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

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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

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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 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 $\mathrm{DNP} < 12$ 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

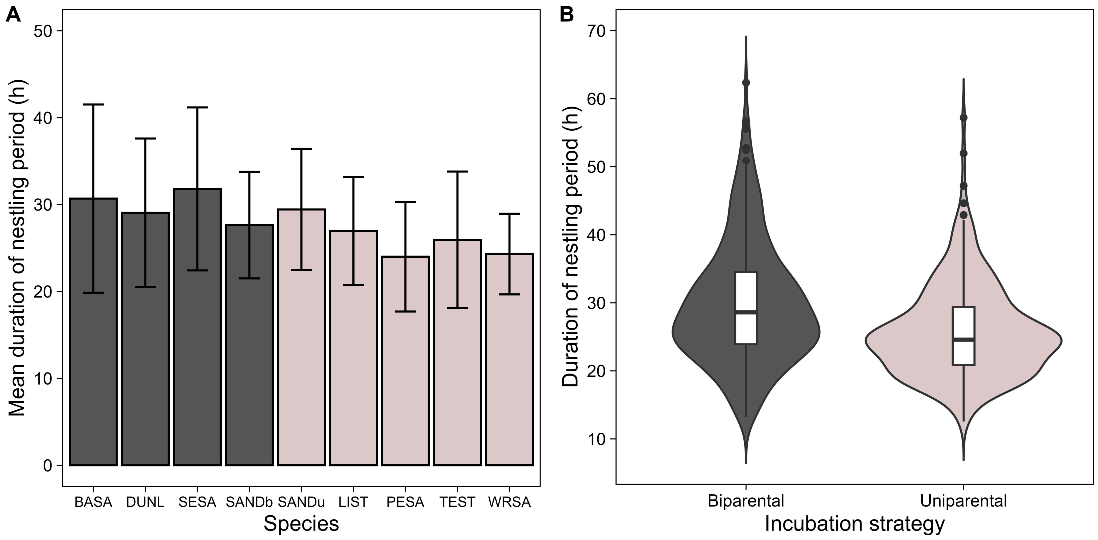

Figure 1. Differences in DNP among species (mean with the standard error; A) and between incubation strategies (medians, interquartile ranges and value distributions; B) in eight species of Arctic-breeding shorebirds. Colour in panels refers to the incubation strategy (dark grey: biparental; light grey: 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 $[0, 2\pi]$ 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 $\Delta\text{AICc} < 2$ 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 $\beta = -0.059$, 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 $\beta = 0.016$, 95% CI: 0.002 to 0.029; i.e.+3.7%; sine, i.e. 18.00 to 06.00 axis: averaged $\beta = 0.014$, 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 $\beta = 0.014$, 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 $\chi^2 = 0.826$, $p = 0.363$). Finally, the relative abundance of avian predators (averaged $\beta = 0.0001$, 95% CI: −0.0100 to 0.0102) and the relative abundance of foxes (averaged $\beta = -0.005$, 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.

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

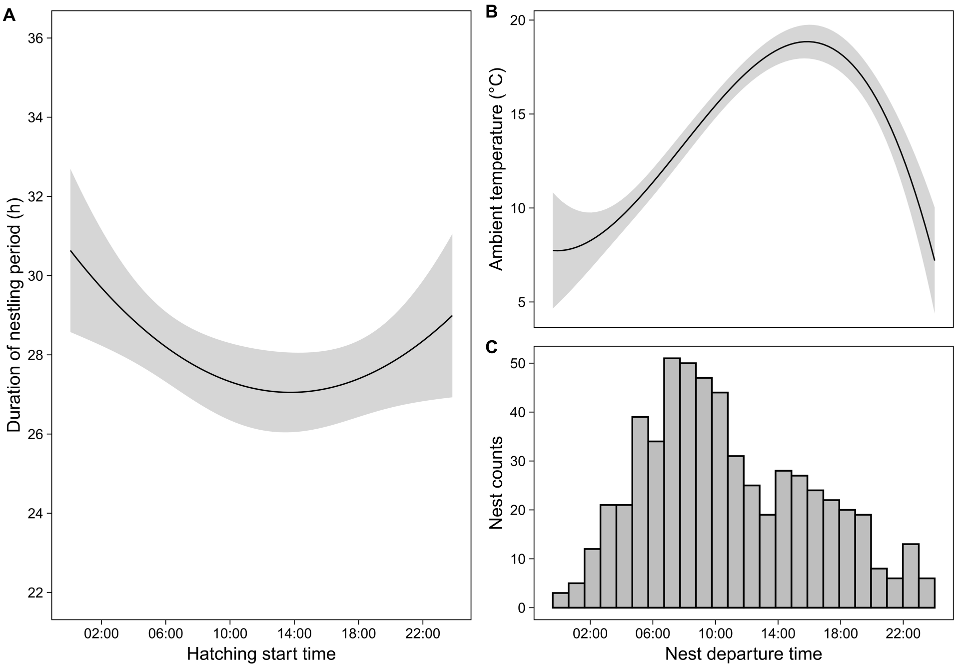

Figure 2. Effect of hatching start time on DNP (A), ambient temperature recorded at nest departure time (B) and general pattern of nest departure time (C) in eight species of Arctic-breeding sandpipers. Curves were obtained from polynomial models. All species from all sites are merged in all figures.

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 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.

