RESEARCH ARTICLE

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

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

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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, cache-reliant, year-round residents of boreal and sub-alpine environments that breed in the late winter/early spring and have female-only incubation. Females had high levels of daytime nest attentiveness (92 ± 3% of daytime spent on the nest; ± SD), taking an average of only 5.5 (± 0.1) off-bouts per day with a mean duration of 13.3 (± 0.2) min. 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 nest 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 suggest that incubation strategies of Canada Jays are likely not shaped by 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: ambient temperature, iButtons, incubation, nest attentiveness, off-bout, rainfall, reproduction, winter breeding

LAY SUMMARY

- We used temperature loggers in the nests of Canada Jays in Denali National Park and Preserve, Alaska, to examine how the number of off-bouts and off-bout duration influenced daily nest attentiveness (total time on nest) and whether variation in rainfall and temperature predicted these behaviours. Canada Jays breed in the late winter/early spring and have female-only incubation.
- On average, females spent 92% of daytime hours incubating, leaving the nest only 5.5 times per day for an average of 13 min each off-bout. Off-bout duration was a better predictor of nest attentiveness than number of off-bouts but females did not adjust their incubation behaviour in response to daily variation in temperature or precipitation.
- Our results suggest that incubation in Canada Jays is shaped by the threat of predation, which influences the level of activity around the nest, and availability of caches, which provides a reliable source of food the few times they leave the nest each day.

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). 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 lower hatching success (MacDonald et al. 2014) and 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 reduces the likelihood of 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. However, because most species nest during the spring and summer, nearly all our understanding about the ecology of incubation behaviour comes from relatively warm periods of the annual cycle (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 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, 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 (Biebach 1986). Conversely, a strategy of longer, less frequent off-bouts, which would reduce the total activity around the nest, could be adopted by to mitigate high risk of nest predation, as has been observed in multiple corvid species (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). Ambient temperature 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-bout foraging forays, 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 would under dry conditions at the same temperature (Coe et al. 2015). In addition to annual variation in weather conditions, individuals within the same season may also experience markedly different environments depending on their relative timing of reproduction and incubation.

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 predicting 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 socially and genetically monogamous year-round pair bonds (Strickland & Ouellet 2020; Fuirst et al. 2021). Once all eggs are laid (range = 1 – 5 eggs; mode = 3), females are the sole incubators (incubation period: 18–19 d) and, despite some provisioning by the male when the female is on the nest, females primarily acquire food during incubation through the retrieval of caches while off nest (Strickland & Ouellet 2020).

To explore incubation behaviour in Canada Jays, we first examined two competing behavioural hypotheses to explain daily variation in nest attentiveness. The first was that the number of off-bouts would be a better predictor of nest attentiveness because eggs left unattended for too long would risk becoming inviable in cold temperatures (thus constraining variation in off-bout duration), whereas females would be able leave the nest multiple times during a day while still being able to maintain eggs at viable temperatures. Conversely, we hypothesized that off-bout duration may be the primary factor influencing nest attentiveness because the number of times females leave the nest during the day, not the duration that they are absent, is limited by the need to avoid attracting 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). 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), despite presumably being capable of feeding females more frequently from their cached food supply. In addition, both adults may be attempting to minimize betraying the nest location since, for example, they bring larger loads of food to nestlings less often compared to smaller loads of food more frequently after young have fledged (Strickland & Waite 2001). Finally, when breeding pairs have a dominant juvenile from the previous year on their territory, they aggressively deter that juvenile from the nest area but allow it to feed their younger siblings immediately after they have fledged the nest (Strickland & Waite 2001). Thus, while females clearly benefit from additional food resources, their behaviour, both on the nest and towards their own juveniles, suggests that it is important to reduce activity during incubation and that this is likely related to the threat of predation.

Next, we 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. We have outlined the mechanisms underlying these hypotheses and their associated predictions for both number of off-bouts and off-bout duration in Table 1.

METHODS

General Field Methods

We conducted fieldwork in Denali NPP, Alaska, USA (63.129887°N, 151.197418°W) during the 2018 and 2019 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 from approx. 480 m to 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, females are not likely maintaining eggs at 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* below). 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* below).

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 lay period (Smith et al. 2015), we deployed iButtons so they logged temperatures on 13 – 16 d 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 moved west to east and we wanted to assess differences, if any, in ambient temperatures caused by elevation gradients between sub-sections.

