ORIGINAL ARTICLE

Incubation behaviour of a boreal, food-caching passerine nesting in sub-zero temperatures

Joseph B. Burant[1,*], Roxan Chicalo[2], Emily J. Williams[3,4], Laura Phillips[3,5], Matthew Fuirst[2,6], D. Ryan Norris[2,*]

[1] Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen, Netherlands

[2] Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

[3] Denali National Park and Preserve, Alaska, USA

[4] Department of Biology, Georgetown University, Washington, D.C., USA

[5] Townsend, Georgia, USA

[6] Birds Canada, Port Rowan, Ontario, Canada

[*] Corresponding authors: (J.B.B.) j.burant@nioo.knaw.nl, (D.R.N.) rnorris@uoguelph.ca

RUNNING HEAD: Balancing the number and duration of off-bouts during incubation

ACKNOWLEDGEMENTS

We thank R. Galvan, N. Hunt, T. Grigsby, K. Swift, C. Peterson, S. Robeson, C. Callo-Simonnet, W. Korecki for assisting with data collection and A. Newman, A. McAdam, and D. Strickland for providing valuable comments on earlier drafts of the manuscript.

Funding statement: Funding was provided through U.S. National Park Service and Denali National Park & Preserve (L.P., E.J.W.), a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (D.R.N.), ECO Canada (D.R.N.), an Ontario Graduate Scholarship (R.C.), and a University of Guelph Graduate Tuition Scholarship (R.C.).

Ethics statement: Canada Jays were ringed under permit from the US Geological Survey (no. 24141) and research permits from the Alaska Department of Fish and Game (no. 19-138) and Denali National Park & Preserve (DENA-2017-SCI-0004). All animal use was in compliance with the Animal Care Committee at the University of Guelph (animal use protocol no. 4003) and the National Park Service (protocol no. AKR DENA Williams Corvids 2018.A3).

Author contributions: R.C., D.R.N., and L.P. contributed to the idea and research design. R.C., E.J.W., L.P., and D.R.N. developed the field methods and collected the data. R.C., J.B.B., M.F. analysed the data. R.C. and D.R.N wrote the first draft. J.B.B. and D.R.N. led subsequent drafts and revisions. J.B.B. developed the statistical analyses as presented in the manuscript. D.R.N., L.P., and E.J.W. contributed materials, resources, and funding. All authors reviewed the manuscript prior to initial submission for publication.

Data availability: Analyses reported in this article can be reproduced using data and code provided on Figshare: https://doi.org/10.6084/m9.figshare.21377955 (Burant et al. 2025).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests, financial or otherwise.

ABSTRACT

Our understanding of avian incubation behaviour is primarily derived from species that nest in the temperate conditions of spring and summer. This leaves uncertainties about strategies employed by a relatively small number of species adapted to breed under sub-zero, winter-like conditions. We used in-nest temperature loggers (iButtons) to monitor incubation behaviours of Canada Jays (*Perisoreus canadensis*), cache-reliant, year-round residents of boreal and sub-alpine environments that breed in late winter/early spring and have female-only incubation. On average, females had high levels of mean daytime nest attentiveness (92 ± 2% of daytime spent on the nest; ± SD), taking an average of only 5.5 (± 0.6) off-bouts per day with a mean duration of 13.3 (± 1.4) minutes per bout. Variation in nest attentiveness was primarily driven by off-bout duration, suggesting that the number of off-bouts per day may be limited to reduce activity around the nest and avoid attracting nest predators. In contrast to expectations, weather conditions (mean daily temperature and total daily rainfall) were not associated with variation in either the number or duration of off-bouts. Our results provide indirect evidence that incubation strategies of Canada Jays are likely not shaped by within-year variation in prevailing weather conditions but instead by predation threat and availability of cached food, the latter of which reduces foraging opportunity costs by allowing females to reliably acquire sufficient food during the few times they leave the nest each day.

KEYWORDS

Incubation, nest attentiveness, off-bout duration, *Perisoreus canadensis*, winter breeding

INTRODUCTION

Feeding young in the nest has traditionally been considered the most energetically costly period of reproduction in birds (Lack 1948; King 1972), but more recent evidence also highlights the considerable energetic investment required during incubation (Visser & Lessells 2001; Thomson et al. 2007), stemming from the thermal demands of embryonic development (Webb 1987; Turner 1994). The energetic demands of incubation can have downstream fitness consequences for both adults and offspring. For example, compared to controls, adult passerines and waterfowl with experimentally enlarged clutches have higher energetic costs during nocturnal incubation (de Heij et al. 2007), reduced future fecundity (Hanssen et al. 2005), and lower survival (Visser & Lessells 2001). Eggs incubated at sub-optimal temperatures have reduced growth efficiency (Olson et al. 2006) and lower hatching success (MacDonald et al. 2014), while nestlings hatched from eggs incubated at low temperatures tend to have lower than average body condition (Eiby & Booth 2009; Ardia et al. 2010) and slower growth rates (Ospina et al. 2018), which reduce the likelihood of subsequent recruitment (Hepp & Kennamer 2012). There may also be opportunity costs to incubation, such that time spent incubating reduces the amount of time available for foraging and self-maintenance. Because most species nest during the spring and summer, nearly all our understanding about the ecology and physiology of incubation behaviour comes from relatively warm periods of the annual cycle (but see MacDonald et al. 2014). Despite this, there are species that nest under sub-zero, winter-like conditions (Rousseu & Drolet 2017) and gaining insight into how these species modulate their incubation behaviour could shed light on the strategies used to successfully reproduce under what are presumably more adverse environmental conditions.

Nest attentiveness, defined here as the proportion of time spent on the nest over the total active time (i.e. for diurnal species, the proportion of daylight hours), is a common metric used to study incubation behaviour (Weathers & Sullivan 1989). A more in-depth understanding might be gained by analyzing the two components that constitute nest attentiveness: the number of times an incubator leaves the nest (hereafter, 'number of off-bouts') and the length of time an incubator spends off the nest during an off-bout (hereafter, 'off-bout duration'; Coe et al. 2015). Because nest attentiveness is a product of these two behaviours, which are likely to be negatively correlated with each other, similar levels of nest attentiveness can be achieved with different combinations of off-bout number and off-bout duration and there are likely specific ecological mechanisms that influence the optimal combination in any particular circumstance. For example, in colder climates, shorter, more frequent off-bouts may be advantageous given the risk of eggs freezing when left unattended and the energetic costs of re-warming them (hereafter, the 'egg cooling hypothesis'; Biebach 1986). Conversely, a strategy of longer, less frequent off-bouts, which would reduce the total activity around the nest, could be adopted to mitigate high risk of nest predation, as has been observed in multiple corvid species (hereafter, the 'predation avoidance hypothesis'; Conway & Martin 2000a).

The number and duration of off-bouts can be modulated by abiotic factors such as ambient temperature (Conway & Martin 2000b), rainfall (Coe et al. 2015), and their interaction (Coe et al. 2015). Under most circumstances, increasing ambient temperature negatively influences energetic costs of incubation (Nord & Williams 2015) and rates of egg cooling when the nest is unattended (Coe et al. 2015). The number of off-bouts, therefore, may increase when ambient temperatures are low, yet off-bout duration may be reduced because of faster rates of egg cooling. Females may spend more time on the nest when it rains (Cresswell et al. 2003) to protect nests and eggs from becoming sodden and cold (Marasco & Spencer 2015). High intensity rainfall can even supress the effects of ambient temperature on the number of off-bouts, such that females take fewer off-bouts than they otherwise might under dry conditions at the same temperature (Coe et al. 2015).

Other biotic and intrinsic factors can also influence the number and duration of off-bouts, including predation risk (Conway & Martin 2000a), mate-feeding rates (Matysioková & Remeš 2014), food availability (Vafidis et al. 2018), and developmental stages like day of incubation (i.e., day relative to the start of an individual's incubation period; Aldrich et al. 1983). Intrinsic factors such as adult body condition prior to laying (Wiebe & Martin 1997) and breeding experience (Zuberogoitia et al. 2018), which are correlated in our study species (Sechley et al. 2014), also modulate incubation behaviour. Interestingly, biotic and intrinsic effects may become more apparent when weather conditions are unfavourable (Marasco & Spencer 2015), highlighting the importance of including multiple, potentially interactive effects in models to predict variation in incubation behaviours.

To address the causes of variation in incubation behaviour in a species that nests in below-freezing temperatures, we collected incubation data from a population of Canada Jays (*Perisoreus canadensis*) in Denali National Park and Preserve (hereafter, 'Denali NPP'), Alaska, USA. Canada Jays are year-round residents of North American boreal and subalpine forests that cache a wide variety of perishable food items, such as vertebrate flesh, invertebrates, berries, and fungi, during late summer and autumn, which they subsequently rely on for survival over winter and into the breeding season (March to May) when fresh food may not be readily available (Swift et al. 2022). Canada Jays form persistent, socially and genetically monogamous pair bonds (Strickland & Ouellet 2020; Fuirst et al. 2021). As the sole incubators and despite some food provisioning by male when on-nest, females primarily acquire food during incubation through retrieval of cached food while off-nest (Strickland & Ouellet 2020). Incubating females in an eastern population of Canada Jays only leave the nest 3 – 4 times per day (Ontario; Strickland & Ouellet 2020) and males provision incubating females, on average, only once per day (Strickland & Waite 2001).

