

EFFECTS OF ENVIRONMENTAL FACTORS ON INCUBATION PATTERNS OF GREATER SAGE-GROUSE

PETER S. COATES¹ AND DAVID J. DELEHANTY

Department of Biological Sciences, Idaho State University, Pocatello, ID 83209-8007

Abstract. Birds in which only one sex incubates the eggs are often faced with a direct conflict between foraging to meet metabolic needs and incubation. Knowledge of environmental and ecological factors that shape life-history strategies of incubation is limited. We used continuous videography to make precise measurements of female Greater Sage-Grouse (*Centrocercus urophasianus*) incubation constancy (percentage of time spent at the nest in a 24-hour period) and recess duration. We used an information-theoretic approach to evaluate incubation patterns in relation to grouse age, timing of incubation, raven abundance, microhabitat, weather, and food availability. Overall, sage-grouse females showed an incubation constancy of 96% and a distinctive bimodal distribution of brief incubation recesses that peaked at sunset and 30 min prior to sunrise. Grouse typically returned to their nests during low light conditions. Incubation constancy of yearlings was lower than that of adults, particularly in the later stages of incubation. Yearlings spent more time away from nests later in the morning and earlier in the evening compared to adults. Video images revealed that nearly all predation events by Common Ravens (*Corvus corax*), the most frequently recorded predator at sage-grouse nests, took place during mornings and evenings after sunrise and before sunset, respectively. These were the times of the day when sage-grouse typically returned from incubation recesses. Recess duration was negatively related to raven abundance. We found evidence that incubation constancy increased with greater visual obstruction, usually from vegetation, of nests. An understanding of how incubation patterns relate to environmental factors will help managers make decisions aimed at increasing productivity through successful incubation.

Key words: *Centrocercus urophasianus*, *Common Raven*, *Greater Sage-Grouse*, *incubation*, *nest*, *predation*, *video*.

Efectos de los Factores Ambientales sobre los Patrones de Incubación de *Centrocercus urophasianus*

Resumen. Las aves en las que sólo un sexo incuba los huevos se enfrentan frecuentemente con un conflicto directo entre forrajear para alcanzar las necesidades metabólicas e incubar. El conocimiento de los factores ambientales y ecológicos que modelan las estrategias de incubación de las historias de vida es limitado. Empleamos registros de video continuos para realizar medidas precisas de la constancia de incubación (porcentaje de tiempo transcurrido en el nido en un periodo de 24 horas) y la duración de los recesos en hembras de *Centrocercus urophasianus*. Utilizamos un enfoque basado en la teoría de la información para evaluar los patrones de incubación en relación con la edad, el momento de incubación, la abundancia de cuervos, el micro hábitat, el clima y la disponibilidad de alimento. En general, las hembras de *C. urophasianus* mostraron una constancia de incubación del 96% y una distribución bimodal caracterizada por breves recesos en la incubación con un pico al atardecer y 30 minutos antes del amanecer. Las aves típicamente regresaron a sus nidos bajo condiciones de poca luz. La constancia de incubación de las aves del primer año fue menor que la de los adultos, particularmente en los estadios finales de la incubación. Las aves de un año gastaron más tiempo alejadas de los nidos al final de la mañana y al principio de la tarde comparadas con las adultas. Las imágenes de video revelaron que casi todos los eventos de depredación por parte de *Corvus corax*, el depredador más frecuentemente registrado en los nidos de *C. urophasianus*, ocurrieron en las mañanas y en las tardes luego del amanecer y antes del atardecer, respectivamente. Estos fueron los momentos del día en que típicamente *C. urophasianus* regresaba de sus recesos de incubación. La duración de los recesos estuvo negativamente relacionada con la abundancia de cuervos. Encontramos evidencia de que la constancia de incubación incrementó con una mayor obstrucción visual de los nidos, usualmente dada por vegetación. El entendimiento de cómo los patrones de incubación se relacionan con los factores ambientales ayudará a que los encargados de tomar decisiones apunten a incrementar la productividad a través de la incubación exitosa.

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¹Present address: U.S. Geological Survey, Western Ecological Research Center, Dixon Field Station, Dixon, CA 95620.

E-mail: pcoates@usgs.gov

INTRODUCTION

In bird species in which only one sex incubates a given clutch of eggs, the parent must balance its own self-maintenance needs (e.g., foraging) with increased risks to eggs (e.g., egg cooling or heating, and predation) during incubation recesses (Conway and Martin 2000, Deeming 2002). Achieving a successful balance may involve many subtle trade-offs. For example, adults that take fewer but longer recesses may lessen the risk of egg predation by moving to and from the nest less often (Conway and Martin 2000), but may risk impairing embryonic development due to egg cooling during long incubation recesses (Clark and Wilson 1985, Naylor et al. 1988). Adults that take crepuscular recesses (Erikstad 1986) may need to reduce recess duration because of increased egg cooling rates during cool crepuscular periods relative to warm daytime periods (Naylor et al. 1988).

Our understanding of incubation patterns in relation to different environmental factors is limited, despite incubation behavior being central to reproductive success in birds (Deeming 2002). For example, knowledge of the relative importance of vegetation surrounding nests in aiding the thermoregulation of nests (Hansell and Deeming 2002) versus visually obstructing nests from predators (Martin 1995) is limited due to the difficulty of making fine-scale measurements of incubation in the wild. For species in decline due to habitat degradation, like the Greater Sage-Grouse (*Centrocercus urophasianus*), a large, ground-nesting galliform of the American West (Schroeder et al. 1999), understanding incubation patterns and environmental influences on these patterns can become central to conservation action.

The principal objective of our study was to use continuous videography to make fine-scale measurements of incubation constancy and recess patterns of sage-grouse and examine relationships with environmental factors using an information-theoretic approach (Anderson 2008). We examined timing of incubation recesses in relation to nest predation events captured on videotape. Additionally, we compared incubation patterns of yearling versus older females to test three a priori hypotheses related to grouse age: (1) that adult grouse take fewer daily incubation recesses than yearling grouse, (2) that a greater proportion of incubation recesses by adults occur during low light conditions (e.g., dawn and dusk) compared to yearlings, (3) and that incubation recess duration is less variable among adults than among yearlings. We based these hypotheses on the results of studies of other large-bodied birds (Erikstad 1986, Murphy and Boag 1989).