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 (e.g., on-bout) and a score of 0 indicates a significant drop in nest temperature (e.g., 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 or more between 4-min. intervals was scored as an off-bout if followed by a 1°C or more 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.

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 (see Supplementary Materials). In both models, a nested random intercept of nest ID within female ID was used to account for non-independence of daily values collected from the same nest. We compared these two models for the difference in their expected predictive accuracy based on the theoretical 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).

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 (see, e.g., the analysis in Browne et al. 2007) but this proved difficult 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) and cumulative daily rainfall (mm), as well as 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 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).

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 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 ± 0.3 cm (± SE) in 2018 and 2.2 ± 0.1 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. Females spent 92.2 ± 3.4% (mean ± SD) 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).

Before analyzing the environmental drivers of variation in incubation behaviour, we first examined the relationship between number of off-bouts and off-bout duration and assessed which of these measures best predicted nest attentiveness. As we predicted, there was a moderate negative correlation between number and duration of off-bouts (Pearson's r = -0.32, $t_{(1,27)}$ = -1.77, p = 0.044; Figures S1, S2), such that a higher number of off-bouts per day was associated with off-bouts of shorter duration. Consistent with the predator activity hypothesis, off-bout duration (elpd = 859.5, LOOIC = -1719.0) provided greater predictive accuracy for variation in nest attentiveness than did the number off-bout (elpd = 855.4, LOOIC = -1710.7; Δelpd = -4.2 ± 2.7, ΔLOOIC = 8.3).

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 (β = -0.01 off-bouts/°C, *95% CI* = (-0.02, 0.01); Figure 3a) or the average duration of off-bouts (β = 0.00 min/°C, *95% CI* = (-0.12, 0.12); Figure 4a). Likewise, there was no support for an effect of cumulative daily rainfall on either the number (β = 0.00 off-bouts/mm rain, *95% CI* = (-0.04, 0.04); Figure 3b) or the duration of off-bouts (β = -0.12 min/mm rain, *95% CI* = (-0.49, 0.24); Figure 4b; Table 3), nor for an interactive effect of temperature and rainfall on either behaviour (Figure 3c; Figure 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 (Figure 3d; Figure 4d).

Finally, we found evidence that the day of incubation influenced both off-bout number (β = 0.02 off-bouts/day advance, *95% CI* = (0.01, 0.03); Figure 3e) and off-bout duration (β = -0.15 min/day advance, *95% CI* = (-0.25, -0.05); Figure 4e), such that, on average, females took shorter and more frequent off-bouts as their nests developed (Table 3). Our models also indicated that, on average, off-bout durations were longer in 2019 than in 2018 (β = 1.36 min/year, *95% CI* = (0.06, 2.74); Figure 4f) but there was no difference in the number of off-bouts between years (β = 0.07 off-bouts/year, *95% CI* = (-0.06, 0.20); Figure 3f). 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 78.2 ± 10.4% of their time on the nest (range: 51.0 – 97.1%, n = 156 species) and even species in which sexes shared incubation duties had an average nest attentiveness of only 87 ± 13.3% (range: 58.2 – 100%, n = 124 species; Matysioková and Remeš 2014). On one hand, the high level of nest attentiveness shown in Canada Jays is perhaps not surprising given females are incubating in much colder temperatures than are typical for most other passerines. However, because of cold temperatures, females must 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 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>, *unpubl. data*), it seems likely that similar male feeding rates occur in Alaska. Rather, to satisfy the energetic demands of incubating in cold temperatures, females appear to gather as much food as possible 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.

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, suggesting that the number of off-bouts may be more of a fixed behavioural trait. We hypothesized that this is caused by selective pressure to reduce predator-attracting activity around the nest, which 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 is consistent with the notion that variation in the number of off-bouts is somewhat fixed. 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 suggest that the incubation behaviours of female Canada Jays are simultaneously shaped by their cold environment and the threat of nest predation.

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. One possibility is 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. In contrast to rainfall, most females experienced 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 probably 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 offspring condition and self-maintenance intensifies since shorter off-bouts presumably improve offspring condition 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 March; 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 climate and the fitness of wild animals, in which long-term changes in weather conditions may have dramatic effects on individual reproductive performance depending on the period of the annual cycle in which they occur.

