BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

CC BY

Research

Cite this article: Pagnon T *et al*. 2026 Incubation strategy and hatching start time affect the duration of the nestling period in precocial Arctic-breeding sandpipers. *Biol. Lett.* **22**: 20250670.
https://doi.org/10.1098/rsbl.2025.0670

Received: 17 October 2025
Accepted: 12 March 2026

Subject Category:
Animal behaviour

Subject Areas:
behaviour

Keywords:
brooding, food availability, parental care, predation, shorebirds, temperature

Author for correspondence:
Thomas Pagnon
e-mail: thomas.pagnon@gmail.com

Incubation strategy and hatching start time affect the duration of the nestling period in precocial Arctic-breeding sandpipers

Thomas Pagnon[1,2], François-Xavier Dechaume-Moncharmont[3], Anders Angerbjörn[4], Joël Bêty[5], Julien Bouvet[2,3], Glen S. Brown[6], Eric Buchel[2], Dorothee Ehrich[7], Léa Etchart[1,8], Ivan Fufachev[9], Jannik Hansen[10], Richard B. Lanctot[11], Johannes Lang[2,12], Christopher J. Latty[13], Nicolas Lecomte[8], Laura McKinnon[14], Jérôme Moreau[2,15], Jeroen Reneerkens[10,16], Sarah T. Saalfeld[11], Brigitte Sabard[2], Niels M. Schmidt[10], Benoit Sittler[2,17], Paul A. Smith[18], Aleksandr Sokolov[9], Vasiliy Sokolov[19], Natalia Sokolova[9], Rob S. A. van Bemmelen[20], Glenn Yannic[2,21], Loïc Bollache[1,22] and Olivier Gilg[1,2]

[1]Chrono-environnement UMR 6249, Université Marie et Louis Pasteur, CNRS, Besançon, France
[2]Groupe de Recherche en Ecologie Arctique, Francheville, France
[3]LEHNA UMR 5023, Universite Claude Bernard Lyon 1, CNRS, ENTPE, Villeurbanne, France
[4]Department of Zoology, Stockholm University, Stockholm, Sweden
[5]Département de Biologie, Chimie et Géographie and Centre d'Études Nordiques, Université du Québec à Rimouski, Rimouski, Québec, Canada
[6]Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada
[7]Department of Arctic and Marine Biology, Arctic University of Norway, Tromsø, Norway
[8]Canada Research Chair in Polar and Boreal Ecology and Centre d'Études Nordiques, Université de Moncton, Moncton, New Brunswick, Canada
[9]Arctic Research Station of Institute of Plant and Animal Ecology, Russian Academy of Sciences, Labytnangi, Russia
[10]Arctic Research Centre and Department of Ecoscience, Aarhus University, Roskilde, Denmark
[11]Migratory Bird Program, US Fish and Wildlife Service, Anchorage, AK, USA
[12]Clinic for Birds, Reptiles, Amphibians and Fish, Justus Liebig University, Giessen, Germany
[13]Arctic National Wildlife Refuge, US Fish and Wildlife Service, Fairbanks, AK, USA
[14]Department of Science, York University Glendon Campus, Toronto, Ontario, Canada
[15]Centre d'Études Biologiques de Chizé UMR 7372, Université de La Rochelle, CNRS, Villiers en Bois, France
[16]Conservation Ecology Group, University of Groningen, Groningen, The Netherlands
[17]Chair for Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany
[18]Wildlife Research Division, Environment and Climate Change Canada, Ottawa, Ontario, Canada
[19]Institute of Plant and Animal Ecology, Russian Academy of Sciences, Ekaterinburg, Russia
[20]Waardenburg Ecology, Culemborg, The Netherlands
[21]Laboratoire d'Ecologie Alpine, Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, Grenoble, France
[22]Université Bourgogne Europe, Dijon, France

TP, 0009-0003-1204-5230; F-XD-M, 0000-0001-7607-8224; AA, 0000-0001-5535-9086; JB, 0000-0002-8775-6411; JB, 0009-0009-6602-608X; GSB, 0000-0002-0825-9274; DE, 0000-0002-3028-9488; LE, 0009-0004-0095-1196; IF, 0000-0002-9531-3127; JH, 0000-0002-2716-9928; RBL, 0000-0001-9873-0199; JL, 0000-0002-7387-795X; CJL, 0000-0002-0522-8333; NL, 0000-0002-8473-5375; LMK, 0000-0002-5237-1538; JM, 0000-0001-9984-0998; JR, 0000-0003-0674-8143; STS, 0000-0002-6837-9729; NMS, 0000-0002-4166-6218; PAS, 0000-0001-9573-5218; AS, 0000-0002-1521-3856; VS, 0000-0002-0115-3151; NS, 0000-0002-6692-4375; RSAvB, 0000-0002-0688-7058; GY, 0000-0002-6477-2312; LB, 0000-0003-0316-6746; OG, 0000-0002-9083-4492

In bird species with precocial development, i.e. chicks acquire abilities to leave the nest soon after hatching, the nestling period during which parents warm their young in the nest by brooding them is short but

Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8405301.

THE ROYAL SOCIETY PUBLISHING

© 2026 The Authors. Published by the Royal Society under the terms of the Creative Commons Attribution License http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, provided the original author and source are credited.

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

critical to breeding success. The duration of the nestling period (DNP) depends on the hatching synchrony of eggs and the speed at which chicks acquire these abilities but may be indirectly affected by parental behaviour and temporal variations in temperature and predation. We assessed the effects of incubation strategy (bi- or uniparental), hatching start time, incubation initiation date and predation risk on the DNP in Arctic-breeding sandpipers. We found that the DNP was longer in biparental species (29.75 ± 8.95 h) compared with uniparental ones (25.82 ± 6.87 h) and was extended in nests where chicks began hatching during the colder 'night' hours. No effect of incubation initiation date or predation pressure was found on the DNP. We suggest that parental investment strategies and constraints related to circadian variations in temperature in chicks drive the DNP in Arctic-breeding sandpipers. These results help us better understand how different species may exhibit different behavioural responses during nesting to impending climate change.