METHODS

STUDY AREA

We monitored a sample of sage-grouse nests within an area of approximately 1430 km² in Elko County, Nevada (41°31'N, 114°57'W) during 2002–2005. Dominant plant communities

consisted of sagebrush-steppe at lower elevations and mountain shrub at higher elevations. In sagebrush-steppe, shrub cover predominantly consisted of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*). Crested wheatgrass (*Agropyron cristatum*), an introduced grass, and native bluebunch wheatgrass (*Pseudoroegneria spicata*) characterized the understory. Mountain big sagebrush (*A. t. vaseyana*), serviceberry (*Amelanchier alnifolia*), and native bunchgrasses characterized the mountain shrub. Utah juniper (*Juniperus osteosperma*) occurred in the adjacent landscape at two of the four sites.

Climate at the study area consisted of cool, dry winters and hot, dry summers, with most annual precipitation occurring during the spring. Long-term (1952–2005) average daily temperatures ranged from –3° to 15°C. During the sage-grouse nesting season (March to July), long-term average daily temperatures ranged from 0° to 18°C. During this study, temperatures during the sage-grouse nesting season averaged 1° to 19°C. Long-term precipitation averaged 26 cm per year and 12 cm during the sage-grouse nesting season (U.S. Climatological Database, Gibbs Ranch, 41°20'N, 115°7'W). During this study, precipitation averaged 11 cm during the grouse nesting seasons.

The Nevada Department of Wildlife, in cooperation with U.S. Department of Agriculture, Animal Health Inspection Service, Wildlife Services carried out Common Raven (*Corvus corax*) removal activities (Coates et al. 2007) at the southernmost lek. The purpose of raven removal was to protect a recently reestablished population of Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*; Coates and Delehanty 2006), for which ravens were suspected to be nest predators (PSC, unpubl. data). The Sharp-tailed Grouse had established a lek within the southernmost sage-grouse lek. A variety of potential sage-grouse egg predators, reported in Schroeder et al. (1999), were observed within the study areas, including Common Ravens, coyotes (*Canis latrans*), weasels (*Mustela* spp.), American badgers (*Taxidea taxus*), ground squirrels (*Spermophilus* spp.), Black-billed Magpies (*Pica hudsonia*), and American Crows (*Corvus brachyrhynchos*).

CAPTURING AND MONITORING OF GROUSE

We captured female grouse from four lek complexes. A lek complex was defined as an area of 1–3 breeding grounds (leks). No leks within a complex were >2 km apart. Each lek complex was separated by ≥15 km. We captured grouse using spotlights and hand-held nets at night (Giesen et al. 1982). Captured grouse were fitted with 17–21g (<4% body mass) necklace-style, battery-powered radio-transmitters with 22 cm antennas (Advanced Telemetry Systems, Isanti, Minnesota). We classified grouse by age (yearling or adult) based on plumage (Ammann 1944). After capture, we located grouse every 2–3 days and recorded locations with a handheld GPS unit. We located nests by approaching female grouse that had been

recorded at the same set of coordinates three times. We sought to locate grouse nests either during the egg-laying period or during the initial days of incubation.

We monitored nests with camouflaged videorecording systems (Fuhrman Diversified, Inc., Seabrook, Texas, and Supercircuits, Austin, Texas; Coates et al., in press). We placed miniature, infrared-equipped cameras approximately 1 m from the nests. We placed time-lapse VCRs and power sources (deep-cycle batteries) 15–25 m from nests and connected them to cameras with camouflaged electrical cords buried beneath dirt and plant debris. VCRs were programmed to capture 1–2 images per second to allow us to record all movements of grouse to and from nests. We installed video systems ≥ 7 days following the onset of incubation to avoid researcher-induced nest abandonment (Renfrew and Ribic 2003). We electronically recorded date, time, and frame number on video images and we changed videotapes and batteries every 2–3 days during a brief visit. Prior to visits, we used binoculars to search the surrounding area for nest predators (e.g., ravens), and delayed maintenance of video systems if a predator was seen. We used a hand-held video monitor temporarily attached to VCRs to check for the presence of the grouse on the nest, and we rarely flushed grouse during our visits. We sought to install video equipment during morning hours while grouse were thought to be away from nests (Schroeder et al. 1999). We did not install cameras during extreme weather conditions to prevent researcher-induced egg mortality.

VEGETATION MEASUREMENTS

One to three days following the termination of a nesting effort, we measured habitat characteristics at the nest bowl and within a 50 m diameter area centered on the nest. In all years (2002–2005) we measured visual obstruction at the nest. We established 16 sample points at random directions and distances from nests (range: 0–25 m), at which we used a cover board (modified from Jones 1968) to estimate percentage of visual obstruction (50VO). The cover board consisted of three sides. Each side was 625 cm² and consisted of 25 squares of 25 cm² in a checkerboard pattern. We placed the three-sided board upright at each sample point facing in a random direction. We counted the number of squares that were 0%–50% visually obstructed from 2 m. We subtracted this number from the total number of squares. Measurements were taken at zero degrees (10–15 cm from the ground) and at approximately 45° (2 m from the ground) for each side of the board. We also estimated visual obstruction at nest bowls (NVO). We placed the board directly over the bowl and took measurements at 0° and 45° for each side. Then, we laid the board flat and measured obstruction at 90° (2 m directly over the board). Values from each of the three sides of the board were averaged at each measurement height to estimate visual obstruction (%).

In 2004 and 2005, we also measured total shrub cover (TSC), sagebrush cover (SC), and forb biomass (FBM) in the

nesting areas. We estimated total shrub cover by establishing four orthogonal ground transects of 25 m beginning in a random direction and intersecting at the nest bowl. Using a line-intercept technique (Canfield 1941), we measured the length of intersections of shrubs by species and calculated percentages of total shrub and sagebrush cover. To measure forb biomass, we clipped all forbs within a 25 × 50 cm plot centered at each random sample point. Samples were labeled and stored in paper bags and subsequently dried and weighed (g) in the laboratory. Plots with no forbs were noted and calculated into averages for the nest areas.

