



Extended incubation recesses increase before nest abandonment in a high-arctic shorebird

Léa Etchart^{1,2} · Nicolas Lecomte² · François-Xavier Dechaume-Moncharmont³ · Jérôme Moreau^{4,5} · Johannes Lang^{5,6} · Thomas Pagnon^{1,5} · Benoit Sittler^{5,7} · Maria Teixeira⁸ · Loïc Bollache^{1,5} · Olivier Gilg^{1,5}

Received: 2 May 2024 / Accepted: 8 May 2025

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2025

Abstract

Parents can abandon their current clutch when reaching a physiological threshold to prioritise their survival and future breeding in the trade-off against current reproduction. Incubation is metabolically costly, and regular recesses are necessary to replenish energy reserves. Thus, an increase in the duration of these foraging trips may signal diminishing reserves and perhaps impending abandonment. Here, we tested the hypothesis that the probability of abandonment of uniparental nest is directly linked to the duration of extended recesses (i.e., recesses > 120 min). Analysing 13 years of breeding behaviour from Sanderlings (*Calidris alba*) using thermologgers placed in 120 nests, we found that both the frequency and duration of extended recesses were higher in nests that were ultimately abandoned. The probability of nest abandonment increased with time spent in extended recesses during incubation, with the final day before abandonment proving critical in the decision-making. In contrast, short recesses showed no relationship with abandonment probability, and neither recess type changed significantly as nests approached hatching, confirming the specificity of extended recesses as indicators of abandonment. With such results, parents likely remain at the nest until their reserves fall below a physiological threshold, when they have no choice but to leave the nest when the costs-benefits balance becomes unsustainable for the parent. Our study suggests the key link between extended recesses and nest abandonment; it paves the way for quantifying foraging success and variations in energy reserves of individuals to provide deeper insights into the mechanisms driving reproductive decisions and their impact on population dynamics.

Keywords Nest failure · Parental care · Incubation strategy · Sanderling · Greenland

Introduction

Nest abandonment is a definitive reproductive decision, particularly in species that only breed once per season (Pogány et al. 2008; Székely et al. 1996). Life-history theories suggest different scenarios under which parents could

Communicated by Thomas Koert Lameris.

✉ Olivier Gilg
olivier.gilg@gmail.com

¹ CNRS, Chrono-Environnement (UMR 6249), Université Marie et Louis Pasteur, 25000 Besançon, France

² Canada Research Chair in Polar and Boreal Ecology and Centre d'Études Nordiques, Université de Moncton, Moncton, NB, Canada

³ Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, 69622 Villeurbanne, France

⁴ Centre d'Études Biologiques de Chizé, UMR 7372, CNRS & La Rochelle Université, 79360 Villiers-en-Bois, France

⁵ Groupe de Recherche en Ecologie Arctique, 21440 Francheville, France

⁶ Working Group for Wildlife Research at the Clinic for Birds, Reptiles, Amphibians and Fish, Justus Liebig University Giessen, 35392 Giessen, Germany

⁷ Chair for Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany

⁸ CNRS, Biogéosciences (UMR 6282), Université de Bourgogne Europe, 6 Boulevard Gabriel, 21000 Dijon, France

abandon their clutch according to their individual conditions (Székely et al. 1996). In long-lived species, individuals may, for instance, prioritise their survival over their offspring's when the energetic cost of breeding hinders future breeding attempts or increases their mortality risk (e.g., Verboven & Tinbergen 2002). This classical trade-off between current and future reproduction highlights the significance of an organism's physiological state (i.e., condition) in parental care decisions (McNamara & Houston 1996). Thus, parents abandoning their clutch when they reach a physiological or condition threshold could preserve their residual reproductive value (Jones et al. 2002; Zangmeister et al. 2009). Signs preceding nest abandonment are diverse. They can be hormonal signals, such as an increase in corticosterone levels (Ouyang et al. 2012; Spée et al. 2011; Turcotte-van de Rydt et al. 2022), morphological signals when the body condition of individuals is altered (Dubiec 2011), and more rarely behavioural signals such as a decline in parental care investment (Spée et al. 2011; Zangmeister et al. 2009). This later can be difficult to detect because it requires constant incubation monitoring (Zangmeister et al. 2009).

Coupled with the monitoring of biotic and abiotic conditions, behavioural observations can help identify environmental stressors behind reproductive failure. Under adverse conditions (e.g., high or low temperatures, extreme climatic events, low food availability), incubating birds, already under heavy metabolic stress (20–50% increase in their metabolic rate compared to non-breeders; Tinbergen & Williams 2002) may perform extended incubation recesses (Bambini et al. 2019; Bueno-Enciso et al. 2017; Haftorn 1988; Jia et al. 2010; Macdonald et al. 2013; Morton & Pereyra 1985; Smith et al. 2012; Tulp & Schekkerman 2006). Extended recesses (sometimes referred to as “prolonged egg neglect”) deserve specific attention and must be studied per se in an ecological context (Deeming and Reynolds 2015), since they respond to different pressures to those of classic short foraging recesses (Etchart et al. 2024). They could be a key breeding strategy to overcome costs of incubation (Etchart et al. 2024). For instance, common guillemots (*Uria aalge*), adapted to conserve heat, can make extended recesses during heatwaves to temporally avoid unfavourable nesting conditions and spend more time cooling off in the sea (Olin et al. 2023). Extended recesses may also help balance the energetic deficits and maintain body condition under harsh conditions, allowing more time for foraging. Indeed, Etchart et al. (2024) demonstrated that income breeders such as small shorebirds, who do not store significant reserves to cover breeding and are therefore very dependent on their environment (Klaassen et al. 2001), performed extended recesses. These extended recesses were primarily performed under cold temperatures and were longer for individuals in poor body condition. This suggests that they may represent a shift towards self-maintenance, at the expense of the eggs. If extended recesses

are not sufficient to allow incubating birds to restore their energy reserves, individuals could ultimately be forced to abandon their nests in order to avoid mortality. Accordingly, birds abandoning their nest due to reserve depletion should perform extended incubation recesses before abandonment, and the duration of those recesses should be linked with abandonment in combination with their body condition.