1. Introduction

In birds, various forms of parental care are provided by one or both parents throughout the breeding stage, from incubating eggs to feeding and protecting offspring until they become independent [1]. Parental care is proximately determined by endocrine processes and ultimately responds to diverse selective pressures, with variations depending on the degree of cooperation between parents [2,3]. Various biotic and abiotic factors can exert pressures, thereby influencing the care strategies used by the parent(s) to maximize reproductive success. The nestling period is the period during which chicks are cared for at the nest. Two phases are generally recognized: the first phase includes the time from the hatching of the first egg until the hatching of the last egg (i.e. the hatching synchrony), and the second phase corresponds to the time when chicks are in the nest until the departure of the last one. The duration of time parents keep nestlings in the nest (i.e. duration of the nestling period = time from first chick hatching to no chicks in nest, hereafter referred to as DNP) is one key parental strategy, which appears to be determined by complex interactions between chick development, parent behaviour and environmental conditions [4].

In species with a precocial mode of chick development, chicks hatch with open eyes, wet downy feathers and limited homeothermy capacity. Besides predator defence, the only care provided by parents is to brood young to maintain high and stable body temperatures [5–7]. Chicks are nidifugous, but only leave the nest after first drying their feathers for body insulation and developing sufficient endothermy and locomotion skills to walk away from the nest to feed [8,9]. The DNP is relatively short, but critical for the survival of nestlings [10]. However, the DNP and factors that affect it remain largely unknown.

The duration of the hatching phase appears mainly driven by the onset of incubation during egg-laying, with early attentiveness before clutch completion leading to differential embryo development and less synchronized hatching [11,12], which appears more frequently when both parents share incubation [13]. Hence, with a given speed of chick maturation, the incubation strategy (going from biparental incubation, where both mates cooperate, to uniparental incubation, where only one parent incubates [10]) would determine a minimum DNP.

Chick departure from the nest, which is the end of the second phase of the nestling period, is predicted to occur at the most favourable time to optimize brood survival [10,14]. If departure occurs during low ambient temperatures, chicks will experience high-energetic costs associated with greater thermoregulation and shorten their foraging bout lengths [15,16]. If departure is delayed, chicks remaining in the nest may experience higher predation risk as smells are concentrated [4,17,18]. As a result, the timing of leaving the nest must be determined based on the chick foraging needs, the thermal environment and predation risk, and the parent(s) appear to be the primary decision-maker(s) [10]. Chick needs are essentially fixed, but environmental constraints vary over daily, seasonal and multi-annual timescales. Hence, hatching time, breeding phenology and predator abundance could be factors indirectly affecting DNP.

In the current context of climate-mediated environmental change, understanding what factors shape the life-history traits of birds, such as DNP, would help biologists model the behavioural responses and adaptive potential of birds. Our study explores behavioural and environmental factors expected to affect DNP in precocial species. We focused on eight Arctic-breeding sandpiper species that have all comparable brood size and incubation duration but differ markedly in their incubation strategies [19–21]. All the species investigated nest in cold environments with 24 h daylight, where temperatures and nest predation risk vary greatly over time [22–25]. Chicks hatch from energy-rich eggs and rely on nutrients from an invaginated yolk sac for the first 1–2 days after hatching [26]. Bold chicks may begin to explore the immediate surroundings of the nest while their siblings are still being brooded in the nest, but they return to the nest when their parents call them. At about one day old, all chicks leave the nest and feed on invertebrates by themselves [27]. The brood is then attended together by one parent until chicks can fully thermoregulate, forage and escape predators independently [28].

Here, we hypothesized that DNP varies with incubation strategy due to differences in hatching synchrony (parental cooperation hypothesis). We predicted that (i) uniparental birds would have a shorter DNP than biparental birds due to more synchronous hatching patterns. We also hypothesized that DNP will be determined by circadian and seasonal variations in ambient temperatures and the ability of chicks to maintain body temperature (thermoregulatory constraint hypothesis). Under this hypothesis, we predicted that (ii) chick departure from nests would occur preferentially during the warm 'daytime' hours and, consequently, DNP would be extended until daily temperatures rise in nests hatching during colder 'night' hours, (iii) chicks hatching late in the breeding season would experience warmer ambient temperatures when leaving the nest, reducing their thermoregulation costs and thus requiring less brooding in the nest and resulting in a shorter DNP, and (iv) incubation strategy may magnify seasonal temperature effects, with the generally later laying uniparental species [29] having even shorter DNP. Finally, we hypothesized that the DNP would reflect a trade-off between chick thermal needs and predation

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

risk minimization (predation avoidance hypothesis). We predicted that (v) parents would strive to minimize nest exposure by favouring shorter DNP when predators are numerous.

2. Material and methods

(a) Study sites and species

We examined the nests of eight sandpiper species (genus *Calidris*) distributed across 14 Arctic sites between 2016 and 2023 (electronic supplementary material, table S1). All species usually lay four eggs in a shallow nest scrape on the tundra during summer, but their incubation strategies differ. Four species are uniparental (little stint *C. minuta*, pectoral sandpiper *C. melanotos*, Temminck's stint *C. temminckii*, white-rumped sandpiper *C. fuscicollis*), three species are biparental (Baird's sandpiper *C. bairdii*, dunlin *C. alpina*, semipalmated sandpiper *C. pusilla*), and one species shows a mixed strategy (sanderling *C. alba*) [30,31].

(b) Incubation, nest fate, hatching start time and duration of the nestling period

In 1651 nests, we monitored incubation behaviour using a temperature probe (Flylead thermistor PB 5009) placed between the eggs and connected to a buried datalogger (Tinytag Plus2 TGP-4020; Gemini Data Loggers Inc., West Sussex, UK; see full methods in [20,32,33]). Nest temperatures were recorded every minute with ±0.2°C accuracy. Temperature patterns were used to identify nest fate using standardized procedures [20,34]. All nests identified as predated at the egg stage or suspected of early predation of chicks in the nest (i.e. when DNP < 12 h) were discarded, and only nests that we estimated successfully produced young that left the nest ($n = 590$) were retained for subsequent analyses. For sanderling, the incubation strategy was assigned for each nest based on the patterns of incubation recesses following [35], but 15 nests were excluded due to an unclear strategy (too short recordings, desertions of one of the biparental breeders before hatching). In the remaining 575 nests, the DNP (i.e. based on the beginning and the end of the nestling period) was determined from the visual inspection of the temperature records (e.g. fig. A1 in [20], fig. 2 in [36]). During the nestling period, the mean temperatures recorded within the nests typically followed a sawtooth pattern from the hatching of the first egg (defined as the hatching start time; electronic supplementary material, figures S1, S2) until the entire brood left the nest (i.e. when recorded temperatures in the nest dropped so as to match ambient air temperature). This temperature pattern contrasts strikingly with the pattern of nests with unhatched eggs being incubated, when the median temperature measured in the nest remains stable and high (i.e. close to the adult body temperature). This empirical method is very consistent with our repeated field observations of the hatching status of eggs and young (see examples in electronic supplementary material, figure S2). All interpretations of temperature patterns were independently assessed by at least two observers and cross-validated to look for inconsistencies. Additionally, we noted the ambient temperature at nest departure time.