RAVEN ABUNDANCE

We conducted transect surveys ($n = 124$) to index raven abundance (Garton et al. 2005) between 17 March and 25 July (the period of sage-grouse nesting) during 2002–2005. One survey was conducted every 3–7 days at each lek complex. Survey transects totaled 27 km in 2002 and 2003 and 20 km in 2004 and 2005. We established 25 and 33 survey points along each 20 and 27 km transect, respectively. At each survey point, we used binoculars to count the number of ravens, flying or perched, during a 3 min period. We avoided recounting individual ravens by separating survey points by 800 m and by keeping track of ravens previously counted as we moved to the next survey point.

STATISTICAL ANALYSES

We reviewed videotapes in the laboratory to determine incubation constancy (percentage of time spent attending the nest within a 24-hour period) and the duration of incubation recesses (time spent away from the nest during each recess averaged over a 24 hr period) per individual. Days of camera installation or video failure were not included in calculations of incubation constancy or mean recess duration. We calculated the ordinal date of incubation (the number of days elapsed from 01 January to the date of incubation under consideration) and the day of incubation (number of days elapsed since the initiation of incubation). We compared the mean duration of recesses initiated before noon (am) and after noon (pm) using a two-sample *t*-test. We calculated a coefficient of variation (CV) for recess duration for each grouse and used one-way ANOVA to measure differences in within-individual variation between the two age classes (yearling and adult). If a grouse nested more than once in a year or in more than one year, we randomly selected one nest to use in analyses for that grouse. In post-hoc analyses, we tested differences in nest understory visual obstruction between age classes using ANOVA. These analyses were performed using Minitab® release 14 (Minitab, Inc., State College, Pennsylvania).

We obtained sunrise and sunset data (U.S. Navy Observatory, Astronomical Applications Department, Washington, DC) for each day of videorecorded recesses and expressed recess times relative to sunrise, noon, and sunset. We calculated

the number and duration of recesses and measured differences among age classes using a Pearson's Chi-square test (Test of Independence in Minitab® release 14) as a post-hoc analysis after observing recess timing frequencies. We defined recesses as crepuscular if they began within a 180 min interval centered on sunrise or sunset. These intervals encompassed nautical twilight periods (defined as starting when the sun is 18° below the horizon before sunrise and after sunset, respectively).

We acquired weather data (U.S. National Climate Data Center, Asheville, North Carolina) from two nearby weather stations, Gibbs Ranch (41°20'N, 115°7'W) and Jackpot (41°35'N, 114°30'W). We matched dates of precipitation and daily maximum and minimum temperatures with dates of videorecorded incubation for each grouse nest. To investigate weather effects further, we divided daily maximum ambient temperature by precipitation (DMT/PRC).

We indexed raven abundance by averaging the number of observed ravens per 10 km of transect surveyed. Because variation was observed in raven numbers through time, and grouse initiated incubation on different dates, we calculated a raven abundance index for each grouse by averaging values from surveys that were performed throughout the incubation period of each grouse.

We used an information-theoretic approach (Anderson and Burnham 2002), based on Kullback-Leibler information (Kullback and Leibler 1951) and maximum likelihood (de Leeuw 1992), to develop predictive models of incubation constancy and recess duration using explanatory variables describing raven abundance, grouse age, weather, timing of incubation, and microhabitat vegetation (Table 1). Explanatory variables in models were chosen based on reported effects on incubation patterns of large-bodied, ground-nesting birds (Erikstad 1986, Brown and Frederickson 1987, Wiebe and Martin 1997, Hansell and Deeming 2002). We included quadratic functions describing the influences of timing variables because these effects have been found in other large-bodied,

ground-nesting birds (Yerkes 1998). Also, we included timing and age interactions to better understand variation in incubation constancy among ages of grouse, as reported in the literature for other birds (Murphy and Boag 1989).

We modeled the two response variables—incubation constancy and recess duration—separately to understand the ecology of incubation patterns, because limitations in inferences may arise when considering only one response variable. Both responses are slightly different from each other and modeling both allowed us to distinguish between factors that affected total daily time off the nest in 24 hr versus the average amount of time spent off the nest during a recess.

We developed candidate models for incubation constancy and recess duration based on combinations of ≤ 3 variables because the analyses were exploratory and many combinations of variables were biologically feasible. We avoided the generation of spurious results by not developing more models than sample units, as suggested by Burnham and Anderson (1998). To avoid multicollinearity, we performed a Pearson's product-moment correlation matrix using 16 variables and excluded one variable of any pairwise comparison that covaried ($r \geq 0.65$). This resulted in 13 variables being used in the analyses. We used Akaike's information criterion (Akaike 1973) corrected for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i) to compare models (Anderson and Burnham 2002). The relative importance of each variable was determined by summing the weights of models in which the variable was present (Burnham and Anderson 1998).

We conducted modeling analyses in two steps. In step one, we identified sets of models that shared an overarching theme, such as weather effects or vegetation effects, and compared only models within each set (1–8 within-group models in each set). To account for additional vegetation measurements taken in 2004 and 2005, we compared models using a restricted dataset that included total shrub cover and dried forb biomass. The purpose of this step was to identify the most influential

TABLE 1. Means \pm SE of continuous explanatory variables used in mixed model analyses of incubation constancy and recess duration of Greater Sage-Grouse in northeastern Nevada, 2002–2005. The sample size (n) is the number of nests used in analyses.

Variable abbreviation ^a	Description	n	Mean \pm SE
RVN	Index of raven abundance (ravens per 10 km of transect)	37	2.9 \pm 0.3
PRC	Daily precipitation (cm)	37	7.2 \pm 1.0
DMT	Daily maximum temperature (°C)	37	19.9 \pm 0.3
NVO	Visual obstruction of nest by understory vegetation (%)	37	76.1 \pm 0.8
50VO	Visual obstruction of nest by understory vegetation at 16 sample points within 25 m (%)	37	56.5 \pm 0.8
TSC	Total shrub cover within 25 m of nest (%) ^b	22	40.5 \pm 1.1
MFB	Dry weight (g) of forb biomass within a 25 \times 50 cm plot centered at 16 sample points within 25 m of nest ^b	22	1.9 \pm 0.1

^aAdditional variables used in mixed model analyses were grouse age (AGE) and linear and quadratic functions of ordinal date (ORD, ORD²) and day of incubation (INC, INC²).

