Multi-scale landscape effects on incubation behaviours in boreal nesting ducks

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Abstract

Incubation plays a crucial role in embryonic development and influences nest and adult survival in birds. Among most North American duck species, only females incubate eggs and therefore face a trade-off between self-maintenance and incubation. These patterns of attendance represent incubation behaviour and are influenced by various external factors that can affect the overall fitness of females and their offspring, but we lack an understanding of how habitat structure and composition affects incubation behaviour. We measured incubation recess frequency, duration and incubation constancy in four ground-nesting duck species (at five nests of Mallard *Anas platyrhynchos*, 12 Blue-winged Teal *Spatula discors*, five Green-winged Teal *Anas crecca*, and seven American Wigeon *Mareca americana*) across a gradient of natural resource development in the western boreal forest of Alberta, Canada. To quantify incubation patterns, we developed a behaviour identification method using a combination of observer-mediated changepoint analyses and generalized additive models. We then examined the effects of important land cover (*e.g.* marsh), land use (*e.g.* roads) and temperature on incubation behaviour using generalized linear mixed-effect models. Average (± s.e.) daily recess frequency for all species was 2.81 ± 0.251 breaks per day, with an average break duration of 3 h (183.49 ± 29.52 min). Across species, individuals spent on average 67% (0.67 ± 0.038) of their day incubating. Daily recess frequency was positively correlated with secondary roads (*e.g.* winter roads, trails, unmaintained roads), overhead cover at the nest site, marsh habitat and air temperature. Recess duration was positively correlated with average air temperature; incubation constancy was negatively correlated with average air temperature and overhead cover. The results suggested that incubating females take more recesses per day in response to increased land cover, land use and temperature;

and that they adjust the duration of recesses and incubation constancy in response to warmer weather. This research yields baseline information on the incubation behaviour of boreal ducks, and uses a new quantitative approach to describe the effects of habitat structure and composition on the incubation behaviour of ground-nesting ducks in the western boreal forest.

Key words: boreal forest, disturbance, iButton, industrial development, nest attendance.

Nest attendance plays a crucial role in avian reproductive success (White & Kinney 1974; Afton & Paulus 1992) by maintaining temperatures within a narrow range promoting optimal embryonic development (Prince *et al.* 1969; Webb 1987; Manlove & Hepp 2000; Hepp *et al.* 2005; Hepp & Kennamer 2012). Prolonged periods of active incubation also results in faster development rates and healthier, more viable offspring while reducing the risk of nest depredation (Afton & Paulus 1992; Hepp *et al.* 2006; DuRant *et al.* 2013b; Carter *et al.* 2014; Croston *et al.* 2020). However, maintaining incubation temperatures for embryonic development is energetically costly (White & Kinney 1974; Tinbergen & Williams 2002; DuRant *et al.* 2013a; Ringelman & Stupaczuk 2013; Croston *et al.* 2020); therefore, incubating individuals face a trade-off between competing requirements of incubation and self-maintenance (Brown & Fredrickson 1987).

Incubation behaviour varies widely across duck species, linked to life history traits. Ducks exhibit various incubation strategies (Afton & Paulus 1992; Hepp *et al.* 2006), including the energetically demanding uniparental or female-only incubation, which emphasises the stark trade-off between nest attendance and self-maintenance (Johnson *et al.* 1999; Cockburn 2006). The incubating female receives no assistance from the male parent in the form of food provisioning, predator vigilance or nest defence while foraging (Fedy & Martin 2009). Thus, the incubating female must meet her own metabolic needs through resource allocation strategies whereby the female passively relies on limited endogenous reserves, intermittent foraging bouts for compensatory supplementation, or a combination of both to meet the nutritional requirements of incubation (Ankney 1984; Jönsson 1997; Langin *et al.* 2006; Houston *et al.* 2007; Stephens *et al.* 2009). Compensatory foraging results in characteristically similar inattentive periods when females leave the nest to replenish energy reserves (Croston *et al.* 2020), producing a highly variable incubation pattern (Skutch 1957, 1962; Manlove & Hepp 2000). These behaviours are quantifiable and can provide valuable insight into extrinsic factors that influence incubation and reproductive success.

Given the importance of nest attendance for reproductive success, there is a long history of research investigating patterns of attendance (*i.e.* sessions and recesses: Baldwin & Kendeigh 1927; Skutch 1962) and constancy of incubation (Skutch

1962). These patterns have been described in ducks (Skutch 1957; White & Kinney 1974; Afton & Paulus 1992; Deeming 2002) and highlight the significance of incubation temperature for embryonic development (Prince *et al.* 1969; Batt & Cornwell 1972; Webb 1987; Hepp & Kennamer 2012; DuRant *et al.* 2013b), and the physiological demands of incubation on the attending parent (Korschgen 1977; Tinbergen & Williams 2002; DuRant *et al.* 2013a). The extrinsic effects of factors such as weather (Afton 1980; Croston *et al.* 2020; Setash *et al.* 2020), food availability (Maccluskie & Sedinger 1999; Bentzen *et al.* 2010) and depredation (Ringelman & Stupaczuk 2013; Croston *et al.* 2018a) on attendance patterns in ducks have also been well documented, and results vary. Remarkably though, few studies have investigated the effects of habitat structure and composition on incubation, and no one has explored these effects at the macro (*i.e.* home range) and micro (*i.e.* nest site, home range) spatial scales. Furthermore, we do not know how industrial development might affect incubation patterns. Given that habitat characteristics influence duck nest site selection (Dyson *et al.* 2019, 2022; Dyson 2020) across multiple scales, and industrial development alters predator–prey dynamics (Abrams & Ginzburg 2000; Dickie *et al.* 2017, 2020; Muhly *et al.* 2019; Mumma *et al.* 2019), exploring the effects of habitat structure and composition may reveal the mechanisms that influence incubation behaviour in boreal ducks.

It is difficult to obtain accurate data on incubation patterns and nest attendance (Ringelman & Stupaczuk 2013) because it requires constant monitoring of the nesting individual (Croston *et al.* 2018b) which can be detrimental to both the incubating female and nests (Korschgen & Dahlgren 1992; Esler & Grand 1993; Olson & Rohwer 1998; Bolduc & Guillemette 2003). Several solutions exist, including the use of temperature sensors placed in the nest to infer the presence or absence of a female *(*Afton 1980; Flint & Maccluskie 1995; Loos & Rohwer 2004; Bentzen *et al.* 2010; Croston *et al.* 2020), visual identification of the female's attendance behaviour using cameras (Hoover *et al.* 2004; Croston *et al.* 2018a,b; Setash *et al.* 2020), or the use of radio telemetry (Ringelman *et al.* 1982). Each of these approaches and their variations, of course, come with concomitant trade-offs. For example, false eggs with temperature probes accurately measure incubation temperatures experienced by eggs (Flint & Maccluskie 1995), but the addition of one egg can increase energetic demands for incubating females (Tinbergen & Williams 2002; DuRant *et al.* 2013a). The use of simple temperature sensors that do not involve the addition of a false egg is less invasive and has been used to track nest attendance behaviour in various avian species (Cooper & Mills 2005; Schneider & McWilliams 2007; Fedy & Martin 2009; Dallmann *et al.* 2016). The use of cameras may act as a visual cue for potential nest predators but are often inefficient for documenting ground-nesting species because nest activity can be challenging to document through dense ground vegetation (DeGregorio *et al.* 2016; Weston *et al.* 2017).

Accurate identification of incubation rhythms traditionally required challenging analysis of large volumes of temperature sensor data (Hepp *et al.* 2005; Bentzen *et al.* 2010) or camera imagery (Manlove & Hepp 2000; Hoover *et al.* 2004; Loos & Rohwer 2004; Dallmann *et al.* 2016; Setash *et al.* 2020), which necessitated visual inspection to identify incubation recesses manually. Concerns have been raised regarding the objectivity, replicability and internal consistency where multiple researchers are involved (Hoover *et al.* 2004; Schneider & McWilliams 2007; Capilla-Lasheras 2018). Sole use of temperature data to identify recess periods has been criticised due to the high sensor sensitivity causing indistinct temperature fluctuations. However, solutions to this are limited in application with large datasets (Capilla-Lasheras 2018), depend upon specialised software (Cooper & Mills 2005), or require *a priori* knowledge of species incubation temperatures and behaviour to establish required temperature thresholds to identify incubation recesses (Croston *et al.* 2018b). Therefore, an approach that is capable of processing high volume temperature data in open access software, is replicable, applicable to novel species and environments, and identifies incubation recesses in highly variable temperature data, would prove useful for quantifying incubation behaviour.

Canada's western boreal forest is the second most important breeding area for North American duck populations (Slattery *et al.* 2011; Singer *et al.* 2020), making it ideal for exploring duck incubation behaviour. Despite its importance (Slattery *et al.* 2011), however, we know relatively little about the basic life history traits of boreal-nesting ducks compared with ducks in prairie and arctic ecosystems. The boreal region has also recently experienced major industrial development (Fahrig 2003; Slattery *et al.* 2011; Steffen *et al.* 2011; Wells 2011; Hebblewhite 2017; Fisher & Burton 2018) causing extensive landscape alteration and habitat fragmentation (Schmiegelow & Mönkkönen 2002; Fahrig 2003; Fisher & Burton 2018) through resource exploration and infrastructure (*e.g.* road networks and extraction sites: Wells 2011; Hebblewhite 2017). Concomitantly, anthropogenic landscape modifications have shown to benefit predator communities (DeGregorio *et al.* 2014) by facilitating movement (DeMars & Boutin 2017; Dickie *et al.* 2017, 2020; Finnegan *et al.* 2018) and enhancing prey capture efficiency (Abrams & Ginzburg 2000; Muhly *et al.* 2019; Mumma *et al.* 2019). Although nest survival is unaffected by industrial development in this region (Dyson 2020), investigating multi-scale effects of habitat structure on incubation attendance may reveal how incubating females adopt adaptive behaviours in response to increased predator activity.