(c) Relative incubation start date

For each nest, the incubation start date was estimated following a multi-approach method [33,37] (see descriptions in electronic supplementary material, table S2). As the incubation start date mainly varies according to species and local environmental conditions [38,39], we calculated the mean incubation start date for each species, site and year across all discovered nests. We then calculated the relative incubation start date for each of the 575 nests by subtracting the mean incubation start date from the individual incubation start date, centring the data around zero for all sites and years, for each species.

(d) Relative abundance of nest predators

Parental care strategies are affected by predation risk perceived by parent(s) [40]. This perceived predation risk is shaped in particular by encounters with predators [41]. Foxes (*Vulpes* spp.) and large birds (jaegers *Stercorarius* spp., gulls *Larus* spp., corvids *Corvus* spp.) are the primary predators of shorebird nests in the Arctic [20,42]. We assumed that fox and avian predators would be detected differently by the shorebirds and thus considered them separately. To assess predation risks perceived by sandpipers, we used incidental observations as a proxy for predator abundance (e.g. [38,43]). Daily counts were conducted by observers who independently recorded all predators (i.e. adult-sized foxes and avian predators) seen within the study area throughout the day. For each site, year and predator type, we calculated an index of relative abundance, defined as the number of predator observations per 100 h of observation (see details in electronic supplementary material, appendix 1, table S3 and figure S3).

(e) Statistical analyses

All analyses were performed with R (v. 4.5.0) [44]. First, DNP, as the dependent variable in the following analysis, was log-transformed to meet parametric assumptions associated with using linear models. All numeric explanatory variables tested were standardized with the 'scale' function [45]. To test whether DNP varied with time-varying factors and among incubation strategies, we built a full set of competitive linear mixed-effect models, including the following fixed factors: (i) hatching start

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

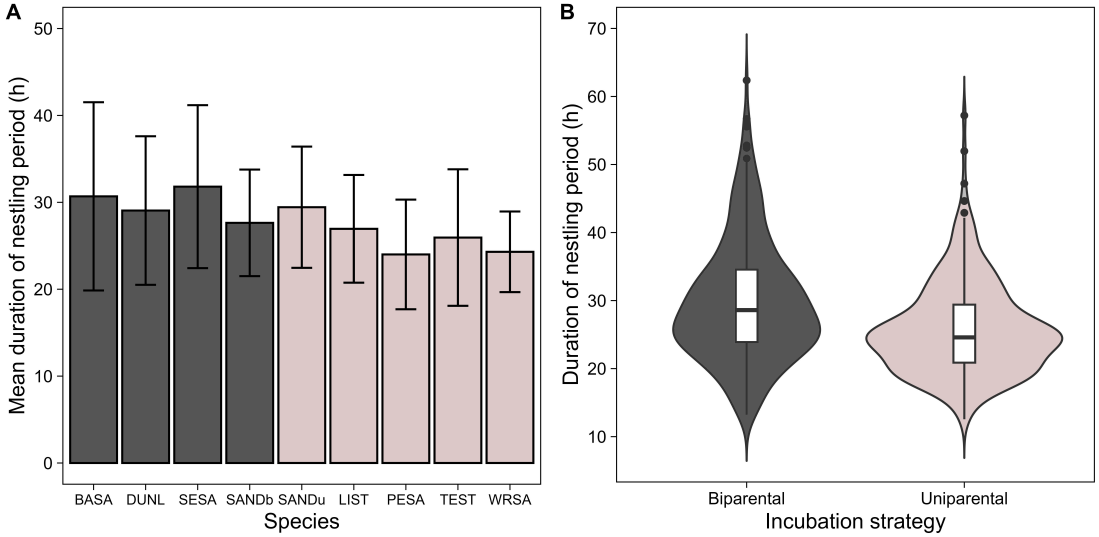


Figure 1. Differences in DNP among species (mean with the standard error; A) and between incubation strategies (medians, interquartile ranges and value distributions; B) in eight species of Arctic-breeding shorebirds. Colour in panels refers to the incubation strategy (dark grey: biparental; light grey: uniparental). BASA: Baird's sandpiper, DUNL: dunlin, SESA: semipalmated sandpiper, SANDb: sanderling biparental, SANDu: sanderling uniparental, LIST: little stint, PESA: pectoral sandpiper, TEST: Temminck's stint, WRSA: white-rumped sandpiper.

time (circular data t in hours normalized to the range [0, 2π] and decomposed into two variables: $\sin(2\pi \times t/24)$ and $\cos(2\pi \times t/24)$ [46]), (ii) relative incubation start date interacting with incubation strategy, (iii) relative abundance of avian predators, (iv) relative abundance of foxes and year as random intercept. Species was modelled with a random slope (by relative incubation start date) and intercept. All possible models were ranked with the corrected Akaike's information criterion (AICc) using the 'dredge' function, and ΔAICc was used to select the best-fitting models [47]. To reduce the risk of retaining spurious variables, only factors present in all models with a ΔAICc < 2 were considered to have relevant effects [48]. For each factor, we calculated its averaged parameter estimate β and its 95% CI by performing model-averaging procedures [47]. Model selection and averaging were conducted using the 'MuMIn' package [49]. Then, we inspected the pattern of nest departure time with all species merged using a frequency histogram. Finally, to test whether chicks experience different temperature conditions at nest departure over the breeding season, we built a linear mixed-effect model with temperature at nest departure time as the dependent variable, nest departure date as fixed factor and site and nest departure hour as random intercepts. All models were built using the 'lme4' package [50].

