

Temperature, wind, vegetation, and roads influence incubation patterns of Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) in the Nebraska Sandhills, USA

Ian R. Hoppe, Jocelyn O. Harrison, Edward J. Raynor IV, Mary Bomberger Brown, Larkin A. Powell, and Andrew J. Tyre

Abstract: Avian incubation involves behavioral decisions that must balance trade-offs between the incubating bird's survival and current and future reproductive success. We evaluated variation in incubation off-bout duration and frequency among Greater Prairie-Chickens (*Tympanuchus cupido pinnatus* (Brewster, 1885)) in the Nebraska Sandhills, USA. Greater Prairie-Chicken life history favors incubation behaviors that prioritize success of the current breeding attempt over adult survival. Previous observations suggest incubating females make these behavioral decisions based on ambient temperature conditions, their own body condition, and predation risk. We monitored nest attendance by females at 30 Greater Prairie-Chicken nests to identify proximate cues used to make behavioral decisions regarding incubation. We recorded 930 incubation off-bouts. Females took 1.9 ± 0.7 off-bouts/day (mean \pm SD), each with a mean (\pm SD) duration of 43.3 ± 24.1 min. Off-bouts were shorter in duration at higher wind speeds, at lower ambient temperatures, at nests with less cover, and at nests closer to roads. Females were most likely to leave the nest during mid-morning and evening, as are most gallinaceous birds, and incubation off-bouts became less frequent later in the season. We did not observe differences in incubation behavior between nests that failed and those that successfully hatched one or more chicks.

Key words: Greater Prairie-Chicken, iButton temperature loggers, incubation behavior, mixed-effects models, nest attendance, *Tympanuchus cupido pinnatus*.

Résumé : Des décisions comportementales interviennent durant la couvaison par les oiseaux pour ajuster des compromis entre la survie de l'oiseau qui couve et son succès de reproduction présent et futur. Nous avons évalué les variations de la durée et de la fréquence des pauses dans la couvaison chez des tétras des prairies (*Tympanuchus cupido pinnatus* (Brewster, 1885)) dans les Sandhills du Nebraska (États-Unis). Le cycle biologique des tétras des prairies favorise des comportements de couvaison priorisant le succès de la tentative de reproduction en cours plutôt que la survie des adultes. Des observations antérieures indiqueraient que les femelles couveuses prennent ces décisions comportementales sur la base des conditions de température ambiante, de leur propre embonpoint et du risque de prédation. Nous avons surveillé la présence au nid de femelles pour 30 nids de tétras des prairies afin de cerner les signaux proximaux utilisés dans la prise de décisions comportementales touchant à la couvaison. Nous avons enregistré 930 pauses dans la couvaison. Les femelles faisaient $1,9 \pm 0,7$ pause/jour (moyenne \pm ÉT), d'une durée moyenne (\pm ÉT) de $43,3 \pm 24,1$ min. Ces pauses étaient de plus courte durée à de plus grandes vitesses du vent, à des températures ambiantes plus faibles, là où la couverture du nid était plus faible et où le nid était plus proche d'une route. Les femelles étaient plus susceptibles de quitter le nid en milieu de matinée et en soirée, à l'instar de la plupart des gallinacés, et les pauses dans la couvaison devenaient moins fréquentes plus tard durant la saison. Nous n'avons observé aucune différence de comportement de couvaison entre les nids non éclos et ceux dans lesquels un oisillon ou plus avait éclos avec succès. [Traduit par la Rédaction]

Mots-clés : tétras des prairies, enregistreurs de température iButton, comportement de couvaison, modèles à effets mixtes, présence au nid, *Tympanuchus cupido pinnatus*.

Introduction

Avian incubation can be costly in terms of energetic resources (Moreno and Carlson 1989; Tinbergen and Williams 2002) and deferred breeding opportunities (de Heij et al. 2006) for the incubating adults. Increased nest attentiveness may improve the hatching success of eggs, but it may also expose the incubating adults and developing chicks to elevated risk of mortality or even

reduced immune competence (Cichoń 2000; Visser and Lessells 2001; Engstrand and Bryant 2002; de Heij et al. 2006; DuRant et al. 2012). Birds evolved a variety of incubation strategies in effort to balance these competing concerns. In nearly 50% of avian families, both male and female contribute to incubation, but in approximately 37% of avian families, only the female contributes to incubation (Deeming 2002); in grouse, only the female attends the nest and incubates the eggs (Coates and Delehanty 2008).

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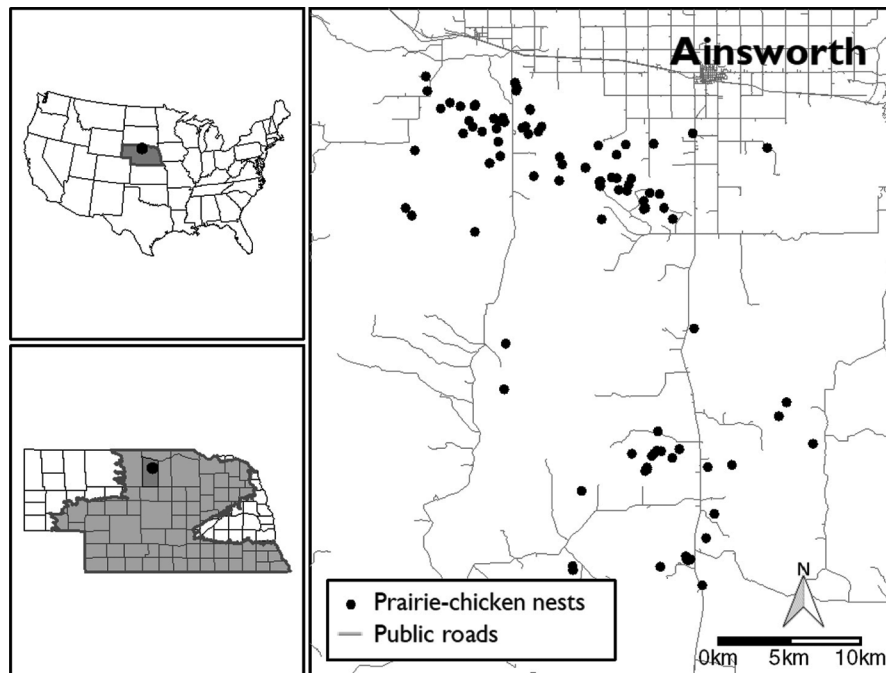
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Fig. 1. Location of our study site within the contiguous USA (upper left panel), in Nebraska (lower left panel; shaded region shows Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) within the state), and locally, near Ainsworth, Brown County, Nebraska (right panel). Nests of Greater Prairie-Chickens are depicted in relation to the locations of public roads.