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Supplementary materials

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

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This document includes:

- Supplementary Tables
- Supplementary Figures
- Appendix 1: Protocol used to document the relative abundance of predators

Table S1. Study sites with ranges of monitoring years and the number of monitored nests per species and site. Non-monitoring years are illustrated within square brackets. For each species and each site, the first number indicates the number of nests that produced young (used for analyses), and the numbers in brackets indicate the total number of monitored nests. BASA: Baird's sandpiper, DUNL: Dunlin, LIST: Little stint, PESA: Pectoral sandpiper, SAND: Sanderling, SESA: Semipalmated sandpiper, TEST: Temminck's stint, WRSA: White-rumped sandpiper. Four-letter acronyms, and genus/species names are in Table S4.

Country	Site name	Location (latitude, longitude)	Years (range)	Species							
				BASA	DUNL	LIST	PESA	SAND	SESA	TEST	WRSA
Russia	Sabetta	71.24°N, 71.80°E	2016-2023	—	15 (82)	41 (138)	—	—	—	24 (119)	—
Russia	Erkuta	68.22°N, 69.15°E	2016-2023	—	4 (5)	—	—	—	—	74 (146)	—
Norway	Varanger	70.53°N, 29.21°E	2023	—	14 (20)	—	—	—	—	9 (18)	—
Sweden	Ammarnäs	69.96°N, 16.29°E	2016-2019	—	10 (28)	—	—	—	—	—	—
Greenland	Hochstetter Forland	75.15°N, 19.70°W	2017-2023	—	18 (36)	—	—	28 (97)	—	—	—
Greenland	Zackenberg	74.47°N, 20.57°W	2016-2020	—	9 (16)	—	—	19 (61)	—	—	—
Greenland	Karupelv valley	72.50°N, 24°W	2016-2023	—	—	—	—	13 (47)	—	—	—
Canada	Bylot	73.15°N, 80.00°W	2016-[2020-2021]-2023	50 (111)	—	—	—	—	—	—	8 (28)
Canada	Igloolik	69.40°N, 81.60°W	2016-[2020-2022]-2023	—	—	—	—	—	—	—	39 (105)
Canada	East Bay	63.98°N, 81.67°W	2017-2019	—	—	—	—	—	—	—	7 (57)
Canada	Burnpoint creek	55.14°N, 84.20°W	2018-[2020]-2023	—	34 (56)	—	—	—	—	—	—
Canada	Churchill	58.70°N, 94.08°W	2016-2018	—	14 (29)	—	—	—	—	—	—
USA	Canning river	70.12°N, 145.82°W	2019	—	—	—	29 (94)	—	14 (153)	—	—
USA	Barrow/Utqiaġvik	71.23°N, 156.75°W	2016-2023	—	43 (157)	—	—	—	59 (148)	—	—
Total				**50 (111)**	**161 (429)**	**41 (138)**	**29 (94)**	**60 (205)**	**73 (201)**	**107 (283)**	**54 (190)**

Table S2. Methods to estimate the incubation start date for nests found with incomplete and complete clutches (see conceptual figure S2 in Etchart et al. 2024).

Nest at discovery	Nest fate	Method to estimate incubation start date	References
Uncomplete clutch (generally <4 eggs)	Hatched/unsuccessful	Assumes one egg laid per day, incubation starting with the penultimate egg and relies on subsequent visits to nests to verify final clutch size	Liebezeit et al. 2014 Saalfeld and Lanctot 2015
Complete clutch	Hatched	Subtract the mean incubation period of the species from the known hatching date, which is determined by temperature patterns in nest (see Figures S2) or by direct observations of hatching eggs/young in nest cup.	Liebezeit et al. 2014
	Unsuccessful	Subtract estimated age of embryos (based on egg floatation) from date eggs are floated in the nest	Liebezeit et al. 2007 Mabee et al. 2006

Table S3. Annual predator observation effort expressed as the total number hours of observation per site per year.

	Monitoring year							
	2016	2017	2018	2019	2020	2021	2022	2023
Ammarnäs	96.3	145.2	187.9	146.0				
Barrow/Utqiagvik	318.0	407.5	219.4	361.2	49.0	213.8	188.0	206.0
Burnpoint creek			191.4	237.1		475.3	269.2	232.8
Bylot	626.8	429.4	878.3	607.7			529.2	414.2
Canning river				599.7				
Churchill	94.5	171.0	169.4					
East Bay		430.3	718.8	285.2				
Erkuta	134.3	436.4	253.8	294.3	95.7	287.4	127.9	189.3
Hochstetter Forland		576.8	140.1	236.9	237.7	216.2	170.4	262.0
Igloolik	292.3	362.5	373.2	282.7				135.5
Karupelv valley	193.8	142.3	187.6	210.6	164.8	237.5	248.7	208.4
Sabetta	109.9	169.6	183.3	213.3	143.8	134.5	121.5	195.7
Varanger								99.9
Zackenberg	412.8	387.0	473.8	341.0	271.7			

Table S4. Descriptive statistics of the duration (in hours) of the nestling period (i.e., time between when nest temperatures showed a sawtooth pattern indicating start of hatch to an empty nest, see Figures S2) for the eight species of arctic sandpiper in this study. Sanderlings are also shown according to their incubation strategy.