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FIGURES & TABLES

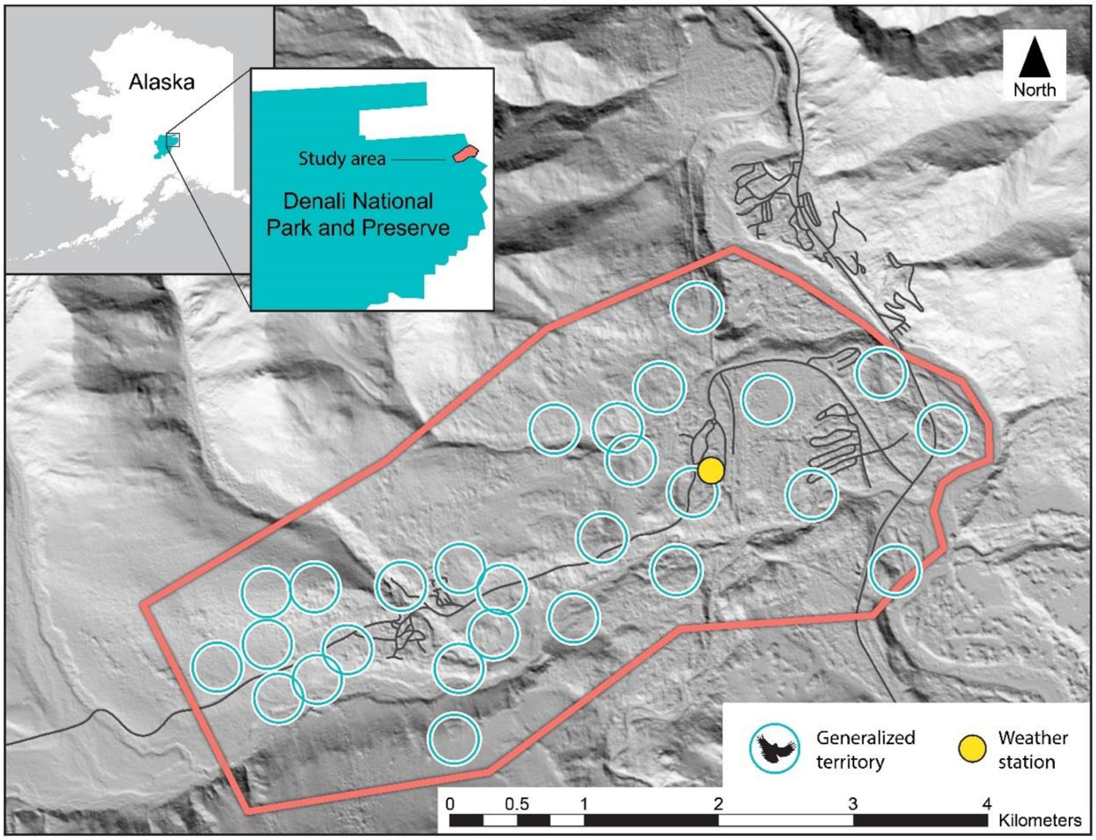

Figure 1. Study area (outlined in pink) along the first 6.4 km of park road within Denali National Park and Preserve, Alaska, USA. Territories of colour-banded Canada Jays were monitored in 2018 and 2019 during the breeding season (Feb. – May). Black lines represent main roads. Yellow circle represents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