We first investigated which component of incubation behaviour —the number of off-bouts or duration of off-bouts— best explains variation in nest attentiveness within and among incubating Canada Jays. Following the egg cooling hypothesis, we predicted that the number of off-bouts, rather than off-bout duration, would be the primary factor influencing variation in nest attentiveness because the latter (duration) would be more constrained by embryonic development. Following the predation avoidance hypothesis, we predicted that off-bout duration, not the number of off-bouts, would be the primary factor influencing nest attentiveness because the number of times females leave the nest during the day would be limited by a desire to avoid attracting would-be nest predators (e.g. American Red Squirrel *Tamiasciurus hudsonicus,* Common Raven *Corvus corax*, Black-billed Magpie *Pica hudsonia*, Northern Hawk-owl *Surnia ulula*, Northern Goshawk *Accipiter gentilis*; Strickland & Waite 2001; Strickland & Ouellet 2020).We then examined the extent to which incubating female Canada Jays responded to prevailing weather conditions by taking advantage of natural variation over the course of the incubation period of a single female and that, because nest initiation was asynchronous, females tended to experience different weather conditions over their respective incubation periods. In doing so, we examined hypotheses related to how temperature, rainfall, and their interaction, as well as day of incubation influenced the number of off-bouts and off-bout duration (Table 1).

MATERIALS & METHODS

General Field Methods

We conducted fieldwork in Denali NPP, Alaska, USA (63.129887°N, 151.197418°W) during the 2018 and 2019 (pre-)breeding seasons (Feb – May) and periodically during the 2017 and 2018 non-breeding periods (Jun – Nov). The study site encompassed a 6.4 km stretch of the Denali park road (mile 0 – mile 4), extending 1 – 2 km into the forest on either side (Figure 1). The elevation within the study site ranged approx. 480 – 680 m above sea level. The forest consisted primarily of white spruce (*Picea glauca*), black spruce (*Picea mariana*), and quaking aspen (*Populus tremuloides*), with occasional open bogs. Within the study area, we monitored individuals breeding on 28 territories in 2018 and 33 territories in 2019. We captured adults during either the non-breeding period or pre-breeding period (late Feb) using either a Potter trap (Third Wheel Ringing Supplies, Devon, UK) or a mist net (Avinet Research Supplies, Portland, Maine, USA) baited with white bread. Upon capture, we fitted each adult with a unique combination of three plastic colour leg bands and a standard U.S. Geological Survey (USGS) aluminum leg band and collected the following morphometrics: mass (g), tarsus length (mm), wing length (mm), tail length (mm), and bill length (mm).

Canada Jays in Denali NPP lay their eggs in mid- to late-March (clutch size range: 2 – 5 eggs, mode: 3 eggs) and, unlike most other passerines that begin incubation upon laying the ultimate or penultimate egg, female Canada Jays begin sitting on the nest after the first egg is laid. However, during the laying stage, it is unlikely that females maintain egg temperatures that induce embryonic development since all eggs hatch on the same day (Strickland & Ouellet 2020). In Denali NPP, the nestling period typically lasts for 23 d prior to fledging, with eggs hatching in mid- to late-April.

We located nests during the breeding season by providing jays with nesting material such as cotton or feathers and following them when they flew to the nest with these materials (Derbyshire et al. 2015). We visited nests every 3 d until nest construction was complete and then every other day until the clutch was initiated (i.e., lay date is the first observation of a sitting female; Strickland & Ouellet 2020). On days 2 – 5 of incubation of the full clutch (5 – 7 d after clutch initiation assuming a clutch of 3 – 5 eggs), we used a ladder to access nests, count eggs and insert an iButton (Maxim Integrated, San Jose, CA, USA) temperature logger (see *Incubation Behaviour*). During the incubation stage, we visited nests less frequently (approx. every 5 d) because iButtons provided precise data on nest activity. On days 18 – 19 of true incubation (i.e., 20 – 21 d following first instance of sitting), we checked nests using a telescoping mirror and, if eggs showed signs of hatching, we accessed the nest to remove the iButton and count the number of hatched young (see *Incubation Behaviour*).

Capture and handling of Canada Jays was conducted under a USGS banding permit (no. 24141) and research permits with the Alaska Department of Fish and Game (no. 19-138) and Denali NPP (DENA-2017-SCI-0004). All animal use protocols, including nest monitoring, were reviewed by and complied with the Animal Care Committee at the University of <REDACTED> (protocol no. 4003) and the National Park Service (protocol no. <REDACTED>).

Incubation Behaviour

Following previous studies (Hartman & Oring 2006; Dallmann et al. 2016), to determine when a female was incubating eggs (termed ‘on-bout’) versus when a female was away from the nest (‘off-bout’), we deployed iButtons —small, dime-sized temperature loggers (17 mm in diameter, 6 mm thick)— into nests during the incubation period. To minimize risk of abandonment due to disturbance during the laying period (Smith et al. 2015), we deployed iButtons so they logged temperatures for 13 – 16 days of the 18 – 19 d incubation period. We secured iButtons to the nest lining as close to the eggs as possible without running the risk of damaging them (approx. 10 – 20 mm from the eggs). To keep iButtons in place, they were either wrapped in parafilm and glued to velcro or had the circumference wrapped in electrical tape, which was then fixed (using velcro or electrical tape) to a small shirt button with a thin wire threaded through the wall of the nest (Smith et al. 2015). In 2018, in an effort to minimize disturbance at the nest, we used parafilm and velcro to attach the iButtons to the shirt button/wire combo so that iButtons could be easily extracted upon retrieval, which was planned to occur while accessing nests to band and measure nestlings on day 13. Unfortunately, half of the nesting pairs (n = 8) removed the iButtons, likely when they were increasing space in the nest cup for growing nestlings (Strickland & Ouellet 2020). In 2019, we instead collected iButtons at the end of the incubation period (days 18 – 19 of the incubation period) and increased attachment security by using electrical tape instead of velcro and parafilm, resulting in no loss. To ensure we were only measuring incubation behaviour, we removed 1 – 2 d of recordings on occasions when iButtons were collected on and soon after hatch day and excluded recordings from the day of deployment or retrieval if collected before hatch day. Since Canada Jays have previously been observed leaving the nest for 4 – 12 min. every 3 – 4 h (Strickland & Ouellet 2020), we used a 4-min. temperature recording interval to capture off-bouts.

In addition to the iButtons placed in the nest, we collected local ambient temperatures (every 4 min.) by fastening three iButtons to the shaded side of three different tree trunks (Hartman & Oring 2006; Dallmann et al. 2016). The locations of ambient iButtons were determined by stratifying the study site into three sub-sections: eastern, middle, and western. We chose this configuration because the low-to-high elevation gradient ran west-to-east and we wanted to assess differences, if any, in ambient temperatures caused by elevation gradients between subsections of our study area.

We analyzed nest temperature profiles using *incR* (Capilla-Lasheras 2018), an R package that automatically provides daily nest attentiveness proportions, number of off-bouts, and off-bout duration. In *incR*, a score of 1 is given in cases when nest temperatures are consistently warmer than ambient temperatures (i.e., on-bout) and a score of 0 indicates a significant drop in nest temperature (i.e., off-bout), as determined by a threshold temperature set by the user (e.g., nest temperature must drop by ≥ 1.5°C to warrant a score of 0). Then, *incR* produces daily values for nest attentiveness (i.e., the number of ones divided by the total number of ones and zeroes), number of off-bouts (i.e., the number of times a zero or a group of zeroes occurs over a fixed period), and off-bout duration (i.e., average number of consecutive zeroes per group multiplied by the 4-min. sampling interval).

We found that *incR* did not always score off- and on-bouts accurately, likely because the universal threshold temperature applied to all nests was not always useful given variation in nest temperature profiles (see Figure 2a for an example plot of iButton-derived nest temperatures over a 24-h period). Variation among nest temperature profiles was likely caused by differences in nest microclimate (not captured by the three ambient iButtons) and structure, as well as variation in iButton placement between nests. While *incR* expedited the process of plotting temperature profiles and automated the creation of datasets from which incubation metrics were derived (i.e., nest attentiveness, number of off-bouts, and off-bout durations), we still visually scrutinized all temperature profiles to confirm off- and on-bout assignments and subsequently adjusted the values generated automatically by *incR*. When doing this, we applied the following criteria for off-bouts: (a) any drop of ≥ 1.5°C between 4-min. intervals was scored as an off-bout if followed by a ≥ 1°C increase in temperature (indicating the female returned), (b) a recording with a slight temperature drop (< 1.5°C) was scored as an off bout if it preceded a significant temperature increase (> 1.5°C). Criterion (a) corrected for gradual night-time cooling (i.e., a decrease of approx. 0.5 – 1.5°C every 4 min. until nest temperature stabilized around 10 – 15°C above ambient temperature) that was originally scored as an off-bout by *incR* and criterion (b) added 4-min. to an off-bout to capture the time when females left nests between two temperature recordings. An example of criterion (b) is an off-bout where nest temperature was decreasing at a rate of 3°C per 4-min. interval and later within the last interval, the female returned to the nest and began re-warming yet did not warm the nest enough to log a higher temperature than the previous recording. Therefore, the temperature profile displayed a temperature drop < 1.5°C, which would originally have been scored as an 'on-bout' by *incR,* while in reality the female was likely off the nest for the majority of that 4-min. interval.

Weather Data

We obtained daily values for total rainfall (mm) from a climate station at Denali NPP Visitor Centre (63.732222°N, 148.905556°W) located within the study area (Figure 1). We selected daily (sunrise to sunset; adjusted each day to account for day length) weather data corresponding to dates for which we had incubation data; 29 Mar – 9 May for 2018 and 23 Mar – 2 May for 2019. We opted to use daily mean ambient temperatures averaged from three iButtons deployed near jay nests (see *Incubation Behaviour* for programming and placement details) to maintain consistent temperature recordings. Snowfall data were not available from this or nearby weather stations so 'precipitation' (the combination of rain and snowfall) was not included in models.

Snow depth (cm), however, was available and was used to describe weather differences between years (Table 2).

Statistical Analyses

To examine the relationship between the number of off-bouts and average off-bout duration, we conducted two Pearson's correlation tests: one for the daily values (i.e., the number and average duration of off-bouts per day; n = 391 incubation days) and second using the mean values from each nest (i.e., the mean number and mean duration of off-bouts per nest across the entire incubation period; n = 29 nests). These were one-tailed tests because we had hypothesized *a priori* that the number and duration of off-bouts would be negatively correlated.

