Nest attentiveness drives nest predation in arctic sandpipers

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ABSTRACT

Most birds incubate their eggs to allow embryo development. This behaviour limits the ability of adults to perform other activities. Hence, incubating adults trade-off incubation and nest protection with foraging to meet their own needs. Parents can either cooperate to sustain this trade-off or incubate alone. The main cause of reproductive failure at this reproductive stage is predation and adults reduce this risk by keeping the nest location secret. Arctic sandpipers are interesting biological models to investigate parental care evolution as they may use several parental care strategies. The three main incubation strategies include both parents sharing incubation duties ('biparental'), one parent incubating alone ('uniparental'), or a flexible strategy with both uniparental and biparental incubation within a population ('mixed'). By monitoring the incubation behaviour in 714 nests of seven sandpiper species across 12 arctic sites, we studied the relationship between incubation strategy and nest predation. First, we described how the frequency of incubation recesses (NR), their mean duration (MDR), and the daily total duration of recesses (TDR) vary among strategies. Then, we examined how the relationship between the daily predation rate and these components of incubation behaviour varies across strategies using two complementary survival analysis. For uniparental and biparental species, the daily predation rate increased with the daily total duration of recesses and with the mean duration of recesses. In contrast, daily predation rate increased with the daily number of recesses for biparental species only. These patterns may be attributed to two independent mechanisms: cryptic incubating adults are more difficult to locate than unattended nests and adults departing the nest or feeding close to the nest can draw predators' attention. Our results demonstrate that incubation behaviour as mediated by incubation strategy has important consequences for sandpipers' reproductive success.

Keywords: nest survival, breeding behaviour, parental care, incubation strategy, incubation recesses, Arctic shorebirds

INTRODUCTION

Parental care, defined as all types of behaviour displayed by a parent to enhance its offspring fitness, is shaped by the necessity to balance the costs of caring against the benefits of producing good quality offspring (Williams 1966, Sargent and Gross 1985, Gross 2005). Parental care strategies primarily emerge from the partitioning of parental duties between sexes and include a range of parental behaviours: complete absence of care, uniparental care (only one parent provides care), biparental care (both parents provide care), and cooperative breeding (Royle et al. 2012). Evolution has resulted in a diversity of parental care strategies in taxonomic groups of phylogenetically close species (Clutton-Brock 1991, Royle et al. 2012), and even within species (Webb et al. 1999).

In birds, the genus *Calidris* (Charadriiform, Scolopacids; hereafter referred as sandpipers) exhibits a diversity of parental care strategies that are associated with a diversity of social systems (Pitelka et al. 1974, Erckmann, 1983, Oring 1986, Borowik and McLennan 1999, Cockburn 2006). Most sandpipers breed in the Arctic during the short summer season and lay their eggs in a poorly insulated nest scrape that is exposed to the highly variable arctic weather (Reid et al. 2002, but see Tulp et al. 2012). Incubation is hence a crucial parental behaviour as adults must keep their eggs warm (Carey 1980) to ensure their development (Webb 1987) and survival. Indeed, incubating is an energetically costly behaviour, especially in the Arctic (Piersma et al. 2003, Cresswell et al. 2004, Tulp et al. 2009), and it prevents the adult from engaging in other activities such as foraging. Thus, sandpipers must regularly interrupt incubation to refuel (Tulp and Schekkerman 2006), and must balance their time between two mutually exclusive activities: incubation and foraging.

Sandpiper species can be classified in three groups according to their incubation strategy. In some species, both parents share incubation duties (biparental strategy), allowing one parent to forage while its partner is attending the nest. Biparental incubation guarantees a quasi-continuous incubation (Norton 1972, Bulla et al. 2014) and allows long daily feeding periods for each adult to access distant feeding sites and replenish individual reserves with no consequences for incubation (Bulla et al. 2015a). In other species, a single individual incubates (uniparental strategy) and performs the mutually exclusive activities of foraging and incubating alone (Tulp and Schekkerman 2006). Consequently, the nest is left unattended during foraging bouts in uniparental species. Lastly, some sandpiper species have a flexible strategy, with some nests biparentally incubated and other nests being deserted by one of the adults either before or during incubation, resulting in uniparental incubation (Reneerkens et al. 2014, hereafter referred as mixed strategy).

The main cause of nest failure in birds is predation (Skutch 1949, Ricklefs 1969, Martin 1993) and shorebirds are no exception (Smith et al. 2007, Reneerkens et al. 2016). The predation pressure on sandpipers' eggs varies according to the composition and dynamic of local terrestrial communities (Gilg and Yoccoz 2010, McKinnon et al. 2013, 2014). Shorebirds have evolved a diversity of antipredator behaviours (e.g., distraction displays, aggressive behaviours such as mobbing; Gochfeld 1984) as well as mechanisms (e.g. reduction of smell; Reneerkens et al. 2005) to minimize the risk of nest predation. Yet their incubation behaviour is also playing an important role in the probability of a nest being found and depredated (Smith et al. 2012, Bulla et al. 2016), with higher nest survival usually reported for biparental species (Smith et al. 2007, but see Weiser et al. 2018). In addition, interspecific differences in nest survival rates have been related to nest attentiveness (i.e. proportion of time the nest is incubated; Norton 1972), with low attentiveness resulting in lower nest survival rates (Smith et al. 2012). Although incubation behaviour may explain part of the variability in nest survival rate across species, the exact relationship between incubation behaviour (constrained by the incubation strategy) and the probability of nest predation remains unclear, and the variability within these relationships across strategies has not been investigated. For instance, we still do not know how a given change in nest attentiveness affects the predation rate of nests for species that have different strategies.

