2004), and nest failure is thought to be an important factor in those declines (Schroeder and Baydack 2001). The primary source of Sage-Grouse nest failure is predation, accounting for an average of 94% of nest loss (Moynahan et al. 2007). Although nest predators of Sage-Grouse have been reported in the literature (Schroeder and Baydack 2001), identification has generally been based on interpreting ambiguous remains of predated nests rather than unequivocal identification (Holloran and Anderson 2003, Moynahan et al. 2006). However, using nest and egg remains to identify predators can lead to misidentification (Marini and Melo 1998, Larivière 1999).

Confirming the identity of nest predators would aid Sage-Grouse conservation efforts by

---

[3] Corresponding author. Current address: USGS, Western Ecological Research Center, Dixon Field Station, 6924 Tremont Road, Dixon, CA 95620. Email: pcoates@usgs.gov

helping to guide management actions designed to increase or maintain nest success, such as direct predator control or indirectly decreasing the chances of specific predators from locating nests through habitat manipulation. Erroneous identification of nest predators based on conventional methods may lead to poor management decisions. Video monitoring has been shown to be a reliable and accurate method for identifying predators (Cutler and Swann 1999, King et al. 2001). Such monitoring has never been employed at Sage-Grouse nests, but could confirm the identity of nest predators. Thus, our objective was to identify Sage-Grouse nest predators by video monitoring nests and to determine the kinds of sign that predators leave at predated nests.

METHODS

We monitored nests of Sage-Grouse in northeastern Elko County, Nevada (Universal Transverse Mercator [UTM] Zone 11, Range = E 648194–706275, N 4564368–4673994, NAD 83) from March to July 2002–2005. We chose four sites to monitor nests based on known breeding areas (Fig. 1). We also monitored four nests in south-central Idaho (25–35 km from the northernmost study site in Nevada).

Lower elevations (1550–1900 m) were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*), with an understory of grasses. Higher elevations (1900–2350 m) were characterized by mountain big sagebrush (*A. t. vaseyana*), Saskatoon serviceberry (*Amelanchier alnifolia*), and native bunchgrasses. Topography consisted primarily of rolling hills and creek drainages that held surface water throughout the year.

Within the study area, we observed many species of potential egg predators (reported in Schroeder et al. 1999), including coyotes (*Canus latrans*), weasels (*Mustela* spp.), elk (*Cervus elaphus*), American badgers (*Taxidea taxis*), ground squirrels, Black-billed Magpies (*Pica hudsonia*), American Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*). Cattle (*Bos taurus*) grazed most of the study site seasonally every year.

We captured female Sage-Grouse by spotlighting (Wakkinen et al. 1992, Connelly et al. 2003) near lek sites from 15 March to 1 May 2002–2005. We equipped grouse with

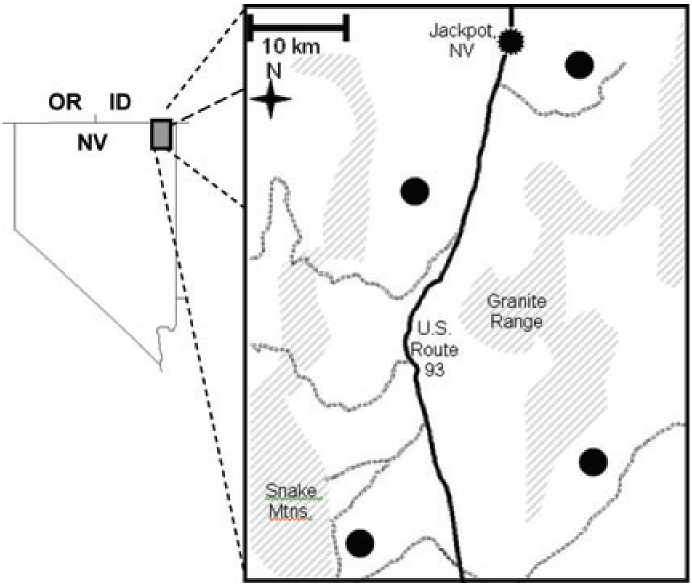

Fig. 1. Greater Sage-Grouse study sites in northeastern Nevada, 2002–2005. Study sites were based on lek routes and were separated by distances $\geq$20 km. We video monitored an additional four nests in south-central Idaho, 25–35 km from the northernmost study site in Nevada. A public landfill was located approximately 7 km from the northernmost Nevada site.