In this study, we focused on uniparental Sanderlings (*Calidris alba*), whose incubation behaviour is responsive to ground-surface temperature (Meyer et al. 2021) and that regularly perform extended recesses (Etchart et al. 2024). In this high-arctic species, replenishing energy reserves daily is essential as they cope with ambient temperatures well below their physiological zero temperature (i.e., 26 °C; Webb 1987) and cannot store significant energy reserves (Klaassen et al. 2001). Using a 13-year dataset from two study sites in Greenland, we hypothesise that the probability of nest abandonment is directly linked to the duration of extended recesses. We predict that (1) the probability of nest abandonment increases with the duration of extended recesses, and that (2) the length of these recesses progressively increases in the days leading up to abandonment, reflecting the physiological stress that drives this decision.

Methods

Study sites and species

The study was conducted on Sanderling nests during 13 breeding seasons (2011–2023) at two locations in Greenland (Hochstetter Forland, 75.15°N 19.70°W, and Karupelv Valley, 72.50°N 24°W). Study sites are located in the uninhabited Northeast Greenland National Park and are part of the ‘prostrate shrub tundra’ bioclimatic zone (Walker et al. 2005). Winters in northeast Greenland are cold, with temperatures between – 15 °C and – 25 °C. In summer, during the sanderling's breeding season, temperatures are usually above zero, with average monthly temperatures between 2 °C and 4 °C. The areas surveyed are 18 km² at Hochstetter Forland and 15 km² at Karupelv Valley.

The Sanderling (44–71 g) is a long-distance migratory shorebird whose breeding range is restricted to a few High-Arctic regions (Cramp and Simmons, 1983). Sanderlings usually arrive at their northeast Greenland breeding strongholds between late May and mid-June (Meltofte et al. 2007). They are generalist insectivores and use both uniparental and biparental incubation strategies, with both sexes able to incubate and rear chicks (Cramp and Simmons, 1983; Reneerkens et al. 2014; Etchart et al. 2024). They are also very flexible in their incubation behaviour, which is mainly driven by temperatures and body condition (Meyer et al. 2021; Etchart et al. 2024).

Nest monitoring, incubation behaviour, and fate determination

Nests were located by flushing incubating adults or by following birds with anti-predator behaviour (Humphreys & Ruxton 2020). Search effort was similar at both sites and for all years, with five to six trained field workers walking across the study areas daily during the breeding season (except in 2015 and 2020, when only two field workers were present at Hochstetter site, and four at Karupelv Valley, respectively).

For each nest, we monitored incubation behaviour using a temperature probe (Flylead thermistor PB 5009 with 60 cm cable) coupled to a data logger (Tinytag Plus2 TGP-4020; Gemini Data Loggers Inc., West Sussex, U.K.; see detailed method in Meyer et al. 2021). Probes were set to record temperature every minute from the date of nest discovery until the fate date (i.e., max. 21–23 days). Recesses were then extracted and all recesses longer than 120 min were considered as extended recesses, while recesses shorter than 120 min were considered short recesses (Etchart et al. 2024).

Two independent observers (LE and OG) assessed whether each nest had hatched, was abandoned, or was depredated based on the pattern of incubating temperatures (for all nests) supplemented by field observations (for non-successful nests only) to distinguish between predated and abandoned nests. A nest was considered hatched if the temperature was erratically declining for 24 h, while both depredated and abandoned nests showed a sudden and permanent drop in temperature (see figure A1 in Meyer et al. 2020). Abandoned nests were further distinguished from depredated nests by the presence of cold eggs left in the nest cups. To prevent extremely long extended recesses from being interpreted as abandonment, the temperature probes were always left in these nests for at least 48 h after the last recorded incubation bout. While a limited number of nests (if any) predated between abandonment and our field visits may have been misclassified as predated, the slight reduction of sample size of abandoned nests did not affect our analyses.

We restricted our study to uniparental nests (see Moreau et al. (2018) for methods), which are the only nests exhibiting extended recesses in this species (Etchart et al. 2024). Nest age and expected hatching date were estimated using four different methods (i.e., observation of uncompleted clutches, observation of hatching eggs or young in the nest cup, flotation of the eggs, exact hatching time documented with thermologgers) assuming an average incubation period of 21.5 days for the species (see figure S2 in Etchart et al. 2024; Liebezeit et al. 2007). The incubation patterns of all nests, with incubation bouts, extended recesses and fates, are presented in Fig. 1.

Statistical analyses

To assess the impact of incubation behaviour on the probability of nest abandonment, we restricted our analyses to successful (i.e., hatched) vs. abandoned nests with at least four days of monitoring. This means excluding predated nests from the analyses, as their potential fate in the absence of predation (i.e., hatching versus abandoned) could not be determined. See Meyer et al. (2020) for detailed analyses of predation and recess patterns.

All our primary analyses were performed with logistic regression with the fate of the nest modelled as a binary response variable coded 0 (hatched) or 1 (abandoned). First, we investigated the effect of the total duration of extended recesses during the total monitored incubation (averaged per day) on the fate. To do so, for each focal nest, the duration of all the extended recesses was summed and divided by the number of days on which the nest was monitored. Second, we investigated the effect of the total duration of extended recesses on the days preceding the fate only, for each period of 24 h from 1 to 7 days before the fate. In this second analysis, a comparison was made between the competing models, with each model based on one of the aforementioned 24-h periods. We also included nest age as a covariate. The model selection procedure was achieved by comparing their Akaike's information criterion for small sample size (AICc; Burnham & Anderson 2002). Third, we performed separate analyses (using categorical nest ages) on hatched and abandoned nests to detect potential differences in the duration of extended recesses between the first (days 1–17) and latest (day 18 until the expected hatching date) stages of the incubation. In these third analyses, we divided the total duration of extended recesses by the total number of days monitored in each group for each nest to obtain a total duration of extended recesses averaged by day (for incubation days 1–17, hatched and abandoned nests were monitored for 154 and 63 days, respectively, and beyond 17 incubation days, for 97 and 14 days, respectively). For all relevant analyses, we presented odds-ratio results (OR) to report the probability ratios of abandonment in our sample (i.e., the larger the OR, the more likely the nest is abandoned when the value of the predictor variable increases).