Species			Mean	SD	Max	Min	N	Incubation strat
BASA	Baird's Sandpiper	*Calidris bairdii*	30.68	10.83	62.37	13.27	50	Biparental
DUNL	Dunlin	*Calidirs alpina*	29.05	8.55	56.36	13.39	161	Biparental
LIST	Little Stint	*Calidris minuta*	26.95	6.19	41.33	18.17	41	Uniparental
PESA	Pectoral Sandpiper	*Calidris melanotos*	24.00	6.31	41.95	12.56	29	Uniparental
SAND	Sanderling	*Calidris alba*	28.27	6.44	42.34	15.39	60	Bi and uniparental
			29.44	*6.97*	*40.9*	*18.18*	*21*	*Uniparental*
			27.64	*6.12*	*42.34*	*15.39*	*39*	*Biparental*
SESA	Semipalmated Sandpiper	*Calidris pusilla*	31.80	9.38	56.70	13.20	73	Biparental
TEST	Temminck's Stint	*Calidris temminckii*	25.95	7.86	57.21	13.13	107	Uniparental
WRSA	White-rumped Sandpiper	*Calidris fuscicollis*	24.31	4.64	34.88	15.13	54	Uniparental

Figure S1. Hatching start time in eight species of arctic-breeding sandpipers. Data from all species throughout the entire breeding seasons across all years are merged.

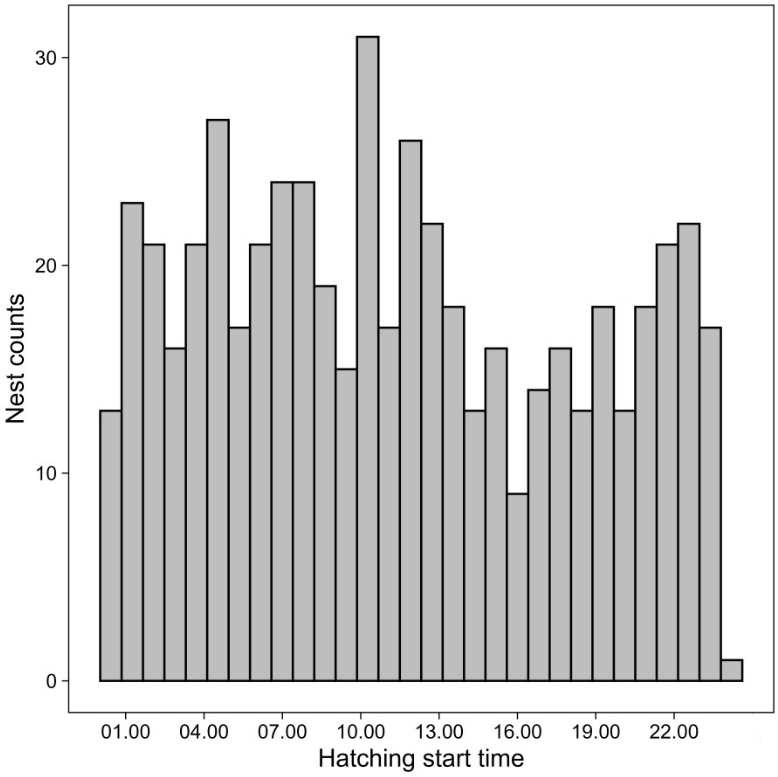
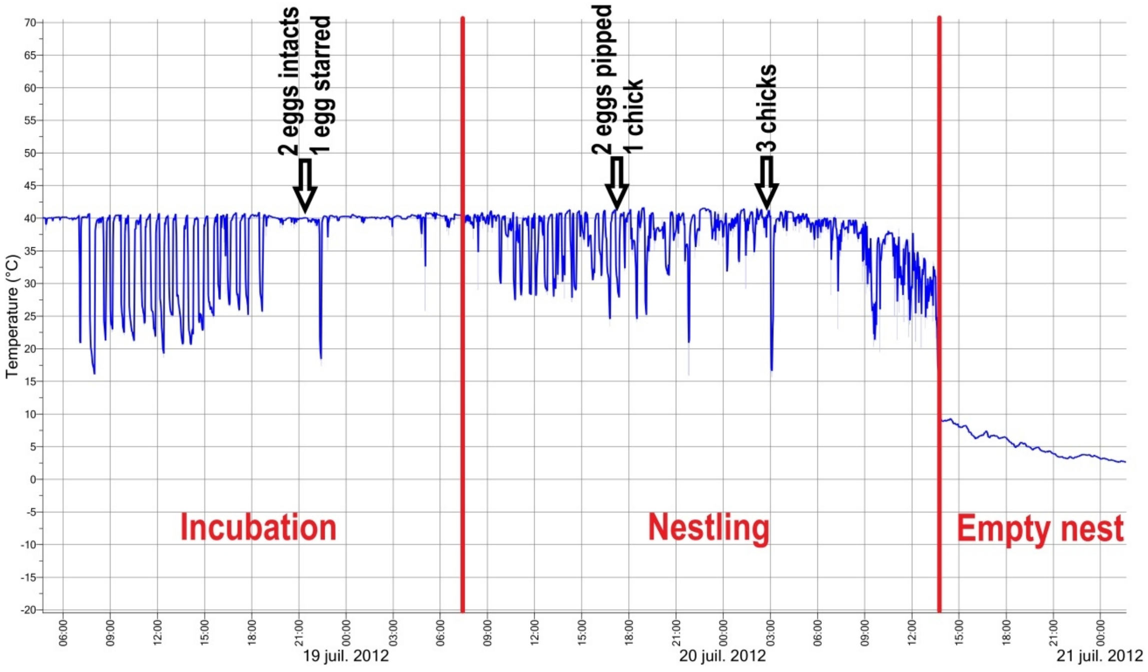
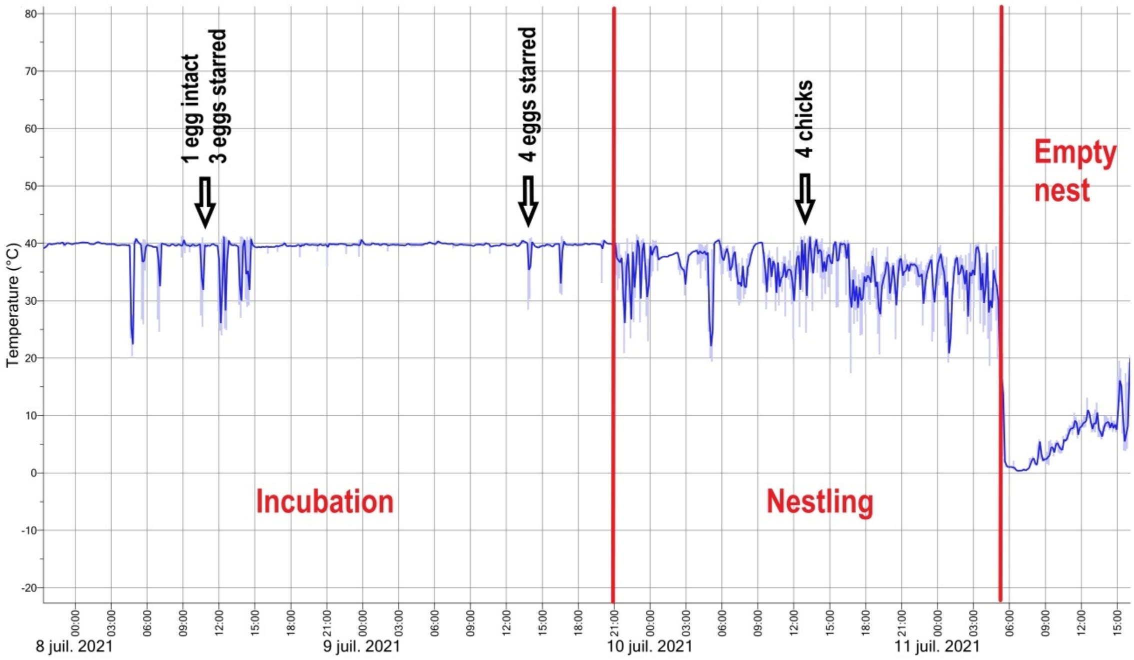