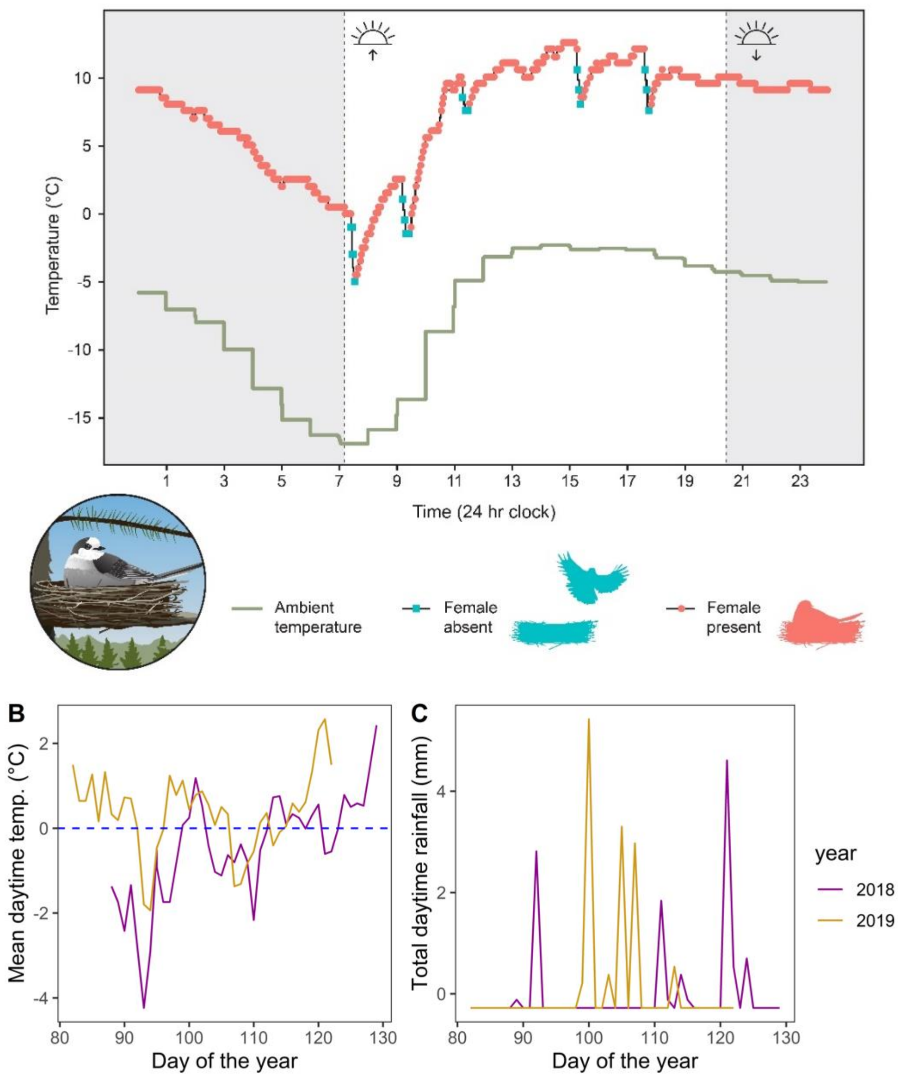

Figure 2. A Canada Jay nest temperature profile and daytime weather conditions in Denali National Park and Preserve, Alaska, USA. **(a)** Nest temperature profile for a single day (Mar. 31, 2018) for an incubating female. Pink dots represent temperature data taken from iButtons (4 min. intervals) when 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.