^bThese additional habitat characteristics were collected in 2004 and 2005 only and included in models within a restricted dataset.

variables within each group. In step two, we developed and compared models using the within-group variables identified as most influential in step one. Variables with $\Delta AIC_c > 2$ were not considered in step two because they lacked support (Burnham and Anderson 1998). This variable selection procedure allowed us to objectively reduce the number of considered variables. We carried out step two (45 between-group models) to better understand the relative ability of different classes of variables to explain incubation patterns.

We fit models using PROC MIXED in SAS version 9.1 (SAS Institute, Inc., Cary, North Carolina), which allowed us to model covariance for repeated-measures of each grouse and to include random effects (Littell et al. 1998) of year and study site. We report values as means \pm SE.

RESULTS

DAILY INCUBATION PATTERNS

We videotaped 392 complete 24-hour days of incubation (2002: $n = 7$; 2003: $n = 123$; 2004: $n = 98$; 2005: $n = 164$) by 43 grouse (2002: $n = 2$; 2003: $n = 9$; 2004: $n = 14$; 2005: $n = 18$). Incubation constancy of all females averaged $96.1\% \pm 0.2\%$ (range: $93.0\% - 97.7\%$). Average incubation constancy was $96.2\% \pm 0.2\%$ for adults and $94.7\% \pm 0.4\%$ for yearlings. We recorded 1042 incubation recesses (2002: $n = 21$; 2003: $n = 332$; 2004: $n = 245$; 2005: $n = 445$) of 46 grouse (2002: $n = 2$; 2003: $n = 9$; 2004: $n = 15$; 2005: $n = 20$). Average recess duration for all females was 26.5 ± 0.9 min (range of averages for each individual female was 14.1–43.9 min). Average recess duration for adult grouse was 24.9 ± 1.0 min ($n = 667$) and for yearlings was 31.4 ± 1.3 min ($n = 370$). The maximum time spent away from the nest during a single recess was 103 min by a yearling grouse. Duration of recesses that were initiated before noon (24.3 ± 1.0 min) was significantly shorter than that of recesses initiated

after noon (28.8 ± 1.2 min; $t_{81} = -2.9, P = 0.005$). Yearlings had greater within-individual variation in recess duration (CV = 43%) than adults (CV = 30%; $F_{1,42} = 5.6, P = 0.01$).

Most incubation recesses (798 of 1037, 77%) were crepuscular, resulting in a bimodal daily recess distribution (Fig. 1). No recesses occurred at night. Using post-hoc analyses, we detected a difference in timing of recesses between age classes ($\chi^2_1 = 13.3, P < 0.001$). Adult recesses were more often crepuscular (537 of 667, 81%) than yearling recesses (261 of 370, 71%). Also, adults were away from their nests before sunrise and after sunset (330 of 667 recesses, 50%) more often than yearlings (121 of 370 recesses, 33%; Fig. 1). Yearling recesses occurred primarily after sunrise, throughout the day, and into the evening, while adults were generally away from their nests before sunrise and nearer to sunset. Overall, female grouse took an average of 2.2 ± 1.0 recesses per day. Adults took fewer daily recesses (2.2 ± 0.1) than yearlings (3.0 ± 0.6) throughout the incubation period ($F_{1,40} = 5.1, P = 0.03$; Fig. 2).

PREDATION EVENTS

We videorecorded nest predation by American badgers ($n = 7$) and Common Ravens ($n = 9$), and directly observed one additional raven predation as it occurred (Coates et al., in press). Grouse were incubating on all occasions when badgers located nests and on eight occasions when ravens found nests. All predation by ravens was diurnal, whereas four predation events by badgers were nocturnal.

INCUBATION CONSTANCY MODELS

Step one. Within the set of models describing timing effects, incubation constancy was best explained by a quadratic effect of ordinal date (Model 3, Table 2). Incubation constancy increased during earlier dates (116 to 126) and decreased during later dates (136 to 176; Fig. 3). Within the set of models

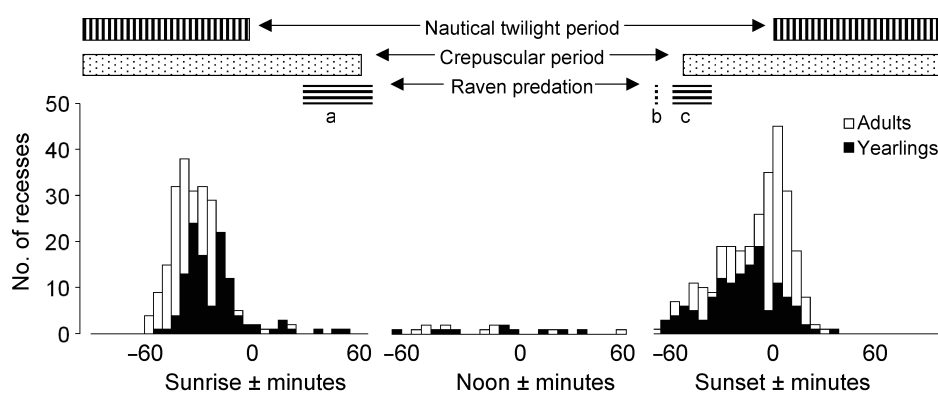


FIGURE 1. Greater Sage-Grouse showed a bimodal frequency distribution in the number of recesses ($n = 1037$) taken during incubation in relation to sunrise and sunset. Zero represents sunrise, noon, and sunset. Adults took recesses more often during the nautical twilight period (represented by vertical striped pattern), earlier in the morning and later in the evening, than yearlings. Raven predation events (represented by horizontal striped pattern) primarily occurred after twilight but during a crepuscular period (represented by dotted pattern). Timing of raven predation events was: (a) 06:22–08:42 ($n = 6$), (b) 13:59–14:04 ($n = 1$), and (c) 17:54–18:31 ($n = 2$). Raven predation events averaged 70.8 ± 24.8 min in duration. Data are from northeastern Nevada, 2002–2005.