Figure S2. Examples of thermic patterns throughout the nestling period based on data from Tiny tag Plus 2 temperature probes deployed in nests. Field observations of nest contents are indicated with black arrows. Temperature patterns during the incubation period are like in Moreau et al. (2018) and Meyer et al. (2020; see figure A1). The start of the sawtooth pattern indicates the hatching of the first egg (1st vertical red bar) and a sudden drop in temperature (2nd vertical red bar) indicates all eggs have hatched and the brood departed the nest. The final drop in temperatures, which indicates an empty nest, matches the ambient air temperature patterns. A sudden drop in temperature after a short time (< 12 hr., based on minimum time of hatching completion and chick drying observed on the field) would indicate that chicks and remaining unhatched eggs have been depredated.

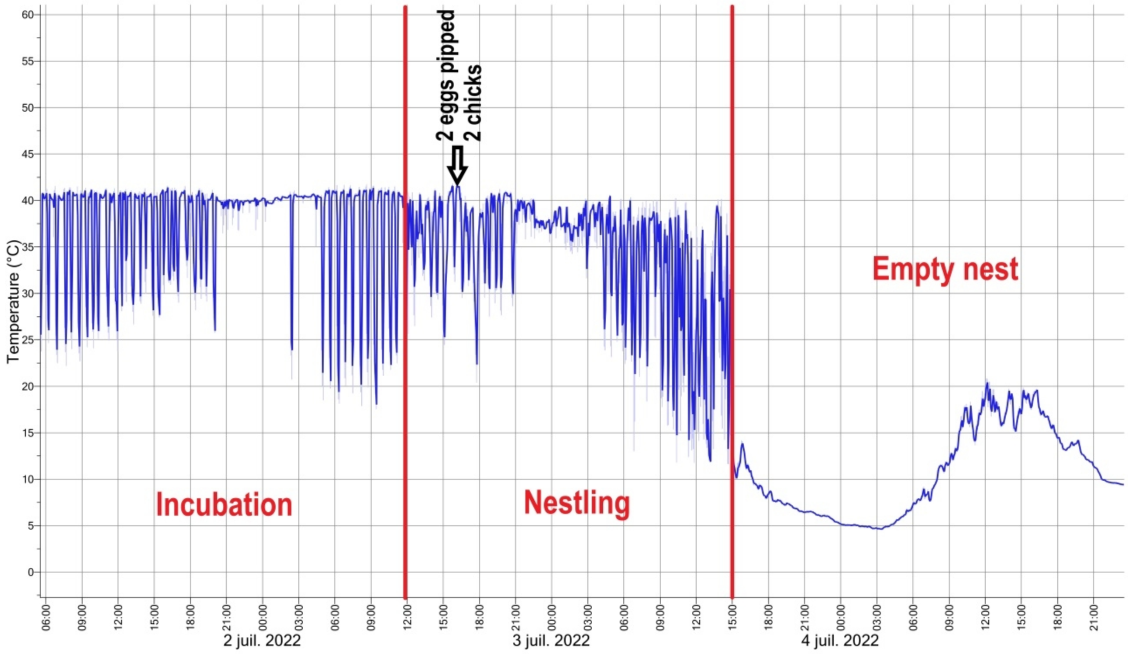
a) Uniparental sanderling nest at Hochstetter (Greenland)