To address potential temporal biases in our analyses and the complementary role of both short and extended recesses, we conducted three additional analyses. First, we examined whether short recesses (< 120 min) showed similar patterns to extended recesses by applying our original logistic regression framework to short recess duration. Second, we tested whether nest attendance patterns change in the days leading up to hatching by comparing both short and extended recess duration across the final three days before hatching using logistic models with nest age as a covariate. Third, we implemented a day-by-day logistic regression approach

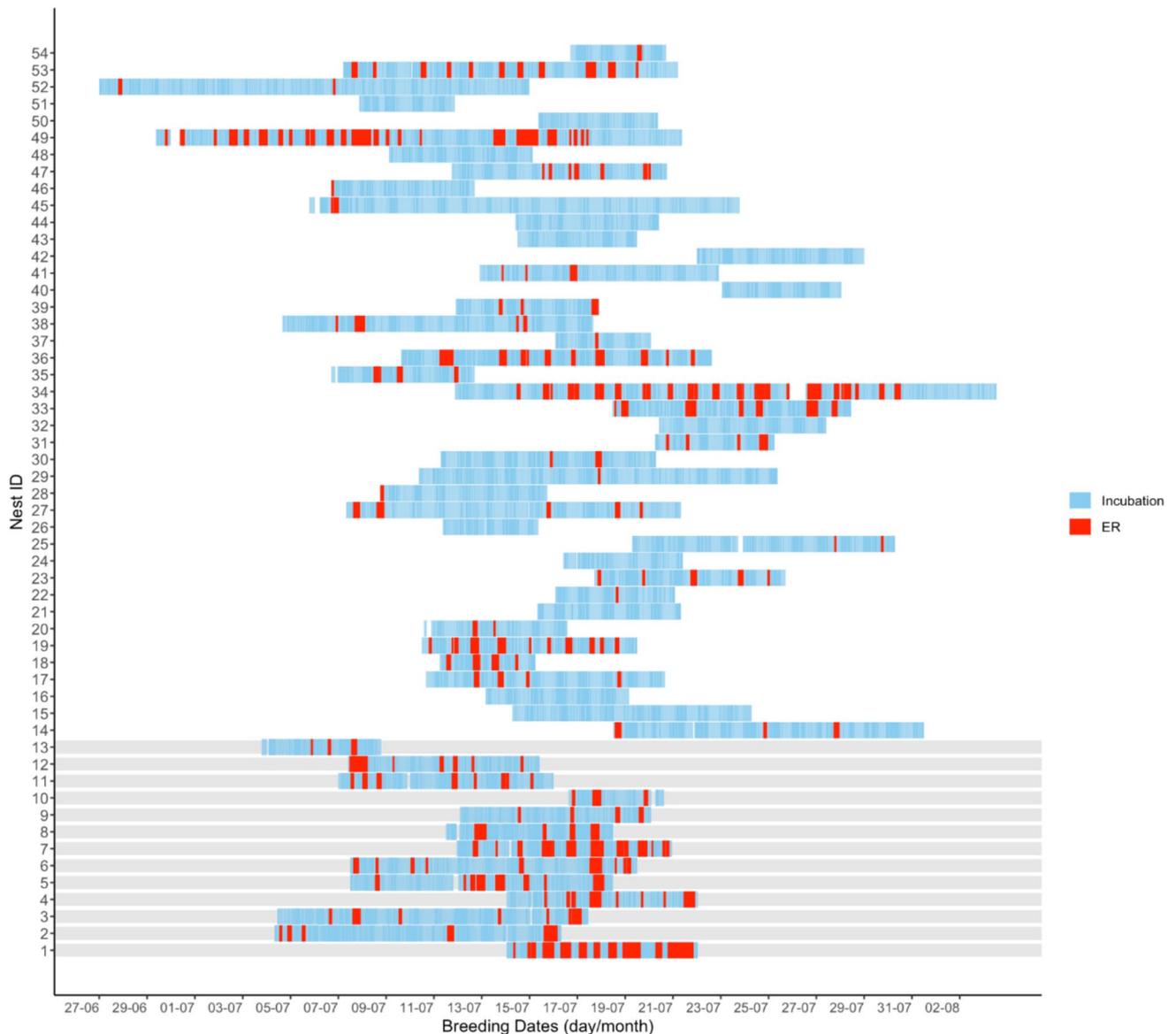


Fig. 1 Actogram presenting raw incubation data of 54 nests of Sanderling in Hochstetter and Karupelv, Greenland (2011–2023). Each segment represents a behavioural state, either incubation bouts (blue) or extended recesses (ER; red). Segment lengths correspond to the duration of each state until the final nest fate (either hatched or abandoned). White segments within the incubation bouts represent miss-

ing data (corresponding to trapping attempts) and are not included in the analyses. On a white background, hatched nests (upper part) are displayed, while abandoned nests (lower part of the figure) are highlighted in grey. In this latter group, nests are ordered by the duration of their extended recesses within the last 24 h before the fate

to predict next-day abandonment probability based on current-day recess duration. In this model, we included both short and extended recesses while controlling for nest age using mixed effects models. These final analyses allowed us to determine whether the observed relationship between extended recesses and abandonment was specific to extended recesses and not confounded by changes in overall attendance patterns or temporal sampling bias.

All statistical analyses were conducted using R freeware Version 4.3.0 (R CoreTeam 2024).

Results

Over the 13-year study, we monitored 120 uniparental nests with thermologgers. Among these nests, 67 hatched, 36 were predated, 15 were abandoned and two were still incubating when we ended our fieldwork. Out of the 82 hatched and abandoned nests, 54 (41 hatched and 13 abandoned) were tracked for four or more days and included in our analyses (mean duration of monitoring: 8.95 days for hatched and 8.77 days for abandoned nests).

Incubating birds spent an average of 2.2 h per day on extended recesses in hatched nests and 4.8 h in abandoned nests (ranges 0–22.3 and 0–19.7 h, respectively). Extended recesses occurred in 28 of the 41 hatched nests and in all 13 abandoned nests (Fig. 1). The frequency was 0.31 extended recesses per day in hatched nests and 0.75 in abandoned nests. In other words (and on average), extended recesses occurred every 3.2 days (and lasted for 7.1 h) in hatched nests, compared to every 1.3 day (for 6.4 h) in abandoned nests (see also figure S6 in Etchart et al. 2024). Generalized linear model predicted a 62% increase in the probability of abandonment for each additional hour spent on extended

recess per day (OR = 1.62, $R^2 = 0.22$, $p < 0.01$, $n = 54$ nests, Fig. 2).