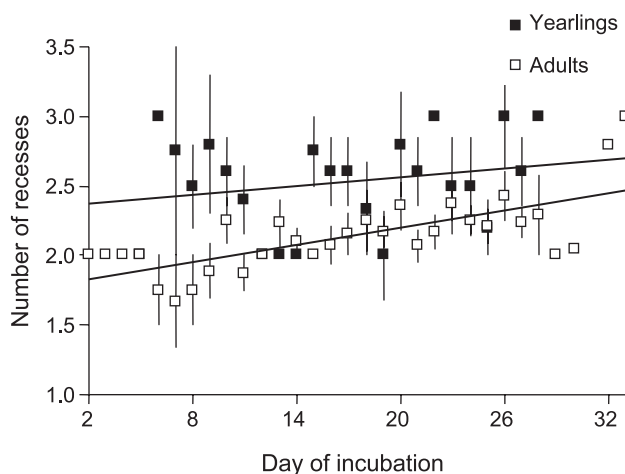


FIGURE 2. Yearling Greater Sage-Grouse ($n = 11$) took more incubation recesses than adults ($n = 32$), although the difference was less pronounced later in the incubation stage. Data are from north-eastern Nevada, 2002–2005. Trend lines were calculated from repeated-measures for each grouse for each day of incubation.

that considered interactions between age and timing, the top two models both included an interaction between age and a quadratic effect of incubation day (Models 5 and 6, Table 2). This interaction and a quadratic effect of ordinal date were the most likely of the variables considered to explain patterns of incubation constancy (Table 3). Incubation constancy of yearlings was substantially different than that of adults throughout the incubation period (Fig. 4). During the first half of the incubation period (days 1 to 14), yearling incubation constancy increased from 93% to 95%. During the second half of the incubation period (days 15 to 27), it decreased from 95% to 92%. Adult incubation constancy remained at approximately 96% throughout the incubation period.

When considering only microhabitat variables, the best-fit model was an additive model of visual obstruction at nests and within 25 m of nests (Model 9, Table 2). As visual obstruction at the nest and within the nesting area increased, grouse spent less time within 24 hours away from their nests. For 2004 and 2005, when we compared models that included total shrub cover and dried forb biomass, the two new variables were not supported by the data better than nest visual obstruction (Table 4).

TABLE 2. Mixed models explaining incubation constancy of Greater Sage-Grouse in northeastern Nevada, 2002–2005. Step 1 compared models within groups of related variables. Models with $\Delta AIC_c > 2$ are not shown. Step 2 evaluated models using the best explanatory variables that were chosen based on the top models ($\Delta AIC_c \leq 2$) in step 1. The number of estimated parameters in a model is denoted by K . The $-2(\log\text{-likelihood})$ value is denoted by $-2LL$. The likelihood R^2 value (LR^2) was based on a likelihood-ratio test, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is the log-likelihood of the model of interest, $\text{Log}L_o$ is the log-likelihood of the null model, and n is the number of observations (Magee 1990). ΔAIC_c represents the difference between the model of interest and the most parsimonious model of the model set. The Akaike weight (w_i) represents the probability that the model of interest is the best predictive model of those within the model set (Anderson 2008).

Model	Explanatory variables ^a	K	$-2LL$	LR^2	ΔAIC_c	w_i
Step 1						
Predator effects (one model)						
1	RVN	4	234.7	0.25	N/A	N/A
Age effects (one model)						
2	AGE	4	202.5	0.33	N/A	N/A
Timing effects (eight models)						
3	ORD ²	5	210.3	0.31	0.0	0.53
4	ORD ² , INC	6	209.1	0.31	0.9	0.34
Age and timing interactions (six models)						
5	AGE*INC ² , ORD ²	9	136.1	0.47	0.0	0.71
6	AGE*INC ² , AGE*ORD ²	10	135.7	0.47	1.8	0.29
Weather effects (three models)						
7	DMT	4	235.1	0.25	0.0	0.69
8	PRC	4	236.6	0.24	1.6	0.31
Vegetation effects (three models)						
9	NVO, 50V0	5	228.1	0.27	0.0	0.61
10	NVO	4	230.8	0.25	1.0	0.37
Step 2						
The three most parsimonious models (45 models)						
11	AGE*INC ² , ORD ² , NVO	10	130.3	0.48	0.0	0.63
12	AGE*INC ² , ORD ² , RVN	10	132.8	0.47	2.5	0.18
13	AGE*INC ² , ORD ²	9	136.1	0.47	3.6	0.10

^aMain effects were included in models with polynomial terms and higher-order interactions. RVN = raven abundance, AGE = age of grouse, ORD² = quadratic function of ordinal date, INC = day of incubation, INC² = quadratic function of day of incubation, DMT = daily maximum temperature, PRC = daily precipitation, NVO = nest visual obstruction, and 50V0 = visual obstruction within 25 m of nest.

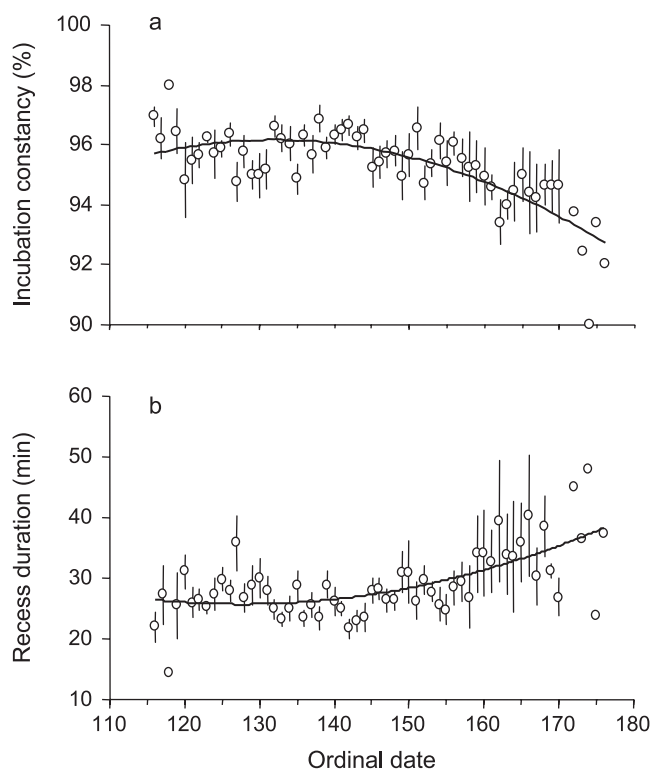


FIGURE 3. (a) Incubation constancy (percentage of time spent on the nest) decreased, and (b) recess duration (minutes) increased in relation to ordinal date (days elapsed between 1 January and date of incubation) for Greater Sage-Grouse ($n = 43$) in northeastern Nevada, 2002–2005. Points along the x axis represent mean values at each date. Bars indicate standard errors. Day 110 = 18 April.