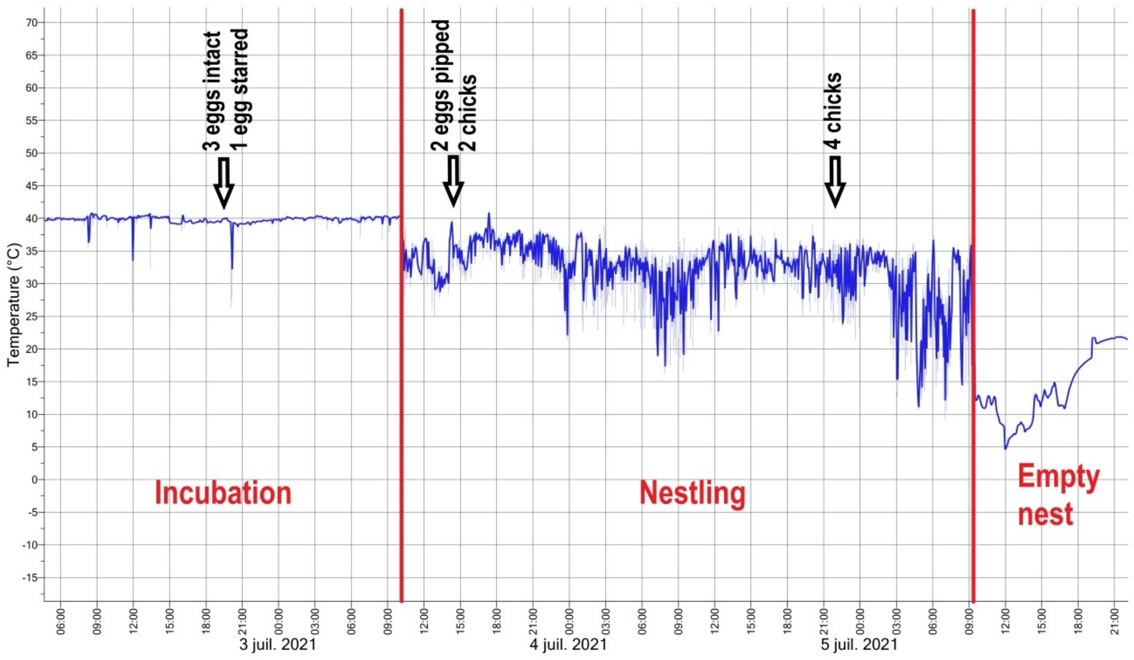
b) Biparental dunlin nest at Barrow/Utqiagvik (USA)



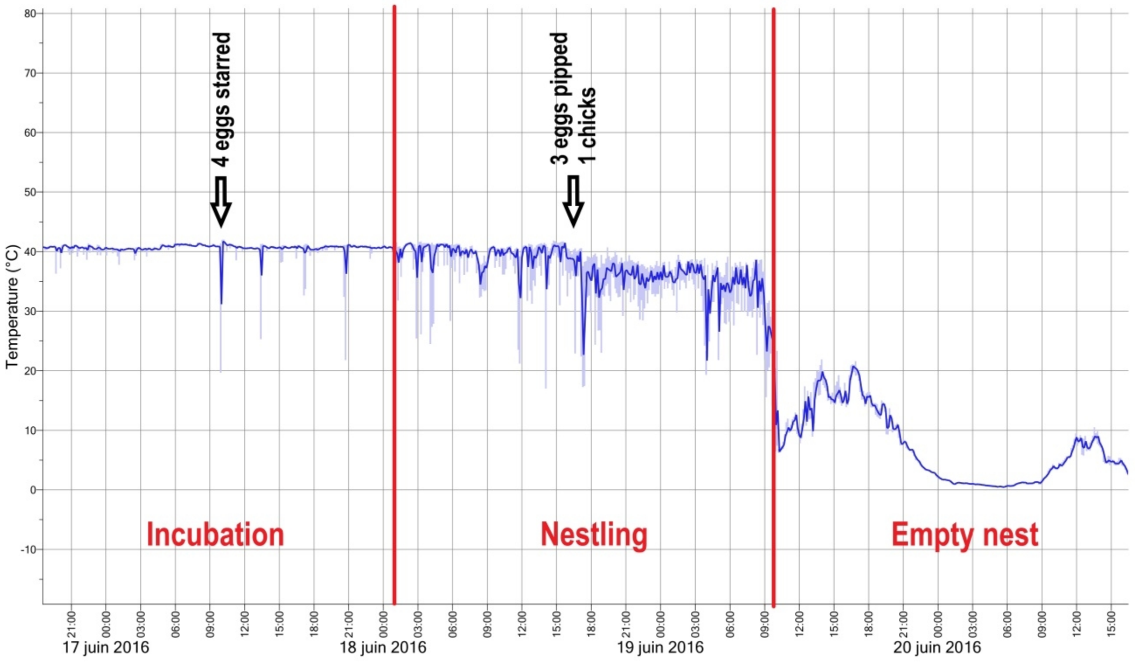
c) Uniparental Temminck's stint nest at Erkuta (Russia)