Here we present the results of a circumpolar effort to monitor the incubation behaviour of seven sandpiper species across 12 study sites during three consecutive years (2016 to 2018). First, we describe the differences in incubation behaviour between species and strategies using three components of the incubation behaviour: the daily total duration of recesses, the daily number of recesses and the daily mean duration of recesses. Second, we studied the relationships between the three components of incubation behaviour and the daily predation rate and assessed whether they differed across strategies, using two different statistical approaches.

MATERIALS AND METHODS

Study sites

The study was conducted at 12 sites across the Arctic (Figure 1) during the summers of 2016 to 2018. Field sessions began in June at the southernmost sites and early July at the high-arctic sites. These sites represent a diversity of climates, topographies, vegetation and vertebrate communities. Churchill and Ammarnäs are the southernmost sites and have a subarctic vegetation profile. Erkuta, in the south of the Yamal Peninsula, is also densely vegetated with mosses and erect shrubs dominating. Most other study sites have discontinuous vegetation cover and are dominated by graminoids, dwarf and prostrated shrubs (see Figure 1; Walker et al. 2005).

Despite these local differences in vegetation and climate, the communities of terrestrial vertebrates found on the 12 sites host similar functional guilds. Among herbivores, small rodents (lemmings and in low arctic sites, voles), geese, ptarmigans and hares are found at all sites. At most sites, one or two large herbivores (i.e., caribou or reindeer, *Rangifer tarandus*, and muskox, *Ovibos moschatus*) are also found, as well as one or a few small passerines (mainly Lapland longspur, *Calcarius lapponicus*, and snow bunting, *Plectrophenax nivalis*). At all sites, one to three species of sandpipers are regular breeders. Regarding predators, all sites host one to several species of avian predators (ravens *Corvus corax*, rough-legged hawks *Buteo lagopus*, snowy owls *Bubo scandiacus*, jaegers, falcons and gulls). Finally, small mustelids (*Mustela* spp.) and the arctic fox (*Vulpes lagopus*), which is usually considered as the main predator of bird nests in the Arctic (Young et al. submitted, Larson 1960, McKinnon and Bêty 2009), are present and breeding at all sites while the red fox (*Vulpes Vulpes*) is only found at the southernmost sites (McKinnon and Bêty 2009).

Nest monitoring

At each site, we monitored the incubation behaviour of one to three species of sandpipers (seven species in total). Three species are uniparental (little stint *Calidris minuta*, Temminck's stint *Calidris temminckii* and white-rumped sandpiper *Calidris fuscicollis*), three species are biparental (dunlin *Calidris alpina*, Baird's sandpiper *Calidris bairdii* and semipalmated sandpiper *Calidris pusilla*), and one species, the sanderling (*Calidris alba*), exhibits a mixed strategy with nests incubated by either two or only one adult in the same population (Reneerkens et al. 2011, Moreau et al. 2018). All species lay a typical clutch of four eggs (rarely three or five) in a shallow nest scrape directly on the tundra's surface (Reid et al. 2002).

Nests were located opportunistically by walking through suitable breeding habitats and flushing incubating birds, or by following birds back to their nests. Nests found with incomplete clutches were visited repeatedly during the following days to determine the exact date of incubation start. For complete clutches, the relative age of the nest (in days since initiation of incubation) was estimated (with a precision of 1-3 days) by floating one to three eggs of the clutch and using flotation curves (Mabee et al. 2006, Liebezeit et al. 2007). Expected hatch dates were then inferred from age estimates and average duration of incubation known for each species (Liebezeit et al. 2007).

Incubation behaviour and nest fate

In each nest, we placed a temperature probe (Flylead thermistor PB 5009 with 60cm cable) coupled to a data logger (Tinytag Plus2 TGP-4020; Gemini Data Loggers Inc., West Sussex, U.K.) to continuously record the nest temperature. This design is widely used to monitor shorebirds' incubation patterns (Tulp and Schekkerman 2006, Smith et al. 2012) as it discriminates between periods of incubation and incubation recesses. The temperature probes were fixed to wooden sticks and anchored into the ground in the centre of the clutch, with the top of the probe levelled with the top of the eggs so as to be in continuous contact with the brood patch of the adults during incubation. Data loggers recorded nest temperature (accuracy of measurements: 0.2°C; temperature range: -40 to +125°C) every minute during the full incubation period, lasting for ca. three weeks (data storage capacity: 22.2 days). Data loggers and the wires connecting it to the probe were buried or concealed using vegetation and substrate to avoid visual attraction of predators. Device deployment took approximately 5-10 minutes and all efforts were made to avoid leaving scent at the nest site to prevent attracting mammalian predators.