We then examined the probability of abandonment as a function of the time spent on extended recesses separately for each of the three days before the fate (i.e., day-1 = 0–24 h before fate; day-2 = 24–48 h; day-3 = 48–72 h). The probability of abandonment increased by 84% for each additional hour spent in extended recess during day-1 (OR_{day-1} = 1.84, $R^2 = 0.73$, $p < 0.01$, Fig. 3a), 42% during day-2 (OR_{day-2} = 1.42, $R^2 = 0.58$, $p < 0.01$, Fig. 3b), and 72% during day-3 (OR_{day-3} = 1.72, $R^2 = 0.56$, $p = 0.02$, Fig. 3c). Although each period from day-2 to day-7 explained part

Fig. 2 Probability for nest abandonment (compared to hatching fate, $y=0$) in Sanderlings, Greenland (2011–2023, $n=54$ nests), as a function of the mean time per day spent on extended recesses during the whole incubation. Dots and shaded areas show the raw data and the 95% confidence intervals, respectively

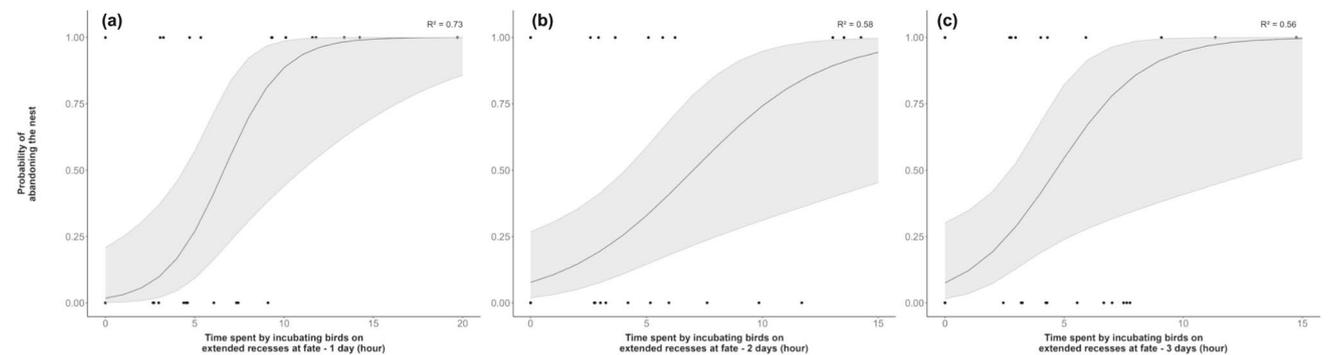
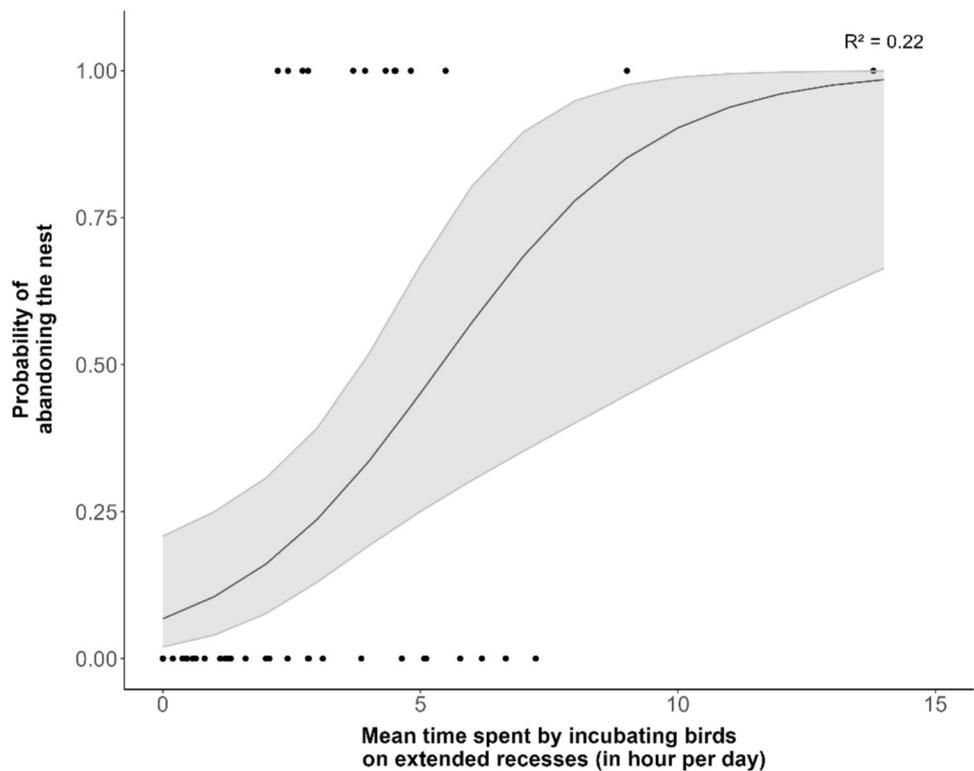


Fig. 3 Probability for nest abandonment (compared to hatching fate, $y=0$) in Sanderlings, Greenland (2011–2023, $n=54$ nests), as a function of the time spent on extended recesses for the three days (24 h

periods) preceding the fate: **a** fate at day-1, **b** fate at day-2, **c** fate at day-3. Dots show the raw data and shaded area the 95% confidence intervals. Nest age is included as a covariate of the model

of the variation (Fig. S1), the model at day-1 best predicted the probability of nest abandonment. However, nest age per se (included as a covariate in this model) did not impact the probability of abandoning the nest.

Finally, our last GLM models using categorical nest ages predicted that, for abandoned nests, the total duration of extended recesses increased more towards the expected hatching date (from day 18 onward; 8 nests) than during the preceding period (days 1 to 17; 13 nests) of the incubation (estimate = 0.35 ± 0.16 , $z = 2.25$, $p = 0.02$, $R^2 = 0.25$). Conversely, we found no difference between the two periods for successful nests (estimate = -0.06 ± 0.11 , $z = -0.59$, $p = 0.55$, $R^2 = 0.003$).