3. Results

Across the eight sandpiper species, the mean DNP was 28.03 ± 8.32 h, and 95% of the observations fell between 15.32 and 48.47 h. Intra- and interspecific variations are shown in figure 1A and electronic supplementary material, table S4.

The top-ranked models investigating the factors influencing DNP always included incubation strategy and hatching start time (table 1). Model selection revealed a substantial influence of incubation strategy (averaged β = −0.059, 95% CI: −0.083 to −0.035; i.e. −12.7%) on DNP, with biparental birds having longer DNP (29.75 ± 8.95 h) than uniparental birds (25.82 ± 6.87 h; figure 1B). DNP depended on hatching start time (cosine, i.e. 12.00 to 00.00 axis: averaged β = 0.016, 95% CI: 0.002 to 0.029; i.e.+3.7%; sine, i.e. 18.00 to 06.00 axis: averaged β = 0.014, 95% CI: −0.001 to 0.028; i.e. +3.2%), with DNP increasing when hatching started during the 'night' hours (figure 2A). The distribution of nest departure time significantly differed from a uniform distribution (asymptotic one-sample Kolmogorov–Smirnov test, D = 0.141, $p < 1 \times 10^{-5}$). Sandpipers appeared to avoid leaving the nest during the cold 'night' hours, with an increase in the number of departures during the warming 'morning' hours, and again fewer departures during the warmest 'afternoon' hours (figure 2B,C).

In contrast, the relative incubation start date had no influence on DNP (averaged β = 0.014, 95% CI: −0.003 to 0.031). Ambient temperatures at nest departure time ranged between 3.9°C and 28.6°C in 95% of the cases and were stable over the season (Wald χ^2 = 0.826, p = 0.363). Finally, the relative abundance of avian predators (averaged β = 0.0001, 95% CI: −0.0100 to 0.0102) and the relative abundance of foxes (averaged β = −0.005, 95% CI: −0.015 to 0.006) had no effect either.

4. Discussion

Breeding of precocial Arctic sandpipers takes place in cold environments during short summers, where nesting is constrained by the incubation strategy and variable environmental conditions. In this context, the care provided in the nest by parent(s) to their newly hatched offspring was expected to influence their development and be tailored to their needs. Our findings support the hypotheses that parental cooperation and certain thermoregulatory constraints affect the duration of time parent(s) brooded their hatchlings in the nest.

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

Table 1. Set of the fifteen top-ranked linear models testing the effects of behavioural and environmental variables on DNP in eight species of Arctic-breeding sandpipers, ranked by differences in AICc. For each model, we calculated its log-likelihood, AICc value, ΔAICc with the best-ranked model, weight w_i and R^2 marginal and conditional. The values given for each variable correspond to their estimates on the log-transformed response variable for each model (estimates of incubation strategy relative to uniparental strategy). Int., intercept; IS, incubation strategy; HST, hatching start time; RISD, relative incubation start date; RAF: relative abundance of foxes; RAAP: relative abundance of avian predators.

predictors								model selectors						
int.	IS	cos(HST)	sin(HST)	RISD	IS*RISD	RAF	RAAP	d.f.	logLik	AICc	ΔAICc	w_i	R^2_m	R^2_c
3.23	−0.059	0.016	0.014	0.016				9	408.7	−799.1	0.00	0.14	0.08	0.12
3.23	−0.058	0.016	0.014	0.016		−0.005		10	409.1	−797.8	1.33	0.07	0.08	0.12
3.23	−0.059	0.016	0.014					8	406.9	−797.5	1.62	0.06	0.07	0.12
3.23	−0.060	0.015		0.015				8	406.9	−797.5	1.65	0.06	0.08	0.11
3.23	−0.059	0.016	0.014	0.011	0.008			10	408.8	−797.3	1.84	0.06	0.08	0.11
3.23	−0.059	0.016	0.014	0.016			0.0003	10	408.7	−797.1	2.07	0.05	0.08	0.12
3.23	−0.058	0.016	0.014			−0.005		9	407.3	−796.3	2.88	0.03	0.07	0.12
3.23	−0.058	0.015		0.015		−0.005		9	407.3	−796.2	2.91	0.03	0.08	0.11
3.23	−0.058	0.016	0.014	0.012	0.007	−0.004		11	409.2	−795.9	3.20	0.03	0.08	0.11
3.23	−0.059		0.013	0.015				8	406.1	−795.9	3.21	0.03	0.07	0.11
3.23	−0.060	0.015						7	405.1	−795.9	3.22	0.03	0.06	0.11
3.23	−0.060	0.015		0.010	0.009			9	407	−795.7	3.41	0.03	0.08	0.10
3.23	−0.058	0.016	0.014	0.016		−0.005	0.0002	11	409.1	−795.7	3.41	0.03	0.08	0.12
3.23	−0.059	0.016	0.014				0.0003	9	406.9	−795.5	3.68	0.02	0.07	0.12
3.23	−0.060	0.015		0.015			0.0002	9	406.9	−795.4	3.71	0.02	0.08	0.11