Data loggers were retrieved after the expected hatch date (unless the nest was still active and then nests were visited again before the end of the fieldwork session) and temperature records were extracted using the software Tinytag Explorer 5.0 (Gemini Data Loggers Inc., West Sussex, U.K.). The fate of each nest (depredated *vs.* hatched) was visually inferred on a temperature plot by two independent observers (OG and NM) according to the temperature pattern recorded during the last 24h of recorded incubation. A nest was considered depredated if the temperature suddenly dropped and permanently stayed at environmental temperatures (usually before the expected hatch date, see Supplementary material Appendix 1 Figure A1, Weidinger 2006) . A nest was considered successful if the temperature was steadily declining for 24h (±12h) within 2 days of the expected day of hatching (Tulp and Schekkerman 2006). In a preliminary step, we used field evidence of nests' fate (e.g. presence of pipped eggs, hatched chicks or small eggshell fragments typical of hatched eggs in the bottom of the nest cup; Mabee 1997, Mabee et al. 2006) to validate that the method of fate determination based on the temperature record was trustworthy, but fate assignments as used in our analyses were only inferred from temperature records.

To describe incubation behaviour, we used the temperatures recorded shortly after the incubating adult had returned to the nest, after thermologgers were first deployed, until either the predation event or the beginning of the hatching event. At our arctic study sites, environmental temperature is always lower than the temperature of incubation (ca. 41°C), resulting in a drop in measured temperatures when the adult leaves the nest. We considered a recess (i.e., a period when eggs are not incubated) to start when the temperature dropped by ≥3°C below the median incubation temperature of a nest (measured over 24h periods) and to end when the temperature returned above this threshold (see Figure 1 in Moreau et al. 2018). Hence, all temperature profiles shorter than 24 hours were excluded from the analyses. For each nest and each day of monitoring, we calculated three components of incubation behaviour: the total duration of recesses (TDR), the number of recesses (NR) and the mean duration of recesses (MDR; equal to TDR/NR). Note that these components describe individual incubation behaviour for uniparental species only. For biparental species, they combine recesses from both incubating adults during their respective incubation bouts.

Data analysis

Temperature measurements were obtained from 714 nests across all seven *Calidris* species monitored on the 12 study sites (Table A1, Figure A2). We removed 104 nests when the thermologgers failed to record temperatures for at least 24 hours (e.g. due to technical malfunctioning). Furthermore, in some of the 610 remaining nests, the temperature probe had moved during the monitoring period (for instance because the nest was built in too soft substrate) and temperature profiles had a decreasing trend, which limited our ability to detect some recesses. To prevent these unreliable records from affecting our analyses, all days when thermologgers recorded a daily median temperature below 36°C (n = 68 nests) were also removed. This approach led to a filtered data set of 542 nests with exploitable nest temperature data.

We first described the inter-specific variability of each component of the incubation behaviour. One linear mixed effect model was performed for each component of the incubation behaviour (i.e. TDR, NR and MDR), with the incubation behaviour component as the response, species as fixed effect and site, year and nest as nested random effects to account for non-independencies. We compared all pairs of species for each of the incubation behaviour components using a Tukey test with Holm-Bonferroni correction method. Linear mixed effect models were conducted using the “lme4” package (Bates et al. 2019) while the “multcomp” package (Hothorn et al. 2019) was used to perform post-hoc analysis in Program R (version 3.6.1; R Core Team 2019).

We described the incubation behaviour of adults by the daily TDR, NR and MDR by averaging values over the entire monitoring period for each nest. To ensure that the averaged behaviour was representative, we only kept nests with a daily median temperature over 36°C for at least 20% of the monitoring period; this approach resulted in the removal of 16 additional nests from the remaining 542 nests. Moreover, an additional 17 nests were excluded from analyses carried on their fates (hatched *vs.* depredated), as 9 nests were abandoned after the beginning of the monitoring and 8 had unclear fate (i.e. the two observers disagreed on the nest's fate). Then, only data sub-sets with more than one suitable recording per species/site/year combination were kept. As the following models (see next paragraphs) can handle right censoring, nests with unknown fates were kept in our models. This approach resulted in a dataset of 505 nests (with 208 hatched and 229 depredated; see second column in Table A1 and Figure A2).

We used generalized linear mixed-effect models (GLMMs) with a binomial error distribution and a logistic-exposure link function to test the effect of the average incubation behaviour on nest fate (hatched *vs.* depredated). These "logistic-exposure models" are similar to logistic models but integrate the exposure time between nest visits in the link function to explicitly take into account the delayed entry of nests in the study and the fact that early depredated nests are overlooked (Shaffer 2004). Logistic-exposure models yield the effect of predictors on the odds of daily nest predation. After running a model to test the effect of the strategy alone on the probability of nest predation, we also constructed separate models for each incubation behaviour component since some explanatory variables were mutually incompatible. For instance, TDR and NR were highly correlated (Pearson product-moment correlation coefficient r = 0.615, p-value < 0.001) and could not be used in the same model because such an extreme collinearity was likely to strongly bias the analyses (Freckleton 2011). The fate of a nest was considered as the response and the incubation behaviour component as a fixed effect. Interactions between incubation behaviour components and incubation strategy (biparental, mixed and uniparental strategies) were tested using likelihood ratio tests to help select our most robust model. Finally, we also used one model per strategy to illustrate the strategy-specific relationship between incubation behaviour components and the probability of nest predation. For every logistic-exposure model, years nested within study sites were included as random effects (random intercepts) to account for the variability of environmental conditions across sites and between years at each site. Species, initially included as a random effect, were removed during model selection since the intraspecific variability was high compared to the interspecific variability (i.e. low repeatability) within strategies. GLMMs were conducted using the "lme4" package (Bates et al. 2019) in Program R.