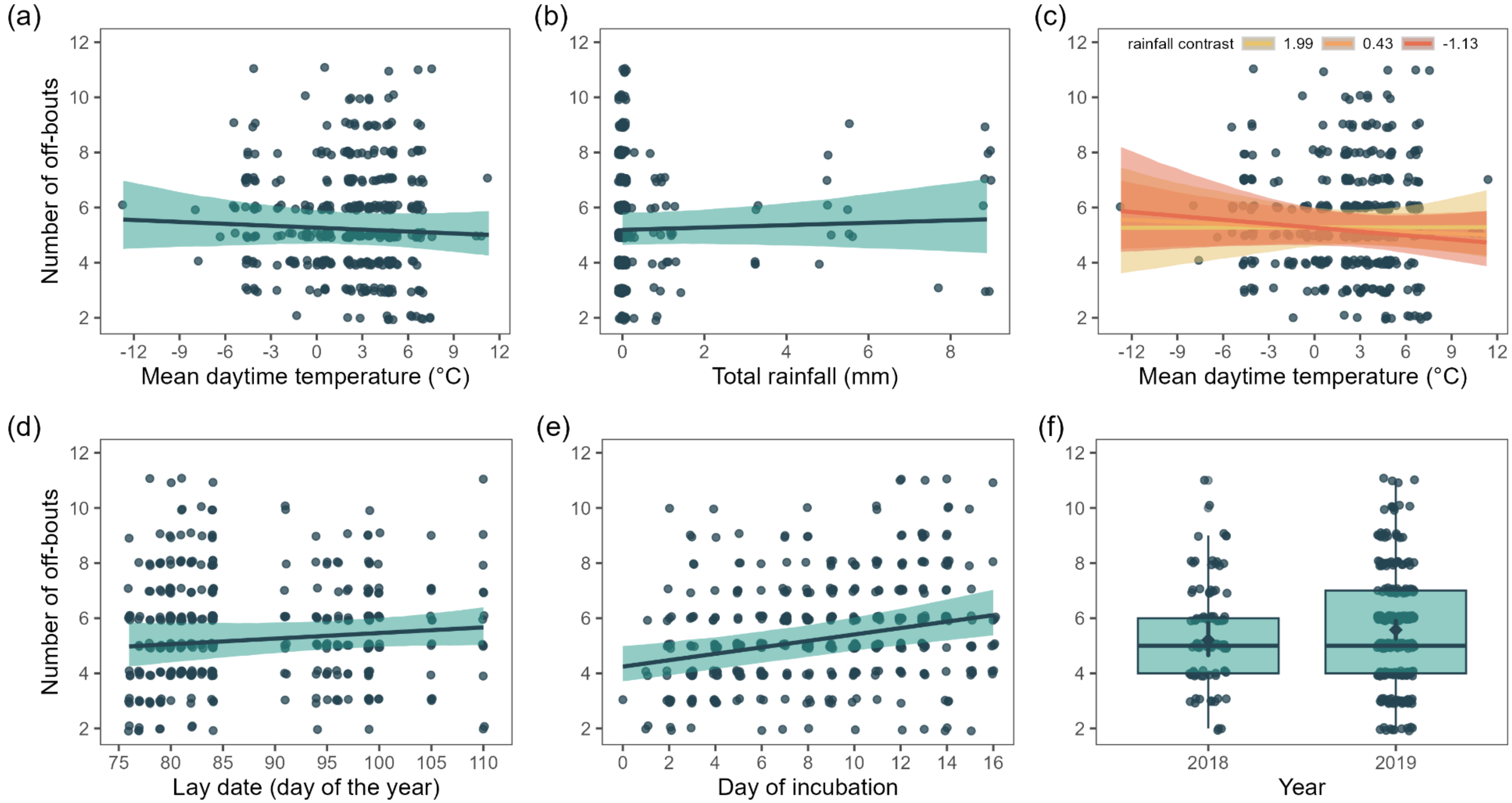

Figure 3. Partial plots of variables hypothesized to influence the daily number of off-bouts of female Canada Jays in Denali National Park and Preserve, Alaska (see hypotheses in Table 1). We investigated whether females adjusted the number of off-bouts in response to two environmental variables: **(a)** 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.