Previous studies of incubation in grouse show a pattern of high incubation constancy punctuated by relatively few off-bouts of long duration — White-tailed Ptarmigan (*Lagopus leucura* (Richardson, 1831)): 93.9%–95.7% of day spent on nest (Wiebe and Martin 1997); Greater Sage-Grouse (*Centrocercus urophasianus* (Bonaparte, 1827)): 96.2% (Coates and Delehanty 2008). High incubation constancy may function to reduce the overall length of the incubation period, limiting total nest exposure to predation and adverse environmental conditions (Deeming 2002; Winder et al. 2016). Female grouse receive neither relief from the nest nor food from the male, and nesting activity may increase the risk of mortality for female grouse (Hagen et al. 2007). Female grouse are thus faced with a recurrent decision about how to appropriately allocate time for foraging and incubation in the context of risk of exposure for themselves and their eggs (Tulp and Schekkerman 2006). How then do female grouse decide when and for how long to leave their nests during incubation?

Proximately, these decisions are influenced by body condition, ambient weather conditions, and predation risk (Wiebe and Martin 1997; Conway and Martin 2000). Energetic costs and the risk of predation during incubation can be partially mitigated by nest-site selection (Wiebe and Martin 1998; Amat and Masero 2004; Carroll et al. 2015; Grisham et al. 2016), but this may be insufficient to counteract the negative effects of ambient weather conditions and predation. Nest-site selection may reflect environmental and predation considerations early in the nesting cycle, but nest-attendance behavior may reflect more immediate concerns arising during incubation.

Greater Prairie-Chickens (*Tympanuchus cupido pinnatus* (Brewster, 1885); hereafter Prairie-Chickens) are a grassland-nesting grouse species (Phasianidae: Tetraoninae) that historically occurred throughout much of the central United States and Canada, with isolated populations in the Mid-Atlantic States (BirdLife International 2017). Reproduction in Prairie-Chickens is characterized by large clutch sizes, precocial young, and low juvenile and adult survival (Ricklefs 1969; Johnsgard 1973; Hagen and Giesen 2005; Johnson et al. 2011). This suite of life-history traits typifies species whose

demographic rates are strongly influenced by fecundity (Sæther and Bakke 2000; Hagen et al. 2009).

We investigated nest-attendance patterns by female Prairie-Chickens in the Nebraska Sandhills, USA, to identify the proximate cues that they use to make behavioral decisions with respect to incubation. Our objectives were to (i) describe the frequency, timing, and duration of female recesses from the nest during incubation and (ii) explore the influences of nest-specific and incubation-bout-specific variables on nest attendance. Our hypotheses are the following: if incubating female Prairie-Chickens prioritize nest success, then (i) we expect them to reduce the duration of incubation off-bouts when ambient temperatures are unfavorable for embryonic development (high or low temperatures); (ii) we expect them to initiate incubation off-bouts at times of day when ambient temperatures are favorable for continued embryonic development; (iii) we expect them to reduce incubation off-bout duration and frequency as nest age increases, since the value of the clutch is higher as more incubation effort has been expended; and (iv) we expect them to show increased incubation off-bout duration at nests with greater vegetation cover and (or) at greater distances from roads because of lower risk of predation in these conditions.

Materials and methods

Study area and population

During the 2013 and 2014 breeding seasons (May–July), we monitored Prairie-Chicken nests in a 490 km² area (centered at 42.41°N, 99.94°W) in Brown County, Nebraska, USA (Fig. 1). Our study population is in the core of the largest intact population of Prairie-Chickens in South Dakota, Nebraska, and Kansas, USA (BirdLife International 2017). The area is part of the Nebraska Sandhills, a largely unfragmented 50 000 km² region spanning the north-central portion of the state and dominated by dunes of sandy soil stabilized by mixed-grass prairie and interspersed with shallow lakes and wetlands (Schneider et al. 2011). Between 1981 and 2010, the study area received a mean of 593 mm of precipita-

tion annually (May–July; HPRCC 2017). Temperatures ranged from a mean monthly low of -9.2 °C in January to a mean monthly high of 30.5 °C in July (HPRCC 2017). Mean monthly temperatures during the breeding season were 15.1 °C in May, 20.3 °C in June, and 23.7 °C in July (HPRCC 2017). Annual mean wind speeds ranged from 7.0 to 7.5 m/s at a height of 50 m (Elliott et al. 1986). The study site includes a wind energy facility owned and operated by the Nebraska Public Power District (NPPD 2017). Although our study design did not allow us to evaluate the impacts of the wind turbines on incubation behavior, we did include a nest's proximity to the nearest turbine in our analyses to account for their presence on the landscape.

Field methods

We captured female Prairie-Chickens using walk-in traps and drop nets during the pre-nesting period and fitted them with necklace-style very high frequency (VHF) radio transmitters (A4050; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). We identified the locations of birds five to seven times per week using radiotelemetry (for details see Harrison 2015; Harrison et al. 2017). When the location of an individual went unchanged over a 3-day period, we approached its last known location to determine whether a nest was present. Upon locating a nest, we recorded the coordinates on a handheld global positioning system (GPS) device (eTrex Vista; Garmin International Inc., Olathe, Kansas, USA). At a subset of the nests, we used Thermochron® iButton® temperature loggers (DS1922L; Maxim Integrated, Dallas, Texas, USA; hereafter iButtons) to record nest temperature as a method of identifying nest-attendance patterns. Each iButton was wrapped in a fine mesh cloth, tied to a thick wire pushed into the ground, and concealed with nesting material just beneath the eggs at the edge of the nest, but within the nest bowl. We placed the iButtons variously before or after clutch completion (and initiation of incubation) depending on when the nest was located; we retrieved them after the eggs hatched or the nest failed (or was abandoned).