The goals of our research were to describe the patterns of incubation for multiple species of ground-nesting ducks, and to assess the effect of important macro and micro habitat characteristics that influence nest site selection (Dyson *et al.* 2019, 2022) and incubation patterns. We developed an efficient and replicable approach for processing high volume temperature data, obtained from common and affordable temperature sensors (Ringelman & Stupaczuk 2013; Croston *et al.* 2018, 2021; Stephenson *et al.* 2021) using standard analysis software (*e.g.* Program R) to identify incubation sessions and recesses and address the gaps in our notions of life history and ecological processes of incubation. We examined incubation attendance in four ground-nesting species of ducks (Mallard *Anas platyrhynchos*, Blue-winged Teal *Spatula discors*, Green-winged Teal *Anas crecca* and American Wigeon *Mareca americana*) across a gradient of industrial development in the western boreal forest of Alberta, Canada during the 2017 and 2018 breeding seasons. We hypothesised that land cover, land use and weather would affect incubation attendance. More specifically, we predicted that nesting habitats with greater amounts of linear features (*e.g.* seismic lines, primary and secondary roads) and industrial block features (*e.g.* oil and gas buildings) would result in shorter and more frequent incubation breaks due to avoidance of increased predator and industrial activity. We also predicted that increased amounts of marsh habitat within proximity to the nest would result in shorter, more frequent incubation breaks due to increased accessibility of foraging habitat. Additionally, increased air temperatures and nest site concealment (*i.e.* lateral and overhead cover) would increase the number of breaks taken and prolong the time females spent off the nest due to reduced risk of embryonic shock and detection of the nest. Finally, we predicted no effect of land cover or land use variables on incubation constancy as females would adjust the frequency and duration of their incubation breaks to maintain nest microclimates, but warmer weather would decrease incubation constancy due to reduced need for nest microclimate regulation.

Methods

Study area

Our study area was located within the western boreal forest of Alberta, Canada, north of Slave Lake and south of Red Earth Creek, within a *c.* 100 km radius of Utikuma Lake (Fig. 1). Upland habitats included mixed-wood, deciduous-dominated forests that consist primarily of Trembling Aspen *Populus tremuloides*, Balsam Poplar *Populus balsamifera* and Jack Pine *Pinus banksiana*. Lowland habitats were characterised by conifer-dominated forests, consisting primarily of Black Spruce *Picea mariana*, and multiple wetland communities. In the boreal forest, terrestrial and aquatic communities are regularly influenced by large-scale natural disturbance such as wildfire and insect outbreaks (Schmiegelow & Mönkkönen 2002; Carlson *et al.* 2015; Thom & Seidl 2016). The western boreal forest has also experienced an increased demand for natural resources (*i.e.* oil and gas, and forestry), which adds to the existing anthropogenic footprint (Schmiegelow & Mönkkönen 2002; Slattery *et al.* 2011; Wells 2011; Pasher *et al.* 2014). We selected study sites that represented the natural landscape and anthropogenic disturbance gradients by incorporating development intensities based on cumulative energy development and land cover characteristics. In addition, we considered regional duck density estimates (Ducks Unlimited Canada 2014) and site accessibility. We did not consider any sites that experienced wildfire or logging activity within 20 years. More details on study site selection and description can be found in Dyson *et al.* (2019).

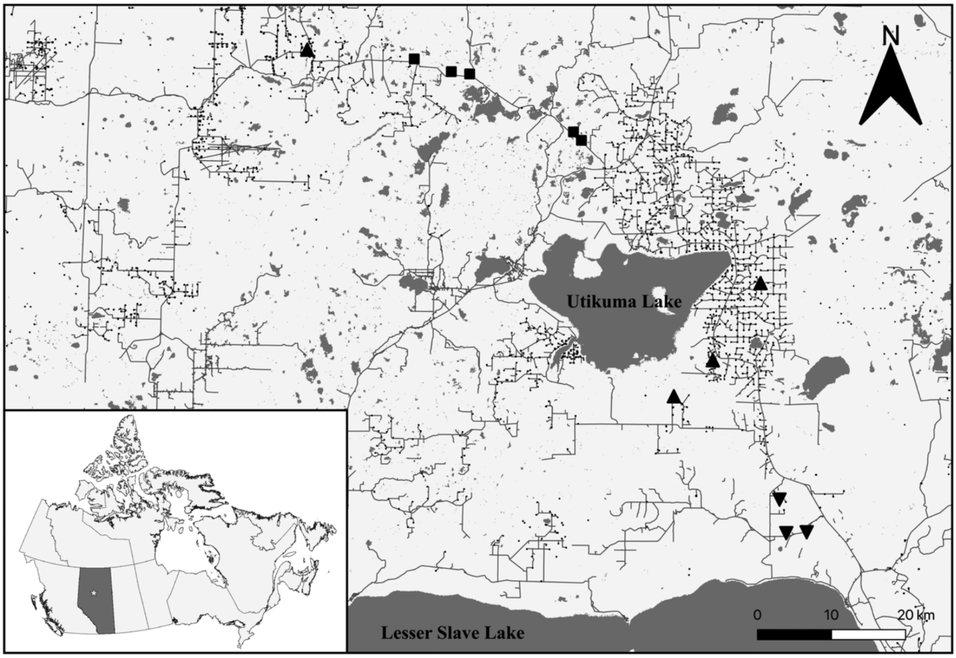

Figure 1. Map of the study area in the Slave Lake Region of Alberta, Canada. Points indicate study site locations where nests were located and are categorised by the cumulative extent of industrial development (low: ▼, medium: ■, high: ▲). The inset map indicates the location of the study area relative to the province of Alberta and Canada.

Nest searching

We searched for nests at 24 sites in 2017, and 25 sites in 2018 on a three-week rotation (15–25 days) between 08:00 h and 16:00 h. We conducted nest-searches on foot with a "willow switch" (*c.* 1.2 m willow branch) to disturb vegetation and increase the probability of flushing an incubating female (Klett *et al.* 1986). The searching process involved three to six technicians walking in unison around wetlands *c.* 5–20 m apart and parallel with the shore. In 2018, we piloted the use of transmitters in addition to nest searching and located three Mallard nests using radio telemetry. At each nest, we identified the species, recorded the number of eggs and estimated the incubation stage using a combination of egg candling and floating (Weller 1956). We recorded nest site variables including lateral and overhead cover, which were measured within five days of a nests predicted or actual hatch date (McConnell *et al.* 2017). We estimated overhead cover of nest bowl vegetation using a 12.5 × 12.5 cm grid with individual 2.5 × 2.5 cm squares from 120 cm above the nest bowl (Guyn & Clark 1997; Borgo & Conover 2016; Dyson *et al.* 2019) and lateral cover using a Robel pole (Robel *et al.* 1970; Nudds 1977; Dyson *et al.* 2019). For a complete description of nest searching and vegetation sampling methods, see Dyson *et al.* (2019).

Nest temperature recording

Nest bowl temperatures were recorded using a Maxim Integrated iButton® temperature datalogger (Maxim Integrated Products Inc., San Jose, CA, USA; Model Number DS1921G-F5; hereafter iButton) from date of nest discovery until termination at 5 min intervals. Up to 30 nests of upland nesting ducks were sampled each year using iButtons. To optimise the spatial distribution of our nest bowl temperature samples, we opportunistically placed iButtons in a limited number of nests to avoid oversampling a site with iButtons. We attached iButtons to 5.8 cm roofing nails using silicone and pressed iButtons into the ground through the bottom of the nest bowl making sure the iButton was slightly protruding above the nest bottom and in contact with the eggs (Ringelman & Stupaczuk 2013). We replaced iButtons on a 7–10 day schedule during regular nest monitoring activities and chose the 5 min interval to ensure we did not exceed the internal storage capacity of the iButton between monitoring events. The location of the iButton meant that temperatures recorded were not indicative of true incubation temperatures experienced by eggs, but served as an index of nest activity (Stephenson *et al.* 2021) which were used to identify incubation sessions and recesses (Ringelman & Stupaczuk 2013; Croston *et al.* 2018b, 2021).

Data processing and recess detection

Temperature data were uploaded from each iButton using Maxim's iButton Blue Dot™ receptor (Model DS1402D-DR8) and OneWireViewer software (Maxim Integrated Products Inc., San Jose, CA, USA). This produced files for each iButton, which included a unique identifier, date, time and temperature records for the predefined time intervals. We replaced iButtons during nest monitoring; therefore, most nests had data contributed from multiple iButtons. We referred to these unique iButton temperature time series within nests as "segments". As a precaution, we trimmed all temperature time series using deployment and removal dates to ensure temperatures recorded during transport were not included. All temperature time series data were processed using a four-step approach including: 1) trim the temperature time series data using a changepoint analysis to isolate the incubation period, 2) smooth incubation rhythms using generalized additive models to better represent the cyclic pattern of the data, 3) identify sessions and recesses using peak and trough identification and variation in temperature change to estimate the duration and patterns of incubation attendance, and 4) a final visual refinement of incubation rhythms to ensure accurate and precise quantification of incubation patterns. Our approaches to each step are outlined below.

We trimmed the raw temperature data to identify behavioural changes (*e.g.* laying, incubating, termination) in our temperature times series and restrict the data to the incubation periods. We identified changepoints based on the raw temperatures for each nest segment using the pruned exact linear time (PELT) algorithm (Killick *et al.* 2012) with a manual penalty of 2*log(number of temperature records) in the *changepoint* package (Killick & Eckley

2014) in Program R (R Core Team 2019). This approach allowed us to detect distinct changepoints in the nest attendance temperature time series (*e.g.* laying, incubating, termination). We visually inspected each identified changepoint (Fig. 2A) and selected the changepoints that identified the initiation and termination of the incubation period (Fig. 2B). This resulted in the removal of segments that did not represent incubation (*i.e.* laying, abandonment, or post-termination).