To examine which incubation behaviour had the strongest influence on variation in daily values of nest attentiveness, we compared two Bayesian generalized linear mixed effect models (GLMMs; Bolker et al. 2009; Fong et al. 2010) for nest attentiveness (Beta distribution), one with daily number of off-bouts as the fixed effect and the second with daily mean duration off-bouts as the fixed effect. These two separate models were generated because the number and duration of off-bouts were moderately correlated (Supplementary Online Material, Figures S1 and S2). In both models, we included a nested random intercept of nest ID within female ID since we had multiple incubation days per nest and, for a few individuals (n = 4 females with 2 nests, 1 female with 3 nests), multiple nests either within or between years (n = 12 – 15 d from one nest for 18 unique females; 24 – 30 d over two or three nests for 5 unique females). We compared these two models for the difference in their expected predictive accuracy based on the expected log pointwise predictive density (ELPD) values, estimated using leave-one-out (LOO) cross-validation in the *loo* R package (Vehtari et al. 2023). In the model comparison, a positive difference in ELPD values between model 1 and model 2 indicates higher expected predictive accuracy for model 2; negative difference indicates model 1 is preferred (Vehtari et al. 2017). In general, a ΔELPD of ≤ 4 indicates a negligible difference in the predictive capacity of the compared models, while ΔELPD > 4 with small standard errors (i.e., error smaller than the point estimate) point to differences in predictive value (Sivula et al. 2020).

To investigate whether ambient temperature and rainfall explained variation in the number or duration of off-bouts, we constructed two Bayesian GLMMs: one for each of the response variables. We attempted to model these in a bi-variate response model (Hadfield et al. 2007) to explore the covariation of number and duration of off-bouts in response to advancing incubation and changing environmental conditions (e.g., as in Browne et al. 2007) but this proved technically challenging due to differences in the error distributions for each variable (Poisson for number of off-bouts, Gaussian for off-bout duration). In lieu, the two response variables were modelled separately and any comparisons are strictly qualitative. For each model, we included mean daily temperature (°C), cumulative daily rainfall (mm), and their interaction as the primary environmental effects. Year (two-level factor: 2018, 2019), lay date (integer; day of the year; range = 76 – 110), and day of incubation (integer; range = 0 – 16) were also included as covariates. We included a nested random intercept term for nest ID within female ID to account for non-independence of daily values collected from the same nest.

All data manipulation and statistical analyses were conducted in the R statistical environment (v. 4.2.3; R Core Team 2023). Bayesian models were fitted in Stan using the *brms* R package (Bürkner 2017). Models were specified using uniform priors and each model consisted of five parallel chains of 40,000 iterations, with a burn-in interval of 20,000 iterations per chain and thinning to every 50th run, for a total post-thinning sample of 2,000 draws per model. To confirm model convergence, we consulted *R-hat* values (equal to 1 at convergence), bulk effective sample sizes (*ESS*; greater than 1,000 for stable estimates), and visually inspected posterior distributions and caterpillar plots (Bürkner 2017). Summary values are presented as means ± SD (standard deviation). Model-derived parameter estimates (β) were taken from the posterior distributions of model parameters and are accompanied by 95% credible intervals (*95% CIs*) based on the 2,000 draws (Cumming and Finch 2005). Credible intervals were used to evaluate the strength of support for a given effect (Cohen 1990), with intervals that did not overlap zero showing "strong support" for an effect. Model fit was estimated using R^2 as the proportion of variance explained (Gelman et al. 2018). The data and code used in the analysis have been made publicly available on the Figshare repository (<REDACTED>).

RESULTS

Across both years, average daytime ambient temperatures during the incubation period ranged -12.7 – +12.8°C (Table 2). In 2019, there were eight more days above freezing compared to 2018 and average daytime temperatures in 2019 never dropped as low as temperatures in 2018 (Figure 2, Table 2). Average snow depth during the incubation period was 71.1 ± 1.9 cm in 2018 and 2.2 ± 0.6 cm in 2019 (Table 2). While there was little rainfall in both years (Table 2), most of the rain in 2019 fell in the middle of the period when most females were incubating (days of the year 99 – 107; Figure 2).

We found and monitored 56 nests across both years (2018: n = 24, 2019: n = 32). Females began laying earlier and laid more eggs in 2019 compared to 2018 (Table 2). Across both years, we obtained temperature data from 29 nests attributed to 23 unique females. The average female spent 92 ± 2% of the daytime (sunrise to sunset) incubating and never left their nest between sunset and sunrise (i.e., 100% nighttime nest attentiveness). During daylight hours, females took an average of 5.5 ± 0.6 off-bouts (range: 2 – 11) that lasted for 13.3 ± 1.4 min. each (range: 5.3 – 28.0 min; Table 2).

As predicted, there was a moderate negative correlation between number and duration of off-bouts (Supplementary Online Material, Figures S1 and S2), such that a higher number of off-bouts per day was associated with off-bouts of shorter duration. Consistent with the predator avoidance hypothesis, off-bout duration (ELPD = 859.5) provided greater predictive accuracy for variation in nest attentiveness than did the number off-bouts (ELPD = 855.4; ΔELPD = -4.2 ± 2.7), although this difference is only marginally larger than the discrimination threshold (see *Statistical Analysis*) and neither off-bout duration ($R^2_{marginal} = 0.02$, $R^2_{conditional} = 0.25$) nor the number of off-bouts ($R^2_{marginal} = 0.001$, $R^2_{conditional} = 0.23$) explained much of the variation in nest attentiveness alone (presumably because most of the variation is explained by the random effects; Supplementary Online Material, Figure S3).

Factors Influencing Incubation Behaviour

We explored how differences in experienced weather conditions (temperature and rainfall), as well as the day of incubation, influenced female incubation behaviour. In contrast to our hypotheses, there was no evidence that mean daily temperature influenced the number of off-bouts per day (Figure 3a) or the average duration of off-bouts (Figure 4a; Table 3). Likewise, there was no support for an effect of cumulative daily rainfall on either the number (Figure 3b) or the duration of off-bouts (Figure 4b), nor for an interactive effect of temperature and rainfall on either behaviour (Figures 3c and 4c; Table 3). The lack of environmental effects is consistent with an absence of an effect of lay date on variation in either incubation behaviour (Figures 3d and 4d).

Finally, we found evidence that the day of incubation influenced both off-bout number (Figure 3e) and off-bout duration (Figure 4e), such that, on average, females took shorter and more frequent off-bouts as their eggs developed (Table 3). Our models also indicated that, on average, off-bout durations were longer in 2019 than in 2018 (Figure 4f), but there was no difference in the number of off-bouts between years (Figure 3f; Table 3). Consistent with our finding that nest attentiveness was primarily driven by off-bout duration, there was also higher average nest attentiveness in 2019 than in 2018 (Table 2).

DISCUSSION

Our results provide a number of unique insights into the incubation strategies used by a species that breeds during snowy, sub-zero temperatures in North America's boreal forest. First, we show that female Canada Jays in Alaska spent, on average, ~92% of their active time warming eggs. By comparison, a meta-analysis estimated that passerines with mate-assisted, female-only incubation spent 78 ± 10% of their time on the nest (range: 51 – 97%, n = 156 species) and even species in which both sexes shared incubation duties had an average nest attentiveness of only 87 ± 13% (range: 58 – 100%, n = 124 species; Matysioková and Remeš 2014). Second, we provide evidence that variation in nest attentiveness was primarily due to variation in off-bout duration, not in the number of off-bouts. In other words, across days within the incubation period, females tended to adjust how long they were off the nest rather than how many times they left the nest. Third, and somewhat surprisingly, we found that female Canada Jays did not appear to adjust their incubation behaviours in response to variation in either daytime temperature or rainfall.

Instead, females adjusted their nest attentiveness by taking shorter and more frequent off-bouts as incubation progressed. Together, these results suggest that Canada Jays may have relatively strict incubation schedules imposed by the physiological and developmental implications of breeding in cold environments and, thus, are less response to variation in weather conditions.

On one hand, the high level of nest attentiveness we report in Canada Jays is perhaps unsurprising given females are incubating in much colder temperatures than are typical for most other passerines. However, because of cold temperatures, females likely also experience higher energetic demands compared to their warmer-temperature counterparts. An obvious solution to this problem would be for males to frequently feed females while on the nest, a trait that is not uncommon across species (Matysioková and Remeš 2014). While we did not record the frequency of this behaviour in Alaska, previous observations in Algonquin Provincial Park, ON, Canada, have demonstrated that males only feed females 1-2 times per day (Strickland & Ouellet 2020) and, given the similarity in a range of behaviours between these two populations, including their general social systems (<REDACTED>, *unpublished data*), it seems likely that similar male feeding rates occur in Alaska. Rather, to satisfy the energetic demands of incubating in cold temperatures, females may need to be more efficient in their food acquisition during the few times they leave the nest each day (Strickland & Waite 2001; Strickland & Ouellet 2020). This strategy is possible because food has been cached by females the previous late summer or fall, thereby reducing search effort when off the nest. Essentially cached food acts as an external capital resource that females draw upon during the incubation period. That said, females also likely rely on ‘internal’ capital resources during the incubation period: a previous study in Algonquin Provincial Park demonstrated that females gain 25% of their initial weight, presumably also primarily from cached food, prior to the commencement of egg laying (Sechley et al. 2014). We suspect that, if female Canada Jays had to rely only on finding fresh food to satisfy energetic requirements during incubation, then total nest attentiveness would decline to a point where eggs could not be maintained at a viable temperature for embryogenesis. However, this scenario may never actually occur given that the appearance of fresh food during the incubation period would likely coincide with warmer than average temperatures, alleviating some of the thermoregulatory costs incurred in a typical breeding season.