Dallmann et al. (2016) used iButtons and video cameras to demonstrate that temperature loggers offer an effective and accurate means of identifying and measuring nest-attendance patterns throughout the incubation period in Prairie-Chickens. This study also showed the presence of female Prairie-Chickens at the nest (nest attendance) during incubation is almost always associated with physical incubation of the eggs. Here, we use nest-attendance patterns to infer incubation patterns. Also, we use the term off-bout to refer to the periods of time a female Prairie-Chicken interrupts incubation by moving away from the eggs.

We determined the location of each female Prairie-Chicken from a distance of at least 30 m throughout the incubation period. When a female was found to be away from her nest for three consecutive days, we approached the nest on foot to assess the nest fate. We evaluated nest fates based on the presence and disposition of eggshells in the nest bowl, as well as signs of predator activity nearby. For nests that successfully hatched, we calculated the approximate date incubation began based on a 28-day incubation period (Johnson et al. 2011). We used this date in determining the nest age used in the off-bout analysis. Nests that could not be reliably aged using egg floatation (Westerskov 1950) or date of clutch completion (and failed or were abandoned prior to hatching) were not included in our model analyses.

At least 5 days after first locating each nest or on the estimated date of clutch completion, we returned to the nest to quantify the structure of the surrounding vegetation. With a Robel pole placed at the center of the nest bowl, we acquired a visual obstruction reading (VOR) from each of the four cardinal directions (North, South, East, West; Robel et al. 1970). The mean VOR for each nest was calculated as the arithmetic mean of the four readings. We used mean VOR to represent vegetation structure at the nest because it has been shown to reflect elements important for nest survival and nest-site selection by female Prairie-Chickens (McNew

et al. 2014; Harrison 2015; Harrison et al. 2017; but see Matthews et al. 2013). We accessed weather data (ambient temperature, precipitation, and wind speed) recorded every 20 min at the nearby Ainsworth Regional Airport ($42^{\circ}55'N$, $99^{\circ}82'W$; see Whalen 2015; Whalen et al. 2017). For each nest, we measured the distance to the nearest road, wind turbine, tree, and open water source using ArcMap version 10.1 (ESRI, Redlands, California, USA). For additional details concerning field methods see Harrison (2015) and Harrison et al. (2017).

The University of Nebraska's Institutional Animal Care and Use Committee approved all field methods involving animal capture and handling (permit No. 901).

Data analyses

iButton data processing

We uploaded readings from each iButton using 1-wire software developer's kit for Windows version 4.00 (Maxim Integrated, Dallas, Texas, USA). After converting the temperature data files into an appropriate format using Rhythm (Cooper and Mills 2005), we manually identified off-bouts and measured their duration in Raven Pro version 1.5 (Cornell Lab of Ornithology, Ithaca, New York, USA). We defined an off-bout as the time interval elapsing between the temperature recording just prior to the female's departure from the nest (indicated by a sharp decrease in temperature in the time series) until the time of the recording made just prior to her return (indicated by a local minimum). Because the precise signature of off-bouts varied, we based our classification on the following three conservative criteria: (1) a minimum duration of 10 min; (2) a total temperature difference of at least 2 °C between temperatures recorded when the female was on and off the nest; (3) a minimum initial absolute slope in the temperature-time plot of 0.1 °C/min (0.4 °C between sequential recordings). We deleted any off-bout recordings that (i) departed from these criteria or (ii) otherwise were aberrant, as we did not collect concurrent observations of the birds and do not know what external factors may have influenced their behavior (see McDonald et al. 2013). We deleted any recordings that appeared to be the result of iButton malfunction. It is conceivable that high temperatures during the early afternoon prevented off-bouts from being detected by the nest temperature loggers which would obscure nest-attendance patterns (Dallmann et al. 2016).

Because iButtons sample temperature instantaneously rather than continuously, off-bout identification and duration measurements are subject to error that is inversely proportional to the sampling rate (Cooper and Mills 2005). We configured the iButtons to record temperatures at 4 min intervals. Therefore, the maximum possible error in a single duration measurement is 8 min. We evaluated the potential measurement error relative to the mean measured off-bout duration (and variation in off-bout duration) to assess the method's precision. Although we cannot be certain that we identified all off-bouts, Dallmann et al. (2016), using simultaneous video and iButton monitoring data demonstrated a high degree of accuracy in identifying incubation off-bouts using this methodology.

Statistical modelling

Eight nests (representing 150 off-bouts) could not be reliably aged, as they were not located until after clutch completion and failed prior to hatching. Because we considered nest age a potentially important factor for females making behavioral decisions regarding incubation, data from those nests were not considered in the modelling analysis (but are included in summary calculations and correlation analysis).

We created (generalized) linear mixed models ((G)LMMs) of off-bout duration and frequency using female ID as a grouping factor in the random-effects structure. This multilevel approach enabled us to consider variables (e.g., mean VOR) that were constant for all observations (off-bouts) at a particular nest as potential covariates

together with those that varied between observations (e.g., wind speed, nest age, and ambient temperature). We tested for correlations between covariates and were prepared to remove variables from further analysis if correlations were found.

We constructed 26 fixed-effects models of off-bout duration and 19 fixed-effects models of off-bout frequency. Each set of competing models (Anderson 2008) included a global model, a null (intercept-only) model, and a series of hypothesis-based models nested within the global model. We included nest age in many of the models because we anticipated that the stage of incubation would have important implications for incubation behavior. We included wind speed, temperature-related variables, and the distance between the nest and the nearest wind turbine because we were interested in accounting for the potential effects of these variables. We constrained the analysis to linear predictors for each individual main effect, as we felt our limited sample size ($n = 30$ nests) would provide insufficient power to detect nonlinear effects (Powell et al. 2017). We did not find any obvious uncaptured trends in the residuals of either the off-bout duration or the off-bout frequency models.

