Free meals during breeding: increased resource access does not benefit Arcic-

nesting shorebirds

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ABSTRACT

Arctic ecosystems are facing intensifying impacts of climate change, notably an increase

in air temperature that can boost local productivity. Yet whether such resource surge can

benefit declining migratory birds is unclear. Here we experimentally increased prey

abundance and measure its effect on the body condition, nesting patterns, and nesting

success of the white-rumped sandpiper (*Calidris fuscicollis*). We captured females at the

beginning and at the end of their incubation to assess body condition and we installed

small temperature probes inside their nests to measure their incubation recess. To

estimate nest survival, we regularly monitored experimental and control nests during two

consecutive summers (2016–2017). For both experimental years with contrasting nest

success (73% vs. 21%), we found no evidence of an effect of our supplementation

experiment mimicking an increased abundance of arthropods in the Canadian Arctic. This

suggests that *in situ* resources are not limiting during incubation. Breeding strategies and

success in shorebirds seem to be driven by inter-individual traits related to body condition

upon the initiation of incubation.

Keywords: Resource allocation, food supplementation, breeding strategies, shorebirds

INTRODUCTION

INTRODUCTION

The migration of Arctic-breeding birds often entails high energetic costs related to

travelling great distances (Klaassen 1996). Upon arrival on their arctic breeding grounds,

income breeders (Drent and Daan 1980, Morrison and Hobson 2004) like sandpipers

must regain fat reserves and reconstitute their reproductive organs as quickly as possible.

Unlike some other birds, they must also feed during incubation as well. On the opposite

end of the spectrum, purely capital breeders such as eiders rely exclusively on their

energy stores accumulated prior to arriving on the breeding grounds (Drent & Daan 1980;

Morrison & Hobson 2004). However, for most other capital and income breeders, the

quantities of both body stores upon arrival and *in situ* resources are important. Thus,

carry-over effects influencing the physical shape of birds when they arrive in the Arctic

such as migration (Legagneux et al. 2012, 2016) and wintering (Marra et al. 1998)

combined with feeding strategies and the availability of resources on the breeding ground

should be critical components influencing incubation and nesting success of Arctic-

breeding birds.

Incubation is a complex period as one or both parents must maintain the

temperature of their eggs above a threshold, deter nest predators, and feed. Generally, in

order for embryos to develop correctly, nest temperatures should not drop below a

temperature threshold of 35 °C (White and Kinney 1974). In High Arctic environments

where average air temperatures usually range from -10 to 10 °C in the summer, this

means that birds often cannot leave their nest unattended for long periods of time (Cantar

and Montgomerie 1985, Olson et al. 2006). However, income breeders also regularly

need to feed in order to maintain sufficient body stores reserves (Cresswell 2004,

Reneerkens et al. 2011, Bulla et al. 2016) and compensate for high daily energy

expenditure (Piersma et al. 2003). Cold Arctic temperatures, wind, and rain intensify

energetic demands and have been shown to modulate the frequency of foraging recesses

of income breeders (Cantar and Montgomerie 1985, Tulp and Schekkerman 2006,

Lecomte et al. 2009). Despite lower predation pressure at higher latitudes (McKinnon et

al. 2010), avian and terrestrial nest predators can cause depredation to be the leading

cause of nest failure (Bêty et al. 2001, Weiser et al. 2017). Parents can limit these impacts

by actively deterring predators (Samelius and Alisauskas 2001) or diverting attention

away from the nest through distraction displays (Bengtson 1970, Jehl 1973). In this way,

leaving the nest to feed is linked to certain costs (e.g., cooling of the eggs, increased risks

of nest predation) and benefits (e.g., resource acquisition), all of which must be managed

in order to successfully hatch a clutch of eggs (Lecomte et al. 2008, Smith et al. 2012).

These trade-offs dictating parental decisions are managed through strategies that can

differ among species, most notably for mono-parental species in which the incubating

parent is never replaced by the other (Reneerkens et al. 2011, Moreau et al. 2018).

Whatever the type of parental care, incubation and its trade-offs remain important in the

life history of Arctic-breeding birds.