Short recesses and nest age

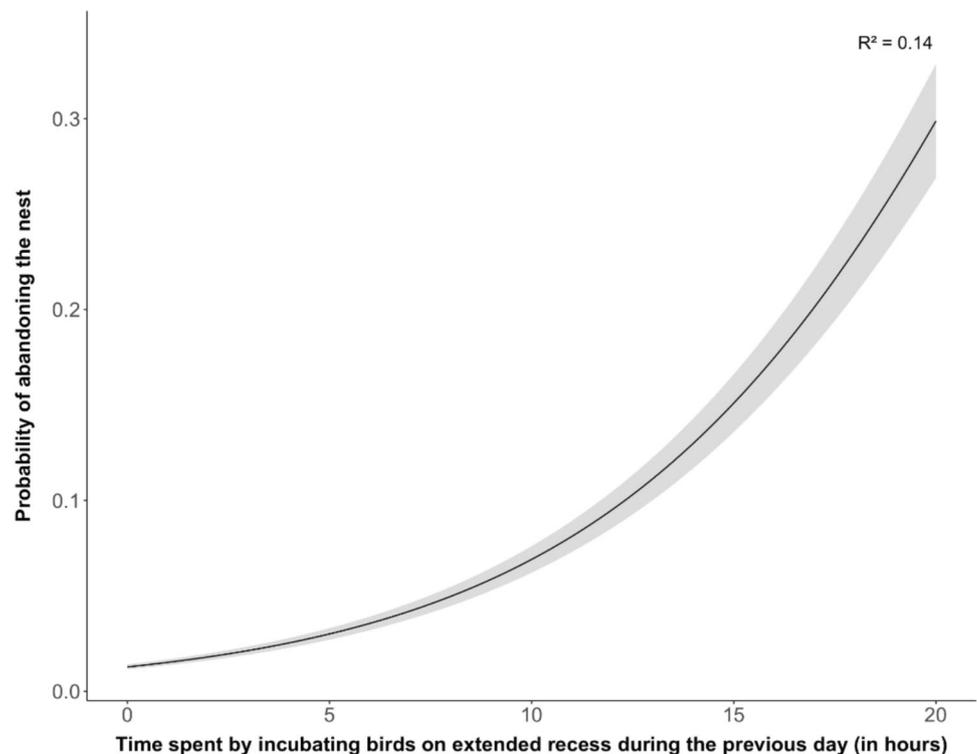
Unlike extended recesses, the duration of short recesses (< 120 min) showed no relationship with nest abandonment probability. Neither the overall duration of short recesses during incubation (GLM: $\beta = 0.08$, $SE = 0.19$, $p = 0.67$, $R^2 = 0.003$) nor the duration in the days immediately preceding the fate (day-1: $\beta = -0.04$, $SE = 0.31$, $p = 0.89$, $R^2 = 0.001$; day-2: $\beta = 0.11$, $SE = 0.28$, $p = 0.71$, $R^2 = 0.002$; day-3: $\beta = -0.07$, $SE = 0.26$, $p = 0.81$, $R^2 = 0.001$) predicted whether nests would be abandoned.

Additionally, our analysis of attendance patterns in the days leading up to hatching revealed that neither

short recesses ($F = 0.84$, $p = 0.43$) nor extended recesses ($F = 0.91$, $p = 0.38$) changed significantly as successful nests approached hatching. This consistency in attendance patterns before hatching contrasted with the significant increase in extended recess duration observed before abandonment.

Our day-by-day prediction analysis on all the nests during the whole incubation period confirmed that extended recess duration significantly predicted next-day abandonment probability ($\beta = 0.47$, $SE = 0.18$, $p = 0.009$; Fig. 4), while short recess duration did not ($\beta = -0.12$, $SE = 0.22$, $p = 0.58$). However, this day-by-day analysis showed lower overall probabilities of immediate abandonment (maximum probability ~ 0.30), even with extended recesses. This suggests that, while extended recesses consistently increased abandonment risk throughout incubation, they were especially predictive in the final days before actual abandonment events occurred (Figs. 2–3 and related analyses). For the final days of nests abandoned by the parent, extended recesses exceeding approximately 5–6 h/day were associated with abandonment probabilities greater than 50%, potentially representing a critical threshold beyond which birds were substantially more likely to abandon their nests (Figs. 2–3). This threshold effect was not observed for short recesses, regardless of their duration, further highlighting the specific relationship between extended recesses and the abandonment decision.

Fig. 4 Probability of nest abandonment (compared to hatching fate, $y = 0$) in Sanderlings, Greenland (2011–2023, $n = 54$ nests), as a function of the time spent on extended recesses during the previous day (24-h period). The shaded area shows the 95% confidence interval. Note the lower overall probabilities of immediate abandonment (max. ca. 0.30) compared to Figs. 1 and 2. Both short and extended recesses were included in this model while controlling for nest age using mixed effects models



Discussion

Our study reveals significant differences in the incubation behaviour documented in hatched and abandoned Sanderling nests. On average, individuals from abandoned nests spent 2.1 times more time in extended recesses (per day) than those from successful nests. Additionally, all parents abandoning their nest performed extended recesses during incubation. The probability of nest abandonment increased with the total duration of extended recesses (averaged per day) across incubation, and the day before abandonment was particularly notable for its extended duration of recesses compared to successful nests (Figs. 1, 2 and 3).

The specificity of extended recesses as indicators of impending abandonment is further supported by our finding that short recesses show no relationship with abandonment probability. This dichotomy suggests that extended and short recesses likely represent fundamentally different behavioural strategies: while short recesses could reflect routine foraging needs that remain consistent throughout incubation (Meyer et al. 2021), extended recesses appear to signal physiological stress and possible resource depletion (Etchart et al. 2024). Furthermore, the stability of both recess types in the days leading up to hatching indicates that Sanderlings maintain consistent attendance patterns even during this critical period, a finding that, to our knowledge, has not been previously documented in Arctic shorebirds. We argue that this is also strengthening our interpretation that the increased extended recesses before abandonment represent a specific behavioural response to deteriorating conditions rather than a temporal artifact of our sampling design.