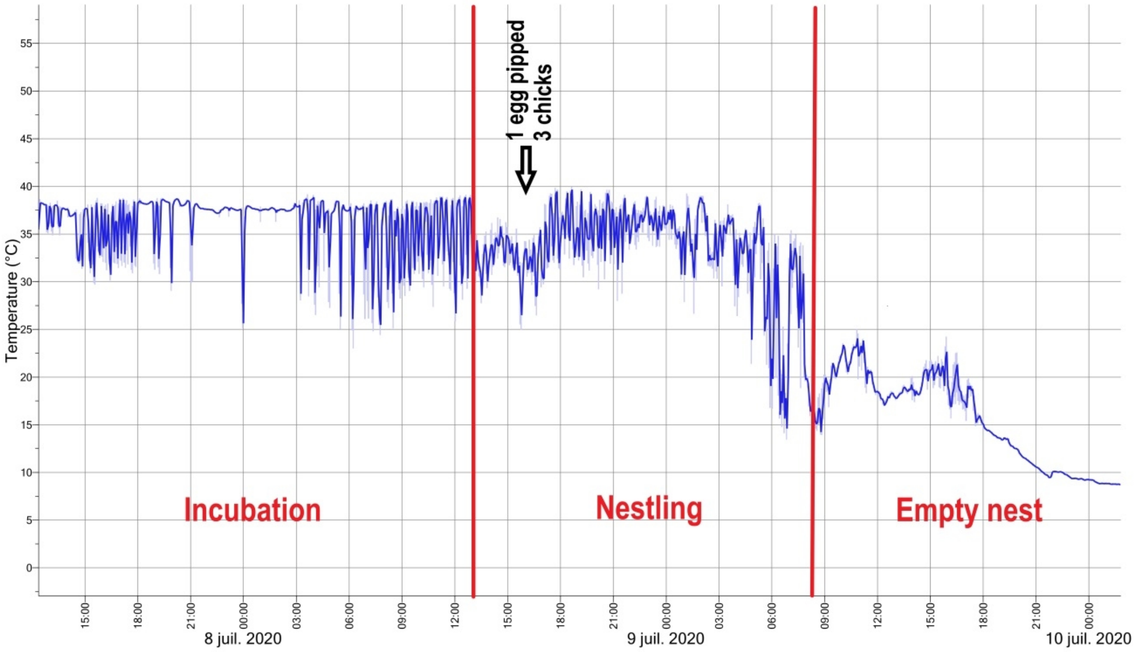
d) Biparental semipalmated sandpiper nest at Barrow/Utqiagvik (USA)



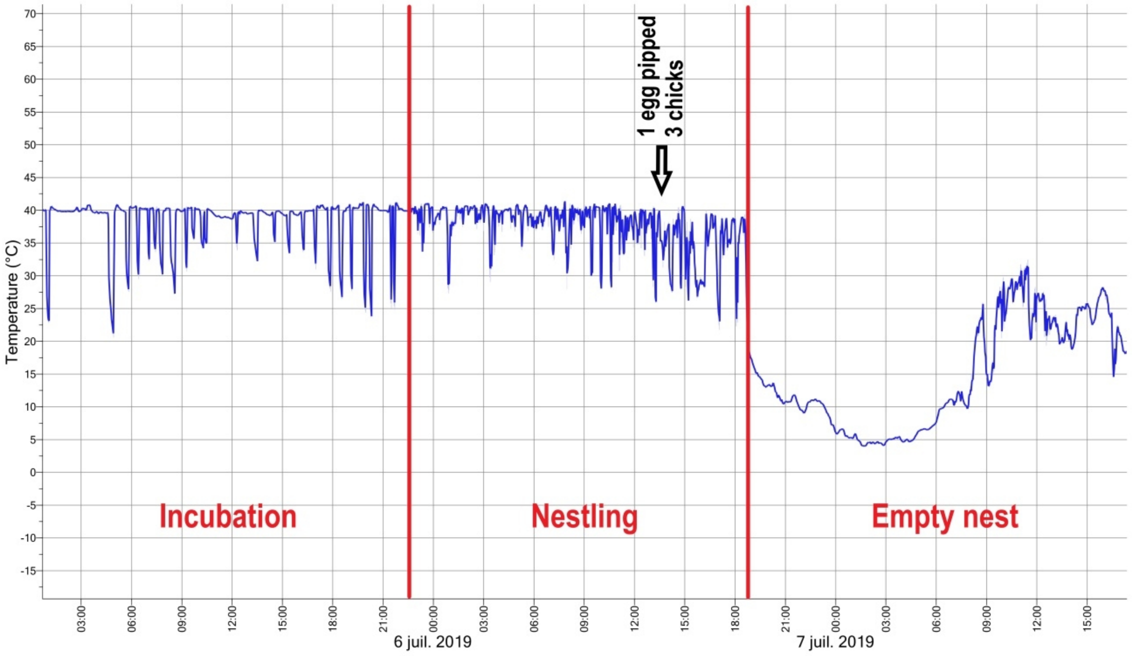
e) Biparental semipalmated sandpiper nest at Barrow/Utqiagvik (USA)