We provide some indirect evidence in support of the hypothesis that variation in the number of off-bouts is constrained by selection to reduce predator-attracting activity around the nest. This evidence is consistent with several other Canada Jay behaviours, including low feeding rates by the male while the female is incubating despite the fact that males help build the nest and frequently perform courtship feeding (Strickland & Ouellet 2020) and aggression towards the one-year-old, dominant juvenile when it is near the nest during the incubation period, despite parents allowing it to feed its younger siblings once they have fledged (Strickland 1991; Strickland & Waite 2001). Furthermore, our finding of differences in nest attentiveness between the two years of study, in the absence of differences in the number of off-bouts (Tables 1 and 2), is consistent with the notion that variation in the number of off-bouts may be relatively constrained and, thus, off-bout duration is a better predictor of nest attentiveness. Early in the incubation period of 2019, unseasonably warm and dry conditions melted the snow on the forest floor, revealing food that would have otherwise been inaccessible (e.g., berries, dormant insects, etc.). As a result, both males and females spent 85% of their foraging time on the ground, as opposed to 100% of their time in trees (presumably retrieving cached foods) in 2018 (Swift et al. 2022). Most importantly, however, females responded to warm temperatures in 2019 by increasing off-bout duration, not the number of off-bouts. While circumstantial, these lines of evidence, in combination with the overall high nest attentiveness compared to other species, suggest that the incubation behaviours of female Canada Jays are simultaneously shaped by their cold environment and the threat of nest predation.

We found that females did not adjust their incubation behaviours in response to weather conditions. It is possible that there was simply insufficient variation in these weather variables over the incubation period to influence incubation behaviours. This may be particularly relevant for rainfall given that rainfall patterns over the incubation period were sporadic, causing only a few females to experience heavy bouts of rain, and only for a brief period of time, while most others experienced virtually none. That most females experienced no rainfall is not surprising since most precipitation events during this period were in the form of snowfall; weather data that we were, unfortunately, unable to obtain. Indeed, the lack of rainfall effects here does not imply that snowfall or cumulative precipitation do not influence incubation decisions. In contrast to rainfall, most females experienced daytime temperatures spanning ~12 °C between the coldest and warmest value (range of ranges: 6.3 – 18.9 °C) over the course of an incubation period. Thus, it is more likely that, save for extreme weather events, which may include heavy snowfall or rainfall and high winds, females may be largely immune to daily fluctuations in temperature during the incubation period. Again, the presence of cached food likely plays a role in this lack of response: a constant, reliable food supply means that females only need to leave their nest a few times per day to acquire sufficient resources to satisfy their daily energetic requirements.

Finally, we provide evidence that females took shorter, more frequent off-bouts as their incubation period progressed. Shorter off bouts later in the incubation period may be explained by females perceiving that their eggs are more susceptible to temperature fluctuations as the embryos develop (e.g., Diez-Méndez et al. 2021). An experimental study demonstrated that developing embryos of Black-capped Chickadees (*Poecile atricapillus*) are more susceptible to heat loss, which explained why female chickadees took shorter off-bouts later in the incubation period (Cooper and Voss 2013). Similar behaviours have been documented in Carolina Chickadees (*Poecile carolinensis*; Walters et al. 2016), Wood Ducks (*Aix sponsa*; McClintock et al. 2014), and Great Tits (*Parus major*; Álvarez & Barba 2014). In a possibly similar response to shorter off-bouts later in the incubation period, female Canada Jays may need to take more off-bouts to support foraging demands, especially since body fat stores have likely dwindled by the end of the incubation period. Hence, the late incubation period may be a time when the trade-off between embryonic condition and self-maintenance intensifies because shorter off-bouts presumably improve embryonic viability yet more off-bouts are required to fuel energetic costs.

In addition to providing unique insight into the incubation behaviour of a cold-weather breeding species, our study also happened to sample incubation patterns and reproductive performance over two record-setting years. The late winter/early spring in 2019 was the second warmest on record and beat the record for earliest snow melt by two weeks (31 Mar; Weather and Climate Summary, Denali NPP). In contrast, while spring 2018 had average temperatures, it was the seventh snowiest year on record, with snow melting ~1 week later than average (17 May, Weather and Climate Summary, Denali NPP). The warm temperatures and early snow melt in 2019 likely allowed jays to conserve energy and, perhaps more importantly, capitalize on fresh food available on the forest floor, ultimately leading to higher reproductive output compared to 2018 (Table 2). Interestingly, opposing trends related to warmer ambient temperatures have been observed in an eastern population of Canada Jays: warmer temperatures during incubation are associated with reduced reproductive performance (Whelan et al. 2017) and higher fall temperatures and frequency of freeze-thaw events (related to higher temperatures) have been linked to long-term population decline, likely by influencing the rate of cache spoilage (Waite & Strickland 2006; Sutton et al. 2021). Our two years of data from Denali NPP suggests that the timing of snow melt may also be an important factor to consider, particularly if it permits access to fresh food. Taken together, results from past studies and those presented here highlight the complex interplay between weather, context, and incubation behaviours. This is especially relevant in light of long-term changes in climatic conditions, with some of the most extreme changes in cold climates. Studies of animals breeding in these cold places, such as the one presented here, are essential if we are to understand how they will respond to these changes.

LITERATURE CITED

Aldrich, T. W., D. G. Raveling (1983). Effects of experience and body weight on incubation behavior of Canada geese. The Auk 100(3):670–679. https://doi.org/10.1093/auk/100.3.670

Álvarez, E., E. Barba (2014). Within and between population variations of incubation rhythm of great tits *Parus major*. Behaviour 151(13):1827–1845. https://doi.org/10.1163/1568539X-00003218

Ardia, D. R., J. H. Pérez, E. D. Clotfelter (2010). Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. Proceedings of the Royal Society, London: Biological Sciences 277(1689):1881–1888. https://doi.org/10.1098/rspb.2009.2138

Biebach, H. (1986). Energetics of rewarming a clutch in starlings (*Sturnus vulgaris*). Physiological Zoology 59(1):69–75. https://doi.org/10.1086/physzool.59.1.30156092

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, J.-S. S. White (2009). Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24(3):127-135. https://doi.org/10.1016/j.tree.2008.10.008

Browne, W. J., R. H. McCleery, B. C. Sheldon, R. A. Pettifor (2007). Using cross-classified multivariate mixed response models with application to life history traits in great tits (*Parus major*). Statistical Modeling 7(3):217-238. https://doi.org/10.1177/1471082X0700700301

Bürkner, P. (2017). brms: an R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80(1):1–28. https://doi.org/10.18637/jss.v080.i01

Capilla-Lasheras, P. (2018). incR: a new R package to analyse incubation behaviour. Journal of Avian Biology 49(8):e01710. https://doi.org/10.1111/jav.01710

Coe, B. H., M. L. Beck, S. Y. Chin, C. M. B. Jachowski, W. A. Hopkins (2015). Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. Journal of Avian Biology 46(4):385–394. https://doi.org/10.1111/jav.00581

Cohen, J. (1990). Things I have learned (so far). The American Psychologist 45(12):1304–1312. https://doi.org/10.1037/0003-066X.45.12.1304

Conway, C. J., T. E. Martin (2000a). Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54(2):670–685. https://doi.org/10.1111/j.0014-3820.2000.tb00068.x

Conway, C. J, T. E. Martin (2000b). Effects of ambient temperature on avian incubation behavior. Behavioral Ecology 11(2):178–188. https://doi.org/10.1093/beheco/11.2.178

Cooper, C. B., M. A. Voss (2013). Avian incubation patterns reflect temporal changes in developing clutches. Public Library of Science ONE 8(6): p.e65521. https://doi.org/10.1371/journal.pone.0065521

Cresswell, W., S. Holt, J. M. Reid, D. P. Whitfield, R. J. Mellanby (2003). Do energetic demands constrain incubation scheduling in a biparental species? Behavioral Ecology 14(1):97–102. https://doi.org/10.1093/beheco/14.1.97

Cumming, G., S. Finch (2005). Inference by eye: confidence intervals and how to read pictures of data. The American Psychologist 60(2):170–180. https://doi.org/10.1037/0003-066X.60.2.170

Dallmann, J. D., L. C. Anderson, E. J. Raynor, L. A. Powell, W. H. Schacht (2016). iButton temperature loggers effectively determine prairie grouse nest absences. Great Plains Research 26:117–123. https://www.jstor.org/stable/i40196054

Derbyshire, R., D. Strickland, and D. R. Norris (2015). Experimental evidence and 43 years of monitoring data show that food limits reproduction in a food-caching passerine. Ecology 96(11):3005–3015. https://doi.org/10.1890/15-0191.1

Diez-Méndez, D., J. J. Sanz, E. Barba (2021). Impacts of ambient temperature and clutch size on incubation behaviour onset in a female-only incubator songbird. Ibis 163(3):1056–1071. https://doi.org/10.1111/ibi.12937

Eiby, Y. A., D. T. Booth (2009). The effects of incubation temperature on the morphology and composition of Australian Brush-turkey (*Alectura lathami*) chicks. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 179(7):875–882. https://doi.org/10.1007/s00360-009-0370-4

Fong, Y., H. Rue, J. Wakefield (2010). Bayesian inference for generalized linear mixed models. Biostatistics 11(3):397–412. https://doi.org/10.1093/biostatistics/kxp053

Fuirst, M., D. Strickland, D. R. Norris (2021). Patterns and causes of breeding dispersal in a declining population of Canada Jays, *Perisoreus canadensis*, over 55 years. Animal Behaviour 182:31–41. https://doi.org/10.1016/j.anbehav.2021.09.015

Gelman, A., B. Goodrich, J. Gabry, A. Vehtari (2018). R-squared for Bayesian regression models. The American Statistician 79(3):307–309. https://doi.org/10.1080/00031305.2018.1549100

Hadfield, J. D., A. Nutall, D. Osorio, I. P. F. Owens (2007). Testing the phenotypic gambit: phenotypic, genetic and environmental correlations of colour. Journal of Evolutionary Biology 20(2): 549–557. https://doi.org/10.1111/j.1420-9101.2006.01262.x

Hanssen, S. A., D. Hasselquist, I. Folstad, K. E. Erikstad (2005). Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proceedings of the Royal Society, London: Biological Sciences 272(1567):1039–1046. https://doi.org/10.1098/rspb.2005.3057

Hartman, C. A., L. W. Oring (2006). An inexpensive method for remotely monitoring nest activity. Journal of Field Ornithology 77(4):418–424. https://doi.org/10.1111/j.1557-9263.2006.00073.x

de Heij, M. E., A. J. van der Graaf, D. Hafner, J. M. Tinbergen (2007). Metabolic rate of nocturnal incubation in female great tits, *Parus major*, in relation to clutch size measured in a natural environment. Journal of Experimental Biology 210(11):2006–2012. https://doi.org/10.1242/jeb.001420

Hepp, G. R., R. A. Kennamer (2012). Warm is better: incubation temperature influences apparent survival and recruitment of wood ducks (*Aix sponsa*). PLoS One 7(10):e47777. https://doi.org/10.1371/journal.pone.0047777

King, J. R. (1972). Energetics of reproduction in birds. Pages 78–107 in Breeding Biology of Birds. National Academy of Sciences, Washington, DC.