Step two involved smoothing the temperature time series data to better reveal the cyclic patterns of nest bowl temperatures during incubation. This approach reduced the noise and helped us to identify sessions and recesses in an effective and objective manner. We smoothed incubation rhythms by fitting a generalized additive model (GAM) with a Gaussian distribution (Fig. 2C). The degrees of freedom (d.f.) used for smoothing were calculated by multiplying the length of the time series for each segment by 0.25. This represented a good trade-off between retaining the detail in the raw data and identifying the major patterns in the data. All GAMs were fitted using the mgcv (Wood 2011) package in R (R Core Team 2019). All subsequent steps were implemented on the model-predicted values.

Step three required the identification of the start and end of incubation sessions and recesses. This was achieved by identifying the peaks and troughs (local minima and maxima) which indicated the start and end points of incubation sessions and recesses using model-predicted temperature values and an inflection function. We used a conservative threshold in the inflection function for the identification of peaks and troughs, intentionally biasing our data towards Type I errors and identifying all peaks and troughs (Fig. 2D). Incubation sessions were indicated by an increase in temperature and recesses were indicated by a decrease in temperature. A false positive in these types of data represents the identification of either the beginning or end of an incubation recess or session. Filtering false positives is commonly completed using a change in temperature (Δtemp) threshold where any temperature change that is < x°C is not considered a "true" change in the incubation status.

Various thresholds have been reported for recess detection in waterfowl (Manlove & Hepp 2000; Hoover *et al.* 2004; Loos & Rohwer 2004; Bentzen *et al.* 2010; Croston *et al.* 2018b); however, variation among individuals and species means these thresholds are likely not appropriate for all temperature data (Loos 1999; Hoover *et al.* 2004). This is important because small variations in temperature (*e.g.* 1°C) can have dramatic effects on the estimation of the duration and frequency of incubation sessions and recesses. Rather than choosing an absolute change in temperature value for all nests and species, and since we are working with model-predicted values, the distribution of the model-predicted temperature data for each nest segment was used to inform the selection of an appropriate value. We calculated the change between sequential peaks and troughs and refer to these values as the *Trend Temperature* (TT). For example, the change in

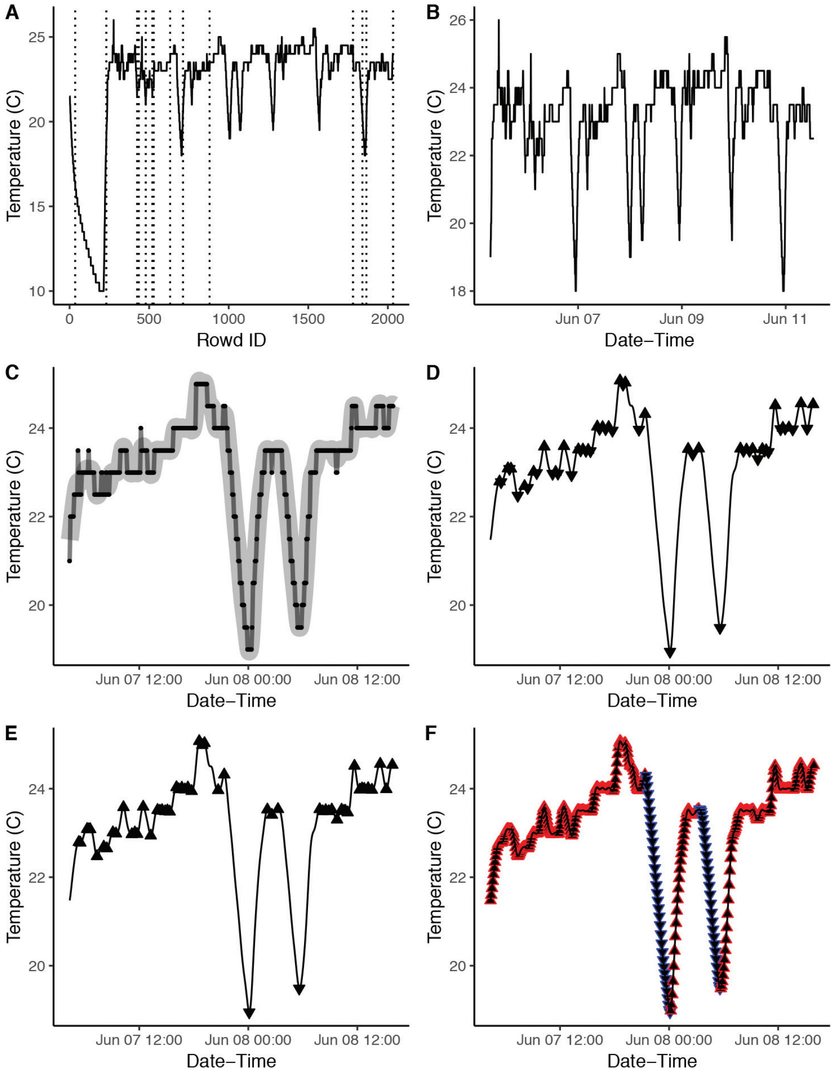

Figure 2. Process plots highlighting key steps in the analysis for temperature time series data from a single nest segment. A) Raw temperature data collected from iButton probes (solid black line) with changepoint locations (hashed line); B) Changepoint adjusted temperature time series representing the incubation rhythm in the segment; C) 48 h segment of the model-predicted incubation rhythm (bolded grey buffer) with raw incubation rhythm overlay (dark grey line) and raw temperature records (black points) overlay; D) 48 h portion of the model-predicted incubation rhythm (black line) with over-estimated peaks (▲) and troughs (▼); E) 48 h portion of the model-predicted incubation rhythm (black line) with threshold-adjusted peaks (▲) and troughs (▲); F) 48 h portion of the model predicted incubation rhythm (black line) with colour-coded sessions (▲) and recesses (▼).

temperature between a peak and trough is assigned a recess *Trend Temperature* ($\text{Recess}_{\text{TT}}$), and the change in temperature between that trough and the next sequential peak is assigned session *Trend Temperature* ($\text{Session}_{\text{TT}}$). We then used the distribution of each nest's specific *Trend Temperature* (*i.e.* $\text{Session}_{\text{TT}}$ and $\text{Recess}_{\text{TT}}$) to set a nest-dependent change in temperature value. The change in temperature value was determined for each individual nest segment using the standard deviation (s.d.) of *Trend Temperature* in each segment. If the *Trend Temperature* between adjacent peaks and troughs was greater than the *Trend Temperature* s.d, we considered it a "true" session or recess. Using the "true" peaks and troughs (Fig. 2E), we filled the gaps with our remaining model-predicted values and assigned behaviour-specific identifiers (Fig. 2F).

As the final (4th) step, we trimmed nest segments that started or finished with a recess to the first and last distinct session to remove any recesses caused by technician disturbance or termination (*e.g.* hatch, abandonment, depredation). In addition, we removed all nests with ≤ 48 h of data following session and recess identification.

Analysis

Variable development. We used three daily metrics that describe incubation behaviour. Recess frequency was a count of the incubation breaks (*i.e.* recesses) taken between 00:00 and 23:59 h. Recess duration was measured as the average amount of time a female spent in recess, between 00:00 and 23:59 h each day. Incubation constancy was measured as the proportion of time a female spent incubating (*i.e.* in session) each day. We calculated daily constancy by dividing the total daily duration of sessions by the sum of the duration of all sessions and recess for a given day (Skutch 1962). We estimated sunrise/sunset time (05:30–21:30 h) across the study period and considered a recess to have occurred during the day if it took place between 05:30 h and 21:30 h, and at night if it occurred outside of those hours. We did not always have nest temperature records for an entire 24-hour period (*e.g.* date of discovery, memory shortage) but felt it was unnecessary to remove incomplete days (< 24 h) that were part of complete segments. Therefore, we included all temperature records for incomplete days during the incubation period and accounted for varying period lengths statistically. We report means and standard errors for each metric unless otherwise noted.

To measure effects of habitat on incubation behaviour, we evaluated important nest site characteristics (*e.g.* lateral and overhead cover) that influence nest site selection at fine spatial scales (Dyson *et al.* 2019). In addition, we developed landscape covariates using spatial layers that represented land cover (*i.e.* habitat) and land use (*i.e.* industrial development) features known to influence nest site selection at broader spatial scales in the region (Dyson *et al.* 2022). Land cover variables were developed from Ducks Unlimited Canada's Enhanced Wetland Classification layer (Ducks Unlimited Canada 2011), and included nest site variables. Land use layers were developed from the Alberta Biodiversity Monitoring Institutes (ABMI) Human Features Inventory database (ABMI

2017). Polygonal features, such as well pads and pump stations, represented the per cent area within a 30 m × 30 m pixel; and line features, such as pipelines and roads, were represented as the sum of the length of each line feature (km) in a 30 m × 30 m pixel. All land use and land cover covariates were then summarised based on a 1,000 m radial buffer with the nest location as the centroid (Table 1).

Table 1. Descriptions and unstandardised ranges for fixed-effect land cover and land use predictors used in our frequency, duration, and incubation constancy models for four species of upland nesting ducks in Alberta's western boreal forest.

Covariate	Scale	Description	Range
Land cover			
Marsh	Landscape	Land cover – Aquatic Bed, Mudflats, Emergent, and Meadow Marsh measured as proportional area (%)	0–10
Lateral Cover	Nest site	Land cover – Nest site measurement of per cent lateral cover from all cardinal directions represented as average proportion for all directions (%)	9.08–83.96
Overhead Cover	Nest site	Land cover – Nest site measurement of per cent overhead cover from 1m above the nest presented as average proportion (%)	7.6–100
Land use			
Primary Roads	Landscape	Land use – Maintained roads (*i.e.* paved and gravel roads) measured as total length (km)	0–13.69
Secondary Roads	Landscape	Land use – Unmaintained roads (*i.e.* winter roads and trails) measured as total length (km)	0–3.89
Seismic Lines	Landscape	Land use – All seismic lines measured as total length (km)	5.81–35.07
Industrials	Landscape	Land use – Industrial block features (*i.e.* camps, facilities, oil and gas buildings, gas plants etc.) measured as proportional area (%)	0–2
Weather			
Air temperature	Landscape	Average air temperature for a 24-hour period (°C)	5.09–20.50

To assess the influence of weather, we paired each nest with local climate data from the nearest active weather station. Average daily temperatures (°C) were obtained from the Alberta Agriculture and Forestry meteorological station in Marten Hills (55.53°N, 114.56°W), accessed through the Alberta Climate Information Service (ACIS) systems.