Off-bout duration

We used a Box-Cox log-likelihood profile (Box and Cox 1964) to determine that off-bout durations were approximately log-normally distributed with respect to the independent variables, so we used a Gaussian error distribution and identity link function to model the natural-log-transformed duration. We considered the following covariates in models of log-transformed off-bout duration: year (a categorical variable with two levels); nest age (days since the initiation of incubation); mean VOR; wind speed; ordinal date; the signed difference between the temperature of the nest just prior to off-bout initiation and the ambient temperature (hereafter temperature gradient); and the distances from the nest to the nearest turbine, road, and water source. We also considered the possibility of first-order interactions between nest age and temperature gradient, between wind speed and the distance to the nearest wind turbine, and between ordinal date and the distance to the nearest water source.

Off-bout frequency

We define off-bout frequency as the mean number of off-bouts taken by a female per day during incubation. We modeled off-bout frequency as the log-odds that a Prairie-Chicken initiated an off-bout during a particular 3 h block of time during the recording period (from the date of the first recorded off-bout until the nest hatched or failed). We used a Bernoulli error distribution and a logit link function to model the response. In addition, and using ambient temperature rather than the nest – ambient temperature gradient, we considered precipitation and time of day as potential influences on the log-likelihood of off-bout initiation. We also considered the possibility of first-order interactions between nest age and ambient temperature, between wind speed and distance to the nearest wind turbine, between turbine distance and time block, between wind speed and time block, and between distance to the nearest water source and ordinal date. We found that precipitation, wind speed, and ambient temperature were associated with time block, so these variables (along with their associated interactions) were removed from the global model prior to model-fitting.

To improve model convergence for all analyses, we centered all continuous covariates on their respective means and scaled them by one standard deviation (SD) prior to fitting. We also used sum-to-zero contrasts on categorical predictors having >2 levels (i.e., time block) to simplify the interpretation of parameter estimates as the log-odds of off-bout initiation during a particular time block relative to the log-odds of initiation averaged across all off-bouts.

Table 1. Mean (\pm SD) values of ambient temperature ($^{\circ}$ C) and wind speed (km/h) during four 3 h time blocks during two Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) breeding seasons (May–June, 2013–2014).

Time block	Mean (\pm SD) ambient temperature ($^{\circ}$ C)	Mean (\pm SD) wind speed (km/h)
0130–0429	14.22 \pm 4.44	12.67 \pm 6.82
0730–1029	18.50 \pm 4.41	17.25 \pm 5.94
1330–1629	23.68 \pm 5.36	19.76 \pm 9.29
1930–2229	18.31 \pm 4.38	13.34 \pm 7.84

Note: Ambient temperature and wind speed were recorded at \sim 20 min intervals at Ainsworth Regional Airport (42 $^{\circ}$ 55'N, 99 $^{\circ}$ 82'W), Brown County, Nebraska, USA.

Table 2. Duration and frequency of incubation off-bouts by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) nesting in Brown County, Nebraska, USA.

Nest fate	n	Mean (\pm SD) off-bout duration (min)	Mean (\pm SD) off-bout frequency per day
Successful	22	41.4 \pm 8.7	1.9 \pm 0.3
Failed	8	48.3 \pm 23.5	1.7 \pm 0.4
Depredated	5	36.6 \pm 9.9	1.9 \pm 0.3
Nondepredated	25	44.6 \pm 14.5	1.9 \pm 0.4

Note: Comparison was made between nests that failed and those that successfully hatched one or more chicks, and between nests that failed due to predation and those that succeeded (or failed for other reasons). No differences in either the duration or the frequency of off-bouts was observed (Welch's unequal variances t tests, $P > 0.05$).

Table 3. Center and spread of covariates considered in a mixed-effects modelling analysis of the duration and frequency of incubation off-bouts by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) nesting near Ainsworth, Brown County, Nebraska, USA.

Variable	Mean \pm SD	Minimum	Maximum
Ambient temperature ($^{\circ}$ C)	19.01 \pm 4.89	1.30	31.84
Temperature gradient ($^{\circ}$ C)	9.52 \pm 4.72	-6.70	23.28
Wind speed (km/h)	16.46 \pm 6.15	0	48.68
Distance (m) from nest to nearest			
Trees	579.7 \pm 387.7	104.5	1 601.6
Road	887.9 \pm 639.8	31.0	2 451.6
Open water	1 654.9 \pm 1 290.1	160.8	5 198.3
Wind turbine	10 607.5 \pm 7 220.9	133.2	24 126.7
Visual obstruction reading (dm)	1.2 \pm 0.7	0.3	3.3

Note: Ambient temperature ($^{\circ}$ C) and wind speed (km/h) were recorded every \sim 20 min at Ainsworth Regional Airport (42 $^{\circ}$ 55'N, 99 $^{\circ}$ 82'W); averaged across recordings made just prior to off-bout initiation), and nest temperatures were recorded every 4 min at each of 30 nests using Thermochron[®] iButton[®] temperature loggers. The temperature gradient represents the difference between the nest bowl and the ambient temperatures just prior to off-bout initiation. For bout-specific variables (temperature, wind speed), $n = 930$. For nest-specific variables (distances, visual obstruction reading), $n = 30$.

We used a two-phase procedure similar to that described by Zuur et al. (2009) to select random- and fixed-effects structures for both off-bout duration and frequency model sets. Using a global (maximal) fixed-effects structure, we fit models with different random-effects structures and selected from among them using Akaike's information criterion with a second-order correction for small sample size (AIC_c; Anderson 2008). The different random-effects structures represented our hypotheses regarding how unmeasured variation between Prairie-Chickens may manifest. In constructing candidate random-effects structures, we considered the possibility that this unmeasured variation between individuals may influence an individual's baseline behavior (random intercept), the individual's response to a particular covariate (random slope), or both. This approach allowed us to account for as much interbout variation as possible with fixed effects while

Table 4. Parameter estimates of the top-ranked (ΔAIC_c) linear mixed-effects model of natural-log-transformed off-bout duration by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) incubating nests in Brown County, Nebraska, USA.