In addition, we investigated the relation between average incubation behaviour and daily predation rates by using Cox Proportional Hazards models (hereafter Cox models). The most striking difference with logistic-exposure models is that Cox models do not assume constant probability of nest predation during the incubation period but consider that groups have proportional hazard functions and that only the baseline hazard function depends on time (Manolis et al. 2000, Shaffer 2004, Nur et al. 2004). Cox models return the effect of a one-unit change of the covariate on the change in hazard rate at a given age. To account for the dataset structure, mixed effect Cox models were implemented using each nest estimated age at the time the temperature probe was installed as the beginning of the exposure period, and the nest's estimated age when fate was determined (or the probe retrieved) as the end of the exposure period. The fate of the nest was used as its status at the end of the exposure (hatched, depredated or censored if the nest was still incubated at the end of the monitoring period). In the end, Cox models were run using 469 nests for which an age could be estimated, for seven species and 12 sites (including 209 depredated nests; see third column in Table A1) with a median age at discovery of ca. 6 days (Figure A3). In these analyses, incubation behaviour components were still used as predictors in separate models to avoid collinearity, and sites and years (nested into sites) were still considered as nested random effects. Interactions between incubation behaviour components and the incubation strategy were tested. Survival analysis was conducted using the "coxme" package (Bates et al. 2019) in the Program R.

RESULTS

Incubation behaviour differed between species and across strategies (Figure 2). TDR varied significantly with incubation strategies, with biparental species showing a lower TDR than both mixed and uniparental species. Regarding NR of each species, uniparental and biparental strategies also differed significantly: biparental species showed a lower NR than all other species, while sanderling and white-rumped sandpiper had lower NR than both little stint and Temminck's stint. Finally, only Temminck's stint had a significantly higher MDR than biparental species. Conversely, semipalmated sandpiper was the only biparental species with a significantly lower MDR than dunlin, mixed and uniparental species (Figure 2).

After checking that the probability of nest predation did not significantly vary across strategies when only strategy was entered in the models (Likelihood ratio test, $\chi^2 = 1.8$, p-value = 0.359), we found that the effect of TDR on the daily predation rate significantly varied between strategies (Likelihood ratio test, $\chi^2 = 6.6$, p-value = 0.037). However, it did not significantly vary between uniparental and biparental strategies (Likelihood ratio test, $\chi^2 = 1.4$, p-value = 0.244) but only between biparental and mixed strategies (Likelihood ratio test, $\chi^2 = 6.3$, p-value = 0.012; Figure 3A). This relationship was not significant for mixed species (Wald's test: z = 0.2, p-value = 0.811, odds ratio = 1.000), but it was positive for uniparental species with a 0.4% increase of the odds of daily nest predation for every one minute of increase in TDR (Wald's test: z = 2.1, p-value = 0.036, odds ratio = 1.004; Figure 3A), as well as for biparental species with a 0.6% increase in odds of daily nest predation for every minute of increase in TDR (Wald's test: z = 4.0, p-value < 0.001, odds ratio = 1.006). These results are corroborated by the overall pattern shown on Figure 4, where depredated nests had a higher TDR than successful nests for most subsets.

Comparatively, the effect of NR on the daily predation rate varied significantly between strategies (Likelihood ratio test, $\chi^2 = 10.4$, p-value = 0.005; Figure 3B). The daily predation rate was positively related to NR for biparental species (Wald's test: z = 3.7, p-value < 0.001, odds ratio = 1.006), with a 6% increase of the odds of daily nest predation for each additional recess. Species with a mixed incubation strategy showed a similar but non-significant trend (Wald's test: z = 0.2, p-value = 0.874, odds ratio = 1.003). Conversely, uniparental species showed a negative but non-significant relation between NR and the daily predation rate (Wald's test: z = -0.8, p-value = 0.392, odds ratio = 0.988).

The effect of MDR did not significantly vary between incubation strategies (Likelihood ratio test, $\chi^2 = 0.4$, p-value = 0.797; Figure 3C), but an increase in MDR was related to an increase of the daily predation rate (Wald's test: z = 2.4, p-value = 0.018, odds ratio = 1.042), with a 4% increase of the odds of daily nest predation for every minute of increase in MDR.