Lack, D. (1948). The significance of clutch-size: part III—some interspecific comparisons. Ibis 90(1): 25–45. https://doi.org/10.1111/j.1474-919X.1948.tb01399.x

MacDonald, E. C., A. F. Camfield, J. E. Jankowski, K. Martin (2014). An alpine-breeding songbird can adjust dawn incubation rhythms to annual thermal regimes. The Auk 131(4):495–506. https://doi.org/10.1642/AUK-13-234.1

Marasco, V., K. A. Spencer (2015). Improvements in our understanding of behaviour during incubation. Pages 142-151 in Nests, eggs and incubation: new ideas about avian incubation (Deeming D. C., Reynolds S. J., editors) Oxford University Press, USA; 2015. https://doi.org/10.1093/acprof:oso/9780198718666.003.0012

Matysioková, B., V. Remeš (2014). The importance of having a partner: male help releases females from time limitation during incubation in birds. Frontiers in Zoology 11(1):1–10. https://doi.org/10.1186/1742-9994-11-24

McClintock, M. E., G. R. Hepp, R. A. Kennamer (2014). Plasticity of incubation behaviors helps wood ducks (*Aix sponsa*) maintain an optimal thermal environment for developing embryos. The Auk 131(4):672–680. https://doi.org/10.1642/AUK-14-57.1

Nord, A., J. Nilsson (2012). Context-dependent costs of incubation in the pied flycatcher. Animal Behaviour 84(2):427–436. https://doi.org/10.1016/j.anbehav.2012.05.017

Nord, A., J. B. Williams (2015). The energetic costs of incubation. Pages 152-170 in Nests, eggs and incubation: new ideas about avian incubation (Deeming DC, Reynolds SJ, editors) Oxford University Press, USA. https://doi.org/10.1093/acprof:oso/9780198718666.003.0013

Olson, C. R., C. M. Vleck, D. Vleck (2006). Periodic cooling of bird eggs reduces embryonic growth efficiency. Physiological and Biochemical Zoology 79(5):927-936. https://doi.org/10.1086/506003

Ospina, E. A., L. Merrill, T. J. Benson (2018). Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. Ecology and Evolution 8(6):3270–3279. https://doi.org/10.1002/ece3.3911

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Remeŝ, V., T. E. Martin (2002). Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56(12):2505–2518. https://doi.org/10.1111/j.0014-3820.2002.tb00175.x

Rousseu, F., B. Drolet (2017). The nesting phenology of birds in Canada. Canadian Wildlife Service, Technical Report Series No. 533, Environment and Climate Change Canada, Québec Region, Québec, Canada.

Sechley, T. H., D. Strickland, D. R. Norris (2014). Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. Journal of Avian Biology 45(1):85-93. https://doi.org/10.1111/j.1600-048X.2013.00296.x

Sivula, T., M. Magnusson, A. A. Matamoros, A. Vehtari (2020). Uncertainty in Bayesian leave-one-out cross-validation based model comparison (version 4). arXiv: 2008.10296. https://doi.org/10.48550/arXiv.2008.10296

Smith, J. A., C. B. Cooper, S. J. Reynolds (2015). Advances in techniques to study incubation. Pages 179-195 in Nests, eggs and incubation: new ideas about avian incubation (Deeming D. C., Reynolds S. J., editors) Oxford University Press, USA. https://doi.org/10.1093/acprof:oso/9780198718666.003.0015

Strickland, D. (1991). Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. Canadian Journal of Zoology 69(12): 2935–2945. https://doi.org/10.1139/z91-414

Strickland, D., H. Ouellet (2020). Canada Jay (*Perisoreus canadensis*). In *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.gryjay.01

Strickland, D., T. A. Waite (2001). Does initial suppression of allofeeding in small jays help to conceal their nests? Canadian Journal of Zoology 79(12):2128–2146. https://doi.org/10.1139/z01-171

Sutton, A. O., D. Strickland, N. E. Freeman, D. R. Norris (2021). Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine. Global Change Biology 27(5):983–992. https://doi.org/10.1111/gcb.15445

Swift, K. N., E. J. Williams, J. M. Marzluff (2022). An observational analysis of Canada Jay (*Perisoreus canadensis*) foraging and caching ecology in Denali National Park and Preserve, Alaska, USA. Canadian Journal of Zoology 100(999):133–146. https://doi.org/10.1139/cjz-2021-0053

Thomson, D. L., P. Monaghan, R. W. Furness (2007). The demands of incubation and avian clutch size. Biological Reviews 73(3):293–304. https://doi.org/10.1111/j.1469-185X.1998.tb00032.x

Turner, J. S. (1994). Thermal impedance of a contact-incubated bird's egg. Journal of Thermal Biology 19(4):237–44. https://doi.org/10.1016/0306-4565(94)90046-9

Vafidis, J. O., R. J. Facey, D. Leech, R. J. Thomas (2018). Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird. Journal of Avian

Biology 49(8):e01672. https://doi.org/10.1111/jav.01672

Vehtari, A., J. Gabry, M. Magnusson, Y. Yao, P Bürkner, T. Paananen, A. Gelman (2023). loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.6.0. https://mc-stan.org/loo

Vehtari, A., A. Gelman, J. Gabry (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27(1):1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Visser, M. E., C. M. Lessells (2001). The costs of egg production and incubation in great tits (*Parus major*). Proceedings of the Royal Society, London: Biological Sciences 268(1473):1271–1277. https://doi.org/10.1098%2Frspb.2001.1661

Waite, T. A., D. Strickland (2006). Climate change and the demographic demise of a hoarding bird living on the edge. Proceedings of the Royal Society, London: Biological Sciences 273(1603):2809–2813. https://doi.org/10.1098/rspb.2006.3667

Weathers, W. W., K. A. Sullivan (1989). Nest attentiveness and egg temperature in the yellow-eyed junco. The Condor 91(3):628–633. https://doi.org/10.2307/1368113

Webb, D. R. (1987). Thermal tolerance of avian embryos: a review. The Condor 89(4):874–898. https://doi.org/10.2307/1368537

Western Regional Climate Center (WRCC), Denali Visitor Center Alaska, (2021). Web. Accessed on 12 April 2021. Available from https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?akADEN

Whelan, S., D. Strickland, J. Morand-Ferron, D. R. Norris (2017). Reduced reproductive performance associated with warmer ambient temperatures during incubation in a winter-breeding, food-storing passerine. Ecology & Evolution 7(9):3029-3036. https://doi.org/10.1002/ece3.2864

Wiebe, K. L., K. Martin (1997). Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. Wildlife Biology 3(3):219–227. https://doi.org/10.2981/wlb.1997.027

Zuberogoitia, I., J. E. Martínez, M. Larrea, J. Zabala. 2018. Parental investment of male peregrine falcons during incubation: influence of experience and weather. Journal of Ornithology 159(1):275–82. https://doi.org/10.1007/s10336-017-1503-2

FIGURES & TABLES

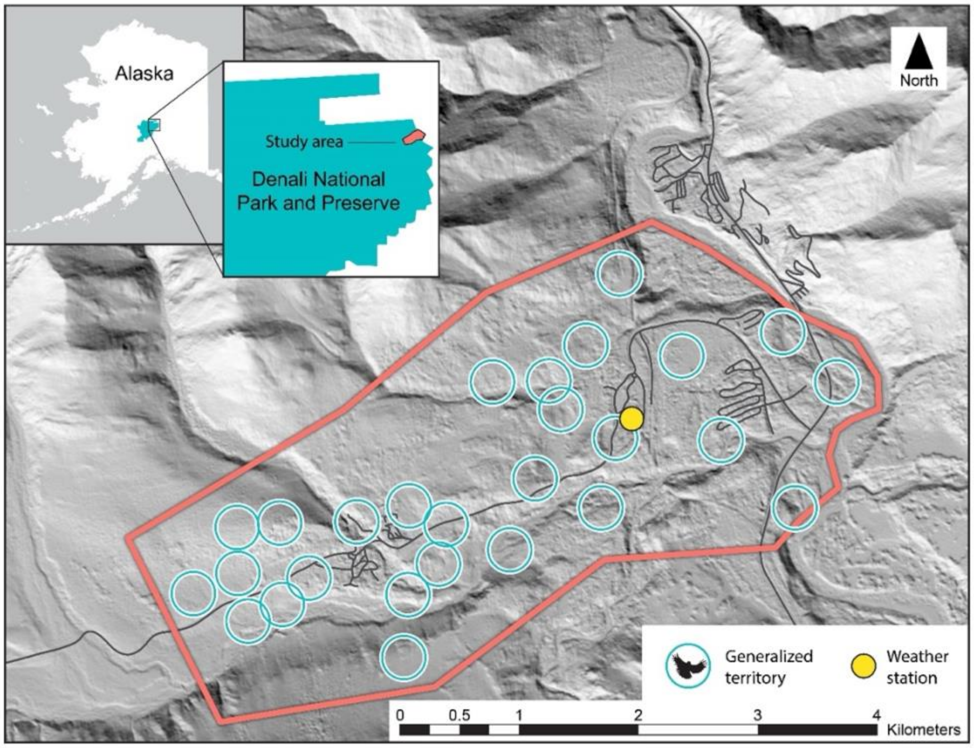

Figure 1. Study area (outlined in pink) along the first 6.4 km of park road within Denali National Park and Preserve, Alaska, USA. Territories of colour-banded Canada Jays were monitored in 2018 and 2019 during the breeding season (Feb – May). Black lines represent main roads. Yellow circle represents location of weather station where rainfall and snow depth data were collected. Teal circles represent generalized locations of territories in 2019.