Main suspected stressors

Extended recesses likely arise in response to harsh environmental conditions and poor body condition (Etchart et al. 2024; Tulp & Schekkerman 2006), serving as an alternative breeding decision when breeding conditions are unfavourable, in stark contrast to the more common “short recess” behaviour seen in many species including Sanderlings (Etchart et al. 2024; Meyer et al. 2021). The positive relationship we found between the duration of extended recesses (per day) and the probability of abandonment indicates that high-Arctic shorebirds are possibly breeding at the limits of their physiological capabilities. Being primarily income breeders, they rely heavily on the current environmental conditions and food availability for breeding success and survival (Klaassen et al. 2001). Furthermore, the increased length of extended recess near the expected hatching date for abandoned nests (while the

increasing ground-level temperatures during the incubation period should rather shorten them; Etchart et al. 2024), but not for hatched ones, suggests that many individuals face constraints as incubation nears completion, leading to significant physiological stress and abandonment (albeit we did not directly measure the physiological conditions of our studied birds). Such constraints might well be stronger for first-time or inexperienced breeders (see below).

While Sanderlings use extended recesses to cope with adverse conditions, there are necessarily energetic and physiological thresholds beyond which it becomes impossible for the adult, or useless for the egg, to prolong or multiply these recesses. Consequently, abandonment likely occurs when the balance between costs and benefits becomes unsustainable for the incubating adult or its eggs. Although shorebird eggs can tolerate long periods of exposure to poor environmental conditions (Norton 1972), they still require a fixed amount of energy to develop and hatch (Deeming and Reynolds 2015). Increasing periods of non-attendance can only be compensated for by an increase in the duration of incubation within certain limits (e.g., four days on average in Blue, *Cyanistes caeruleus*, and Great tits, *Parus major*; Bueno-Enciso et al. 2017). Furthermore, extending the duration of incubation also increases the time of exposure to nest predators (Webb 1987) and hence mechanistically decreases the probability of a nest hatching (i.e., by prolonging exposition time to predation).

Alternative explanations

There are a few other drivers that could potentially explain our results. First, when non-fertile eggs (or dead embryos) are incubated, the fate of the nest can only be predation (excluded from our study) or abandonment. Incubating birds have cues to assess the development of their eggs (Deeming and Reynolds 2015), and the amount of parental care they provide could decline throughout the incubation (e.g., by engaging in more or longer extended recesses) if they suspect that their eggs are unlikely to hatch. In such cases, we would expect the incubation period to last longer than the expected hatching date, as we have observed in non-fertile clutches of Pectoral Sandpipers (*Calidris melanotos*; unpublished data). In contrast, all the abandoned nests analysed in this study were abandoned before their expected hatching date. Furthermore, all the abandoned Sanderling clutches we were able to autopsy during this study (ca. half of the 13 abandoned nests) had been fertilized (i.e., contained embryos).

Secondly, disturbances by humans, predators, parasites, competing individuals (of the same or different species), or changes in habitat quality (e.g., flooding or drought) are also known reasons for nest abandonment in birds (Ellison and Cleary 1978; Frederick and Collopy 1989; Strasser and

Heath 2013; Burga-Dominguez et al., 2020). In our study areas, Sanderlings are particularly tame and resume incubation within minutes of disturbances ceasing, and we did not notice any change in habitat quality around the abandoned nests we found. For these disturbances to explain abandonment through cumulative effects, they would therefore have to last several hours (i.e., of duration similar to that of the > 120 mn extended recesses that we observed), be repeated (to explain the repetition of the extended recesses) or become more intense over time (to explain the increase in the duration of the extended recess before abandonment). To our knowledge, none of the disturbances that occurred in our study areas met these conditions.

Capital breeders vs. income breeders

Nest abandonment and its underlying mechanisms are well studied in capital breeders, where a body mass threshold prompts a shift from lipid catabolism to protein stores (Spée et al. 2011), but remain poorly understood in income breeders like small shorebirds. In contrast to capital breeders, small shorebirds must forage daily (Tulp & Schekkerman 2006), with nest attendance largely depending on the timing of foraging recesses for optimal arthropod intake (Meyer et al. 2021). For these small income breeders, adverse weather likely quickly induces physiological stress in incubating individuals, potentially influencing reproductive decisions such as nest abandonment (Ouyang et al. 2012).

Extended recesses: a make-or-break decision

Extended recesses occur when incubating Sanderlings face poor conditions (Etchart et al. 2024) and were observed in most nests in our study (Fig. 1). Although we did not measure the foraging success during extended recesses, we posit that successful individuals likely succeed in refuelling their energy reserves during their extended recesses. While the total duration of extended recesses (i.e., measured over the entire incubation) increases the probability of abandoning the nest, the strongest signal of this variable was found for the day preceding abandonment. This suggests that individuals likely balance the increasing cost of poor condition until a threshold limit is reached and abandonment becomes inevitable, highlighting the need to monitor foraging success and body condition in tandem.

The fact that individuals can perform extended recesses and be successful, while others are not, might be the result of inter-individual variability in a suite of traits, such as body condition, the ability to cope with stressful conditions, foraging success, residual reproductive value (Tulp and Schekkerman 2006; Deeming and Reynolds 2015). Cumulative effects can also be at play, e.g. when birds face several successive days of poor weather during their incubation compared

to birds facing only one unfavourable day. However, this could also indicate various responses to the same adverse conditions.

Individual experience could also play an important role in their decision. For instance, some ringed Sanderlings have been found breeding in the same territory for more than 10 years (OG, pers. obs.). Experience might well increase over the lifespan of individuals, with older ones being more aware of the risks, costs, and benefits of incubating under changing conditions, and younger, less experienced ones more prone to abandonment. Age can also impact the recess scheduling and attentiveness of individuals (Aldrich & Raveling 1983), as well as their foraging abilities. Experienced individuals could e.g. be more resistant to fasting and tolerate bigger energy depletion (as seen in some polar capital breeders; Groscolas et al. 2000).

While extended incubation recesses are relatively rare compared to short recesses (Etchart et al. 2024), our study demonstrates that they are closely linked to the probability of nest abandonment. The hypothesis of extended recesses as a strategy for coping with adverse conditions needs further tests, especially to decipher the interplay between environmental conditions, resource allocation, and individual variability (but see e.g., Skutch 1962; Conway and Martin 2000). Future research should focus on quantifying foraging success and physiological stress linked to incubation behaviours, which could provide deeper insights into the mechanisms driving reproductive decisions and their impact on population dynamics. Additionally, investigating foraging success of uniparental breeders according to various abiotic and biotic conditions (e.g., body condition, competition, predation risk) could be crucial to predict breeding success and desertion patterns accurately. Such studies will likely require continuous data on body condition throughout incubation (see e.g., Spaans et al. 2007), an experimental and ethical challenge for small free-ranging taxa including shorebirds, but that is nowadays achievable with new technological developments. With such tools at-hand, deciphering the dynamics of breeding trade-offs could then also be scaled up to multitaxon studies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-025-05735-y>.