Parameter	$\beta \pm SE$	t	P	Variance
Intercept	3.8062 \pm 0.0926	41.085	<0.0001	0.0414
Year	-0.2484 \pm 0.1139	-2.180	0.0346	—
Nest age (days)	-0.0432 \pm 0.0384	-1.126	0.2706	—
Temperature gradient ($^{\circ}C$)	-0.0676 \pm 0.0344	-1.963	0.0640	0.0124
Visual obstruction reading (dm)	0.0787 \pm 0.0514	1.532	0.1335	—
Wind speed (km/h)	-0.0348 \pm 0.0151	-2.307	0.0213	—
Distance (m) from nest to nearest				
Turbine	-0.0011 \pm 0.0585	-0.020	0.9847	—
Road	0.1499 \pm 0.0521	2.876	0.0113	—
Open water	0.0724 \pm 0.0494	1.466	0.1602	—
Ordinal date	-0.0094 \pm 0.0764	-0.123	0.9035	—
Residual	—	—	—	0.1631

Note: Significance values (P) and t statistics (t) are based on Satterthwaite's approximation for denominator degrees of freedom. Temperature gradient is calculated as the difference between the ambient temperature and the temperature in the nest bowl just prior to off-bout initiation. Variance estimates for the global intercept and the effect of temperature gradient represent interindividual random variation in off-bout duration. The model is based on 780 off-bout observations made in 2013 and 2014.

finding the best random-effects structure to account for unmeasured interindividual variation. We then selected fixed-effects structures based on relative AIC_c rankings and using the top-ranked random-effects structure. Because we used our hypotheses to construct our models rather than balanced combinations of covariates, we were prepared to remove uninformative parameters from top-ranking models to improve the predictive value of the model. For inference, we focused on parameter estimates within the selected model whose 85% confidence intervals excluded zero (Arnold 2010).

We compared mean off-bout duration and mean off-bout frequency between successful and failed nests and between depredated and nondepredated nests using Welch's unequal variances t test. Our small sample size of depredated nests may limit the inferences that can be made, but patterns may nonetheless be apparent in the analyses.

We performed all calculations and statistical procedures in R version 3.3.1 (R Foundation for Statistical Computing, Vienna, Austria) using the packages lme4 (Bates et al. 2015) and lmerTest (for P value calculations; Kuznetsova et al. 2016) for functionality associated with mixed-effects modelling. We used the MASS package (Venables and Ripley 2002) to calculate Box-Cox log-likelihood profiles.

Results

We recorded 930 incubation off-bouts by 25 female Prairie-Chickens attending 30 nests. Four females were observed in both years of the study. Female Prairie-Chickens took 1.95 ± 0.67 off-bouts/day (mean \pm SD; range: 1–4 off-bouts/day) during incubation. Off-bouts lasted 43.3 ± 24.1 min (mean \pm SD; range: 10.1–311.3 min). Both mean and SD of off-bout duration were large compared with the maximum potential error in off-bout measurement (8 min). A majority (61.8%) of off-bouts occurred between 0730 and 1029 Central Daylight Time (CDT) ($n = 309$) and between 1930 and 2229 CDT ($n = 266$), when both mean ambient temperature and mean wind speed were relatively moderate compared with the highs around midday ($n = 38$) and the lows just after midnight ($n = 10$) (Table 1).

Neither the mean off-bout duration (Welch's $t_{[7,7]} = 0.8132$, $P = 0.4405$) nor the mean off-bout frequency ($t_{[11,1]} = -1.6842$, $P = 0.1201$) differed between successful and unsuccessful nests (Table 2). Mean off-bout duration ($t_{[7,9]} = 1.4970$, $P = 0.1730$) and off-bout frequency ($t_{[7,9]} =$

-0.0195 , $P = 0.9849$) did not differ between depredated nests and nests that were successful or that failed due to other causes (Table 2).

None of the continuous covariates was strongly correlated with any others (all Spearman's $|\rho| < 0.5$). The time block during which an off-bout was initiated was associated with ambient temperature ($\chi^2_{[7]} = 1454.372$, $P < 0.001$), wind speed ($\chi^2_{[7]} = 420.234$, $P < 0.001$), and precipitation ($\chi^2_{[7]} = 48.895$, $P < 0.001$). To avoid the potentially confounding effects of multicollinearity in the model matrix and because we were particularly interested in temporal effects, we eliminated the latter three covariates from consideration in the off-bout frequency model. Summaries of nest-specific and bout-specific covariates are presented in Table 3.