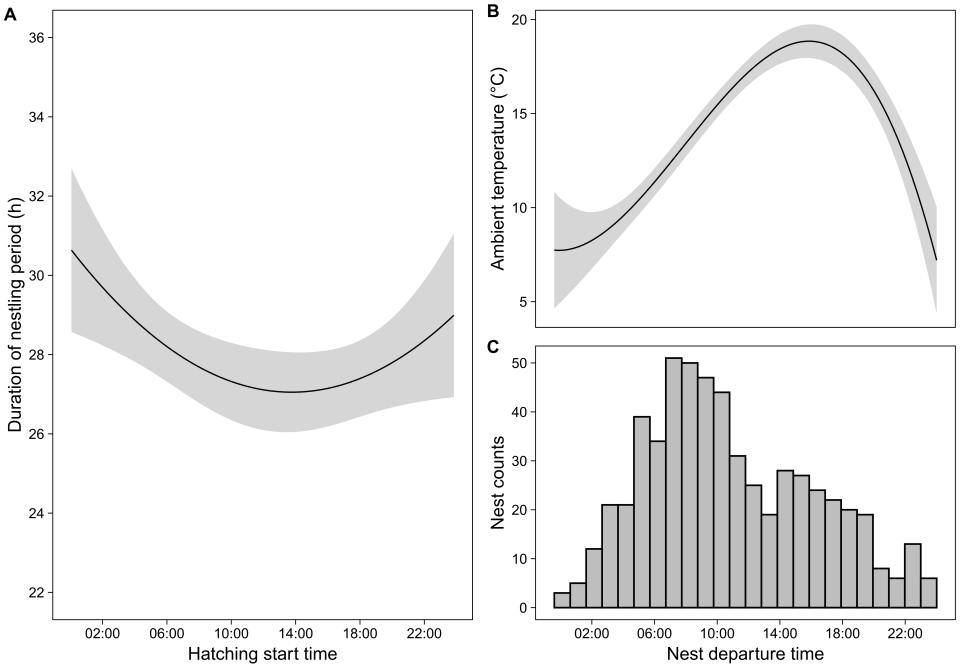


Figure 2. Effect of hatching start time on DNP (A), ambient temperature recorded at nest departure time (B) and general pattern of nest departure time (C) in eight species of Arctic-breeding sandpipers. Curves were obtained from polynomial models. All species from all sites are merged in all figures.

As predicted, a shorter DNP was found in uniparental nests compared with biparental nests. The main explanation for this difference appears to be that biparental species have young that hatch more asynchronously [13]; this prolongs the time parents must wait to allow all eggs to hatch and chicks to mature before leaving the nest. But other explanations are possible. For example, uniparental incubating parents may pursue earlier nest departures of their brood so they can regain the significant amount of mass loss they experienced during the days preceding hatching; mass loss in uniparental parents near hatching is generally thought to be larger than in biparental parents [51]. Given that the average body masses of uniparental and biparental sandpiper species in this study were similar [30], uniparental species might be more prone to leave the nest earlier. Another alternative explanation relates to the greater physiological adaptations in offspring of uniparental species compared with offspring of biparental species. In this case, the greater number and length of recesses by uniparental species during incubation [33,52] might lead to better early thermoregulatory ability of their chicks [53–55]. Indeed, suboptimal incubation temperatures in uniparentally attended nests are likely to increase the metabolic rate in neonates (i.e. higher heat production), improving their cold tolerance [56] and inducing more proactive behaviours, such as rapid exploration of novel environments [57,58]. Therefore, we speculate that nestlings could leave their nest earlier in uniparental than in biparental nests, because the former are faster to reach an efficient thermoregulation system and develop bolder behavioural traits.

Besides the incubation strategy, sandpiper young tended to leave their nests during 'day' hours, and hatching start time was, as predicted, an additional factor influencing DNP. These time-of-day effects are likely due to 'night' hours being colder than 'day' hours (see [24,32]). Broods starting to hatch during the colder 'night' hours may not be ready to leave the nest when the next warm 'day' hours occur. As a result, these young may continue to be brooded at the nest for an additional 'night', until temperatures rise again the following day. Indeed, although the sun never sets in the Arctic summer, higher levels of solar radiation during the day increase ground temperatures, which in turn reduces the thermoregulatory demands on chicks while also increasing the availability of invertebrate prey [24,59,60]. By delaying departure from the nest until warmer 'morning' hours, parents may prioritize warmer temperatures and improved foraging conditions at departure time for their chicks [61].

We also predicted that warmer temperatures later in the season would shorten DNP due to a reduced thermoregulation cost for the chicks at nest departure [62], hence allowing them to leave their nest sooner. However, we found that temperatures at nest departure time did not vary significantly over the breeding season, and DNP was not affected by the incubation start date. This suggests that the choice of optimal thermal conditions for leaving the nest is based on circadian thermal variations, regardless of seasonal temperatures.

Finally, with a high impact of nest predation risk on Arctic sandpiper breeding success [63], DNP could also reflect a trade-off between the risk of predation within and outside the nest [64]. Although the higher risk of depredation of the full brood at the nest site was expected to push adult(s) to shorten the DNP to the minimum when predator abundances are high [18,40,65], we did not find any effect of predation risk. This suggests that the selection pressure from predators on DNP may be low, and the mortality rates due to high cost of thermoregulation could be higher than the losses due to predation during the short nestling period.

These results constitute a first step towards understanding factors affecting the DNP in precocial Arctic-breeding sandpipers; further studies are needed to better unravel the mechanisms behind the DNP patterns revealed here. Our study was limited in the sense that the temperature probes used in our study could not distinguish the hatching phase or determine the individual maturation speed of the chicks. To disentangle the effects of behavioural and environmental factors on each phase of the nestling period, additional devices, such as video cameras, would be needed. Moreover, the ways parents and young interact

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

in the nest and their consequences on the decision to leave it are undocumented. Besides considering environmental factors, parents likely also consider the behaviour and condition of their chicks, and the behavioural interplay between chicks and their caring parents in this decision-making also warrants further investigation [66].

To summarize, our study showed that DNP, an understudied trait of post-hatching parental care in precocial Arctic-breeding sandpipers, varies according to the incubation strategy and strongly responds to diurnal factors related to temperature, highlighting the role of climate in influencing life-history traits. With ambient temperatures predicted to continue increasing in the Arctic and elsewhere [67], thermoregulation costs are likely to be modified in the future [68], which might force sandpipers to adjust their nestling period or their breeding phenology.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and R code are available from the Zenodo repository [69].