At a larger scale, breeding success is an essential component of population

dynamics. Consequently, the breeding period of most shorebirds is especially critical in

the current context where over 44% of shorebird populations are declining (Gratto-Trevor

et al. 2012). This decline is being observed despite the fact that shorebirds could benefit

from climate change in the Arctic (McKinnon et al. 2013, Weiser et al. 2018). Other

authors have suggested that a phenological mismatch caused by climate change between

shorebirds and their prey, terrestrial arthropods (Tulp and Schekkerman 2008), entails

negative impacts on the survival of shorebird chicks (McKinnon et al. 2012, Senner et al.

2017). Although the effects of the responses of arthropods to climate change on

shorebirds have been investigated in terms of the timing of their emergence, it is possible

that this negative effect could be counteracted by a simultaneous increase in the

abundance of arthropods. While food supplementation studies on birds are common in

behavioral and population ecology (Boutin 1990, Ruffino et al. 2014), to our knowledge,

studies have not yet investigated the effects of increased arthropod abundance on

incubating arctic shorebirds. Indeed, if shorebirds are limited by their resources, this

boosted food source could benefit shorebirds during a critical time of their life cycle by

modifying the balance of trade-offs that parents face during incubation.

Our objective is to determine whether an increase in arthropod abundance can

lead to positive effects on the reproductive success of an arctic-nesting shorebird. We

hypothesize that increases in arthropod abundance will improve the nesting success of

female white-rumped sandpipers, a uniparental incubator, by improving their body

condition and/or by allowing them to spend more time incubating (Fig. 1). Improved

body condition should allow females to deter nest predators more efficiently (Wallin

1987) and reduce the risks of nest abandonment (Bustnes et al. 2002, Weiser et al. 2017)

while spending more time incubating should ensure that eggs develop correctly (Olson et

al. 2006, Reneerkens et al. 2011) and reduce detection of the nest by predators (Smith et

al. 2012). We predict that (P1) the daily rate of mass loss will be smaller for females

having received a resource supplementation and/or that (P2) females having received a

resource supplementation will have a lower frequency of incubation recesses and/or that

(P3) females having received a resource supplementation will have a lower mean

duration of incubation recesses. If P2 or P3 is verified, we predict that (P4) females

having received a resource supplementation will spend more time incubating per day.

Lastly, if P1 or P4 is verified, we predict that (P5) nesting success of females that

received a resource supplementation will generally be better than that of females that did

not receive such inputs (Fig. 1). Here we conducted an experiment to test our hypothesis

by adding food resources available to nesting sandpipers and measuring 5 response

variables, which map directly onto our predictions.

MATERIALS AND METHODS

Study species

We chose the white-rumped sandpiper as our model species because they are not globally

threatened, they are abundant on our study site, they are income breeders, and they

possess typical shorebird morphology and phenology. White-rumped sandpipers are

small (15–18 cm, 28–66 g), polygynous, monoparental arctic-nesting shorebirds. Females

will lay 4 (occasionally 3) cryptically coloured eggs, and incubation lasts approximately

21 days. As a long-lived and iteroparous species, white-rumped sandpipers may abandon

their nests near the end of the breeding season to improve their survival and optimize

their southern migration (Weiser et al. 2017).

Study site

Our experiment was conducted on Igloolik Island (Nunavut, Canada, 69 °24'N,

81 °32'W; Fig. 2a, b), an island in the Foxe Basin, located north-east of the Melville

Peninsula during the summers of 2016 and 2017. Our study site covered an area of

approximately 25 km^2 consisting of wet meadows and raised beaches, which comprise

mostly xeric and mesic ridges. Wet meadows, interspersed by lakes and ponds, dominate

the landscape (Forbes *et al.* 1992) and provide optimal breeding grounds for the two most

abundant shorebirds of the island: white-rumped sandpipers (*Calidris fuscicollis*) and red

phalaropes (*Phalaropus fulicarius*). Most shorebirds nesting on the island feed on

terrestrial spiders and insects. In terms of avian nest predators, shorebirds share the island

with nest predators such as long-tailed and parasitic jaegers (*Stercorarius longicaudus*

and *Stercorarius parasiticus*), glaucous gulls (*Larus hyperboreus*), Sabine's gulls (*Xema*

sabini), herring gulls (*Larus argentatus*), Thayer's gulls (*Larus thayeri*), ruddy turnstones

(Arenaria interpres), and common ravens (*Corvus corax*). Terrestrial predators such as

arctic foxes (*Vulpes lagopus*) and stoats (*Mustela ermine*) can also depredate nests.