Model development. The influence of all covariates were modelled for each of our three response variables representing incubation patterns (*i.e.* frequency, duration and constancy) using generalized linear mixed-effects models (lme4 package, Bates *et al.* 2015) in R (R Core Team 2019). We included important land cover and land use variables identified by the top micro and macro nest site selection models proposed by Dyson (2020). Variables were not included in the same model if Pearson's r > |0.65|. On identifying highly correlated variables, we selected individual variables that were the most relevant for exploring our questions and underlying hypotheses for inclusion in the model. For example, roads and pipelines in the western boreal are often constructed in unison and sometimes share the cleared corridors through the dense forest landscape. However, evidence suggests roads (*i.e.* primary and secondary) play an important role in boreal duck nest site selection (Dyson *et al.* 2022), and primary road (*i.e.* paved, gravel) densities are positively correlated with nest survival (Roy 2018; Dyson 2020); thus, we selected roads as a practical predictor variable. Prior to analysis, we standardised all predictor variables and visually inspected the species-specific distribution of the response variables, using box and whisker plots to confirm overlap among species and justify the pooling of all species in the data.

Our global model for each of the three response variables incorporated three land cover, four land use and one weather covariate as fixed effects (Table 1) and a unique nest identifier as a random effect. Recess frequency data are discrete counts and were fitted using a Poisson distribution with a log-link function (Zurr *et al.* 2009). Prior to analysis, we log-transformed recess duration to meet the requirements of homoscedasticity (Zurr *et al.* 2009) and fitted models to these data using a gamma distribution with an inverse logit-link function (Hardin & Hilbe 2007). The incubation constancy data were proportional and therefore linear mixed-effects models were fitted to these data using a weighted binomial distribution with a logit-link function (Bolker *et al.* 2009; Zurr *et al.* 2009; Bates *et al.* 2015). We weighted observations using the combined daily duration of sessions and recesses (*i.e.* daily total) to account for days with < 24 h of data. For each response variable, we ranked models using Akaike's Information Criterion corrected for small sample size (AICc) and removed nested subsets of the top model that contained uninformative parameters and present all competing models within 2 ΔAICc units of the top model (Arnold 2010). The top ranked model with the lowest ΔAICc unit was selected for interpretation (Burnham & Anderson 2004).

Results

We were able to use iButton data from 29 nests (25% iButton failure rate), for five

Mallard, 12 Blue-winged Teal, five Green-winged Teal and seven American Wigeon. Use of the inflection function to detect peaks and troughs identified a total of 823 recesses across all species and nests. We documented 163 incubation recesses for Mallard, of which 73% occurred during the day (05:30–21:30 h). For Blue-winged Teal, we identified 249 recesses, with 81% occurring during the day. Data availability for American Wigeon and Green-winged Teal were similar with 208 and 203 recesses, of which 67% and 72% were taken during the day, respectively. Approximately 35% of recesses were detected at night (213 at night; 610 during daylight) across all species (Fig. 3).

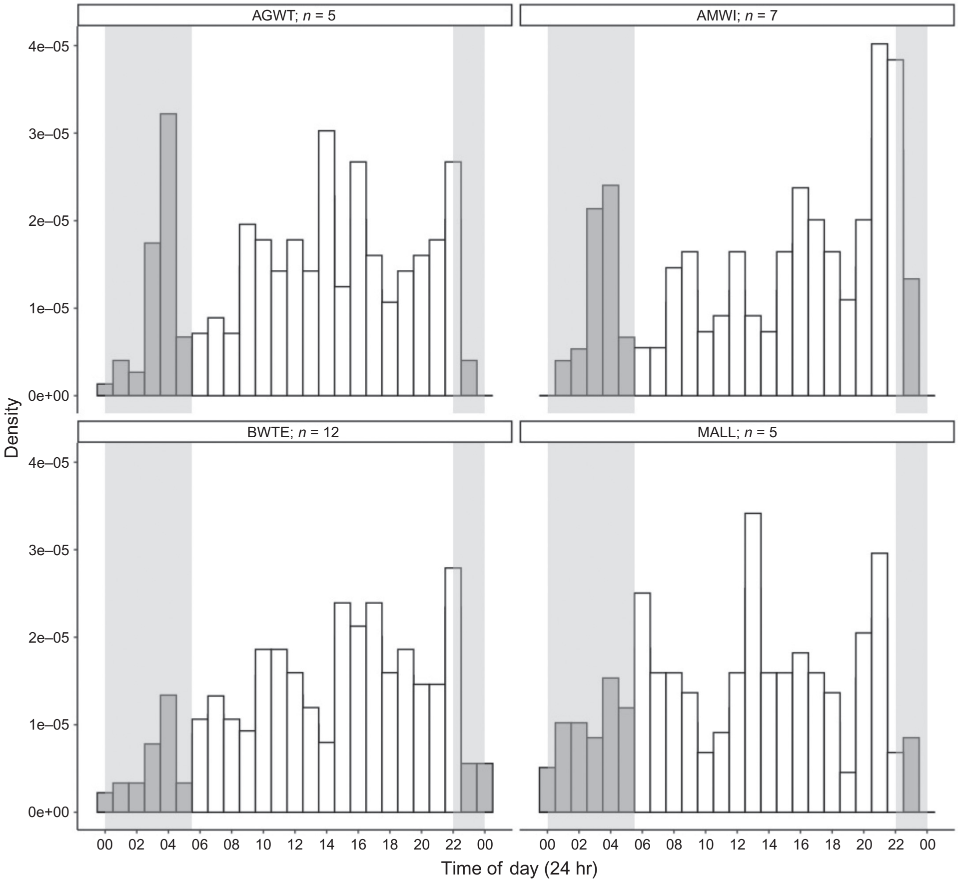

Figure 3. Density distributions of recess start times during the 24-hour day for four species of upland nesting ducks in Alberta's western boreal forest. Shaded areas and dark bars represent estimated night periods (21:30–05:30 h). Individual plot sub-titles indicate species four letter USGS codes, and *n* represents the number of nests. Species codes: AGWT = Green-winged Teal, AMWI = American Wigeon, BWTE = Blue-winged Teal, MALL = Mallard.

Table 2. Summary of recess frequency, duration and incubation constancy in four species of ground-nesting duck species in the boreal forest, Alberta, Canada during the 2017–2018 nesting period. Mean values are given ± s.e.

	All species	**Green-winged Teal (*n* = 5)**	**AmericanWigeon (*n* = 7)**	**Blue-winged Teal (*n* = 12)**	**Mallard (*n* = 5)**
Frequency					
Mean	2.81 ± 0.25	3.45 ± 0.29	2.54 ± 0.21	2.62 ± 0.22	2.85 ± 0.27
Max	–	6	6	6	7
Min	–	1	1	1	1
Duration					
Mean	183.50 ± 29.52	163.52 ± 26.16	208.53 ± 42.78	177.29 ± 19.90	178.23 ± 21.47
Max (h)	–	25.75	32	15.8	22.5
Min (min)	–	20	25	25	25
Constancy					
Mean	0.67 ± 0.038	0.65 ± 0.036	0.66 ± 0.041	0.67 ± 0.037	0.69 ± 0.036
Max	–	0.871	0.925	0.891	0.883
Min	–	0.035	0.010	0.069	0.066

Summary statistics for measures of incubation behaviour varied across species (Table 2). Mean daily recess frequency was the greatest numerically for Green-winged Teal and the lowest for American Wigeon. The maximum number of recesses recorded in a single day was seven for Mallard, and six for all other species. Mean recess duration was greatest numerically in American Wigeon. The minimum recess duration we detected was in Blue-winged Teal and the longest was in American Wigeon. Mean incubation constancy was greatest numerically in Mallard, and the maximum and minimum incubation constancy we observed within a complete 24 h time period was in American Wigeon.

Our top ranked recess frequency model included land cover, land use and weather covariates (Table 3). There were four competing models in our candidate set within 2 ΔAICc units. The remaining models were within *c.* 6 ΔAICc units and included non-nested combinations of the top covariates. There was a response by nesting females to secondary roads (*e.g.*

Table 3. Non-nested generalized linear mixed model set for incubation recess frequency, duration, and constancy in four species of ground-nesting duck species in the boreal forest, Alberta, Canada during the 2017–2018 nesting periods. Model sets represent non-nested competing models within 2 AICc units of the top ranked model.

Model	**K**	**Ll**	**ΔAICc**[a]	w_i
Recess frequency				
Avg. air temperature + Marsh + Secondary roads + Avg. overhead cover	4	–505.4	0	0.26
Marsh + Secondary roads + Avg. overhead cover	3	–506.62	0.35	0.21
Avg. air temperature + Secondary roads + Avg. overhead cover	3	–506.93	0.98	0.16
Marsh + Secondary roads	2	–508	1.06	0.15
Secondary roads + Avg. overhead cover	2	–509.26	1.57	0.12
Recess duration				
Avg. air temperature	1	–253.23	0	0.82
Incubation constancy				
Avg. air temperature + Avg. overhead cover	2	–950.85	0	0.58
Avg. air temperature	1	–952.19	0.62	0.42

[a] Lowest AICc unit for recess frequency = 1,023.09, recess duration = 514.60, and incubation constancy = 1,909.82.