Finally, mixed effect Cox models also confirmed the positive relation between TDR and predation risk (HR = 1.002, z = 3.0, p-value = 0.003), with no significant difference between biparental and uniparental species (Likelihood ratio test, $\chi^2 = 1.2$, p-value = 0.264). As found with the logistic-exposure models, the incubation strategy significantly influenced the relation between NR and the instantaneous risk of nest predation (Likelihood ratio test, $\chi^2 = 9.0$, p-value = 0.011). For biparental species, an increase in the NR was related to an earlier nest predation (HR = 1.048, z = 3.1, p-value = 0.002), whereas mixed species showed non-significant relation (HR = 1.024, z = 0.7, p-value = 0.490) and uniparental species showed an opposite but non-significant relation (HR = 0.978, z = -1.6, p-value = 0.110). Finally, MDR was positively related to the risk of nest predation (HR = 1.044, z = 2.4, p-value = 0.015) and this relation did not significantly vary across strategies (Likelihood ratio test, $\chi^2 = 1.8$, p-value = 0.402).

DISCUSSION

Small shorebirds such as sandpipers mainly rely on camouflage and stillness to keep the nest location undetected by predators (Larsen 1991, Larsen et al. 1996, Reneerkens et al. 2005, Buck 2016). However, adult sandpipers cannot incubate continuously and must regularly leave the nest to “refuel” to ensure their own survival. The incubation behaviour can be described by the frequency and duration of adult foraging trips (i.e., recesses) and the resulting behavioural components vary across strategies (Cresswell et al. 2004, Reneerkens et al. 2011, Bulla et al. 2015a). We found that uniparental species showed a higher frequency and higher total duration of recesses compared to biparental species (Figure 2). Smith *et al.* (2012) showed that the interspecific variability in nest survival could partly be explained by differences in incubation behaviour.

Interestingly, we found that it was not the incubation strategy *per se* that influenced the probability of nest predation. Instead, it was the time during which the nest was unattended (i.e. TDR, MDR) and the frequency of recesses (i.e. NR) that affected nest predation. Hence, when survival rates differ between strategies, this is most probably a result of quantitative differences in their incubation recess behaviour, rather than qualitative differences in the ability of predators to discover nests of a given strategy (see also Smith et al. 2012).

Increasing TDR resulted in a higher probability of nest predation for both uniparental and biparental incubation strategies, supporting the results of Smith *et al.* (2012). However, we found a positive relation between probability of nest predation and NR, consistent with Smith’s *et al.* (2012), for biparental species only. Conversely, statistically non-significant negative relationship was found between NR and the probability of nest predation for uniparental species. Finally, the probability of nest predation was positively related to MDR for both uniparental and biparental strategies. The single mixed species (sanderling) showed no significant relationship between their incubation behaviour and the probability of nest predation, even if they could not be distinguished from other strategies when studying the effect of MDR. Such a result may arise from the high variability of the incubation behaviour of sanderlings, due to their flexible strategy. Interestingly, the Cox and logistic-exposure models produced similar results, which might suggest a constant predation probability during the incubation period.

Two independent mechanisms could explain our findings. First, unattended nests may be more visible to predators. Indeed, sandpipers nest directly on the ground (Reid et al. 2002) and most species monitored in this study choose exposed nest sites that allow early predator detection but confer little nest concealment (Götmark et al. 1995, Koivula and Rönkä 1998, Amat and Masero 2004). Adult presence on the nest could confer passive protection as they cover their eggs with their cryptic upper parts (Weidinger 2002, Buck 2016). Egg camouflage may also be important to reduce predation risk during nest recesses (Šálek and Cepáková 2006) but is probably less effective than plumage crypsis (see e.g. Swanson et al. 2012), although we are not aware of any specific experiment that evaluates these two types of camouflage for *Calidris* species. This could explain why a decrease in the overall attentiveness (i.e., higher TDR) is related to a higher predation probability for both uniparental and biparental species.

Second, movements of adults near the nest may draw the attention of the predator and reveal the nest location as hypothesized by Skutch (1949) for passerines. Several studies support this hypothesis for passerines (Conway and Martin 2000, Matysioková and Remeš 2018), and Smith *et al.* (2012) present similar correlational support for nidifugous shorebirds. Moreover, the fact that sandpipers use distraction behaviour to divert predators from their nests (i.e. active deception; Gochfeld 1984, Montgomerie and Weatherhead 1988, Smith and Edwards 2018) also suggests that arctic predators are attracted to movements.

Considering NR as a proxy for movements to/from the nest, we found that only biparental species seemed to face higher predation rates when more mobile (Figure 3b). The reason for this difference is unclear since, in absolute values, biparental species have much lower number of recesses (NR) values than uniparental and mixed species (Figure 2b). This result might be due to the suspected more conspicuous behaviour (i.e., social interactions) of biparental species when flushed or taking turns at the nest site, as compared to uniparental species that are usually more discrete during these critical events (Larsen 1991). The negative trend found between NR and predation in uniparental species is also counterintuitive as we would expect them to feed closer to the nest due to their much shorter feeding bouts. Indeed, if movements attract predators, then foraging near the nest during recesses should be detrimental in revealing nest location. By showing that it is less risky for uniparental species to have more shorter, rather than few longer recesses, our results do not support such an explanation and rather suggest that uniparental species can feed at safe distances from the nest even during short recesses. However, because NR and MDR are negatively correlated, the higher predation rates observed for large MDR values (associated with low NR) could also simply be the result of longer feeding bouts spent close to the nest. Indeed, if we assume that uniparental species always feed close to the nest (at distances unrelated to MDR), then longer periods of activity near the nest (i.e., larger MDR regardless of NR values) could also explain this relation. Conversely, if larger values of MDR are associated to distant feeding spots, then our results could suggest that passive (crypsis) or active (distraction) protection behaviour of adults

(Weidinger 2002, Lameris et al. 2018) are more important than movements to explain the breeding success of Calidris nests.