Electronic supplementary material is available online [70].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. T.P.: conceptualization, data curation, formal analysis, investigation, methodology, resources, visualization, writing—original draft, writing—review and editing; F.-X.D.-M.: formal analysis, methodology, writing—review and editing; A.A.: investigation, writing—review and editing; J.Be.: investigation, writing—review and editing; J.Bo.: investigation, writing—review and editing; G.S.B.: investigation, writing—review and editing; E.B.: investigation, writing—review and editing; D.E.: investigation, writing—review and editing; L.E.: data curation, investigation, writing—review and editing; I.F.: investigation, writing—review and editing; J.H.: investigation, writing—review and editing; R.L.: investigation, writing—review and editing; J.L.: investigation, writing—review and editing; C.J.L.: investigation, writing—review and editing; N.L.: formal analysis, investigation, writing—review and editing; L. McK.: investigation, writing—review and editing; J.M.: investigation, writing—review and editing; J.R.: investigation, writing—review and editing; S.T.S.: investigation, writing—review and editing; B.Sa.: investigation, writing—review and editing; N.M.S.: investigation, writing—review and editing; B.Si.: investigation, writing—review and editing; P.A.S.: investigation, writing—review and editing; A.S.: investigation, writing—review and editing; V.S.: investigation, writing—review and editing; N.S.: investigation, writing—review and editing; R.S.A.v.B.: investigation, writing—review and editing; G.Y.: investigation, writing—review and editing; L.B.: funding acquisition, project administration, supervision, validation, writing—review and editing; O.G.: conceptualization, data curation, investigation, methodology, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

Funding. This study is part of the long-term Studies in Ecology and Evolution (SEE-Life) Programme of the CNRS and was funded by the French Polar Institute (IPEV) (Programme 'Interactions 1036'), the Agence Nationale de la Recherche (ANR-21-CE02-0024 PACS), the Groupe de Recherche en Ecologie Arctique (GREA), the University of Bourgogne Europe and the University Marie et Louis Pasteur (to Hochstetter Forland and Varanger field sites). Additional funding was granted to field sites as follows: Sabetta and Erkuta (Ministry of Science and Higher Education of Russian Federation Program FUWU-2022-0009), Ammarnas (The Netherlands Organisation for Scientific Research—project 866.13.005), Zackenberg (Danish Environmental Protection Agency), Bylot (Fonds de Recherche du Québec—Nature et Technologies, Indigenous and Northern Affairs Canada, Natural Resources Canada Polar Continental Shelf Program, Natural Sciences and Engineering Research Council of Canada, ArcticNet, Environment and Climate Change Canada, Sirmilik National Park—Parks Canada, Centre d'Études Nordiques), Igloolik (Department of Environment, Government of Nunavut, Natural Sciences and Engineering Research Council, Canada Research Chair Program, Université de Moncton, ArcticNet, Centre d'Études Nordiques, Canadian Foundation of Innovation, Polar Knowledge Canada, Canadian Wildlife Service, Polar Continental Knowledge, Natural Resources Canada, Hunters and Trappers Associations), Burnpoint Creek (Ontario Ministry of Natural Resources, Natural Sciences and Engineering Research Council), Varanger (Navigating the New Arctic—National Science Foundation award 2126796), Churchill (York University Glendon Campus, Northern Scientific Training Program, Churchill Northern Studies Centre's Northern Research Fund), Utqiagvik/Barrow and Canning River (US Fish and Wildlife Service, Arctic Landscape Conservation Cooperative, National Fish and Wildlife Foundation, US Geological Survey's Science Support Program, University of Colorado Denver, Oregon State University, Iowa State University). J.R. was supported by an International Polar Year grant from the Netherlands Organisation for Scientific Research (NWO), by the Metawad project awarded by Waddenfonds (WF209925, www.metawad.nl), by two INTERACT grants for Transnational Access from the European Community's Seventh Framework Programme (grant agreement no. 262693) and by a grant from World Wildlife Fund Netherlands.

Acknowledgements. The authors thank all people who helped collect field data, and the various entities that allowed access to their lands. They also would like to thank the referees for their relevant and useful comments.

References

1. Mota-Rojas D, Marcet-Rius M, Domínguez-Oliva A, Buenhombre J, Daza-Cardona EA, Lezama-García K, Olmos-Hernández A, Verduzco-Mendoza A, Bienboire-Frosini C. 2023 Parental behavior and newborn attachment in birds: life history traits and endocrine responses. *Front. Psychol*. **14**, 1183554. (doi:10.3389/fpsyg.2023.1183554)
2. Zimmer C, Boogert NJ, Spencer KA. 2013 Developmental programming: cumulative effects of increased pre-hatching corticosterone levels and post-hatching unpredictable food availability on physiology and behaviour in adulthood. *Horm. Behav*. **64**, 494–500. (doi:10.1016/j.yhbeh.2013.07.002)
3. Riechert J, Becker PH. 2017 What makes a good parent? Sex-specific relationships between nest attendance, hormone levels, and breeding success in a long-lived seabird. *Auk* **134**, 644–658. (doi:10.1642/auk-17-13.1)
4. Mainwaring MC. 2016 The transition from dependence to independence in birds. *Behav. Ecol. Sociobiol*. **70**, 1419–1431. (doi:10.1007/s00265-016-2186-z)
5. Starck JM, Ricklefs RE. 1998 *Avian growth and development: evolution within the altricial-precocial spectrum*. Oxford, UK: Oxford University Press.
6. Vleck CM, Vleck D. 2011 Hormones and regulation of parental behavior in birds. In *Hormones and reproduction of vertebrates* (eds DO Norris, KH Lopez), pp. 181–203. London, UK: Academic Press. (doi:10.1016/B978-0-12-374932-1.00045-7)
7. Chen CK, Chuang HF, Wu SM, Li WH. 2019 Feather evolution from precocial to altricial birds. *Zool. Stud.* **58**, e24. (doi:10.6620/ZS.2019.58-24)
8. Schekkerman H, Visser GH. 2001 Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *Auk* **118**, 944–957. (doi:10.2307/4089844)
9. Schekkerman H, Tulp I, Piersma T, Visser GH. 2003 Mechanisms promoting higher growth rate in Arctic than in temperate shorebirds. *Oecologia* **134**, 332–342. (doi:10.1007/s00442-002-1124-0)