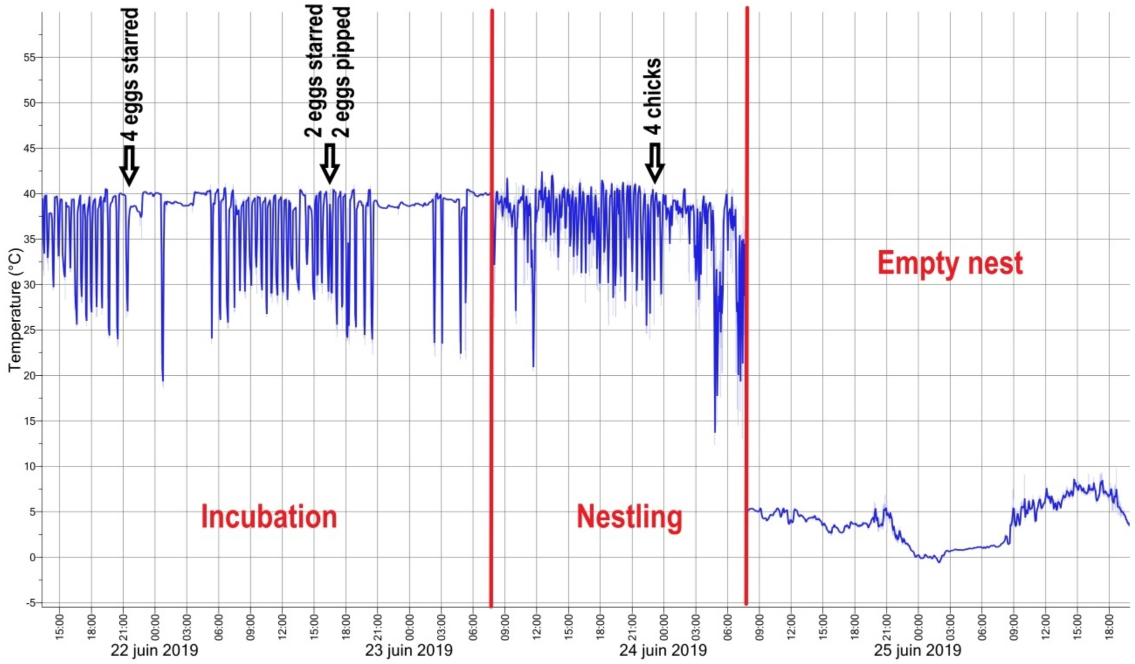
f) Uniparental little stint nest at Sabetta (Russia)



g) Uniparental white-rumped sandpiper nest at Igloolik (Canada)



h) Uniparental pectoral sandpiper nest at Canning River (USA)



i) Biparental Baird's sandpiper nest at Bylot (Canada)