Regardless of what mechanisms lead to our results, a trade-off should emerge for uniparental species regarding the distance from their nest when foraging and their ability to protect their clutch. Unfortunately, too little is known about the off-nest behaviour and feeding range of arctic sandpipers (Bulla et al. 2015b). Investigating how sandpipers behave when off the nest and when departing/returning to their nest would provide important insight on how they manage to keep their nest location undiscovered. We are only aware of a few descriptions of off nest behaviour (see e.g., Cartar and Montgomerie 1985)

Incubation behaviour that prolongs the incubation period may also indirectly influence the probability of nest predation due to the increased length of exposure (Bosque and Bosque 1995, Tombre and Erikstad 1996). Embryo development is directly dependent on nest temperatures maintained during incubation (Webb 1987). Lowered nest attentiveness, exposes eggs to lower temperatures in the Arctic and slows down embryo's development (Olson et al. 2006, Martin et al. 2007). Uniparental species, in particular, may have prolonged nest incubation periods due to their lower attentiveness, but mechanisms such as increasing egg temperature (Hepp et al. 2006, Reneerkens et al. 2011) may help to (partially) compensate. According to our results, a poorly attended nest has a higher probability of being depredated per day, but it may also have a lower survival rate over the entire incubation period due to a possible lengthening of this period.

Weather conditions are highly variable in the Arctic and extreme cold weather events can severely cool eggs left unattended, reduce the prey availability for adults (i.e. terrestrial arthropods; MacLean and Pitelka 1971, Schekkerman et al. 2003), as well as increase the metabolic rate necessary for adults to stay warm (Wiersma and Piersma 1994, Piersma et al. 2003). Hence, sandpipers may adopt a plastic behavioural response to avoid exposing their eggs to unfavourable conditions and to take advantage of the best foraging opportunities. During cold spells, uniparental species perform fewer but longer recesses (Cartar and Montgomerie 1985, Tulp and Schekkerman 2006, Reneerkens et al. 2011), whereas biparental species such as dunlin (*C. alpina*; Tulp and Schekkerman 2006) and semipalmated sandpipers (*C. pusilla*; Norton 1972, Bulla et al. 2015a) show no effect of temperature on their incubation behaviour. Hence, uniparental species should suffer an increased rate of nest predation compared to biparental species during inclement weather. This may become even more problematic due to the increasing variability in weather that is associated with climate change (e.g. Schmidt et al. 2019). In this study, we controlled for the effect of the site and the site-specific effect of year (i.e. average abiotic and biotic conditions may change across years at each site) on the response variable's variance by using both factors as random effects in our models. However, we currently lack a precise description of the immediate and dynamical effects of abiotic conditions on incubation behaviour. Such information is needed to understand the influence of changing conditions on the reproductive success of shorebirds using different incubation strategies (Matysioková and Remeš 2018).

Among biotic factors, the level of predation pressure on sandpipers' nests could also lead to changes in incubation behaviour that ultimately affects nest predation. For example, the arctic fox is the most opportunistic terrestrial predator in the tundra (Larson 1960, Dalerum and Angerbjörn 2000, Elmhagen et al. 2000, Gilg et al. 2006, McKinnon and Bêty 2009) and its density and diet vary according to local community dynamics (Angerbjorn et al. 1999, Gilg et al. 2003) present across years and even within a season (Smith and Wilson 2010). This ultimately influences predation pressure on sandpiper's nests (Blomqvist et al. 2002, Fraser et al. 2013). Furthermore, the perception of predation risk can strongly influence the behaviour of breeding birds (e.g. a decrease in the frequency of feeding trips, Conway and Martin 2000, Ghalambor and Martin 2002, Fontaine and Martin 2006). Hence, the relationship between the incubation behaviour of sandpipers and the probability of nest predation will also depend on their ability to detect and respond to changes in trophic and behavioural interactions with their predators.

Ongoing global changes deeply impact the population dynamics of many arctic species, including changes in predation rate and breeding success of shorebird nests (van der Putten et al. 2004, Ims and Fuglei 2005, Gilg et al. 2009, 2012, Post et al. 2009). In this context, studying variation in parental care and its consequences offers unique opportunities to investigate how future reproductive success may change and to assess adaptive capacities of migratory species under changing environmental conditions.

Declarations:

NM, LB and OG led the design, analyses and writing of this manuscript, with substantial contribution from FXDM. All other authors collected the data and/or significantly contributed to the manuscript.