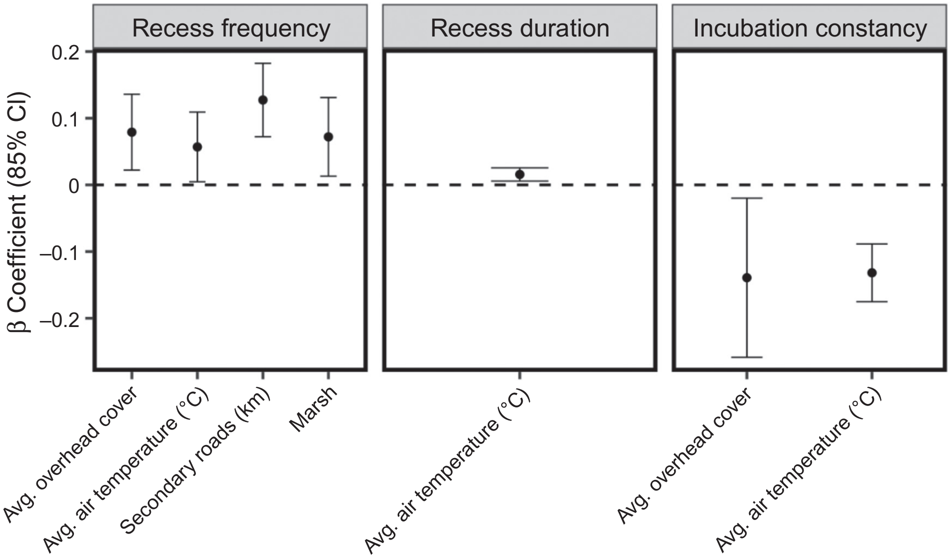

Figure 4. Coefficient estimate plots for fixed effects in the top ranked recess frequency, duration and incubation constancy models for upland nesting ducks in the boreal forest, Alberta, Canada, from 2017–2018. Error bars = 85% confidence intervals.

winter roads, trails, unmaintained roads; Fig. 4), such that an increase in road density (*i.e.* total length) surrounding nests was correlated with an increased number of recesses taken daily (Fig. 5). There was also a positive response to overhead cover at the nest site, suggesting that increased overhead cover increased the number of recesses. We additionally detected an effect of marsh habitat on daily recess frequency, such that increased marsh habitat within 1 km of the nest resulted in increased daily recess frequency.

For recess duration, the best model included only average air temperature and no land cover or land use covariates (Table 3). The next competing model, excluding all nested combinations, was > 3 ΔAICc units and was the null model. We observed a positive effect of average air temperature on recess duration (Fig. 4) suggesting that warmer temperatures resulted in longer incubation recesses (Fig. 5).

The top ranked model in our model set for incubation constancy included average air temperature and overhead cover and did not include land use covariates (Table 3). Excluding all nested combinations, the next competing model was < 1 ΔAICc unit and did not include overhead cover. The remaining model was > 17 ΔAICc units and was the null model. We detected a negative effect of average air temperature on incubation constancy (Fig. 4), such that females spent a greater proportion of time off the nest during warmer weather (Fig. 5). We also observed a negative response to overhead cover at the nest site (Fig. 4), indicating that increased overhead cover

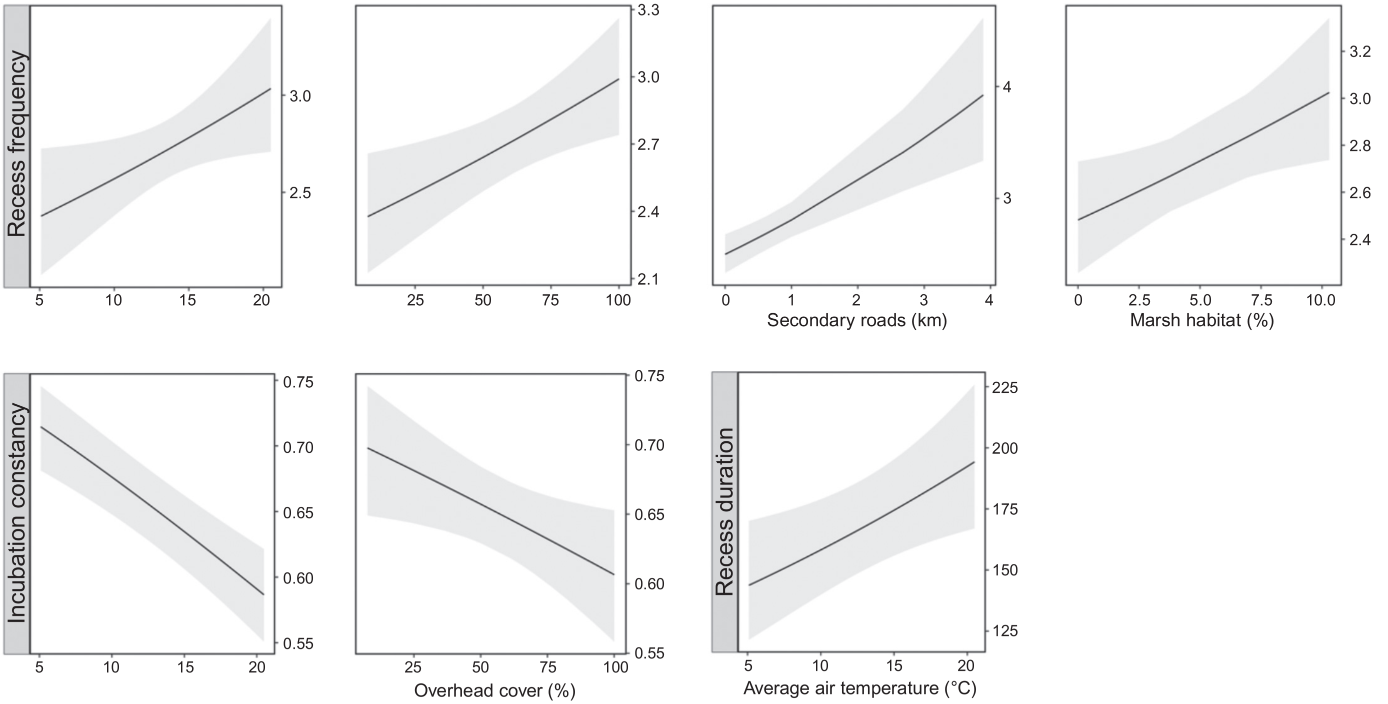

Figure 5. Predicted effects plots for incubation recess frequency, duration and constancy in ground-nesting ducks in the boreal forest, Alberta, Canada from 2017–2018 nesting periods. Plots represent the response from ground-nesting ducks to predictor variables. Shaded areas = 85% confidence intervals.

reduced daily incubation constancy (Fig. 5), although visual inspection of the residuals suggested a weak model fit at the upper and lower extremes of the model. In addition, we did not observe any differences across species for any of our three models.

Discussion

We described incubation patterns and presented quantified measures of incubation attendance for ducks nesting in the western boreal forest using simple nest temperature sensing. The changepoint analysis and use of GAMs provides a rapid and reproducible means of identifying and quantifying incubation duration, sessions and recesses from temperature probe data using standard statistical software across species. Our results provide a valuable baseline for incubation studies in the boreal forest and contribute new information on boreal waterfowl life histories and ecology.

Overall, our findings were generally consistent with our predictions. Greater marsh habitat area and densities of secondary roads (*e.g.* winter roads, trails, unmaintained roads) close to the nest led to increased recess frequencies but did not affect recess duration or incubation constancy. Against our predictions, recess frequency was positively correlated with warmer air temperatures, but recess durations and reduced incubation constancy increased, which was consistent with predictions. Overhead cover at the nest site and incubation constancy were negatively correlated, against expectations and we failed to detect effects of industrial block features on any of our three incubation behaviour measures.

Previous approaches to quantifying incubation behaviour in ducks used time-consuming and costly methods (Hoover *et al.* 2004; Schneider & McWilliams 2007; Capilla-Lasheras 2018) requiring constant observer mediation (Cooper & Mills 2005) or a prior understanding of the study species (Croston *et al.* 2018b). iButtons offer a cost-effective way to record nest bowl activity (Ringelman & Stupaczuk 2013; Croston *et al.* 2018b, 2021) that reduces observer and equipment disturbance at the nest (Stephenson *et al.* 2021) compared with alternative approaches (*i.e.* addition of false eggs: Erikstad & Tveraa 1995; DuRant *et al.* 2013a). The implementation of flexible temperature thresholds based on the distribution of model-predicted nest bowl temperatures, accounting for the inter- and intra-species variation, also eases concerns regarding application of species thresholds. One potential limitation of our approach arises from the dense layers of down that ducks use to insulate their nests, which may have masked minor temperature fluctuations detected by the iButtons, hindering our ability to detect the onset and duration of short recesses and sessions.

Comparison of incubation behaviours across waterfowl species (*i.e.* Mallard *vs.* Blue-winged Teal) can be limited by differences in observed nesting behaviours (*e.g.* cavity, upland, over water) and breeding strategies (*i.e.* capital and income). However, studies of species relatedness (Wilson *et al.* 2012), breeding strategies and nesting behaviours (Connelly & Ball 1984) suggests that Blue-winged Teal and Cinnamon Teal *A. cyanoptera* are similar, and therefore it is reasonable to compare measures of incubation. Breeding Cinnamon Teal have been shown to have an average daily recess frequency of 2.02, with durations ranging from 0.1–1.5 h (6.57–96.8 min) and an incubation constancy of 0.894 (Setash *et al.* 2020). Blue-winged Teal in our study took comparatively more recesses per day (2.54), with longer recess durations (177 min) and lower incubation constancy (0.67). Previous research on Mallard reported a daily recess frequency of 1.69 and recess duration of 1.75–2.5 h (106.11–155.39 min; Croston *et al.* 2020). Similarly, Ringelman & Stupaczuk (2013) reported a combined daily recess frequency in Mallard and Gadwall of 1.7, with recess durations of ~3 h (171 min). Our average daily recess frequency for Mallard was 40% higher (2.85); however, our recess duration in Mallard was similar to the two previous studies at ~3 h (178.23 min). Overall, our results suggests that Mallard and Blue-winged Teal consistently took more daily recesses, which were longer for Blue-winged Teal but similar in duration for Mallard when compared with previous research.