Off-bout duration

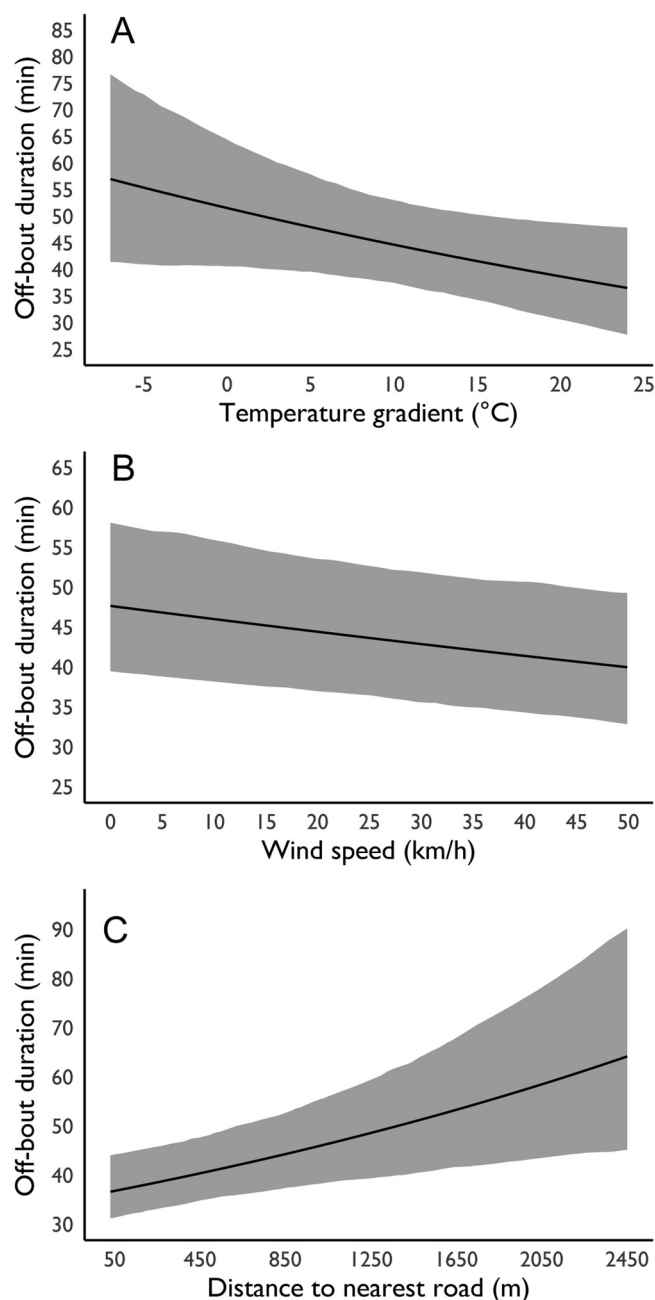
The top-ranked random-effects structure for off-bout duration bore 66.9% of the weight of evidence and included both a random intercept and an uncorrelated random slope of the effect of the temperature gradient on the duration of incubation off-bouts (Supplementary Tables S1 and S2)¹. The top-ranked model for off-bout duration, using the selected structure for random effects, had a fixed-effects structure that predicted negative effects of temperature gradient and wind speed, and positive effects of VOR and the distance from the nest to the nearest road, on log-transformed off-bout duration (Table 4; Supplementary Table S2¹). The model predicted a mean (\pm SE) off-bout duration of 45.0 ± 1.1 min by female Prairie-Chickens nesting at mean nest and environmental conditions (see Table 3). Off-bout duration is predicted to decrease by $\sim 7\%$ for every additional $5^{\circ}C$ increase in temperature gradient (decrease in ambient temperature; Fig. 2A) and by $\sim 3\%$ for every 10 km/h increase in wind speed (Fig. 2B). The off-bout duration is predicted to increase by $\sim 3\%$ for every additional 100 m between the nest and the nearest road (Fig. 2C) and by $\sim 2\%$ for each 2.5 cm added to the mean VOR at the nest. The top-ranked model also predicted random variation among females with respect to the effect of temperature gradient on off-bout duration (Table 4). No other models were competitive (all $\Delta AIC_c > 2$).

Off-bout frequency

The best random-effects structure for explaining off-bout frequency bore 42.5% of the weight of evidence and included a ran-

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0130>.

Fig. 2. Predicted duration of incubation off-bouts ($\pm 95\%$ confidence intervals) by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) with respect to (A) the nest – ambient temperature gradient ($^{\circ}\text{C}$) at the time of off-bout initiation, (B) wind speed (km/h) at the time of off-bout initiation, and (C) the distance (m) from the nest to the nearest public road. Predictions for each variable are made assuming all other variables are held constant at their respective mean observed values. Confidence intervals are bootstrapped using 1000 simulations.



dom slope of the effect of time block on the log-likelihood of off-bout initiation, as well as a correlated random intercept (Supplementary Table S3).¹ The best fixed-effects structure for explaining the log-likelihood of off-bout initiation, hence frequency, included terms for nest age, ordinal date, and time block (Supplementary Table S4).¹ No other models in the candidate set were competitive (all $\Delta\text{AIC}_c > 2$). Females were most likely to leave the nest between 0730 and 1029 CDT ($n = 309$, probability of departure = 94%) and between 1930 and 2229 CDT ($n = 266$, probability of

Table 5. Parameter estimates of the top-ranked (ΔAIC_c) logistic mixed-effects model of the log-odds of off-bout initiation by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) incubating nests in Brown County, Nebraska, USA.

Parameter	$\beta \pm \text{SE}$	z	P	Variance
Intercept	-1.9328 ± 0.1392	-13.884	<0.0001	0.0836
Nest age (days)	0.0672 ± 0.0630	1.066	0.2863	—
Ordinal date (days)	-0.1746 ± 0.0732	-2.385	0.0171	—
Time-block contrasts	—	—	—	—
0130–0429	-2.7183 ± 0.6688	-4.064	<0.0001	1.1521
0430–0729	-0.3382 ± 0.3967	-0.853	0.3939	1.5311
0730–1029	2.8034 ± 0.2904	9.653	<0.0001	1.0121
1030–1329	-0.8733 ± 0.3012	-2.899	0.0037	0.5271
1330–1629	-0.4323 ± 0.2296	-1.883	0.0597	0.2019
1630–1929	1.5902 ± 0.2821	5.636	<0.0001	0.9893
1930–2229	2.3487 ± 0.2341	10.032	<0.0001	0.5540

Note: The contrast effects of each 3 h time block reflect the marginal change in the outcome compared with the reference block (2230–0129), reflected in the global intercept. Variance estimates for the intercept and time-block contrasts represent interindividual random variation in the log-likelihood of off-bout initiation. The model is based on 780 off-bout observations made in 2013 and 2014.