Step two. The overall best-fit model consisted of an interaction between age and a quadratic effect of incubation day, a quadratic effect of ordinal date, and nest visual obstruction (Model 11, Table 2). No other models were closely competitive ($\Delta AIC_c \leq 2$). The second best-fit model was similar but included the index of raven abundance instead of nest visual obstruction (Model 12, Table 2). Mean raven abundance was 2.9 ± 0.3 ravens along 10 km of transect. Model 11 was 3.4 times (w_i/w_j) more likely than model 12 to explain incubation constancy. Among all models, the interaction between age and a quadratic effect of incubation day and a quadratic effect of ordinal date had the greatest relative importance (Table 3).

INCUBATION RECESS MODELS

Step one. A quadratic effect of ordinal date and incubation day (Model 3, Table 5) best explained recess duration when comparing timing variables. A quadratic effect of ordinal date was in all models with $\Delta AIC_c \leq 2$. During early ordinal dates (116–126) recesses were shorter. At later dates recess durations were longer (days 136–176; Fig. 3). There was an interaction between grouse age and both a quadratic effect of incubation day and a quadratic effect of ordinal date (Model 6, Table 5). The recess duration of yearlings varied through time

TABLE 3. Support for and relative importance of explanatory variables used to model incubation constancy and recess duration of Greater Sage-Grouse in northeastern Nevada, 2002–2005. Parameter estimates and standard errors were weighted (using Akaike weights) and averaged across all models. The likelihood R^2 value (LR^2) was based on a likelihood-ratio test of the variable under consideration (without additive effects), $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is the log-likelihood of the model of interest, $\text{Log}L_o$ is the log-likelihood of the null model, and n is the number of observations (Magee 1990). Parameter likelihoods (PL) were calculated by summing Akaike weights for models that included the variable of interest within the model set (Burnham and Anderson 1998). Values < 0.05 are not shown. See Table 1 for variable explanations.

Response variable	Parameter	Estimate \pm SE	LR^2	PL
Incubation constancy	AGE*INC ²	-0.0007 \pm 0.0002	0.35	1.00
	ORD ²	-0.0008 \pm 0.0001	0.31	1.00
	NVO	0.0050 \pm 0.0019	0.26	0.64
	RVN	0.0098 \pm 0.0054	0.25	0.18
Recess duration	AGE*INC ²	0.0021 \pm 0.0005	0.32	1.00
	ORD ²	0.0015 \pm 0.0005	0.32	1.00
	RVN	-0.0449 \pm 0.0164	0.30	0.82
	DMT	0.0291 \pm 0.0088	0.29	0.17

more than that of adults. Specifically, yearling grouse took relatively lengthy recesses earlier in incubation (days 1–15), shorter recesses in midincubation (days 15–20), and lengthier recesses during late incubation (days 20–27), whereas adult recess duration did not change notably through time (Fig. 4).

The model of maximum ambient temperature alone was 2.5 times (w_i/w_j) more likely to fit the data than the model with temperature and precipitation (Table 5). Recess duration was positively related to maximum temperature, meaning grouse stayed away from nests longer during days of increased temperature.

When considering only microhabitat variables, the best-fit model consisted of an additive effect of visual obstruction at nests and in the nesting area (model 9, Table 5). As with the incubation constancy models, the two additional habitat variables of total shrub cover and dry biomass of forbs, measured during 2004 and 2005, were not informative in modeling recess duration (Table 4). Nest visual obstruction was the only parameter that was substantiated by the data using the restricted dataset and was included in step two. We also included 25 m visual obstruction in step two because of its importance when using all four years of data.

Step two. The best model for predicting recess duration consisted of an interaction between age and a quadratic effect of incubation day, a quadratic effect of ordinal date, and the index of raven abundance (Model 10, Table 5). No other models had a $\Delta AIC_c \leq 2$. The effects of timing and age were described above. An increase in raven abundance was inversely related to the duration of incubation recesses; i.e., more ravens were associated with a decrease in recess duration. The second best-fit model was similar but included maximum ambient temperature instead of the raven index (Model 11, Table 5). Model 10 was 4.8 times (w_i/w_j) more likely than model 11

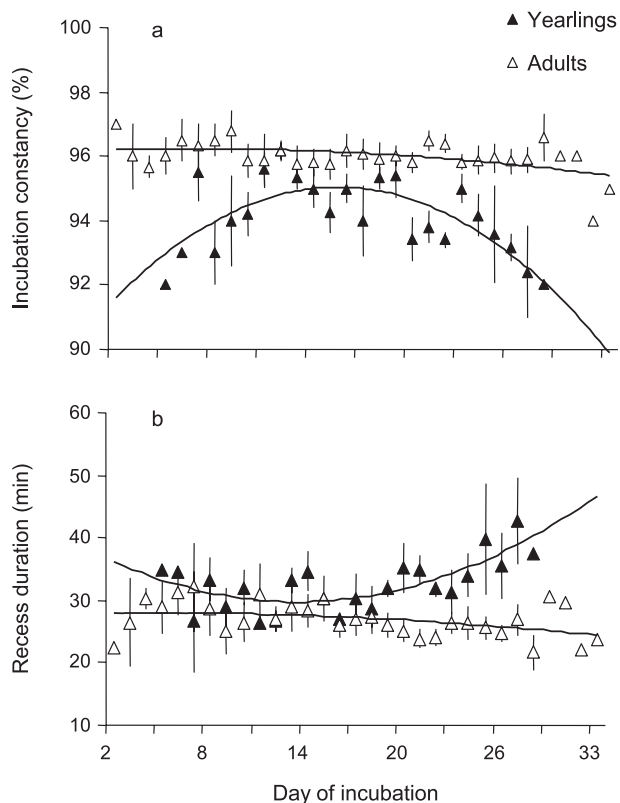


FIGURE 4. (a) Incubation constancy (percentage of time spent on the nest) of yearling Greater Sage-Grouse ($n = 11$) during later days of incubation was less than that of adults ($n = 32$), and (b) recess duration (minutes) of yearlings during later days of incubation was greater than that of adults. Data are from northeastern Nevada, 2002–2005. Points along the x axis represent mean values on each day of incubation. Bars indicate standard errors.

to explain recess duration. The parameters of an interaction between age and a quadratic effect of incubation day and a quadratic effect of ordinal date were most substantiated in explaining recess duration. However, the index of raven abundance also received substantial support (Table 3).