necklace-style, radio transmitters (Series A4000, Advanced Telemetry Systems, Isanti, Minnesota) that were <3% of grouse body mass (1–1.8 kg; Schroeder et al. 1999). Antennae were bent near their bases and rested along the backs of grouse to minimize interference with flight (Marks and Marks 1987). To locate nests, we located radio-marked grouse every 2–3 d using 3-element hand-held Yagi antennae and receivers (Models R4000 and R2000, Advanced Telemetry Systems, Isanti, Minnesota). Aircrafts were used to locate missing grouse, followed by ground surveys to verify grouse location. We recorded UTM coordinates for each grouse location using hand-held Global Positioning System units (eTrex, Legend, Garmin International, Olathe, Kansas).

When a grouse was located within 30 m of the previous position on three consecutive occasions, we visually confirmed the presence of a nest. We located all nests either during the laying period or the initial stages of incubation. We monitored nesting females every 3 d to record their status (present or absent) and determine nest fate. Clutch size was measured when females were away from nests during early stages of incubation or during camera installation if a female was inadvertently flushed.

We identified nest predators and recorded predator and grouse behavior using continuously recording video-monitoring systems (Pietz and Granfors 2000). We used miniature (40 × 40 × 60 mm), camouflaged cameras (Fuhrman Diversified, Seabrook, Texas; Supercircuits, Austin, Texas) equipped with 12 infrared-emitting diodes (850–950 nm wavelength) that allowed night video monitoring using light that was likely undetectable by vertebrates. We used time-lapse VCR systems operating at 2–3 frames/s.

Nests ($N = 55$) were chosen for video monitoring based on fewest estimated days of incubation, but not on distance and access to nests. However, to minimize the risk of abandonment (Renfrew and Ribic 2003), video systems were deployed at nests ≥ 7 d after the onset of incubation. We estimated day of incubation through telemetry monitoring. We placed cameras 0.5–1.0 m from nests and 10–20 cm above ground. We mounted cameras on the nearest shrub trunk or a camouflaged stake using rebar tie wire. Stakes were also covered with grasses and shrub branches. Cables that extended 15–20 m to a VCR system and power source were buried 3–5 cm in the ground to reduce the chances of damage and either attracting or deterring predators. We scattered litter over the buried cord and human tracks. Recorders were housed in camouflaged cases and placed under the canopy of a large shrub. We powered cameras and recorders with two deep-cycle, 12-volt marine batteries. Burlap and vegetation were used to cover the VCR cases and batteries. We replaced batteries and tapes every 3 d.

We camouflaged all cameras and other equipment with camouflage vinyl photography tape and paint that matched the colors of the shrub-steppe microhabitat. Grasses and small sagebrush branches and leaves were secured to camera casings with painted wire. We applied camouflage, adhesive cloth tape over the light emitting diodes (LEDs). We used rubber boots and gloves during video system deployment and maintenance to minimize human scent at nests (Whelan et al. 1994).

Most cameras were installed ($N = 45$, or 82%) while grouse were incubating, and they typically flushed from the nests. To minimize the risk of egg mortality, we did not install cameras during times of snow, rain, high winds, or extreme ambient temperatures. We continued video monitoring nests for 24 h after termination of nesting attempts to identify any subsequent animal encounters and record post-nest-fate behaviors of predators at hatched and predated nests. We then moved cameras to other nests.