Within-species variation in incubation patterns are influenced by several factors including habitat (Ringelman *et al.* 1982; Maccluskie & Sedinger 1999; Bentzen *et al.* 2010). Our results are consistent with patterns reported for other species in which populations further north tend to take more incubation breaks. For example, female Northern Shovelers *Spatula clypeata* took twice as many breaks and had lower constancy at a northern study site in Alaska compared with those nesting further south in Manitoba, but recess duration was similar (Maccluskie & Sedinger 1999). The measures of recess frequency, duration and incubation constancy that we report represent ducks in the western boreal forest and indicate that Mallard and teal take more breaks than their southern breeding conspecifics (Ringelman & Stupaczuk 2013; Croston *et al.* 2020; Setash *et al.* 2020). As habitat and latitude co-vary, these differences may be further evidence of latitudinal variation in incubation patterns (Chalfoun & Martin 2007) and represent behavioural adaptations required to meet the demands of incubation in more northerly habitats such as increased foraging due to food limitations (Maccluskie & Sedinger 1999) and predator avoidance in response to elevated risk of female mortality (Martin 2002). However, the exact mechanisms driving this variation would require further examination.

The influence of local ambient temperature on incubation behaviour has been the focus of many studies which show that warmer ambient temperatures are generally associated with increased recess frequency, longer recess durations and decreased incubation constancy (Afton 1980; Ringelman *et al.* 1982; Ringelman & Stupaczuk 2013; Croston *et al.* 2020). Our results were congruent with this previous research; all three of our top models indicated that females took longer, more frequent breaks, and spent less time on their nest during warmer days. Microclimates differ between nest sites (Gloutney & Clark 1997); therefore, to model ambient temperature effects on incubation behaviour accurately, future research could record ambient temperature using additional iButtons outside of the nest bowl or installing weather stations to report more localised ambient temperature patterns than have we here.

The habitat a species occupies influences all aspects of the individual's behaviour and fitness (Block & Brennan 1993; Jones 2001; Kaminski & Elmberg 2014; Boyce *et al.* 2016). Incubation behaviour can impact both survival and reproduction, and has been studied for multiple duck species across North America (Afton 1980; Ringelman *et al.* 1982; Mallory & Weatherhead 1993; Maccluskie & Sedinger 1999; Hoover *et al.* 2004). However, few studies have quantified the effects of habitat structure on incubation behaviour. Previous research suggested that microscale (*e.g.* nest site) habitat characteristics such as overhead cover did not have an effect on incubation behaviour (Setash *et al.* 2020). However, we observed a positive response to overhead cover in our top recess frequency and incubation constancy models, likely because of the added benefits it provides during incubation (*e.g.* nest concealment and microclimate regulation: Gloutney & Clark 1997; Fogarty *et al.* 2017). Our recess frequency results are consistent with Zicus (1995), in that females took more recesses when functional foraging habitat (*i.e.* marsh) was close to the nest (presumably to forage; Afton 1979, 1980); however, we found no effect of marsh habitat on recess duration nor incubation constancy. This may indicate a trade-off between self-maintenance and incubation attendance, with females reducing the duration of their breaks to maintain overall constancy and optimise microclimate for embryonic development. Remarkably, our findings serve as the first quantified evidence regarding the multi-scale effects of nest site and surrounding habitat characteristics on incubation behaviour in ducks.

The influence of industrial development on nest success in ducks has received attention in prairie (Ludlow & Davis 2018; Skaggs *et al.* 2020) and hemi-boreal (Roy 2018) regions, and we are only beginning to understand the relationship between industrial development and ducks in the western boreal forest (Dyson *et al.* 2019, 2020, 2022; Slattery *et al.* 2011), and industrial development effects on incubation behaviour. The inclusion of road categories was illuminating, as primary road (*i.e.* paved, gravel) densities and nest survival are positively correlated (Roy 2018; Dyson *et al.* 2022), likely because many mammalian predators avoid roads (Tucker *et al.* 2018). However, our results indicated that nest sites surrounded with high densities of secondary roads (*e.g.* winter roads, decommissioned vegetated roads, trails) had a higher recess frequency, which can have a negative influence on survival and embryonic development.

Predator avoidance and increased foraging behaviours are two potential hypotheses that explain the correlations with secondary roads. Certain linear features (*e.g.* secondary roads, seismic lines) have shown to facilitate predator movement (DeMars & Boutin 2017; Finnegan *et al.* 2018), and the characteristics of secondary roads make them ideal travel corridors (Trombulak & Frissell 2000; Randa & Yunger 2006; Fahrig & Rytwinski 2009; Roy 2018) that could increase foraging success rates (Abrams & Ginzburg 2000; Muhly *et al.* 2019; Mumma *et al.* 2019). Depredation is the primary limiting factor of nest success in ducks (Clark & Shutler 1999; Martin 1995; Simpson *et al.* 2005; Pieron & Rohwer 2010; Howerter *et al.* 2014). Flushing off the nest is a defence tactic used by attending females (Forbes *et al.* 1994; Gunness *et al.* 2001; Dassow *et al.* 2012); thus, increased recess frequency may be indicative of females flushing to avoid depredation. For example, if greater secondary roads densities increases nest depredation risk (*i.e.* elevated predator activity), then females should devote less energy to their nest due to reduced likelihood of survival (Ringelman & Stupaczuk 2013) and are more likely to flush from the nest in response to predator-induced disturbance (Dassow *et al.* 2012).

Conversely, nesting habitats with higher densities of secondary roads may have fewer predators and provide females with increased foraging opportunities because of decreased predator pressure. If recesses were taken at appropriate times (*i.e.* during the warmer periods of the day; Brown & Fredrickson 1987), nest microclimates could be maintained for embryonic development (Webb 1987) with limited concern for nest concealment (Kreisinger & Albrecht 2008). Depending on forage availability, this behaviour could also be more energetically costly (Caldwell & Cornwell 1976) and extend the incubation period, increasing the potential for abandonment (Korschgen & Dahlgren 1992; Esler & Grand 1993) and depredation (Afton & Paulus 1992; Bolduc & Guillemette 2003). Secondary roads did not influence incubation constancy or recess duration, suggesting that while females took more breaks, they did not spend more time off the nest, although it is unclear whether these were predator-induced recesses or increased foraging recesses. A companion study investigating the occupancy of boreal duck predators (Dyson *et al.* 2020) found increasing probability of site occupancy for bear *Ursus* sp., Wolves *Canis lupus* and Coyotes *Canis latrans* with increasing human footprint, but was unable to differentiate impacts between primary and secondary roads (Dyson *et al.* 2022). Thus, future research may consider investigating the exact mechanisms driving increased recess frequency.

Ducks nest at low densities in the boreal forest, making it difficult to locate nests. Previous research adapted for the prairie regions suggested that the optimal time to search for duck nests was between 08:00 and 14:00 h (Gloutney *et al.* 1993). We detected incubation recesses at every hour during the entire 24-hour day (Fig. 3). Given that the observers are dependent on flushing the female to locate the nest, traditional upland nest searching methods (Klett *et al.* 1986) and time-frames may not be a feasible option. Though we cannot recommend an optimal time to search for nests, the implementation of alternative nest searching approaches such as drones (Bushaw *et al.* 2020) may allow researchers to cover larger areas in a shorter amount of time, potentially increasing nest discovery rates.

Conclusion

We developed a new method to objectively and efficiently quantify incubation behaviour in ground-nesting ducks, using cost-effective temperature loggers and produced baseline life history information regarding the recess frequency, duration and incubation constancy in four species of boreal ground-nesting ducks. This also allowed us to investigate multi-scale relationships between land cover, land use, weather and incubation behaviour. The findings supported our hypotheses that land cover, land use and weather affect incubation behaviour, and were generally consistent with our predictions. Females took frequent, short recesses during high ambient temperatures, reducing incubation constancy. Females also took more nest recesses when surrounded with greater densities of linear features (*i.e.* secondary roads) and foraging habitat (*i.e.* marsh), and when nests were better concealed with dense overhead cover, reducing incubation constancy. The increased measures of recess frequency reported here are the first quantified effects of land use characteristics on incubation behaviour in ducks and represent the potential impacts of continued industrial development on boreal nesting ducks. Ultimately, our research addresses important questions concerning the behavioural response of ducks to changes in ecosystem structure and function during their most crucial life stage. Therefore, these data and our findings may prove useful for making predictions about waterfowl population trajectories relative to landscape change in the future.

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References

Abrams, P.A. & Ginzburg, L.R. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15: 337–341.

Afton, A.D. 1979. Time budget of breeding Northern Shovelers. *Wilson Bulletin* 91: 42–49.

Afton, A.D. 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* 82: 132–137.

Afton, A.D. & Paulus, S.L. 1992. : Incubation and brood care. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 62–108. University of Minnesota Press, Minneapolis, USA.

Alberta Biodiversity Monitoring Institute. 2020. *Human Footprint Inventory 2018*. Alberta Biodiversity Monitoring Institute, Edmonton, Alberta, Canada.

Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting Brant. *Auk* 101: 361–370.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.

Baldwin, S.P. & Kendeigh, S.C. 1927. Attentiveness and inattentiveness in the nesting behavior of the House Wren. *Auk* 44: 206–216.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Batt, B.D.J. & Cornwell, G.W. 1972. The effects of cold on Mallard embryos. *Journal of Wildlife Management* 36: 745–751.

Bentzen, R.L., Powell, A.N., Phillips, L.M. & Suydam, R.S. 2010. Incubation behavior of King Eiders on the coastal plain of Northern Alaska. *Polar Biology* 33: 1075–1082.

Block, W.M. & Brennan, L.A. 1993. The habitat concept in ornithology: theory and applications. *In* D.M. Power (ed.), *Current Ornithology*, pp. 35–91. Plenum Press, New York, USA.

Bolduc, F. & Guillemette, M. 2003. Human disturbance and nesting success of Common Eiders: interaction between visitors and Gulls. *Biological Conservation* 110: 77–83.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.