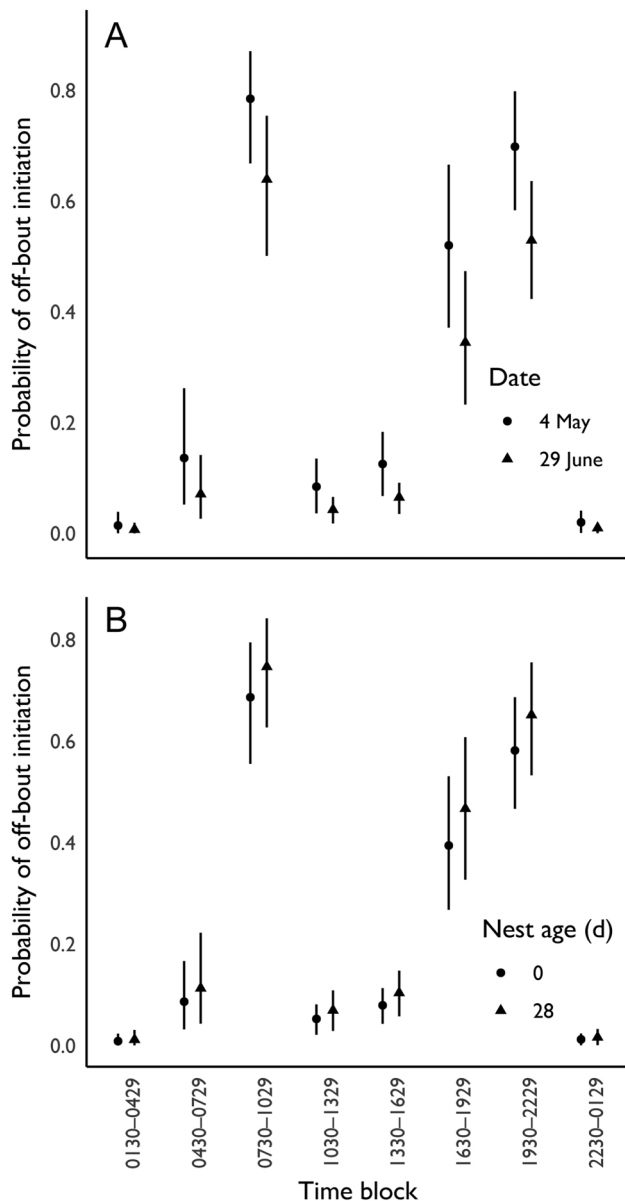
departure = 91%) and were least likely to leave between 0130 and 0430 CDT ($n = 10$, probability of departure = 6%; Table 5). The predicted effects of nest age and ordinal date suggest that the odds of off-bout initiation increase by $\sim 36\%$ over the course of incubation, but decrease by $\sim 54\%$ across the nesting season (Fig. 3). This may be explained by considering that the likelihood that females initiate off-bouts during a particular 3 h time block may decline during the course of the breeding season, whereas individual females experience increases in the odds of off-bout initiation throughout their own incubation periods.

After comparing the predictive power of highly ranked models in the candidate set, we fitted an additional fixed-effects model of off-bout duration. From the top-ranked model, we removed three variables that either appeared to be uninformative (on uninformative parameters see Arnold 2010) or that were predicted to have negligible effects on the response (e.g., ordinal date and distance to the nearest wind turbine). The revised model offers a substantial improvement over previous models in its ability to describe the data ($\Delta\text{AIC}_c = -14.281$ (relative to the top-ranked model); Supplementary Table S2¹). The effects predicted by this exploratory model are qualitatively similar to those of the top-ranked model in the original model set (Table 6) and support the conclusion that both time (nest age) and environmental factors (nest – ambient temperature gradient and wind speed) influence the duration of incubation off-bouts by female Prairie-Chickens.

Discussion

Our results indicate that incubation behavior in female Prairie-Chickens is directed by the temporal and environmental factors of time of day, wind speed, ambient temperature, vegetation density, and proximity to roads. Incubating females made decisions about when to leave their nests principally based on time of day and adjusted the duration of incubation off-bouts based on other variables. We observed a pattern of incubation behavior (few off-bouts of long duration, typically occurring once each in the early to mid-morning and the evening) that was highly consistent among females, similar to patterns observed by others for Prairie-Chickens and other grouse species (Bowen and Simon 1990; Wiebe and Martin 1997; Coates and Delehanty 2008; Winder et al. 2016). Our results indicate that off-bout duration decreases as the difference in temperature between nest and ambient conditions increases; Coates and Delehanty (2008) reported similar observations for Greater Sage-Grouse. Our results also indicate that off-bout duration decreases with higher wind speeds, reduced veg-

Fig. 3. Predicted probability of off-bout initiation ($\pm 95\%$ confidence intervals) by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) during each of eight 3 h time blocks. Model-based predictions are made for (A) nests in the middle of their respective incubation periods (nest age = 14 days) early and late in the nesting season and (B) nests at the start and end of their respective incubation periods in the middle of the nesting season (1 June). Confidence intervals are bootstrapped using 1000 simulations.



etation density in the vicinity of the nest bowl, and closer proximity to roads.

Ambient temperature and nest predation have been suggested as the primary influences on the evolution of incubation patterns (Conway and Martin 2000). If adult activity at the nest attracts nest predators (as it appears to do in grouse (Bowen and Simon 1990; Wiebe and Martin 1997) and passerines (Martin et al. 2000a, 2000b)), then birds subject to high rates of nest predation are expected to exhibit infrequent, long-duration incubation on- and off-bouts (Conway and Martin 2000). Grouse in general experience high rates of nest predation (Ricklefs 1969; Hagen and Giesen 2005; Pitman et al. 2005; Coates et al. 2008; Johnson et al. 2011; Webb et al. 2012; Matthews et al. 2013; Burr et al. 2017); only

one-third of the nests observed during this study were successful (Harrison 2015) and two-thirds of all nest failures were attributed to predation (J.O. Harrison, J.A. Smith, M. Bomberger Brown, and L.A. Powell, unpublished data). Thus, it is expected that Prairie-Chickens should make the infrequent, long-duration on- and off-bouts that we observed in this study and that has been reported elsewhere (Bowen and Simon 1990; Coates and Delehanty 2008; Winder et al. 2016).