We used nests without video systems as controls to measure camera effects and visited these nests every 3 d to document nesting status and control for potential bias caused by our visits to nests. To estimate the camera effect on nest fate, we used the nest survival module in program MARK (White and Burnham 1999) and employed an information-theoretic approach (Anderson and Burnham 2002) based on Kullback-Leibler information (Kullback and Leibler 1951) and maximum likelihood estimation (de Leeuw 1992) to simultaneously evaluate the support for two a priori models: an intercept-only (β_0) model and an intercept with camera covariate ($\beta_0 + \beta_1\mathrm{CAM}$) model. We used Akaike's information criterion (Akaike 1973) corrected for small sample size (AIC_c; Anderson and Burnham 2002) to evaluate the relative support of candidate models using Akaike's differences ($\Delta\mathrm{AIC}_c$) and weights (ω_i) (Anderson and Burnham 2002) for each model. We also performed a likelihood ratio test to determine if the more complex model fit the data significantly better ($\alpha = 0.05$). Values are reported as means ± SE.

Predated nests were classified as either partial (≥ 1 intact egg remained in the nest bowl) or complete (all eggs destroyed or missing from nest bowl). We considered nests successful if ≥ 1 egg hatched (Rearden 1951), as determined by observation of ≥ 1 whole eggshell, egg membrane, or chick in the nest bowl, and unsuccessful if completely predated, abandoned, or partially predated and subsequently abandoned. Descriptions of predated nest remains were recorded, including condition of nest bowl and surrounding vegetation (disturbed or destroyed), missing eggs, eggshell fragments, punctured eggs, and condition of eggshell membranes (missing, fragmented, or intact).

RESULTS

We monitored 87 Sage-Grouse nests ($N = 55$ with camera and $N = 32$ with no camera), with 37 (43%) partially or completely predated, six (7%) abandoned, and 44 (51%) successful. Nests were monitored with cameras for about 15,500 h, or an average of 12.0 ± 0.83 d of incubation per nest. We identified predators at 16 nests, and one predation event was observed in the field at a nest with no camera. At four nests with cameras, predation events were not recorded due to camera failure. Of the video-monitored nests, grouse abandoned all nests that were partially predated.

Model selection indicated no support for an effect of camera presence ($\Delta AIC_c = 1.02$) (Fig. 2). The best-approximating model (β_0, $\omega_i = 0.63$) was 1.7 times (ω_i/ω_j) more likely to

Fig. 2. Images of Sage-Grouse nests in northeastern Nevada: (A) incubating grouse, (B) Common Raven predation with no diagnostic egg remains, (C) badger removing eggs from nest bowl, (D) Wyoming ground squirrels biting intact egg, (E) fragmented (arrow) and crushed eggshells resulting from badger predation, and (F) holes (arrow) in eggshells due to badger predation.

describe the data than the $\beta_0 + \beta_1$CAM model (ΔAIC$_c$ = 1.02, ω_i = 0.37), but β_0 model did not have substantially greater support from the data (Burnham and Anderson 1998). The more complex model ($\beta_0 + \beta_1$CAM) was not the best-fit model (likelihood ratio test, $\chi^2 = 0.98$, $P = 0.32$). The estimated camera effect was 0.330 ± 0.329 (95% CI –0.315 to 0.976). Estimated daily survival rate (DSR) for nests with and without cameras were 0.980 ± 0.004 and 0.973 ± 0.007, respectively. Estimated DSR was 0.978 ± 0.003. Calculated point estimate of nest success was 0.44 (95% CI 0.35–0.55), using 37-d nest survival (laying and incubation period). Point estimates for nests with and without cameras were 0.47 (95% CI 0.34–0.62) and 0.36 (0.20–0.55), respectively.

Raven encounters. We documented predation by ravens at 10 nests (Fig. 2), with three cases of partial predation and seven with complete predation. When a grouse was present ($N = 8$), one or more ravens flushed the female from the nest before predating eggs. We observed differences among ravens and predation events in nest and egg sign.