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

10. Ritchison G. 2023 *In a class of their own: a detailed examination of avian forms and functions*. Cham, Switzerland: Springer. (doi:10.1007/978-%203-031-14852-1)
11. Arnold TW. 2011 Onset of incubation and patterns of hatching in the American coot. *Condor* **113**, 107–118. (doi:10.1525/cond.2011.100001)
12. Temizyürek T, Johannknecht M, Korsten P. 2024 Incubation before clutch completion predicts incubation time and hatching asynchrony in the blue tit *Cyanistes caeruleus*. *Ardea* **110**, 213–225. (doi:10.5253/arde.2022.a6)
13. Stoleson SH, Beissinger SR. 1995 Hatching asynchrony and the onset of incubation in birds, revisited. In *Current ornithology* (ed. DM Power), pp. 191–270. Boston, MA: Springer. (doi:10.1007/978-1-4615-1835-8_6)
14. Jones TM, Kaiser SA, Sillett TS. 2026 Post-fledging ecology of birds: emergent patterns, knowledge gaps, and future frontiers. *Biol. Rev. Camb. Philos. Soc.* **101**, 237–267. (doi:10.1111/brv.70080)
15. Krijgsveld KL, Visser GH, Daan S. 2003 Foraging behavior and physiological changes in precocial quail chicks in response to low temperatures. *Physiol. Behav*. **79**, 311–319. (doi:10.1016/s0031-9384(03)00117-3)
16. Shinder D, Rusal M, Tanny J, Druyan S, Yahav S. 2007 Thermoregulatory responses of chicks (*Gallus domesticus*) to low ambient temperatures at an early age. *Poult. Sci*. **86**, 2200–2209. (doi:10.1093/ps/86.10.2200)
17. Ghalambor CK, Peluc SI, Martin TE. 2013 Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biol. Lett*. **9**, 20130154. (doi:10.1098/rsbl.2013.0154)
18. Ibáñez-Álamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RL, Martin TE. 2015 Nest predation research: recent findings and future perspectives. *J. Ornithol.* **156**, 247–262. (doi:10.1007/s10336-015-1207-4)
19. Weiser EL *et al*. 2018 Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. *Ibis* **160**, 608–623. (doi:10.1111/ibi.12571)
20. Meyer N *et al*. 2020 Nest attentiveness drives nest predation in Arctic sandpipers. *Oikos* **129**, 1481–1492. (doi:10.1111/oik.07311)
21. Etchart L *et al*. 2025 Snowmelt and laying date impact the parental care strategy of a high-Arctic shorebird. *Sci. Rep*. **15**, 19760. (doi:10.1038/s41598-025-02318-y)
22. Eberhardt LE, Hanson WC, Bengtson JL, Garrott RA, Hanson EE. 1982 Arctic fox home range characteristics in an oil-development area. *J. Wildl. Manage*. **46**, 183–190. (doi:10.2307/3808421)
23. Westermann S, Langer M, Boike J. 2011 Spatial and temporal variations of summer surface temperatures of high-Arctic tundra on Svalbard—implications for MODIS LST based permafrost monitoring. *Remote Sens. Environ*. **115**, 908–922. (doi:10.1016/j.rse.2010.11.018)
24. Steiger SS, Valcu M, Spoelstra K, Helm B, Wikelski M, Kempenaers B. 2013 When the sun never sets: diverse activity rhythms under continuous daylight in free-living Arctic-breeding birds. *Proc. R. Soc. B* **280**, 20131016. (doi:10.1098/rspb.2013.1016)
25. Bonnefond L, Pinaud D, Bollache L, Schmidt NM, Lang J, Hansen LH, Sittler B, Moreau J, Gilg O. 2025 Intraseasonal variations in the spatial behaviour of an Arctic predator. *Mov. Ecol.* **13**, 13. (doi:10.1186/s40462-024-00522-5)
26. Norton DW. 1973 *Ecological energetics of calidrine sandpipers breeding in northern Alaska*. Fairbanks, AK: University of Alaska.
27. Grond K, Lanctot RB, Jumpponen A, Sandercock BK. 2017 Recruitment and establishment of the gut microbiome in Arctic shorebirds. *FEMS Microbiol. Ecol.* **93**, fix142. (doi:10.1093/femsec/fix142)
28. Schekkerman H. 2008 *Precocial problems: shorebird chick performance in relation to weather, farming, and predation*. Wageningen, The Netherlands: Wageningen University and Research.
29. Whitfield DP, Tomkovich PS. 1996 Mating system and timing of breeding in Holarctic waders. *Biol. J. Linn. Soc*. **57**, 277–290. (doi:10.1111/j.1095-8312.1996.tb00313.x)
30. Cramp S, Simmons KEL. 1983 *Handbook of the birds of Europe, the Middle East and North Africa, volume III: waders to gulls*. Oxford, UK: Oxford University Press.
31. Reneerkens J, van Veelen P, van der Velde M, Luttikhuizen P, Piersma T. 2014 Within-population variation in mating system and parental care patterns in the sanderling (*Calidris alba*) in northeast Greenland. *Auk* **131**, 235–247. (doi:10.1642/AUK-13-247.1)
32. Meyer N *et al*. 2021 Behavioural responses of breeding arctic sandpipers to ground-surface temperature and primary productivity. *Sci. Total Environ*. **755**, 142485. (doi:10.1016/j.scitotenv.2020.142485)
33. Etchart L *et al*. 2024 Extended incubation recesses in sanderlings are impacted by temperature and body condition. *Proc. R. Soc. B* **291**, 20232264. (doi:10.1098/rspb.2023.2264)
34. Bulla M, Valcu M, Rutten AL, Kempenaers B. 2014 Biparental incubation patterns in a high-Arctic breeding shorebird: how do pairs divide their duties? *Behav. Ecol*. **25**, 152–164. (doi:10.1093/beheco/art098)
35. 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**, 13–22. (doi:10.1111/ibi.12507)
36. Saalfeld ST, Weiser EL, Brown SC, Latty CJ, Schulte S, Lanctot RB. 2026 Reducing bias in shorebird nest survival rates across a large Arctic landscape. *Ibis* **168**, 25–41. (doi:10.1111/ibi.13441)
37. Tavera EA *et al*. 2024 Why do avian responses to change in Arctic green-up vary? *Glob. Chang. Biol*. **30**, e17335. (doi:10.1111/gcb.17335)
38. Smith PA, Gilchrist HG, Forbes MR, Martin J, Allard K. 2010 Inter-annual variation in the breeding chronology of Arctic shorebirds: effects of weather, snow melt and predators. *J. Avian Biol*. **41**, 292–304. (doi:10.1111/j.1600-048x.2009.04815.x)
39. Liebezeit JR, Gurney KEB, Budde M, Zack S, Ward D. 2014 Phenological advancement in Arctic bird species: relative importance of snow melt and ecological factors. *Polar Biol*. **37**, 1309–1320. (doi:10.1007/s00300-014-1522-x)
40. Hua F, Sieving KE, Fletcher RJ, Wright CA. 2014 Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behav. Ecol*. **25**, 509–519. (doi:10.1093/beheco/aru017)
41. Laundré JW, Hernández L, Altendorf KB. 2001 Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Can. J. Zool.* **79**, 1401–1409. (doi:10.1139/z01-094)
42. McKinnon L, Bêty J. 2009 Effect of camera monitoring on survival rates of high-Arctic shorebird nests. *J. Field Ornithol*. **80**, 280–288. (doi:10.1111/j.1557-9263.2009.00231.x)
43. Smith PA, Wilson S. 2010 Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* **163**, 613–624. (doi:10.1007/s00442-010-1644-y)
44. R Core Team. 2025 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
45. Schielzeth H. 2010 Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113. (doi:10.1111/j.2041-210X.2010.00012.x)
46. Pewsey A, Neuhäuser M, Ruxton GD. 2013 *Circular statistics in R*. Oxford, UK: Oxford University Press.
47. Burnham KR, Anderson DR. 2022 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
48. Richards SA, Whittingham MJ, Stephens PA. 2011 Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behav. Ecol. Sociobiol.* **65**, 77–89. (doi:10.1007/s00265-010-1035-8)