Borgo, J.S. & Conover, M.R. 2016. Visual and olfactory concealment of duck nests: influence on nest site selection and success. *Human-Wildlife Interactions* 10: 110–121.

Boyce, M.S., Johnson, C.J., Merrill, E.H., Nielsen, S.E., Solberg, E.J. & van Moorter, B. 2016. Can habitat selection predict abundance? *Journal of Animal Ecology* 85: 11–20.

Brown, P.W. & Fredrickson, L.H. 1987. Time budget and incubation behavior of breeding White-winged Scoters. *Wilson Bulletin* 99: 50–55.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.

Bushaw, J.D., Ringelman, K.M., Johnson, M.K., Rohrer, T. & Rohwer, F.C. 2020. Applications of an unmanned aerial vehicle and thermal-imaging camera to study ducks nesting over water. *Journal of Field Ornithology* 91: 409–420.

Caldwell, P.J. & Cornwell, G.W. 1976. Incubation behaviour and temperatures of the Mallard duck. *Auk* 92: 706–731.

Capilla-Lasheras, P.P. 2018. incR: a new R package to analyse incubation behaviour. *Journal of Avian Biology* 49: e01710.

Carlson, M., Wells, J. & Jacobson, A. 2015. Balancing the relationship between protection and sustainable management in Canada's boreal forest. *Conservation and Society* 13: 13–22.

Carter, A.W., Hopkins, W.A., Moore, I.T. & DuRant, S.E. 2014. Influence of incubation recess patterns on incubation period and hatchling traits in Wood Ducks *Aix sponsa*. *Journal of Avian Biology* 45: 273–279.

Chalfoun, A.D. & Martin, T.E. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Animal Behaviour* 73: 579–585.

Clark, R.G. & Shutler, D. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80: 272–287.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society Series B: Biological Sciences* 273: 1375–1383.

Connelly, J.W. & Ball, I.J. 1984. Comparisons of aspects of breeding Blue-winged and Cinnamon Teal in eastern Washington. *The Wilson Bulletin* 96: 626–633.

Cooper, C.B. & Mills, H. 2005. New software for quantifying incubation behavior from time-series recordings. *Journal of Field Ornithology* 76: 352–356.

Croston, R., Ackerman, J.T., Herzog, M.P., Kohl, J.D., Hartman, C.A., Peterson, S.H., Overton, C.T., Feldheim, C.L. & Casazza, M.L. 2018a. Duck nest depredation, predator behavior, and female response using video. *Journal of Wildlife Management* 82: 1014–1025.

Croston, R., Hartman, C.A., Herzog, M.P., Casazza, M.L. & Ackerman, J.T. 2018b. A new approach to automated incubation recess detection using temperature loggers. *Condor* 120: 739–750.

Croston, R., Hartman, C.A., Herzog, M.P., Casazza, M.L., Feldheim, C.L. & Ackerman, J.T. 2020. Timing, frequency, and duration of incubation recesses in dabbling ducks. *Ecology and Evolution* 10: 2513–2529.

Dallmann, J.D., Anderson, L.C., Raynor, E.J., Powell, L.A. & Schacht, W.H. 2016. iButton® temperature loggers effectively determine Prairie Grouse nest absences. *Great Plains Research* 26: 117–123.

Dassow, J.A., Eichholz, M.W., Stafford, J.D. & Weatherhead, P.J. 2012. Increased nest defence of upland-nesting ducks in response to experimentally reduced risk of nest predation. *Journal of Avian Biology* 43: 61–67.

Deeming, D. C. 2002. Behaviour patterns during incubation. *In* D.C. Deeming (ed.), *Avian Incubation: Behaviour, Environment and Evolution*, p. 415. Oxford University Press, Oxford, UK.

DeGregorio, B.A., Weatherhead, P.J., Sperry, J.H. & Brett DeGregorio, C.A. 2014. Powerlines, roads, and avian nest survival: effects on predator identity and predation intensity. *Ecology and Evolution* 4: 1589–1600.

DeGregorio, B.A., Chiavacci, S.J., Benson, T.J., Sperry, J.H. & Weatherhead, P.J. 2016. Nest predators of North American birds: continental patterns and implications. *BioScience* 66: 655–665.

DeMars, C.A. & Boutin, S. 2017. Nowhere to hide: effects of linear features on predator–prey dynamics in a large mammal system. *Journal of Animal Ecology* 87: 274–284.

Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M. & Avgar, T. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *Journal of Animal Ecology* 89: 623–634.

Dickie, M., Serrouya, R., McNay, R.S. & Boutin, S. 2017. Faster and farther: Wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology* 54: 253–263.

Ducks Unlimited Canada. 2011. *Enhanced Wetland Classification: Inferred Products User Guide*. Duck Unlimited Canada, Stonewall, Manitoba, Canada.

Ducks Unlimited Canada. 2014. *Distribution and Abundance of Waterfowl in the Western Boreal Forest*. Duck Unlimited Canada, Stonewall, Manitoba, Canada.

DuRant, S.E., Hopkins, W.A., Hepp, G.R. & Romero, L.M. 2013a. Energetic constraints and parental care: is corticosterone indicative of energetic costs of incubation in a precocial bird? *Hormones and Behavior* 63: 385–391.

DuRant, S.E., Hopkins, W.A., Hepp, G.R. & Walters, J.R. 2013b. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews* 88: 499–509.

Dyson, M.E. 2020. Nesting ecology of ducks nesting in the boreal forest. Ph.D. thesis, University of Waterloo, Waterloo, Ontario, Canada.

Dyson, M.E., Slattery, S.M. & Fedy, B.C. 2019. Microhabitat nest-site selection by ducks in the boreal forest. *Journal of Field Ornithology* 90: 348–360.

Dyson, M.E., Slattery, S.M. & Fedy, B.C. 2020. Nest predators of ducks in the boreal forest. *Wildlife Society Bulletin* 44: 631–639.

Dyson, M.E., Slattery, S.M. & Fedy, B.C. 2022. Multiscale nest-site selection of ducks in the western boreal forest of Alberta. *Ecology and Evolution* 12: e9139.

Erikstad, K.E. & Tveraa, T. 1995. Does the cost of incubation set limits to clutch size in Common Eiders *Somateria mollissima*? *Oecologia* 103: 270–274.

Esler, D. & Grand, J.B. 1993. Factors influencing depredation of artificial duck nests. *Journal of Wildlife Management* 57: 244–248.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515.

Fahrig, L. & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14: 21–41.

Fedy, B.C. & Martin, T.E. 2009. Male songbirds provide indirect parental care by guarding females during incubation. *Behavioral Ecology* 20: 1034–1038.

Finnegan, L., Pigeon, K.E., Cranston, J., Hebblewhite, M., Musiani, M., Neufeld, L., Schmiegelow, F., Duval, J. & Stenhouse, G.B. 2018. Natural regeneration on seismic lines influences movement behaviour of Wolves and Grizzly Bears. *PLoS ONE* 13: e0195480.

Fisher, J.T. & Burton, A.C. 2018. Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment* 16: 323–328.

Flint, P.L. & Maccluskie, M.C. 1995. A device for simultaneously measuring nest attendance and nest temperature in waterfowl. *Journal of Field Ornithology* 66: 515–521.

Fogarty, D.T., Elmore, R.D., Fuhlendorf, S.D. & Loss, S.R. 2017. Influence of olfactory and visual cover on nest site selection and nest success for grassland-nesting birds. *Ecology and Evolution* 7: 6247–6258.

Forbes, M.R.L., Clark, R.G., Weatherhead, P.J. & Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense Theory. *Behavioral Ecology and Sociobiology* 34: 79–85.

Gloutney, M.L. & Clark, R.G. 1997. Nest-site selection by Mallards and Blue-Winged Teal in relation to microclimate. *Auk* 114: 381–395.

Gloutney, M.L., Clark, R.G., Afton, A.D. & Huff, G.J. 1993. Timing of nest searches for upland nesting waterfowl. *Journal of Wildlife Management* 57: 597–601.

Gunness, M.A., Clark, R.G. & Weatherhead, P.J. 2001. Counterintuitive parental investment by female dabbling ducks in response to variable habitat quality. *Ecology* 82: 1151–1158.

Guyn, K.L. & Clark, R.G. 1997. Cover characteristics and success of natural and artificial duck nests. *Journal of Field Ornithology* 68: 33–41.

Hardin, J.W. & Hilbe, J.M. 2007. *Generalized Linear Models and Extensions. Second Edition*. Stata Press, College Station, Texas, USA.

Hebblewhite, M. 2017. Billion dollar boreal woodland Caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation* 206: 102–111.

Hepp, G.R. & Kennamer, R.A. 2012. Warm is better: incubation temperature influences apparent survival and recruitment of Wood Ducks (*Aix sponsa*). *PLoS ONE* 7: 1–6.

Hepp, G.R., Folk, T.H. & Manlove, C.A. 2005. Nest temperature, incubation period, and investment decisions of incubating Wood Ducks *Aix sponsa*. *Journal of Avian Biology* 36: 523–530.

Hepp, G.R., Kennamer, R.G. & Johnson, M.H. 2006. Maternal effects in Wood Ducks: incubation temperature influences incubation period and neonate phenotype. *Functional Ecology* 20: 307–314.

Hoover, A.K., Rohwer, F.C. & Richkus, K.D. 2004. Evaluation of nest temperatures to assess female nest attendance and use of video cameras to monitor incubating waterfowl. *Wildlife Society Bulletin* 32: 581–587.

Houston, A.I., Stephens, P.A., Boyd, I.L., Harding, K.C. & McNamara, J.M. 2007. Capital or income breeding? A theoretical model of female reproductive strategies. *Behavioral Ecology* 18: 241–250.

Howerter, D.W., Anderson, M.G., Devries, J.H., Joynt, B.L., Armstrong, L.M., Emery, R.B. & Arnold, T.W. 2014. Variation in Mallard vital rates in Canadian Aspen Parklands: the Prairie Habitat Joint Venture Assessment. *Wildlife Monographs* 188: 1–37.