DISCUSSION

Sage-grouse had an incubation constancy similar to that of other large birds with female-only incubation and precocial young (Deeming 2002). For adult sage-grouse, incubation constancy typically was interrupted by only two short, crepuscular recesses. Yearlings often augmented this bimodal recess pattern with additional, irregular daytime recesses, and took slightly longer recesses than adults on average. Our modeling of factors associated with variation in sage-grouse incubation behavior was an effort to explain time away from the nest in a system characterized by high nest attendance.

A plausible explanation for the decrease in incubation constancy in later days of incubation is a reduction of parental

TABLE 4. Support for and relative importance of microhabitat variables used to model incubation constancy and recess duration of Greater Sage-Grouse in northeastern Nevada, 2002–2005. The -2 (log-likelihood) value is denoted by $-2LL$. The likelihood R^2 value (LR^2) was based on a likelihood-ratio test, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is the log-likelihood of the model of interest, $\text{Log}L_o$ is the log-likelihood of the null model, and n is the number of observations (Magee 1990). ΔAIC_c represents the difference between the model of interest and the most parsimonious model of the model set. The Akaike weight (w_i) represents the probability that the model of interest is the best predictive model of those within the model set (Anderson 2008). Parameter likelihoods (PL) were calculated by summing Akaike weights for models that included the variable of interest within the model set (Burnham and Anderson 1998). See Table 1 for variable explanations.

Response variable	Parameter	$-2LL$	ΔAIC_c	LR^2	PL
Incubation constancy	NVO	136.8	00.0	0.21	1.00
	50VO	153.2	18.6	0.14	0.39
	TSC	154.0	19.4	0.13	0.25
Recess duration	FBM	152.4	17.8	0.14	0.23
	NVO	242.3	00.0	0.28	0.99
	50VO	256.5	16.3	0.22	0.78
	FBM	260.0	19.8	0.21	0.48
	TSC	260.9	20.7	0.20	0.16

energy; that is, a depletion of nutrient reserves as incubation proceeds, which has been reported for waterfowl (Afton and Paulus 1992). Energy requirements for incubation are partly satisfied by lipid and protein reserves stored during a prelaying period. As incubation advances, sage-grouse may experience depleted reserves and increase their reliance on foraging, resulting in reduced incubation constancy later in incubation, as is the case for many birds (Afton 1980, Brown and Frederickson 1987, Yerkes 1998). Perhaps reduced reserves also explain the reduced incubation constancy at later ordinal dates.

Alternative explanations for these patterns include increased embryonic heat production (Drent 1970), increased ambient temperatures (Mallory and Weatherhead 1993), and changes in egg cooling rates during egg development (Turner 2002). Although these explanations are possible, the energetic reserves explanation is more supported by our data by the importance of an interaction between age and day of incubation. Incubation constancy decreased during late incubation (days 20–30) for yearlings but not adults. Adult sage-grouse likely are able to store more reserves for incubation than yearlings, as has been shown for Willow Grouse (*Lagopus lagopus*; Erikstad 1986). Therefore, adults could maintain greater incubation constancy than yearlings, as yearlings are increasingly forced to rely on foraging late in the incubation period. Similar findings were reported for young female Canada Geese (*Branta canadensis*), who lost body mass, increased foraging, and had reduced nest attentiveness toward the later stages of incubation compared to older geese (Murphy and Boag 1989).

TABLE 5. Mixed models explaining the recess duration of Greater Sage-Grouse in northeastern Nevada, 2002–2005. Step 1 compared models within groups of related variables. Models with $\Delta AIC_c > 2$ are not shown. Step 2 evaluated models using the best explanatory variables that were chosen based on the top models ($\Delta AIC_c \leq 2$) of step 1. The number of estimated parameters in a model is denoted by K . The $-2(\log\text{-likelihood})$ value is denoted by $-2LL$. The likelihood R^2 value (LR^2) was based on a likelihood-ratio test, $1 - \exp(-2/n(\text{Log}L_m - \text{Log}L_o))$, where $\text{Log}L_m$ is the log-likelihood of the single-variable model, $\text{Log}L_o$ is the log-likelihood of the null model, and n is the number of observations (Magee 1990). ΔAIC_c represents the difference between the model of interest and the most parsimonious model of the model set. The Akaike weight (w_i) represents the probability that the model of interest is the best predictive model of those within the model set (Anderson 2008).

Model	Explanatory variables ^a	K	$-2LL$	LR^2	ΔAIC_c	w_i
Step 1						
Predator effects (one model)						
1	RVN	4	695.6	0.30	N/A	N/A
Age effects (one model)						
2	AGE	4	701.2	0.28	N/A	N/A
Timing effects (eight models)						
3	ORD ² , INC	6	684.1	0.33	0.0	0.55
4	ORD ² , INC ²	7	683.7	0.33	1.7	0.23
5	ORD ²	5	688.1	0.32	1.9	0.21
Age and timing with interactions (six models)						
6	AGE*INC ² , AGE*ORD ²	9	650.9	0.40	0.0	1.00
Weather effects (three models)						
7	DMT	4	700.1	0.29	0.0	0.70
8	DMT, PRC	4	699.8	0.29	1.8	0.28
Vegetation effects (three models)						
9	NVO, 50V0	4	687.2	0.32	0.0	0.96
Step 2						
The three most parsimonious models (45 models)						
10	AGE*INC ² , ORD ² , RVN	10	636.9	0.43	0.0	0.82
11	AGE*INC ² , ORD ² , DMT	10	640.1	0.42	3.2	0.17
12	AGE*INC ² , ORD ² , NVO	10	646.5	0.42	9.5	0.01

^aMain effects were included in models with polynomial terms and higher-order interactions. RVN = raven abundance, AGE = age of grouse, ORD² = quadratic function of ordinal date, INC = day of incubation, INC² = quadratic function of day of incubation, DMT = daily maximum temperature, PRC = daily precipitation, NVO = nest visual obstruction, and 50V0 = visual obstruction within 25 m of nest.