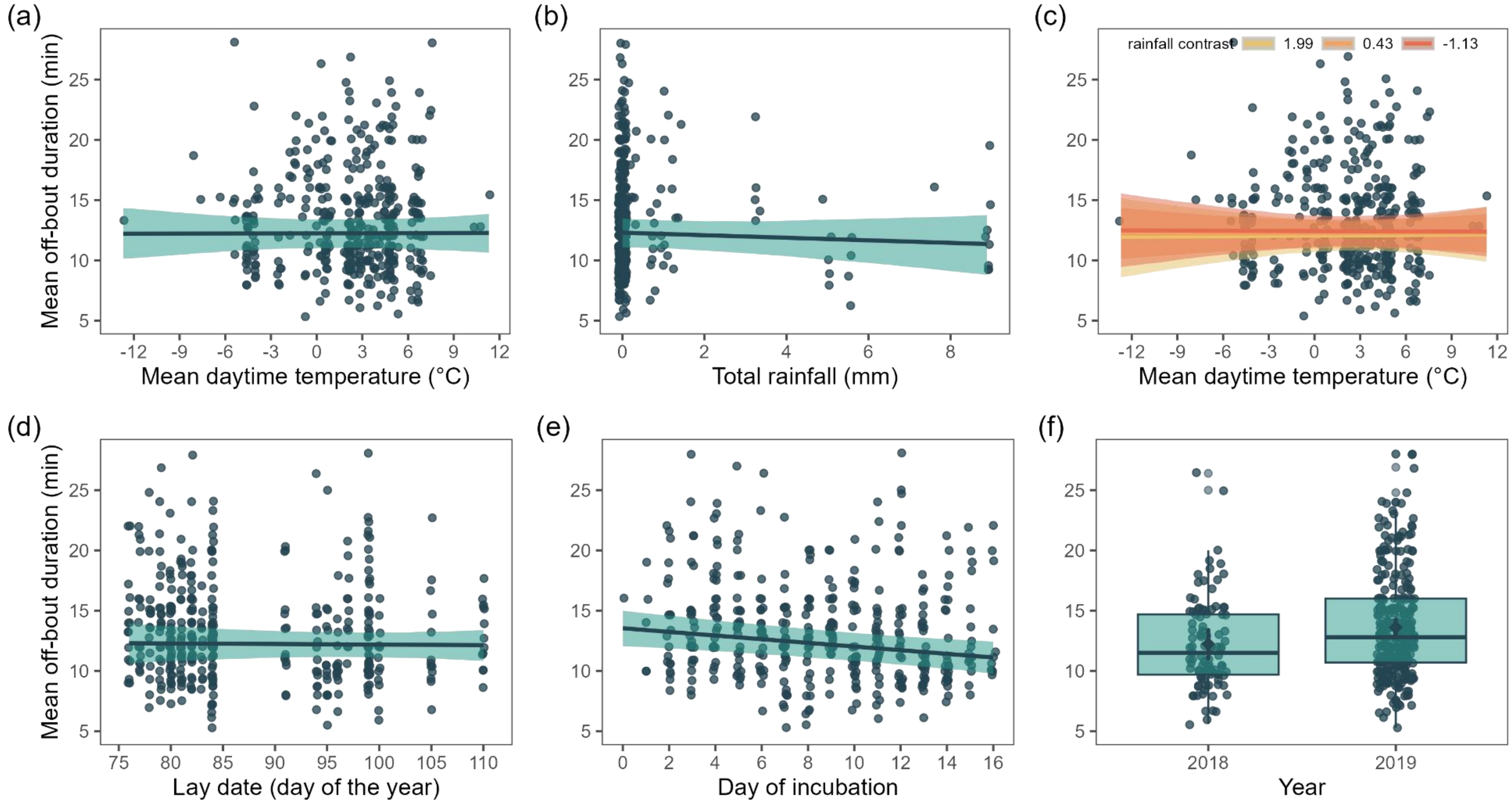

Figure 4. Partial plots of variables hypothesized to influence the daily mean off-bout duration of female Canada Jays in Denali National Park and Preserve, Alaska (see hypotheses in Table 1). We investigated whether females adjusted the number of off-bouts in response to two environmental variables: **(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
		Females that experience warmer temperatures throughout their incubation period will take more off-bouts	Females that experience warmer temperatures throughout their incubation period will take longer off-bouts
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
		Females that experience higher amounts of rainfall during their incubation period will take fewer off-bouts	Females that experience higher amounts of rainfall during their incubation period will take shorter off-bouts
Interaction between temperature and rainfall	The instinct to cover nest and eggs from rainfall trumps self-maintenance activities (e.g., foraging)	Individuals will respond to temperature on days with low rainfall but not on days with high rainfall	Individuals will respond to temperature on days with low rainfall but not on days with high rainfall
		Females that experience low rainfall will show a negative effect of temperature on number of off-bouts, but not those who experience high rainfall	Females that experience low rainfall will show a positive effect of temperature on off-bout duration, but not those who experience 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, standard errors (SE), 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 ± SE	range	mean ± SE	range	mean ± SE	range
Weather						
daytime ambient temperature (°C)[a,b]	0.8 ± 0.4	-12.7 – 12.8	2.8 ± 0.2	-4.6 – 11.3	2.2 ± 0.2	-12.7 – 12.8
daytime rainfall (mm)[b,c]	0.4 ± 0.1	0 – 7.2	0.5 ± 0.1	0 – 8.9	0.4 ± 0.1	0 – 8.9
snow depth (cm) [d]	71.1 ± 0.3	58.0 – 91.4	2.2 ± 0.1	0 – 17.8	19.3 ± 1.5	0 – 91.4
Reproductive parameters						
lay date (day of the year)[e]	92.5 ± 1.3	82 – 101	83.5 ± 1.0	76 – 97	87.3 ± 1.0	76 – 101
cutch size[f]	3.1 ± 0.1	3 – 4	3.8 ± 0.1	3 – 5	3.6 ± .08	3 – 5
Incubation metrics						
daytime nest attentiveness (%)[b,g]	93.6 ± 0.2	85.7 – 97.1	91.8 ± 0.2	74.6 – 97.5	92.2 ± 0.2	74.6 – 97.5
number of off-bouts[b,g]	4.8 ± 0.2	2.0 – 9.0	5.8 ± 0.1	2.0 – 11.0	5.5 ± 0.1	2.0 – 11.0
off-bout duration (min)[b,g]	16.5 ± 0.4	9.0 – 28.0	12.3 ± 0.2	5.0 – 28.0	13.3 ± 0.2	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 Jays in Denali NPP, AK. 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 MATERIAL