Johnson, K.P., McKinney, F. & Sorenson, M.D. 1999. Phylogenetic constraint on male parental care in the dabbling ducks. *Proceedings of the Royal Society Series B: Biological Sciences* 266: 759–763.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118: 557–562.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78: 57–66.

Kaminski, R.M. & Elmberg, J. 2014. An introduction to habitat use and selection by waterfowl in the Northern Hemisphere. *Wildfowl* (Special Issue No. 4): 9–16.

Killick, R. & Eckley, I.A. 2014. changepoint: An R Package for Changepoint Analysis. *Journal of Statistical Software* 58: 1–19.

Killick, R., Fearnhead, P. & Eckley, I.A. 2012. Optimal detection of changepoints with a linear computational cost. *Journal of the American Statistical Association* 107: 1590–1598.

Klett, A.T., Duebbert, H.F., Faanes, C.A. & Higgins, K.F. 1986. *Techniques for Studying Nest Success of Ducks in Upland Habitats in the Prairie Pothole Region.* United States Department of the Interior, Fish and Wildlife Service Publication No. 158. United States Department of the Interior, Washington D.C., USA.

Korschgen, C.E. 1977. Breeding stress of female Eiders in Maine. *Journal of Wildlife Management* 41: 360–373.

Korschgen, C.E. & Dahlgren, R.B. 1992. 13.2.15. Human disturbances of waterfowl: causes, effects, and management. U.S. Fish and Wildlife Service: Waterfowl Management Handbook No. 12. University of Nebraska, Lincoln, USA. Available at https://digitalcommons.unl.edu/icwdmwfm/12 (last accessed 29 August 2023).

Kreisinger, J. & Albrecht, T. 2008. Nest protection in Mallards *Anas platyrhynchos*: untangling the role of crypsis and parental behaviour. *Functional Ecology* 22: 872–879.

Langin, K.M., Norris, D.R., Kyser, T.K., Marra, P.P. & Ratcliffe, L.M. 2006. Capital versus income breeding in a migratory passerine bird: evidence from stable-carbon isotopes. *Canadian Journal of Zoology* 84: 947–953.

Loos, E.R. 1999. Incubation ecology of Blue-Winged Teal (*Anas discors*): testing hypotheses of incubation constancy, recess frequency, weight loss, and nest success. M.Sc. thesis, Louisiana State University, Baton Rouge, USA.

Loos, E.R. & Rohwer, F.C. 2004. Laying-stage nest attendance and onset of incubation in prairie nesting ducks. *Auk* 121: 587–599.

Ludlow, S.M. & Davis, S.K. 2018. Oil and natural gas development influence nest-site selection and nest survival of upland-nesting waterfowl and shorebirds. *Wildlife Society Bulletin* 42: 57–66.

Maccluskie, M.C. & Sedinger, J.S. 1999. Incubation behaviour of Northern Shovelers in the subarctic: a contrast to the prairies. *Condor* 101: 417–421.

Mallory, M.L. & Weatherhead, P.J. 1993. Incubation rhythms and mass loss of Common Goldeneyes. *Condor* 95: 849–859.

Manlove, C.A. & Hepp, G.R. 2000. Patterns of nest attendance in female Wood Ducks. *Condor* 102: 286–291.

Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.

Martin, T.E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society Series B: Biological Sciences* 269: 309–316.

McConnell, M.D., Monroe, A.P., Burger, L.W. & Martin, J.A. 2017. Timing of nest vegetation measurement may obscure adaptive significance of nest-site characteristics: a simulation study. *Ecology and Evolution* 7: 1259–1270.

Muhly, T.B., Johnson, C.A., Hebblewhite, M., Neilson, E.W., Fortin, D., Fryxell, J.M., Latham, A.D.M., Latham, M.C., McLoughlin, P.D., Merrill, E., Paquet, P.C., Patterson, B.R., Schmiegelow, F., Scurrah, F. & Musiani, M. 2019. Functional response of Wolves to human development across boreal North America. *Ecology and Evolution* 9: 10801–10815.

Mumma, M.A., Gillingham, M.P., Johnson, C.J. & Parker, K.L. 2019. Functional responses to anthropogenic linear features in a complex predator-multi-prey system. *Landscape Ecology* 34: 2575–2597.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 5: 113–117.

Olson, R. & Rohwer, F.C. 1998. Effects of human disturbance on success of artificial duck nests. *Journal of Wildlife Management* 62: 1142–1146.

Pasher, J., Seed, E. & Duffe, J. 2014. Development of boreal ecosystem anthropogenic disturbance layers for Canada based on 2008 to 2010 Landsat imagery. *Canadian Journal of Remote Sensing* 39: 42–58.

Pieron, M.R. & Rohwer, F.C. 2010. Effects of large-scale predator reduction on nest success of upland nesting ducks. *Journal of Wildlife Management* 74: 124–132.

Prince, H.H., Siegel, P.B. & Cornwell, G.W. 1969. Incubation environment and the development of Mallard embryos. *Journal of Wildlife Management* 33: 589–595.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Randa, L.A. & Yunger, J.A. 2006. Carnivore occurrence along an urban-rural gradient: a landscape-level analysis. *Journal of Mammalogy* 87: 1154–1164.

Ringelman, J., Longcore, J. & Owen, R. 1982. Nest and brood attentiveness in female Black Ducks. *Condor* 84: 110.

Ringelman, K.M. & Stupaczuk, M.J. 2013. Dabbling ducks increase nest defense after partial clutch loss. *Condor* 115: 290–297.

Robel, R.J., Briggs, J.N., Dayton, A.D. & Hulbert, L.C. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23: 295–297.

Roy, C.L. 2018. Nest and brood survival of Ring-necked Ducks in relation to anthropogenic development and wetland attributes. *Avian Conservation and Ecology* 13: 20.

Schmiegelow, F.K.A. & Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* 12: 375–389.

Schneider, E.G. & McWilliams, S.R. 2007. Using nest temperature to estimate nest attendance of Piping Plovers. *Journal of Wildlife Management* 71: 1998–2006.

Setash, C.M., Kendall, W.L. & Olson, D. 2020. Factors influencing Cinnamon Teal nest attendance patterns. *Ibis* 163: 125–136.

Simpson, J.W., Yerkes, T.J., Smith, B.D. & Nudds, T.D. 2005. Mallard duckling survival in the Great Lakes Region. *Condor* 107: 898–909.

Singer, H.V., Slattery, S.M., Armstrong, L. & Witherly, S. 2020. Assessing breeding duck population trends relative to anthropogenic disturbances across the boreal plains of Canada, 1960–2007. *Avian Conservation and Ecology* 15: 1.

Skaggs, C.G., Ringelman, K.M., Loesch, C.R., Szymanski, M.L., Rohwer, F.C. & Kemink, K.M. 2020. Proximity to oil wells in North Dakota does not impact nest success of ducks but lowers nest densities. *Condor* 122: 1–15.

Skutch, A.F. 1957. The incubation patterns of birds. *Ibis* 99: 69–93.

Skutch, A.F. 1962. The constancy of incubation. *Wilson Bulletin* 74: 115–152.

Slattery, S.M., Morissette, J.L., Mack, G.G. & Butterworth, E.W. 2011. Waterfowl conservation planning. *In* J.V. Wells (ed.), *Boreal Birds of North America: A Hemispheric View of Their Conservation Links and Significance*, Issue 41, pp. 23–40. University of California Press, Berkeley, USA.

Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockström, J., Scheffer, M., Schellnhuber, H.J. & Svedin, U. 2011. The anthropocene: from global change to planetary stewardship. *Ambio* 40: 739–761.

Stephens, P.A., Boyd, I.L., McNamara, J.M. & Houston, A.I. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90: 2057–2067.

Stephenson, M.D., Schulte, L.A., Klaver, R.W. & Niemi, J. 2021. Miniature temperature data loggers increase precision and reduce bias when estimating the daily survival rate for bird nests. *Journal of Field Ornithology* 92: 492–505.

Thom, D. & Seidl, R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews* 91: 760–781.

Tinbergen, J.M. & Williams, J.B. 2002. Energetics of incubation. *In* D.C. Deeming (ed.), *Avian Incubation Behaviour, Environment and Evolution*, pp. 299–313. Oxford University Press, Oxford, UK.

Trombulak, S.C. & Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Moorter, B. Van, Alberts, S.C., Ali, A. H., Allen, A.M., Attias, N., Avgar, T., Bartlam-brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., Beest, F.M. Van, Blake, S., Blaum, N., … Rimmler, M. 2018. Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science* 359: 466–469.

Webb, D.R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89: 874–898.

Weller, M.W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20: 111–113.

Wells, J.V. 2011. Boreal forest threats and conservation status. *In* J.V. Wells (ed.), *Boreal Birds of North America: A Hemispheric View of Their Conservation Links and Significance*, Issue 41, pp. 1–6. University of California Press, Berkeley, USA.

Weston, M.A., Ekanayake, K.B., Lomas, S., Glover, H.K., Mead, R.E., Cribbin, A., Tan, L.X.L., Whisson, D.A., Maguire, G.S. & Cardilini, A.P.A. 2017. Case studies of motion-sensing cameras to study clutch survival and fate of real and artificial ground-nests in Australia. *Bird Study* 64: 476–491.

White, F.N. & Kinney, J.L. 1974. Avian incubation. *Science* 186: 107–115.

Wilson, R.E., Eaton, M.D. & McCracken, K.G. 2012. Plumage and body size differentiation in Blue-winged Teal and Cinnamon Teal. *Avian Biology Research* 5: 107–116.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73: 3–36.

Zicus, M.C. 1995. Common Goldeneye nest attendance patterns. *Condor* 97: 461–472.

Zurr, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science+Business Media, New York, USA.

Photograph: iButton temperature probe placement in a down-lined nest bowl of a female Mallard in the western boreal forest of Alberta, Canada in 2016, by Matthew E. Dyson.