The hypothesis that yearlings rely on supplemental foraging more than adults is also supported by the interaction between age and day of incubation in the best-fit model of recess duration. Yearlings took longer recesses in the later stages of incubation, a pattern that would be expected if yearlings require more foraging time than adults. Unfortunately, little information exists on foraging activity during incubation recesses for sage-grouse, although White-tailed Ptarmigan (*Lagopus leucura*) forage vigorously during incubation recesses (Wiebe and Martin 1997).

It is also possible that prior nesting experience contributed to different incubation patterns between ages. Experienced adult sage-grouse may have exhibited greater incubation constancy to help conceal eggs from predators, while inexperienced yearlings employed a more risky incubation strategy. Some portion of variation in incubation behavior could be learned through positive or negative association with nest success or failure. Species subject to high nest predation rates show great behavioral plasticity in antipredator strategies (Conway and Martin 2000, Ghalambor and Martin 2000, Martin 2002). The higher incubation constancy that we observed in adults may have multiple antipredator advantages. High constancy

is associated with fewer overall days of incubation, which almost certainly decreases the chance of predators finding nests, and increases the proportion of time that eggs are camouflaged (Marzluff 1985, Thompson and Raveling 1987, Wiebe and Martin 1997). Because they are more capable of meeting metabolic requirements, adults may speed embryonic development through high incubation constancy to avoid predation (Wiebe and Martin 1997). Both mechanisms, grouse nesting experience and grouse energetic reserves, probably would favor the expression of greater incubation constancy in adults relative to yearlings, even though the two processes are not mutually exclusive. An important conservation consequence of the differences between yearling and adult sage-grouse in incubation patterns is that events that skew populations toward yearlings may result in reduced annual nest success rates.

The strongly bimodal pattern of timing in daily recesses is most likely a result of behavior aimed at avoiding visually cued, diurnal predators such as ravens and other corvids, something that has been suggested for other grouse (Angelstam 1984, Erikstad 1986). If grouse avoid nocturnal activity, but use low light levels to avoid diurnal predators, then we would expect peak frequencies of recesses to occur sometime near dawn and

dusk, as we observed. In the morning, most females left their nests at times that allowed them to return at low light. In the evening, we observed a sharp reduction in recess initiation 30 min after sunset, resulting in most females returning to the nest just prior to dark. Timing of return in the evening may also be influenced by egg temperature flux, with birds returning to incubate eggs when egg cooling rates start increasing.

Videographic documentation of raven predation of sage-grouse nests (Coates et al., in press) showed that ravens depredated nests primarily in the morning following sunrise (06:30 to 09:30) and immediately preceding sunset (18:00 to 19:00). Ravens appear to cue in on the movements of grouse to and from their nests. The fact that grouse typically take recesses during low light, when foraging efficiency may be impaired and when, at least during the morning, egg cooling rates are relatively high, may reflect the importance of diurnal predation pressure. Additionally, the best-fit model of recess duration included a parameter for raven abundance. Longer recesses may increase the chance of ravens finding nests because they extend off-nest parental activities into high light conditions. Diurnal activity by passerines near nests was found to be positively related to nest predation and attributed to visually cued predators (Martin et al. 2000). We found no pattern in the timing of badger predation events; perhaps because badgers forage during the day and night and primarily rely on olfactory senses (Messick 1987).

It is possible that ravens may have gone unnoticed by us and could have used our movements to locate nests. However, this is unlikely because of our precautions and because video images revealed that >3 hours elapsed between our nest visits and predation events. Most predation occurred 1–2 days after nest visits. Also, it is possible that we did not observe midday predation by ravens simply because ravens were less active at this time. However, others have found that detection of corvids during surveys was not affected by time between sunrise and midday (Luginbuhl et al. 2001). Nonetheless, grouse appear to use low-light conditions because ravens, regardless of their abundance, are hindered in their ability to find nests during these conditions.

An alternative explanation for the bimodal recess pattern we observed is that the amount of time spent on the nest between recesses is limited by the amount of food the crop can contain, as was suggested for White-tailed Ptarmigan (Wiebe and Martin 1997). Specifically, grouse fast during dark hours. Then, when enough illumination is available, grouse forage due to hunger until their crops are full. Grouse forage again in the evening and may choose the latest possible time to gather enough food to sustain them throughout the night. This hypothesis, however, does not adequately explain the differences we saw in daytime recesses between adults and yearlings.

If yearling grouse are energetically constrained and need more recess time to meet metabolic requirements, we would expect to observe yearlings engaging in incubation recesses

during times when egg cooling rates are reduced, to allow more time to forage in a single bout. Indeed, yearlings were away from their nests more often during high light periods when eggs cool at slower rates, which is consistent with reports for other grouse (Erikstad 1986). It may be difficult for yearlings to acquire enough food during low light conditions to meet their metabolic needs (Naylor et al. 1988) due to reduced foraging efficiency compared to adults. The effect of prevailing conditions on egg cooling rates can make adjusting the duration of recess rather than recess frequency advantageous because of the high energetic cost associated with re-warming cool eggs (Hainsworth and Voss 2002).

It is generally accepted that vegetation surrounding the nest can influence incubation patterns, through its effects on nest microclimate (Ar and Sidis 2002). However, one unexamined hypothesis linking nest vegetation to incubation constancy is the possibility that vegetation makes critically needed water available to grouse while on the nest, in the form of captured dew or frost. Birds with long incubation sessions experience high water loss through respiration and skin evaporation (Ar and Sidis 2002) and combat dehydration by consuming surface water (Carey 2002). Unfortunately, water needs of sage-grouse during incubation have not been specifically addressed in the literature.

The positive relationship between vegetation characteristics at sage-grouse nests and nest survival reported in the literature (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005) may be at least partially explained by increased incubation constancy. Populations of sage-grouse are declining, partly as a result of loss of nesting habitat (Connelly et al. 2004). Loss of visual obstruction at nests appears to have detrimental effects on successful nesting behavior by reducing incubation constancy and possibly increasing the exposure of grouse and eggs.

These effects may be particularly important in environments where ravens or other corvids are abundant. Raven numbers have increased with anthropogenic resource subsidies (e.g., transmission lines and landfills; Boarman and Heinrich 1999, Boarman 2003), and predation by ravens has been suggested as one of the factors potentially limiting sage-grouse production at local scales (Batterson and Morse 1948, Autenrieth 1981). Further research on sage-grouse incubation patterns, especially in relation to energetic reserves, food and water availability, and nest predator abundance, would make important contributions to understanding sage-grouse reproduction.

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