Acknowledgements The authors are grateful to all the people who helped collect the field data over the years and to the Joint Arctic Command (Nuuk) for logistic support.

Author contributions OG developed methodology. OG, JL, TP, BS conducted fieldwork. OG, NL, LB, LE originally formulated the idea. LE performed statistical analyses with the help of FD and NL. LE wrote the manuscript with substantial help from NL, OG, and LB. All authors revised and commented on the manuscript.

Funding This study is part of the long-term Studies in Ecology and Evolution (SEE-Life) program of the CNRS and was funded by the

ANR (ANR-21-CE02-0024 PACS to LB) and IPEV (French Polar Institute; Program “Interactions 1036”). NL and LE were supported by the Canada Research Chair program and NSERC.

Data availability Data is available at <https://github.com/leatchart/Extended-recesses-and-abandonment>

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Separate annual research permits were granted by the Government of Greenland, Ministry of Domestic Affairs, Nature and Environment-NNPAN, for the Hochstetter site (permit numbers: C-11-4-12, C-12-4-17, C-13-4-29, C-14-4-23, C-15-4-10, C-16-4-15, C-17-3-28, C-18-3-11, C-19-3-03, C-20-3-19, C-21-3-22) and Karupelv site (permit numbers: C-11-14, C-12-28, C-13-11, C-14-16, C-15-14, C-16-20, C-17-23, C-18-24, C-19-36, C-20-33, C-21-33).

Consent to participate Not applicable.

Consent for publication Not applicable.

References

- Aldrich TW, Raveling DG (1983) Effects of experience and body weight on incubation behavior of Canada Geese. *Auk* 100(3):670–679
- Bambini G, Schlicht E, Kempnaers B (2019) Patterns of female nest attendance and male feeding throughout the incubation period in blue tits *Cyanistes caeruleus*. *Ibis* 161(1):50–65. <https://doi.org/10.1111/ibi.12614>
- Bueno-Enciso J, Barrientos R, Ferrer ES, Sanz JJ (2017) Do extended incubation recesses carry fitness costs in two cavity-nesting birds? *J Field Ornithol* 88(2):146–155. <https://doi.org/10.1111/jfo.12194>
- Burga-Domínguez C, Gonzales-Delcarpio DD, Zavalaga CB (2020) Time-lapse imagery of Peruvian Boobies (*Sula variegata*) reveals nest abandonment caused by tick hyperinfestation. *Mar Ornithol* 48:303–311. <https://doi.org/10.5038/2074-1235.48.2.1385>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin, Springer, Berlin
- Conway CJ, Martin TE (2000) Effects of ambient temperature on avian incubation behavior. *Behav Ecol* 11(2):178–188. <https://doi.org/10.1093/beheco/11.2.178>
- Deeming DC, Reynolds SJ (2015) Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198718666.001.0001>
- Dubiec A (2011) Condition-dependent clutch desertion in Great Tit (*Parus major*) females subjected to human disturbance. *J Ornithol* 152(3):743–749. <https://doi.org/10.1007/s10336-011-0647-8>
- Ellison LN, Cleary L (1978) Effects of human disturbance on breeding of double-crested cormorants. *Auk* 95:510–517
- Etchart L, Lecomte N, Dechaume-Moncharmont F-X, Moreau J, Lang J, Pagnon T, Sittler B, Teixeira M, Bollache L, Gilg O (2024) Extended incubation recesses in sanderlings are impacted by temperature and body condition. *Proceed Royal Societ Biol Sci*. <https://doi.org/10.1098/rspb.2023.2264>
- Frederick PC, Collopy MW (1989) The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. *Condor* 91:860–867. <https://doi.org/10.2307/1368070>
- Groscolas R, Decrock F, Thil M-A, Fayolle C, Boissery C, Robin J-P (2000) Refeeding signal in fasting-incubating king penguins: changes in behavior and egg temperature. *Am J Physiol Integrat Comparat* 279(6):R2104–R2112. <https://doi.org/10.1152/ajpgu.2000.279.6.R2104>
- Haftorn S (1988) Incubating female passerines do not let the egg temperature fall below the “physiological zero temperature” during their absences from the nest. *Ornis Scand* 19(2):97–110. <https://doi.org/10.2307/3676458>
- Humphreys RK, Ruxton GD (2020) Avian distraction displays: a review. *Ibis* 162(4):1125–1145. <https://doi.org/10.1111/ibi.12814>
- Jia CX, Sun YH, Swenson JE (2010) Unusual incubation behavior and embryonic tolerance of hypothermia by the Blood Pheasant (*Ithaginis cruentus*). *Auk* 127(4):926–931. <https://doi.org/10.1525/auk.2010.09254>
- Jones KM, Ruxton GD, Monaghan P (2002) Model parents: is full compensation for reduced partner nest attendance compatible with stable biparental care? *Behav Ecol* 13(6):838–843. <https://doi.org/10.1093/beheco/13.6.838>
- Klaassen M, Lindström Å, Møltøfte H, Piersma T (2001) Arctic waders are not capital breeders. *Nature* 413(6858):794–794. <https://doi.org/10.1038/35101654>
- Liebezeit JR, Smith PA, Lanctot RB, Schekkerman H, Tulp I, Kendall SJ, Tracy DM, Rodrigues RJ, Møltøfte H, Robinson JA, Gratto-Trevor C, Mccaffery BJ, Morse J, Zack SW (2007) Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* 109:32–47. <https://doi.org/10.1093/condor/109.1.32>
- Macdonald EC, Camfield AF, Jankowski JE, Martin K (2013) Extended incubation recesses by alpine-breeding horned larks: a strategy for dealing with inclement weather? *J Field Ornithol* 84(1):58–68. <https://doi.org/10.1111/jfo.12006>
- McNamara JM, Houston AI (1996) State-dependent life histories. *Nature* 380(6571):215–221. <https://doi.org/10.2173/bow.yebti4.t01>
- Møltøfte H, Piersma T, Boyd H, McCaffery B, Ganter B, Golovnyuk VV, Graham K, Gratto-Trevor CL, Morrison RIG, Nol E, Rösner H-U, Schamel D, Schekkerman H, Soloviev MY, Tomkovich PS, Tracy DM, Tulp I, Wennerberg L (2007) Effects of climate variation on the breeding ecology of Arctic shorebirds. *Meddelelser Om Grønland-Biosci* 59:1–48
- Meyer N, Bollache L, Dechaume-Moncharmont F-X, Moreau J, Afonso E, Angerbjörn A, Bêty J, Ehrich D, Gilg V, Giroux MA, Hansen J, Lanctot RB, Lang J, Lecomte N, McKinnon L, Reneerkens J, Saalfeld ST, Sabard B, Schmidt NM, Gilg O (2020) Nest attentiveness drives nest predation in arctic sandpipers. *Oikos* 129(10):1481–1492. <https://doi.org/10.1111/oik.07311>
- Meyer N, Bollache L, Galipaud M, Moreau J, Dechaume-Moncharmont F-X, Afonso E, Angerbjörn A, Bêty J, Brown G, Ehrich D, Gilg V, Giroux MA, Hansen J, Lanctot RB, Lang J, Latty C, Lecomte N, McKinnon L, Kennedy LV, Gilg O (2021) Behavioural responses of breeding arctic sandpipers to ground-surface temperature and primary productivity. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2020.142485>
- Moreau J, Perroud L, Bollache L, Yannic G, Teixeira M, Schmidt NM, Reneerkens J, Gilg O (2018) Discriminating uniparental and biparental breeding strategies by monitoring nest temperature. *Ibis* 160(1):13–22. <https://doi.org/10.1111/ibi.12507>
- Morton ML, Pereyra ME (1985) The regulation of egg temperatures and attentiveness patterns in the dusky flycatcher (*Empidonax oberholseri*). *Auk* 102(1):25–37. <https://doi.org/10.2307/4086819>
- Norton DW (1972) Incubation schedules of four species of calidrine sandpipers at Barrow. *Alaska the Condor* 74(2):164–176