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026

49. Barton K. 2018 MuMIn: multi-model inference. R package. See https://CRAN.Rproject.org/package=MuMIn.
50. Bates D, Mächler M, Bolker B, Walker S. 2015 lme4: linear mixed-effects models using lme4. *J. Stat. Softw*. **67**, 1–48. (doi:10.18637/jss.v067.i01)
51. Moreno J. 1989 Strategies of mass change in breeding birds. *Biol. J. Linn. Soc*. **37**, 297–310. (doi:10.1111/j.1095-8312.1989.tb01907.x)
52. Reneerkens J, Grond K, Schekkerman H, Tulp I, Piersma T. 2011 Do uniparental sanderlings *Calidris alba* increase egg heat input to compensate for low nest attentiveness? *PLoS One* **6**, e16834. (doi:10.1371/journal.pone.0016834)
53. DuRant SE, Hopkins WA, Wilson AF, Hepp GR. 2012 Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird. *Funct. Ecol*. **26**, 416–422. (doi:10.1111/j.1365-2435.2011.01945.x)
54. DuRant SE, Hopkins WA, Hepp GR, Walters JR. 2013 Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biol. Rev.* **88**, 499–509. (doi:10.1111/brv.12015)
55. DuRant SE, Hopkins WA, Carter AW, Stachowiak CM, Hepp GR. 2013 Incubation conditions are more important in determining early thermoregulatory ability than posthatch resource conditions in a precocial bird. *Physiol. Biochem. Zool.* **86**, 410–420. (doi:10.1086/671128)
56. Tzschentke B. 2007 Attainment of thermoregulation as affected by environmental factors. *Poult. Sci.* **86**, 1025–1036. (doi:10.1093/ps/86.5.1025)
57. Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MA, Blokhuis HJ. 1999 Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935. (doi:10.1016/s0149-7634(99)00026-3)
58. Hope SF, Kennamer RA, Moore IT, Hopkins WA. 2018 Incubation temperature influences the behavioral traits of a young precocial bird. *J. Exp. Zool. A* **329**, 191–202. (doi:10.1002/jez.2176)
59. Ricklefs RE, Williams JB. 2003 Metabolic responses of shorebird chicks to cold stress: hysteresis of cooling and warming phases. *J. Exp. Biol.* **206**, 2883–2893. (doi:10.1242/jeb.00482)
60. Zoller L, Bennett JM, Knight TM. 2020 Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. *Sci. Rep*. **10**, 21187. (doi:10.1038/s41598-020-78165-w)
61. Holt S, Whitfield DP. 2003 Timing of nest departure by broods of dotterel *Charadrius morinellus*. *Bird Study* **50**, 88–90. (doi:10.1080/00063650309461296)
62. McKinnon L, Nol E, Juillet C. 2013 Arctic-nesting birds find physiological relief in the face of trophic constraints. *Sci. Rep*. **3**, 1816. (doi:10.1038/srep01816)
63. Bonnefond L, Pinaud D, Bollache L, Pagnon T, Buchel E, Sabard B, Gilg V, Moreau J, Gilg O. 2026 Predation risk does not delay breeding but reduces nest survival in high-Arctic shorebirds. *Ecol. Evol.* **16**, e72997. (doi:10.1002/ece3.72997)
64. Roff DA, Remes V, Martin TE. 2005 The evolution of fledging age in songbirds. *J. Evol. Biol.* **18**, 1425–1433. (doi:10.1111/j.1420-9101.2005.00958.x)
65. Stodola KW, Buehler DA, Kim DH, Franzreb KE, Linder ET. 2010 Biotic and abiotic factors governing nestling-period length in the ovenbird (*Seiurus aurocapilla*). *Auk* **127**, 204–211. (doi:10.1525/auk.2009.09151)
66. Johnson M, Aref S, Walters JR. 2008 Parent–offspring communication in the western sandpiper. *Behav. Ecol*. **19**, 489–501. (doi:10.1093/beheco/arn003)
67. Rummukainen M. 2012 Changes in climate and weather extremes in the 21st century. *Wiley Interdiscip. Rev. Clim. Change* **3**, 115–129. (doi:10.1002/wcc.160)
68. Andreasson F, Nilsson JÅ, Nord A. 2020 Avian reproduction in a warming world. *Front. Ecol. Evol.* **8**, 576331. (doi:10.3389/fevo.2020.576331)
69. Pagnon T. 2026 Incubation strategy and hatching start time affect the duration of the nestling period in precocial Arctic-breeding sandpipers [Data set]. Zenodo. (doi:10.5281/zenodo.18611034)
70. Pagnon T *et al*. 2026 Supplementary material from: Incubation strategy and hatching start time affect the duration of the nestling period in precocial Arctic-breeding sandpipers. Figshare. (doi:10.6084/m9.figshare.c.8405301)

Downloaded from royalsocietypublishing.org/rsbl/article-pdf/doi/10.1098/rsbl.2025.0670/6132352/rsbl.2025.0670.pdf
by BCU Lausanne Site Unitheque user
on 13 October 2026