On three occasions, a female stood over the eggs between ravens that were taking eggs. One grouse actively, but unsuccessfully, defended her nest from two or more ravens. The grouse lunged across the nest, toward a raven, with wings extended on three occasions. However, as the grouse lunged at one raven, another would take an egg on the other side of the nest. All three attempts at nest defense by grouse were unsuccessful and the nests were predated.

During all 10 predation events involving ravens, one or more eggs were consumed or taken from the nest. At two nests, ravens left holes in the sides or tops of eggs and left the rest of the eggshell intact. At two other nests, ravens broke eggshells into fragments.

Badger encounters. We recorded seven predation events by badgers and all resulted in complete nest predation (Fig. 2). Grouse flushed just prior to badgers arriving at nests. Badgers did not attempt to capture fleeing grouse, and grouse did not attempt to deter badgers from eating eggs.

Postpredation badger sign varied within and among predation events (Fig. 2). At four nests, badgers left holes in the sides or tops of eggs and left the rest of the eggshell intact. At five nests, badgers broke eggshells into fragments while consuming egg contents with their tongues. During two events, badgers consumed the entire egg and shell, leaving no eggs or eggshells. During all events, most eggs were consumed by badgers outside the nest bowl. However, on three occasions, badgers ate eggs in the nest bowl and left fragments or largely intact eggshells with holes. Nest material was removed from bowls at five nests destroyed by badgers, whereas, at two nests, nesting material was not disturbed and we found no badger tracks or sign. One badger completely destroyed the nest and removed it from below the shrub.

Rodent encounters. Rodents frequently visited Sage-Grouse nests ($N = 167$), but none consumed eggs. However, rodents often consumed remnant eggshells and membranes following normal hatches or after predation by ravens or badgers ($N = 42$) often leaving the appearance that the nests had been predated by rodents. Rodents identified at nests included least chipmunks (*Tamias minimus*; $N = 73$), Wyoming ground squirrels (*Spermophilus elegans*; $N = 16$), Piute ground squirrels (*S. mollis*; $N = 7$), northern pocket gophers (*Thomomys talpoides*; $N = 3$), Great Basin pocket mice (*Perognathus parvus*; $N = 22$), North American deer mice (*Peromyscus maniculatus*; $N = 31$), and sagebrush voles (*Lemmiscus curtatus*; $N = 2$). Many small rodents visiting nests at night could not be identified by species ($N = 29$).

Least chipmunks regularly consumed or picked up eggshells, eggshell membranes, embryonic membranes, feathers, and nest material. Least chipmunks attempted to perforate eggs twice, but were unsuccessful. No ground squirrel encounters resulted in egg predation. Ground squirrel visits were generally brief (1–3 s) and took place during incubation recesses or at abandoned nests. Wyoming ground squirrels bit intact eggs during four visits, but were unsuccessful at opening them (Fig. 2).

Other encounters. On two occasions, Great Basin gopher snakes (*Pituophis catenifer deserticola*) visited nests during incubation recesses. Each snake appeared to be >1 m long and about 4 cm at maximum body width. Snakes lightly touch eggs with their mouths, but did not attempt to consume them.

One of six encounters by cows resulted in damage to one egg. At one nest, a cow flushed an incubating grouse, causing an egg to be displaced from the nest bowl; the cow subsequently was recorded eating the egg, leaving shell fragments. The cow sniffed and moved, but did not eat, other eggs in the nest bowl, then moved the camera out of position. Following subsequent nest visitation, three other eggs were damaged in the nest and the grouse appeared to abandon the nest. In each of the five other cow encounters, grouse were flushed from their nests and cows sniffed eggs, but did not consume them. We suspected abandonment by a cow flushing the grouse at one other nest.