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Figure Legends

Figure 1: Circumpolar Arctic vegetation Map, adapted from Walker et al. (2005), with numbers showing the location of study sites: 1. Belyi Island (BELY; 73.32N, 70.09E), 2. Sabetta (SABE; 71.24N 71.80E), 3. Erkuta (ERKU; 68.22N 69.15E), 4. Hochstetter Forland (HOCH; 75.15N 19.70W), 5. Zackenberg (ZACK; 74.47N 20.57W), 6. Karupelv (KVPE; 72.50N 24W), 7. Bylot (BYLO; 73.15N 80.00W), 8. Igloolik (IGLOO; 69.40N 81.60W), 9. East Bay (EABA; 63.98N 81.67W), 10. Churchill (CHUR; 58.70N 94.08W), 11. Utqiaġvik/Point Barrow (UTQI; 71.28N 156.61W) and 12. Ammarnäs (AMMA; 69.96N 16.29E). Subzones include subzone: (A) barren vegetation with 5% prostrated vascular plant and 40% mosses and lichens; (B) 5–25% dwarf prostrated vascular plants less than 5–10 cm tall and 60% cryptogams; (C) 5–50% vascular plants with shrubs less than 15 cm tall; (D) 50–80% vascular plants with shrubs 10-40 cm tall; (E) 80–100% vascular plants with shrubs and grass 20–50 cm tall. Density of vegetation increases from subzone A (i.e. patchy vegetation) to subzone E (i.e. continuous vegetation). Shorebird species included in this study are listed on the left of the map with the site numbers where they were investigated.

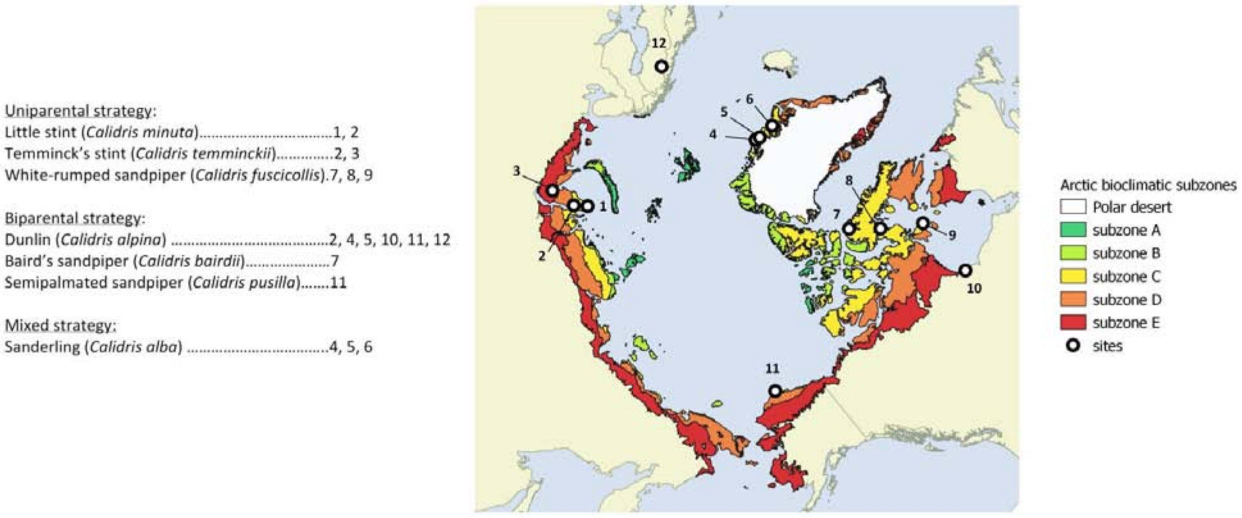

Figure 2: Mean daily total duration of recesses (TDR; panel A), number of recesses (NR; B) and mean duration of recesses (MDR; C) estimated for each species across all sites and years. Means are estimated through linear mixed effect models (see methods). Sample sizes indicated on panel B are the same for all panels. Error bars represent the 95% CI obtained through mean estimation. Species with different letters within each panel are significantly different and result from a post-hoc analysis with paired differences. White, grey, and black bars correspond to species with biparental, mixed, and uniparental incubation strategies, respectively.