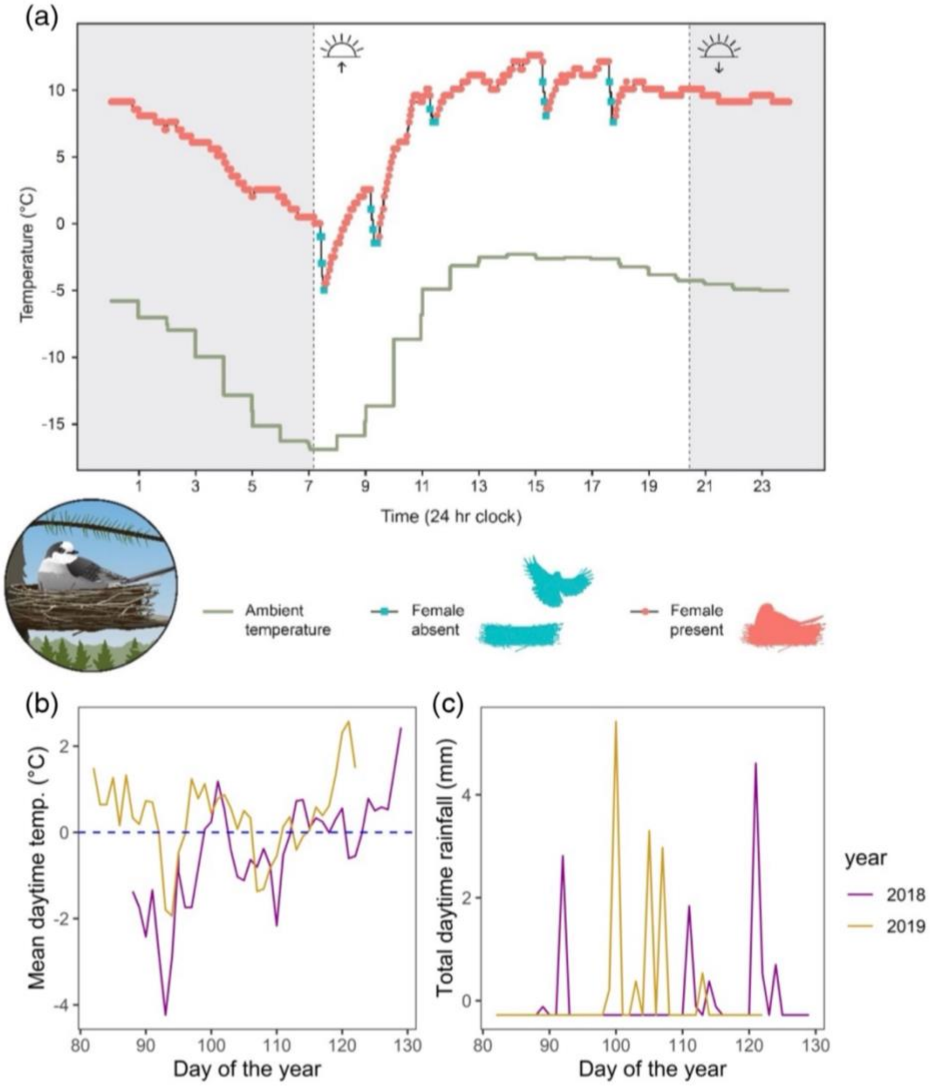

Figure 2. A Canada Jay nest temperature profile and daytime weather conditions in Denali National Park and Preserve, Alaska, USA. **(a)** Nest temperature profile for a single day (31 Mar 2018) for an incubating female. Pink dots represent temperature data taken from iButtons (4 min. intervals) when the female was incubating, and blue squares represent when the female was absent from the nest. The green line is the ambient temperature profile. On this day, this female had five off-bouts of 12 – 16 min. beach. **(b)** Mean daytime (period between sunrise and sunset) ambient temperature (°C) and **(c)** total daytime rainfall (mm) throughout 2018 (purple line) and 2019 (yellow line) incubation periods.

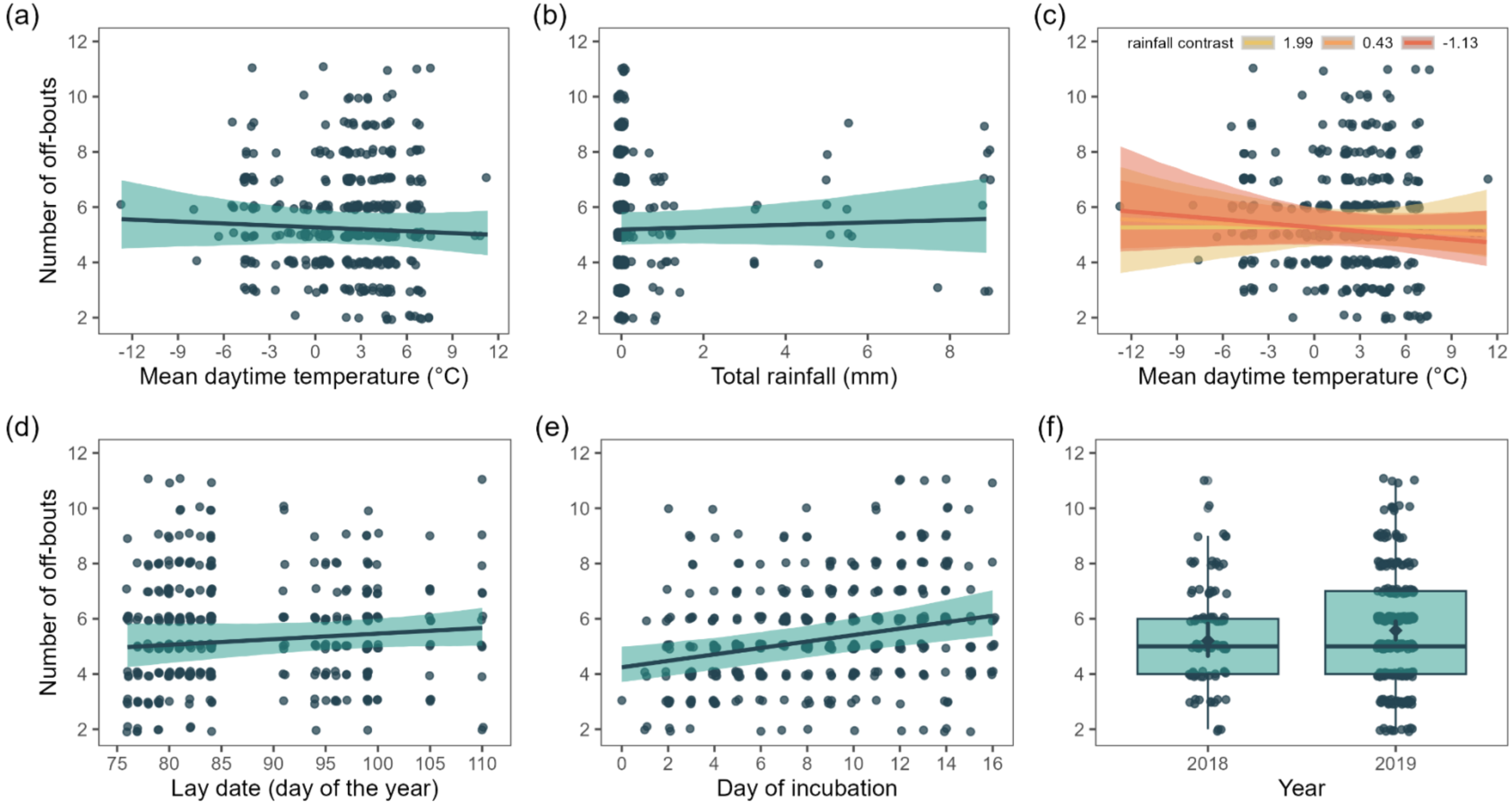

Figure 3. Partial plots of variables hypothesized to influence the daily number of off-bouts of female Canada Jays in Denali National Park and Preserve, Alaska (see hypotheses in Table 1). We investigated whether females adjusted the number of off-bouts in response to two environmental variables: **(a)** daytime temperature (°C) and **(b)** total daily rainfall (mm), as well as **(c)** the interaction between temperature and rainfall. In addition, we tested for effects of **(d)** lay date (day of the year), **(e)** day of incubation, and **(f)** year. In each

panel, points represent the observed daily number of off-bouts (n = 12 – 15 observations per nest), and solid lines indicate the estimated relationship from a Bayesian GLMM (see *Statistical Analysis*). In panel (c), the interaction between temperature and rainfall is visualized at three different rainfall contrasts, although this interaction is not supported by the model (Table 3). In panel (f), the boxplots represent the distribution of the data, and the overlaid dot-and-whisker plots visualise the estimated average (β) and standard error (SE) per year. Points have been jittered along both axes (± 0.1 in either direction) to better visualize the density of the data. See Table 3 for a summary of the model results.