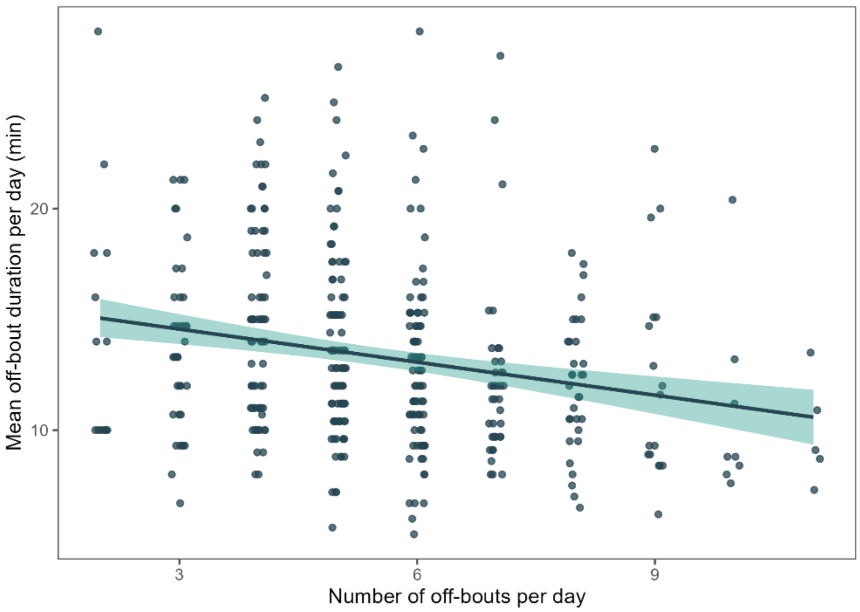

Figure S1. Pearson correlation of daily measurements of the number of off-bouts and mean off-bout duration during the incubation period of Canada Jays in Denali NPP, AK (r = - 0.23, t = - 4.57, p < .00001, n = 391). Points have been jittered along the x-axis in order to better visualize the density of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

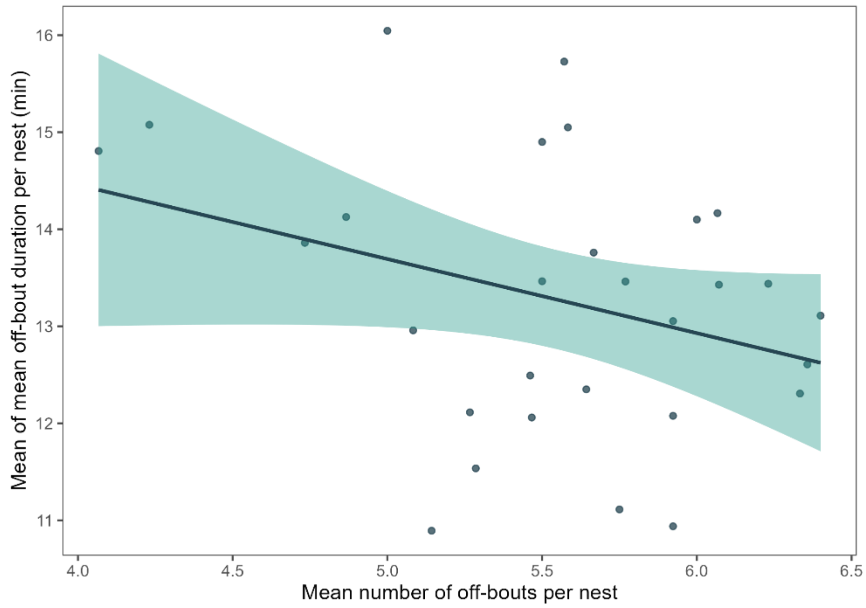

Figure S2. Pearson correlation of average of the number of off-bouts and mean of mean daily off-bout duration (minutes) over the incubation period of 29 nesting attempts from 23 unique Canada Jay females in Denali National Park and Preserve, AK (r = - 0.32, t = -1.77, p = 0.04, n = 29).