Winder et al. (2016) suggest that the bimodal (dawn and dusk) incidence of incubation off-bouts in Prairie Grouse is inconsistent with the hypothesis that nest predation drives incubation patterns. Because predators of grouse nests are frequently crepuscular mammalian mesocarnivores (Bowen and Simon 1990; Coates et al. 2008; Winder et al. 2016), adult departure or arrival at the nest during periods of peak predator activity (dawn and dusk) could alert predators to the presence of the nest (Wiebe and Martin 1997). Winder et al. (2016) argue that if nest predation is the driving force behind incubation patterns in grouse, then incubating birds should leave the nest once per day at around midday to avoid periods of high predator activity; but see Coates and Delehanty (2008) regarding the avian predation of Greater Sage-Grouse. Instead, Winder et al. (2016) suggest that adult physiological requirements determine the timing of incubation off-bouts by constraining the length of time which the female can continuously remain on the nest without foraging. For White-tailed Ptarmigan, Wiebe and Martin (1997) suggested that the interval between incubation off-bouts is determined by the amount of food that can be stored in the crop.

We are not able to provide a test of whether predation or adult physiology drives nest-attendance patterns in Prairie-Chickens using our data. Nevertheless, as our observations are consistent with the model proposed by Conway and Martin (2000) and the hypothesis offered by Winder et al. (2016), we posit that both nest predation and adult physiological requirements are important influences on Prairie-Chicken incubation behavior. The broad nest-attendance pattern (i.e., long duration, infrequent on- and off-bouts) may be due to predation pressure, and adult physiology may constrain the timing and frequency of off-bouts as suggested by Wiebe and Martin (1997) and Coates and Delehanty (2008). Females may optimize their energy expenditures by leaving their nests at dawn and dusk when conditions are moderate, rather than at midday and midnight when they are more extreme; nearly all of the off-bouts that we observed were taken during morning and evening when conditions were comparable. Females may optimize embryo development by leaving the nest at these times so the eggs will not be overheated or chilled (Coates and Delehanty 2008; see Clark and Wilson 1985; Naylor et al. 1988). Our data support the hypothesis that vegetation cover and proximity to roads may influence females' incubation behavior. Vegetation cover type and density (Carroll et al. 2015; Harrison 2015; Grisham et al. 2016; Harrison et al. 2017) and distance to roads (Harrison 2015; Harrison et al. 2017) are important elements of female grouse nest-site selection preferences, with both variables having implications for nest success and juvenile and adult mortality. Greater vegetation density surrounding the nest bowl may provide thermally favorable microclimates by shading or insulating the eggs, protecting them from temperature fluctuations, thus allowing the female to take longer off-bouts (Hansell and Deeming 2002; Carroll et al. 2015; Grisham et al. 2016). However, vegetation surrounding the nest may also serve to obscure the nest from predators allowing the female to take longer off-bouts or remain on the nest for longer on-bouts, as in Greater Sage-Grouse (Martin 1995; Coates and Delehanty 2008). Roads are known to serve as pathways for predators (Latham et al. 2011; Červinka et al. 2013), so females with nests located nearer to roads may take shorter off-bouts to reduce the visibility of their nests to predators or to be present at the nest to attempt to deter predators. Nests subjected to other sorts of anthropogenic disturbance may experience greater risk of predation

Table 6. Parameter estimates of a linear mixed-effects model of natural-log-transformed off-bout duration by Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) incubating nests in Brown County, Nebraska, USA.

Parameter	$\beta \pm SE$	<i>t</i>	<i>P</i>	Variance
Intercept	3.7466±0.0657	57.000	<0.0001	0.0306
Year	-0.1548±0.0697	-2.222	0.0294	—
Nest age (days)	-0.0448±0.0166	-2.691	0.0073	—
Temperature gradient (°C)	-0.0703±0.0336	-2.093	0.0500	0.0118
Wind speed (km/h)	-0.0322±0.0151	-2.136	0.0330	—
Distance (m) from nest to nearest				
Road	0.1376±0.0446	3.083	0.0068	—
Open water	0.0534±0.0413	1.295	0.2088	—
Residual	—	—	—	0.1643

Note: Significance values (*P*) and *t* statistics (*t*) are based on Satterthwaite's approximation for denominator degrees of freedom. Temperature gradient is calculated as the difference between the ambient temperature and the temperature in the nest bowl just prior to off-bout initiation. Variance estimates for the global intercept and the effect of temperature gradient represent interindividual random variation in off-bout duration. The model is based on 780 off-bout observations made in 2013 and 2014.

or desertion by the attending female (Götmark 1992) and the female may modify her off-bout pattern to accommodate these threats.

We observed apparently conflicting effects of nest age and ordinal date on the likelihood of off-bout initiation, yet these two measures appear to represent the same phenomenon (date), although they are not correlated (Spearman's $\rho = 0.427$). We interpret this result to indicate that Prairie-Chicken nest attentiveness increases generally throughout the nesting season, but that individual females become more flexible in their attentiveness as their own incubation period progresses. The former trend possibly serves to counteract seasonal increases in ambient temperature. The nest-age effect seems somewhat counterintuitive, as eggs should gain fitness value for the incubating parent and become less tolerant of temperature fluctuations as incubation progresses, requiring increased female attentiveness and fewer incubation off-bouts; however, we observed the opposite response. One possible explanation for the observed increase in off-bout initiation later in the nesting cycle is that females experience a decline in body condition throughout the incubation period, requiring them to leave the nest more frequently to forage (Wiebe and Martin 1997; Coates and Delehanty 2008). Comparison of a captive female Spruce Grouse (*Falcapennis canadensis* (Linnaeus, 1758)) fed a high-quality diet ad libitum with a free-living, individual showed the captive bird spent proportionately more time incubating than did the free-living bird who interrupted incubation more frequently and for longer periods of time to forage (Pendergast and Boag 1971; McCourt et al 1973). White-tailed Ptarmigan nesting in the area of Mt. Evans, Colorado, USA, experienced an 11% decline in body mass, indicating reduced body condition, during incubation which was associated with an increase in the number of off-bouts taken per day (Wiebe and Martin 1997). Winder et al. (2016) did not observe an effect of either ordinal date or nest age on the number of off-bouts taken each day.

Overall, our results corroborate the notion of a highly conserved general pattern of incubation rhythmicity among gallinaceous birds and demonstrates that female Prairie-Chickens make adjustments to the timing and duration of incubation off-bouts in response to local environmental cues.

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