- Olin AB, Dück L, Berglund PA, Karlsson E, Bohm M, Olsson O, Hentati-Sundberg J (2023) Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Mar Ecol Prog Ser*. <https://doi.org/10.3354/meps14244>
- Ouyang JQ, Quetting M, Hau M (2012) Corticosterone and brood abandonment in a passerine bird. *Anim Behav* 84(1):261–268. <https://doi.org/10.1016/j.anbehav.2012.05.006>
- Pogány Á, Szentirmai I, Komdeur J (2008) Sexual conflict and consistency of offspring desertion in Eurasian penduline tit *Remiz pendulinus*. *BMC Evol Biol* 8(1):242. <https://doi.org/10.1186/1471-2148-8-242>
- R CoreTeam. (2024). *R: A language and environment for statistical computing*. Vienna, Austria. <https://www.r-project.org/>
- Reneerkens J, van Veelen P, van der Velde M, Luttikhuisen P, Piersma T (2014) Within-population variation in mating system and parental care patterns in the Sanderling (*Calidris alba*) in northeast Greenland. *Ornithol Adv*. <https://doi.org/10.1642/AUK-13-247.1>
- Skutch AF (1962) The constancy of incubation. *Wilson Bulletin* 74:115–152
- Smith, P. A., Dauncey, S. A., Gilchrist, H. G., & Forbes, M. R. (2012). The influence of weather on shorebird incubation. In C. Ribic, R. F. Thompson, III, & P. J. Pietz (Eds.), *Video surveillance of nesting birds. Studies in Avian Biology (no. 43)* (pp. 89–104). University of California Press, Berkeley, California. <https://doi.org/10.1038/089062c0>
- Spaans B, Hoff K, van der Veer W, Ebbinge BS (2007) The significance of female body stores for egg laying and incubation in dark-bellied brent geese (*Branta Bernicla Bernicla*). *Ardea* 95(3–15):13. <https://doi.org/10.5253/078.095.0102>
- Spée M, Marchal L, Lazin D, Le Maho Y, Chastel O, Beaulieu M, Raclot T (2011) Exogenous corticosterone and nest abandonment: A study in a long-lived bird, the Adélie penguin. *Horm Behav* 60(4):362–370. <https://doi.org/10.1016/j.yhbeh.2011.07.003>
- Strasser EH, Heath JA (2013) Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *J Appl Ecol* 50:912–919. <https://doi.org/10.1111/1365-2664.12103>
- Székely T, Webb JN, Houston AI, McNamara JM (1996) An evolutionary approach to offspring desertion in birds. *Curr Ornithol* 13:271–330. https://doi.org/10.1007/978-1-4615-5881-1_6
- Tinbergen JM, Williams JB (2002) Energetics of incubation. In: Deeming DC (ed) *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford University Press, New York, pp 299–313
- Tulp I, Schekkerman H (2006) Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *J Avian Biol* 37(3):207–218. <https://doi.org/10.1111/j.2006.0908-8857.03519.x>
- Turcotte-van de Rydt AV, Petalas C, Sblendorio JM, Pearl CA, Gill SA, Guigueno MF (2022) Clutch abandoning parasitised yellow warblers have increased circulating corticosterone with no effect of past corticosterone or differences in egg maculation characteristics. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2022.711732>
- Verboven N, Tinbergen JM (2002) Nest desertion: a trade-off between current and future reproduction. *Anim Behav* 63(5):951–958. <https://doi.org/10.1006/anbe.2001.1971>
- Walker DA, Reynolds MK, Daniëls FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumpolar arctic vegetation map. *J Veget Sci* 16:267–282. <https://doi.org/10.1111/j.1654-1103.2005.tb02365.x>
- Webb DR (1987) Thermal tolerance of avian embryos: a review. *The Condor* 89(4):874. <https://doi.org/10.2307/1368537>
- Zangmeister JL, Haussmann MF, Cerchiara J, Mauck RA (2009) Incubation failure and nest abandonment by leach's storm-petrels detected using PIT tags and temperature loggers. *J Field Ornithol* 80(4):373–379. <https://doi.org/10.1111/j.1557-9263.2009.00243.x>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.