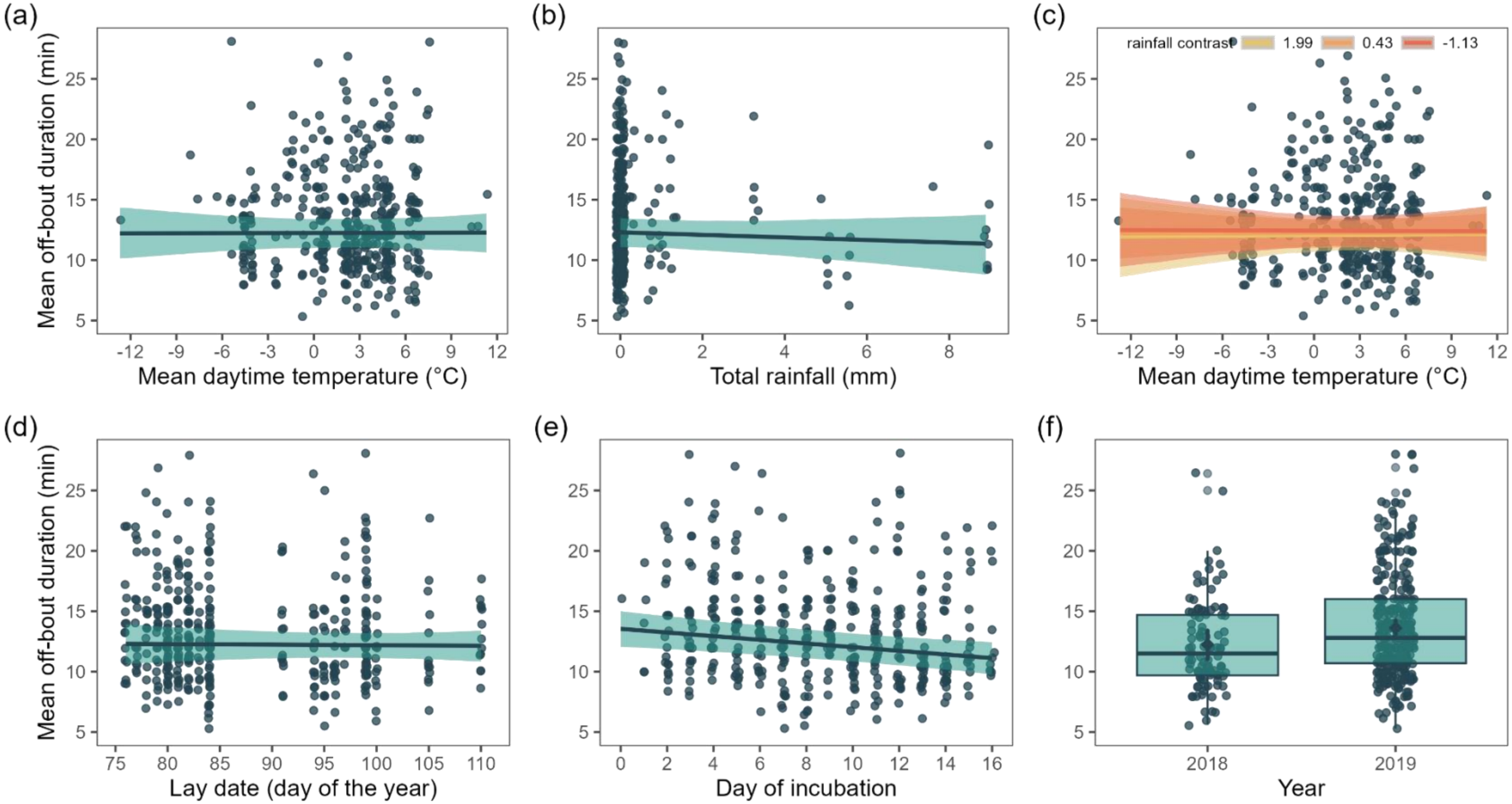

Figure 4. Partial plots of variables hypothesized to influence the daily mean off-bout duration of female Canada Jays in Denali National Park and Preserve, Alaska (see hypotheses in Table 1). We investigated whether females adjusted the number of off-bouts in response to two environmental variables: **(a)** daytime temperature (°C) and **(b)** total daily rainfall (mm), as well as **(c)** the interaction between temperature and rainfall. In addition, we tested for effects of **(d)** lay date (day of the year), **(e)** day of incubation, and **(f)** year.

In each panel, points represent the observed daily number of off-bouts (n = 12 – 15 observations per nest), and solid lines indicate the estimated relationship from a Bayesian GLMM (see *Statistical Analysis*). In panel (c), the interaction between temperature and rainfall is visualized at three different rainfall contrasts, although this interaction is not supported by the model (Table 3). In panel (f), the boxplots represent the distribution of the data, and the overlaid dot-and-whisker plots visualise the estimated average (β) and standard error (SE) per year. Points have been jittered along the both axes (± 0.1 in either direction) to better visualize the density of the data. See Table 3 for a summary of the model results.

Table 1. Hypothesized effects, mechanisms, predictions, and predictor variables regarding the effects of environmental conditions and day of incubation on the number and duration of off-bouts taken by incubating Canada Jays (*Perisoreus canadensis*). Environmental predictor variables are intended to test the facultative behavioural responses of females that experience different weather conditions throughout the breeding period and how females respond to variation in these conditions while incubating.

Hypothesis		Predictions	
Variable	**Mechanism**	**Number of off-bouts**	**Off-bout duration**
Temperature	Temperature influences energetic costs of incubation which in turn affect foraging rates	Individuals will take more frequent off-bouts on warmer days	Individuals will take longer off-bouts on warmer days
Rainfall	Rainfall can result in nests and eggs becoming sodden and cold	Individuals will take fewer off-bouts on days with high levels of rainfall	Individuals will take shorter off-bouts on days with higher amount of rainfall
Interaction between temperature and rainfall	The instinct to cover nest and eggs from rainfall trumps the effect of temperature on incubation behaviour (i.e., the influence temperature could have on foraging activity)	The number of off-bouts will be positively related to temperature on days with low rainfall but there will be no relationship between temperature and off bouts on days with high rainfall	Off bout duration will be positively related to on days with low rainfall but there will be no relationship between temperature and off bout duration on days with high rainfall
Day of incubation	Embryos become more sensitive to temperature fluctuations as they develop	Number of off-bouts is negatively related to day of incubation	Off-bout duration is negatively related to day of incubation

Table 21. Annual and global means and ranges of weather variables, reproductive parameters, and incubation metrics associated with Canada Jay nests in Denali National Park and Preserve, AK.

Variable	2018		2019		Combined	
	mean	range	mean	range	mean	range
Weather						
daytime ambient temperature (°C)[a,b]	0.8	-12.7 – 12.8	2.8	-4.6 – 11.3	2.2	-12.7 – 12.8
daytime rainfall (mm)[b,c]	0.4	0 – 7.2	0.5	0 – 8.9	0.4	0 – 8.9
snow depth (cm) [d]	71.1	58.0 – 91.4	2.2	0 – 17.8	19.3	0 – 91.4
Reproductive parameters						
lay date (day of the year)[e]	92.5	82 – 101	83.5	76 – 97	87.3	76 – 101
cutch size[f]	3.1	3 – 4	3.8	3 – 5	3.6	3 – 5
Incubation metrics						
daytime nest attentiveness (%)[b,g]	93.6	85.7 – 97.1	91.8	74.6 – 97.5	92.2	74.6 – 97.5
number of off-bouts[b,g]	4.8	2.0 – 9.0	5.8	2.0 – 11.0	5.5	2.0 – 11.0
off-bout duration (min)[b, g]	16.5	9.0 – 28.0	12.3	5.0 – 28.0	13.3	5.0 – 28.0

[a] n = 82 daily mean temperatures from samples taken every 4 min. (2018: n = 41 daily averages from 29 March to 9 May 2019: n = 41 daily averages from 23 Mar to 2 May)

[b] daytime' indicates sunrise to sunset, adjusted each day to account for changing day length, which corresponded to activity period of incubating jays.

[c] n = 82 daily mean rainfall and snow depth from samples taken every hr (2018: n = 41 daily averages from 29 March to 9 May 2019: n = 41 daily averages from 23 Mar to 2 May)

[d] not used in analyses but listed here for descriptive purposes.

[e] from n = 45 nests (2018: n = 19, 2019: n = 32); only initial nests included in calculation (no re-nests).

[f] from n = 56 nests (2018: n = 24, 2019: n = 32)

[g] n = 398 daily measurements from 29 nests from 23 unique females (2018: n = 97 daily averages from 6 females, 2019: n = 301 daily averages from 22 females).

Table 3. Model estimates of effects of factors predicted to influence number of off-bouts and mean off-bout duration in incubating Canada. See Table 1 for the list of hypothesized effects of the predictor variables on each response. Both models include a nested random intercept for nest ID within female ID (see *Statistical Analysis*). For each parameter, 95% credible intervals (*95% CI*) around the mean (*β*) were estimated from a posterior sample of 2,000 draws per model.