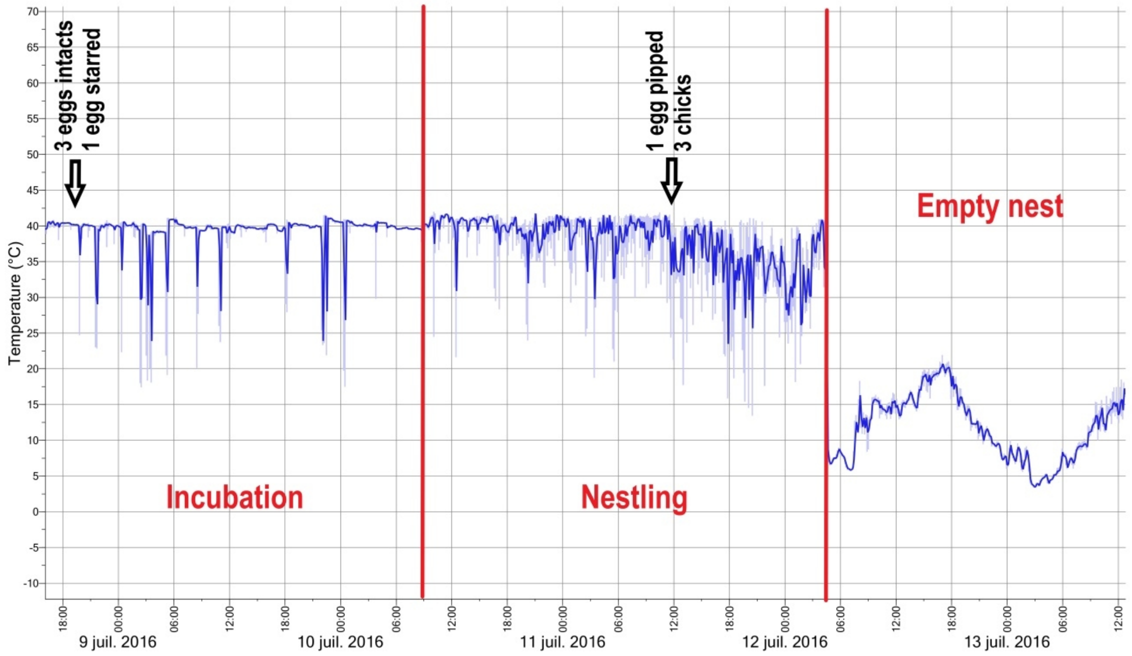
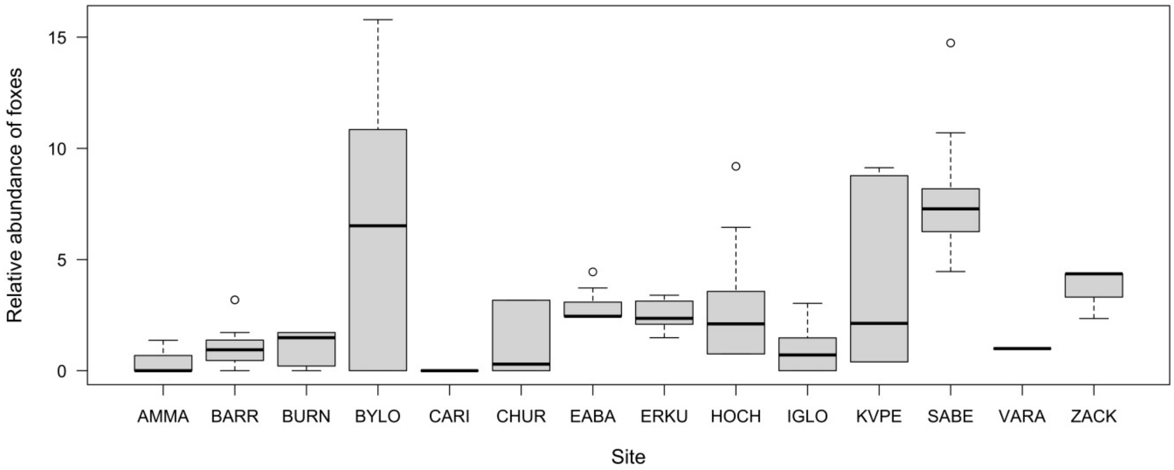
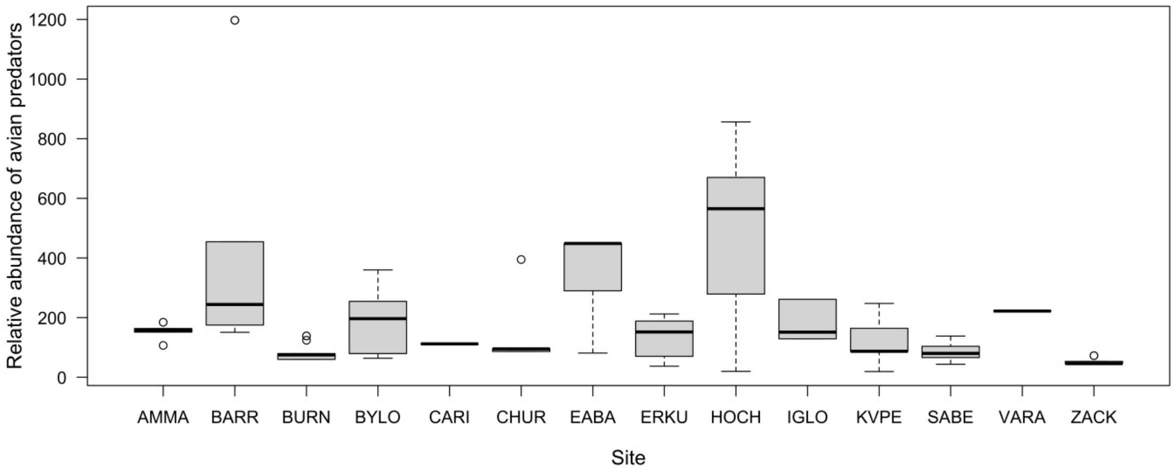


Figure S3. Relative abundances of foxes (a) and avian predators (b) per study site expressed as the number of predator observations for 100h of observation between 2016 and 2023 (see table S3). The boxplots show the medians (thick horizontal lines), interquartile ranges (boxes), ranges (whiskers) and outliers (dots) across all years with data at a site. AMMA: Ammarnäs; BARR: Barrow/Utqiagvik; BURN: Burnpoint creek; BYLO: Bylot; CARI: Canning River; CHUR: Churchill; EABA: East Bay; ERKU: Erkuta; HOCH: Hochstetter Forland; IGLO: Igloolik; KVPE: Karuplev valley; SABE: Sabetta; VARA: Varanger; ZACK: Zackenberg

a)



b)



Appendix 1: Protocol used to document the relative abundance of predators

Incidental observations of all vertebrate predators were used to create an index of predator relative abundance at each study site, which allowed us to investigate the influence of predator abundance estimates on predation risk between years and sites.

Count method: Counts were conducted daily by one or several observers at each study site. Designated counter(s) recorded observations of all predators throughout the day regardless of their primary activity when the observers were alert (e.g. during nest searching, and/or environmental monitoring but NOT during captures). Observers counted predators independently (results were never pooled across several observers) and make efforts to minimize double-counting (see below). If two observers worked together in the field or were in the same area, we only considered the observations from one of observers. If multiple observers counted independently during the same time period but in different areas, we recorded these observations separately and considered them both useful. Predator counts only occurred when people were within the study area and did not include observations gathered during transportation to and from the study area (i.e. assuming people stayed outside the study area) nor incidental observations of predators at camp (some predators are attracted by camps).

Other guidelines:

- In addition to counting predators, observers also counted the predators they heard.
- Observers counted an individual twice if they saw it a second time after not having seen it for at least 20 minutes. However, observers did not count an individual twice if they continuously saw the predator for 20 minutes or more.
- For birds, observers did not count incubating avian predators
- For foxes, observers only counted adult size individuals because they are the only individuals capable of depredating bird nests
- Observers did not count predators not using the “terrestrial” habitats (e.g. Arctic skua following the coastline, Glaucous gulls resting in a delta or flying up and down large rivers, gulls on a landfill)
- For aggregation or group of predators, observers attempted to record the most accurate number of individuals rather than a range of values.

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