DISCUSSION

As also reported by previous investigators, we identified ravens (Connelly et al. 1991, Schroeder et al. 1999, Vander Haegan et al. 2002) and badgers (Petersen 1980, Ritchie et al. 1994) as Sage-Grouse nest predators. Sage-Grouse habitat has become highly fragmented (Knick et al. 2003) and fragmentation may increase nest vulnerability to corvids (Hartley and Hunter 1998, Vander Haegen et al. 2002). Current land-use practices in the Intermountain West favor high raven abundance (Boarman and Heinrich 1999) relative to historic numbers (Sauer et al. 2004).

Rodents were frequently observed at grouse nests in our study, but did not prey on grouse eggs. Other investigators have reported that ground squirrels are Sage-Grouse nest predators (Patterson 1952, Gill 1965, Petersen 1980, Niemuth and Boyce 1995). We found that ground squirrels and other rodents often left sign at predated nests after nest predation or hatch, and such scavenging may result in incorrectly attributing predation events to rodents when nest sign is used to identify predators. Wyoming ground squirrels in our study were limited by their gape-width and were unsuccessful at predating Sage-Grouse eggs, similar to reported observations of Richardson's ground squirrels (*Spermophilus richardsonii*) that encountered eggs of domestic fowl (*Gallus gallus*) and Ring-necked Pheasant (*Phasianus colchicus*; Michener 2005). Ground squirrels may not be capable of opening eggs because the average width of Sage-Grouse eggs (38–39 mm, Schroeder et al. 1999) is greater than their functional gape-width (Richardson's ground squirrel was ≤21 mm, Michener 2005). Using still photography, Holloran and Anderson (2003) also found that thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and Richardson's ground squirrels were unsuccessful at predating Sage-Grouse eggs in Wyoming.

Our observations clearly demonstrate that signs left by ravens and badgers were often indistinguishable following nest predation, and support other observations of interspecific similarities in nest and egg remains (Larivière 1999). For example, one or more eggs or eggshells were missing from 12 nests, with 10 predated by ravens and two by badgers. Moreover, several eggs with holes were observed following raven predation, similar to eggs predated by badgers. In addition, both badgers and ravens sometimes scattered egg shells around the nest bowl. Thus, documenting the removal of eggs from nests does not permit accurate identification of predators even to higher taxonomic levels (i.e., class; Larivière 1999). Furthermore, interpretation of nest sign becomes even more difficult with the confirmation of intraspecific differences in sign (Larivière 1999). For example, some badgers disturbed nest bowls and left crushed egg shells and some did not, and nests predated by ravens were often missing all or most of the eggs whereas others contained eggshells with holes in the sides.

We found no evidence that video monitoring influenced predation rates. Waiting until ≥ 7 d after the initiation of incubation by female Sage-Grouse may have contributed to the tendency of daily survival rates to be higher at nests with video systems. As indicated by other investigators (Moynahan et al. 2006), Sage-Grouse nests that survived to the later stages of incubation were often successful, and we observed more predation at nests during the initial stages of incubation.

Our results confirm that Common Ravens and badgers are predators of Sage-Grouse nests, and suggest that previous investigators have incorrectly identified scavenging rodents as predators. We also found that female Sage-Grouse are not able to defend nests successfully when confronted with ravens or badgers, but are able to escape direct predation. Video monitoring is an effective tool, especially when certain predators are thought responsible for nest predation and identification of those predators must be confirmed. Additional video-monitoring studies would help further our understanding of the causes of Sage-Grouse nest failure in the face of land-use changes in the Intermountain West.