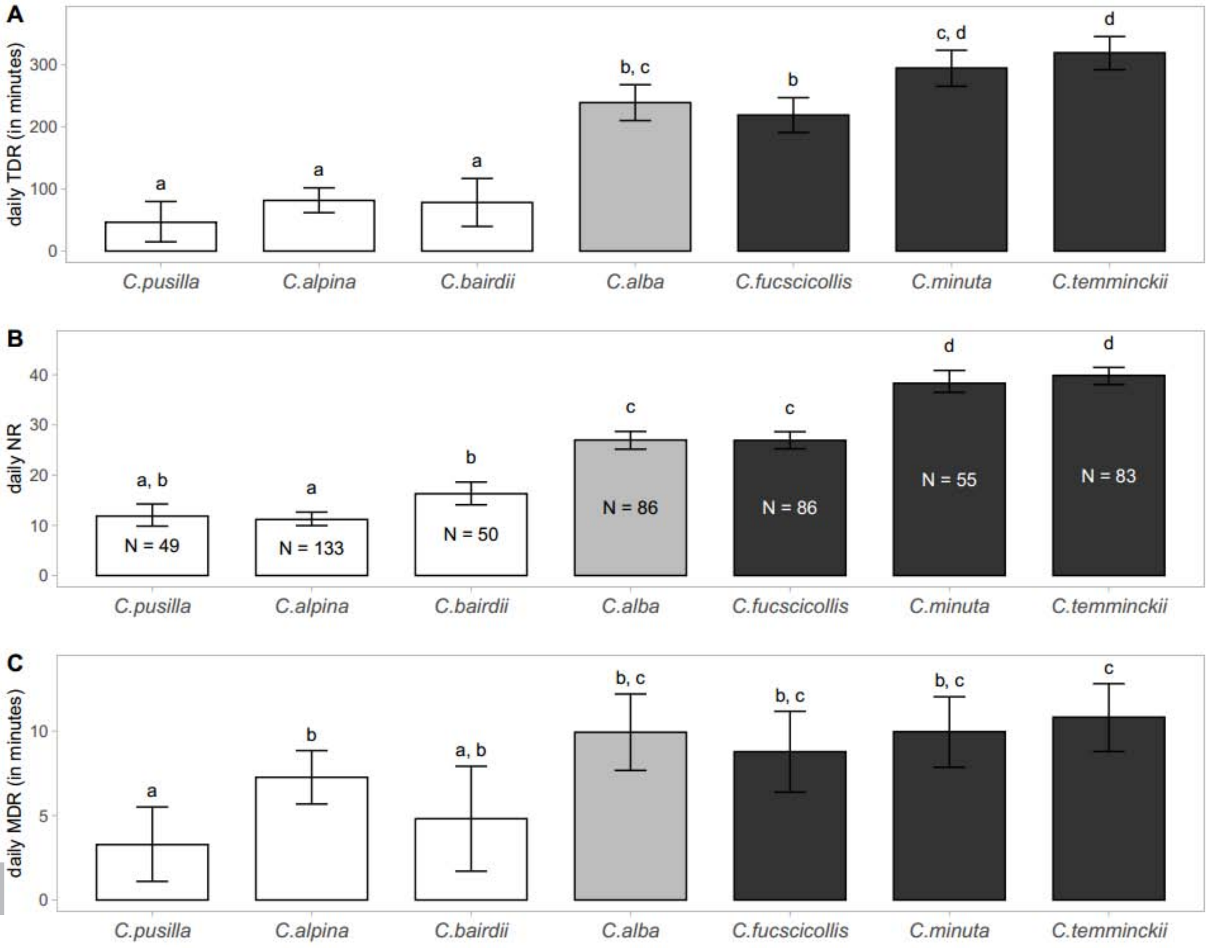

Figure 3: Relations between predation probability (y-axis) and mean daily total duration of recesses (TDR; panel A), number of recesses (NR; B), and mean duration of recesses (MDR; C) for species with biparental, mixed and uniparental incubation strategies. Log odds ratio of daily nest predation and confidence intervals are presented in each panel with the p-values next to corresponding curves (same colour as in legend).

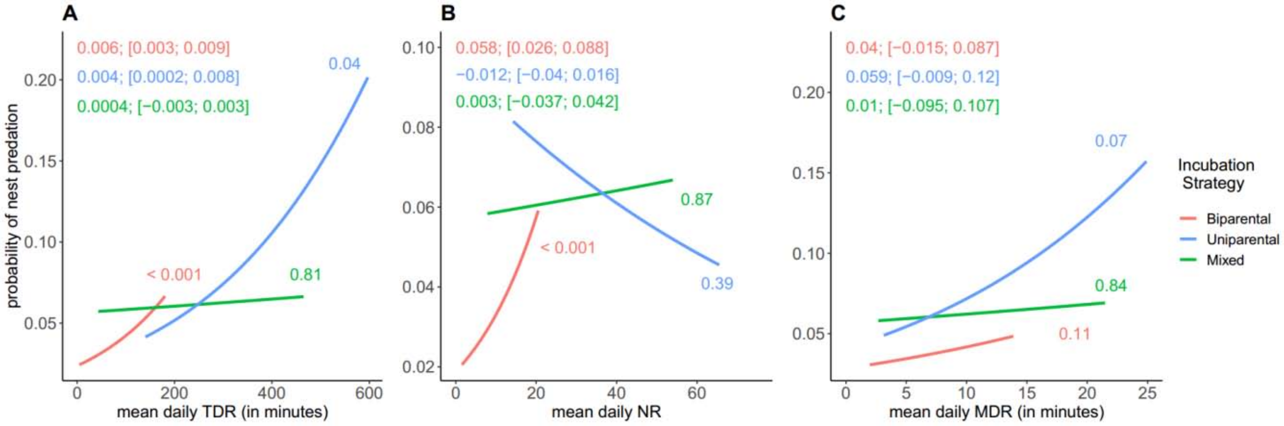

Figure 4: Relation between mean daily total duration of recesses (TDR) of depredated nests and TDR of successful nests (with 95% confidence interval) estimated for each species/study area combination. The black line represents equality for both fates. Means and confidence intervals were estimated using linear mixed effect models to consider intra and inter-nest variabilities. Data were restricted to a single species at a given site and year with a minimum of two nests per modality (i.e. depredated or hatched).