Response variable: Number of off-bouts (counts)			
Fixed effects	**Estimate (β)**	**Error (SE)**	**95% credible interval**
(intercept)	1.14	0.31	(0.52, 1.77)
temperature	-0.01	0.01	(-0.02, 0.01)
rainfall	0.00	0.02	(-0.04, 0.04)
temperature: rainfall	0.00	0.01	(-0.01, 0.01)
lay date	0.00	0.00	(0.00, 0.01)
day of incubation	0.02	0.01	(0.01, 0.03)
year	0.07	0.07	(-0.06, 0.20)
Random effects	**Estimate (SD)**	**Error (SE)**	**95% credible interval**
female ID	0.03	0.03	(0.00, 0.10)
female ID: nest ID	0.04	0.03	(0.00, 0.10)

Response variable: Mean off-bout duration (min)			
Fixed effects	**Estimate (β)**	**Error (SE)**	**95% credible interval**
(intercept)	13.97	3.11	(8.06, 20.15)
temperature	0.00	0.06	(-0.12, 0.12)
rainfall	-0.12	0.19	(-0.49, 0.24)
temperature: rainfall	0.00	0.05	(-0.09, 0.11)
lay date	0.00	0.03	(-0.07, 0.05)
day of incubation	-0.15	0.05	(-0.25, 0.05)
year	1.36	0.69	(0.06, 2.74)
Random effects	**Estimate (SD)**	**Error (SE)**	**95% credible interval**
female ID	0.49	0.32	(0.02, 1.22)
female ID: nest ID	0.47	0.32	(0.02, 1.17)
Family-specific parameter	**Estimate (σ)**	**Error (SE)**	**95% credible interval**
sigma (residual)	4.09	0.15	(3.81, 4.41)

SUPPLEMENTARY ONLINE MATERIAL

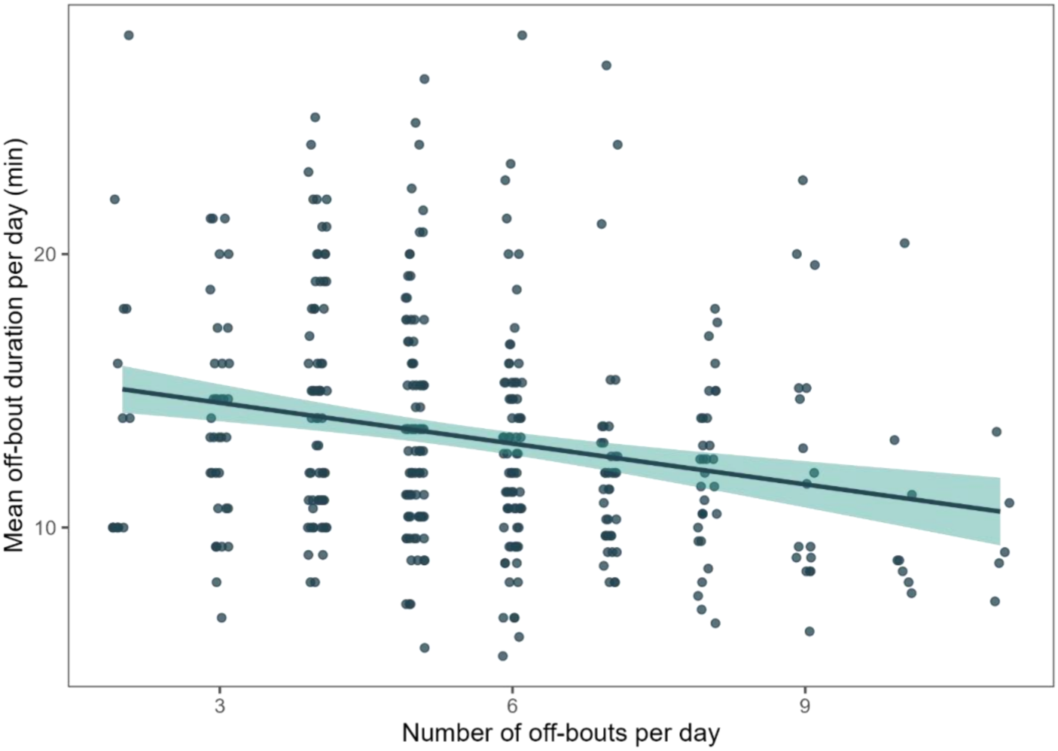

Figure S1. Pearson correlation of daily measurements of the number of off-bouts and mean off-bout duration during the incubation period of Canada Jays in Denali NPP, AK (*r* = - 0.23, *t* = - 4.57, *p* < .00001, *n* = 391). Points have been jittered along the x-axis in order to better visualize the density of the data; in reality, the number of off-bouts per day is an integer value.

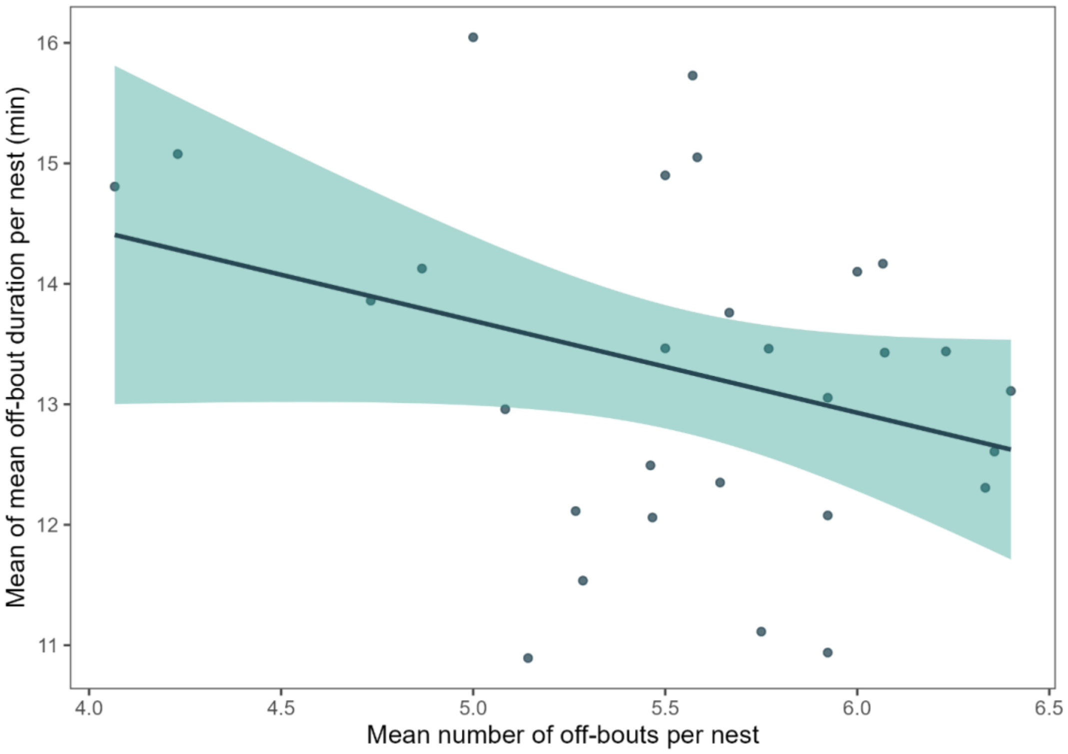

Figure S2. Pearson correlation of average of the number of off-bouts and mean of mean daily off-bout duration (minutes) over the incubation period of 29 nesting attempts from 23 unique Canada Jay females in Denali National Park and Preserve, AK (r = - 0.32, t = -1.77, p = 0.04, n = 29).

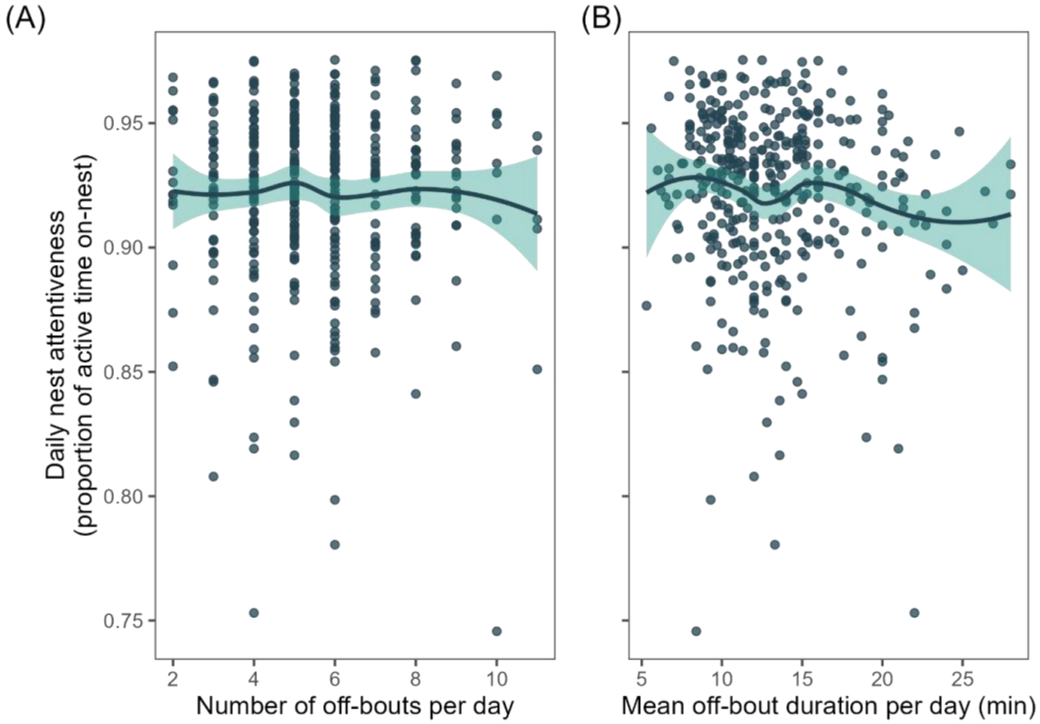

Figure S3. Correlations between incubation behaviours and daily nest attentiveness. Nest attentiveness was calculated as the proportion of daylight hours females spent on the nest. This value is dependent on the combination of the number and duration of off-bouts, which are themselves moderately correlated (Figures S1 and S2). **(A)** The number of off-bouts represents the number of times a female leaves the nest each day. **(B)** The mean off-bout duration is the average time a female spends off the nest during each foray. Comparison of separate GLMMs (see *Statistical Analysis*) showed that off-bout duration better predicts variation in nest attentiveness than does the number of off-bouts (see *Results*).