ACKNOWLEDGMENTS

Jack H. Berryman Institute and Idaho National Engineering Laboratory/Bechtel provided funding for this research with grants to D. J. Delehanty at Idaho State University. Many thanks to the generous sportsman and conservation organizations that provided financial support including Safari Club International (Idaho and Desert and Northern Nevada chapters), Carson Valley Chukar Club, Wildlife and Habitat Improvement of Nevada, Sportsmen for Fish and Wildlife, and Nevada Chukar Foundation. We thank T. Peterson for statistical consulting, and C. Simms, R. Troy, J. Warwick, and N. Sparks for significant field contributions. We are grateful to personnel of the Nevada Department of Wildlife, Idaho Department of Fish and Game, and U. S. Department of Interior, Bureau of Land Management for assistance with data collection and logistical support.

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: Second international symposium on information theory (B. N. Petrov and F. Csaksi, eds.), pp. 267–281. Akademiai Kiado, Budapest, Hungary.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66: 912–918.

Boarman, W. I., and B. Heinrich. 1999. Common Raven (*Covus corax*). In: The birds of North America online (A. Poole, ed.), Cornell Lab of Ornithology, Ithaca, NY. Available at: http://bna.birds.cornell.edu/bna/species/476.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3: 229–234.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of Greater Sage-Grouse habitats and populations. College of Natural Resources Experiment Station, Station Bulletin 80, Moscow, ID.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55: 521–524.

Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27: 571–581.

De Leeuw, J. 1992. Introduction to Akaike (1973) information theory and an extension of the maximum likelihood principle. In: Breakthroughs in statistics (S. Kotz and N. L. Johnson, eds.), pp. 599–609. Springer-Verlag, London.

Gill R. B. 1965. Distribution and abundance of a population of sage grouse in North Park, Colorado. M.S. thesis, Colorado State University, Fort Collins, CO.

Hartley, M. J., and M. L. Hunter, Jr. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12: 465–469.

Holloran, M. J., and S. H. Anderson. 2003. Direct identification of Northern Sage-Grouse, *Centrocercus urophasianus*, nest predators using remote sensing cameras. Canadian Field-Naturalist 117: 308–310.

King, D. I., R. M. DeGraaf, P. J. Champlin, and T. B. Champlin. 2001. A new method for wireless video monitoring of bird nests. Wildlife Society Bulletin 29: 349–353.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105: 611–634.

Kullback, S., and R. A. Leibler. 1951. On information and sufficiency. Annals of Mathematical Statistics 22: 79–86.

Larivière, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101: 718–721.

Marini, M. A., and C. Melo. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. Condor 100: 395–399.

Marks, J. S., and V. S. Marks. 1987. Influence of radio collars on survival of Sharp-tailed Grouse. Journal of Wildlife Management 51: 468–471.

Michener, G. R. 2005. Limitation on egg predation by Richardson's ground squirrels. Canadian Journal of Zoology 83: 1030–1037.

Moynahan, B. J., M. S. Lindburg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater Sage-Grouse in north-central Montana. Journal of Wildlife Management 71: 1773–1783.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female Greater Sage-Grouse in north-central Montana. Ecological Applications 16: 1529–1538.

Niemuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low densities: an experimental study. Canadian Journal of Zoology 73: 819–825.

Patterson, R. L. 1952. The sage grouse of Wyoming. Sage Books, Denver, CO.

Petersen, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. M.S. thesis, Colorado State University, Fort Collins, CO.

Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64: 71–87.

Rearden, J. D. 1951. Identification of waterfowl nest predators. Journal of Wildlife Management 36: 87–98.

Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. Auk 120: 371–383.

Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. Great Basin Naturalist 54: 122–129.

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, results and analysis 1966 – 2003. Version 2004.1. United States Geological Survey. Patuxent Wildlife Research Center, Laurel, MD.

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

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*). In: The birds of North America, online (A. Poole, ed.), Cornell Lab of Ornithology, Ithaca, NY. Available at: http://bna.birds.cornell.edu/bna/species/425.

Vander Haegen, W. M., M. A. Schroeder, and R. M. Degraaf. 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. Condor 104: 496–506.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20: 425–426.

Whelan, C. J., M. L. Dilger, D. Ronson, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial-nest experiments. Auk 111: 945–952.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–138.