Although these two mammals rarely depredate adults, peregrine falcons (*Falco*

peregrinus), gyrfalcons (*Falco rusticolus*), and snowy owls (*Bubo scandiaca*) more

frequently prey upon adult shorebirds.

Nest monitoring

During the summers of 2016 and 2017, we searched for white-rumped sandpiper nests

that were in their laying or incubation stages from around mid-June until our departure at

the end of July over an area of 10 km^2. Nine randomly located circular plots (200m

radius) were defined to estimate nest densities although our nest searching was not

limited to these plots. When nests were found during the laying stage (nests had more

eggs during subsequent visits), we calculated initiation date by considering that one egg

was laid per day; hatching date was then estimated to occur 24 days later (3 days of

laying and 21 days of incubation). To estimate initiation dates and hatching dates for

nests found during the incubation phase, we floated two to three eggs (van Paassen et al.

1984). For nests that eventually hatched, we corrected this date by subtracting 21 days of

incubation and 3 days of laying from the hatch date if the latter was available. We also

installed a small thermistor (Tinytag Talk PB-5005-0M6 [ø 2.5mm] with a Talk 2 logger

TK-4023, Gemini Data Loggers Ltd, Chichester, United Kingdom) within the nest by

attaching it to a thin wooden stick planted at the center of the nest (Fig. 2c). The

thermistor wire and the data logger were both buried to avoid attracting predators. Prior

to deployment, we programmed the logger of each thermistor to start recording

temperature every minute for 21 days. Because white-rumped sandpiper females incubate

for 21 days (Parmelee, 1992) and because it was unlikely that we started the experiment

on the day the clutch was completed, thermistors never stopped recording before the end

of incubation. We revisited nests every 4 days and, when approaching the estimated

hatching date, every 2 days to be able to track nesting success accurately. We considered

that nests in which at least one egg had hatched were successful. Once a nest was found

empty, we searched for clues that could indicate whether the nest was successful or not,

as well as why the incubation might have failed (Brown *et al.*, 2014). Some of these clues

include the presence of hatchlings, eggshell fragments or halves, as well as fox urine and

scat. We also removed the thermistor and data logger at this time and downloaded the

data using the tinytag explorer 4.8 software (Gemini Data Loggers). We cross-checked

the fate determined through nest monitoring with the profiles of incubation obtained from

the thermistors. Around the midway point of the study period, we visited each nest to

estimate vertical cover of vegetation over the nest cup (nest cover; estimated in

increments of 10%) and soil humidity (dry, slightly humid, saturated, flooded) over two

days.

Supplementation experiment

The experiment started as soon as possible with the random designation of control or

supplementation treatments to nests as they were discovered. We chose to use industrially

sold dried mealworms (*Tenebrio molitor*) as our supplementation because they have

previously been used as experimental resources for little stints (Tulp and Schekkerman,

unpubl. data) and red knots (Vézina, unpubl. data) and are commonly used to feed captive

or rescued shorebirds (e.g., Gartell et al. 2014). Additionally, we observed white-rumped

sandpipers feeding on mealworms (video available along with data and code on figshare

taken during preliminary tests in 2015; see link at the end).

For all supplemented nests (n = 15 in 2016, n = 13 in 2017), we placed a plastic cup (~4

cm diameter) filled mealworms 5 m east of the nest (Fig. 2c). Approximately half of the

cup was buried in the ground but remained accessible to sandpipers. This

supplementation was available to the sandpipers for the rest of their incubation; since

refills were not required required, we considered the number of mealworms as *ad libitum*

resources for the breeding individual white-rumped sandpiper. We also used a cup

containing only a rock as a weight to maintain it in the ground and set the cup 5 m east of

each control nest (n = 14 in 2016, n = 15 in 2017) to account for any positive or negative

bias related to the installation of the cup. We later estimated that the average nest age was

8 days (SD = 4.7; n = 57) at the initiation of the experiment.

In 2016, we used bownets to capture females on their nest. We banded each female,

evaluated their body condition, and measured morphometric dimensions at the beginning

of the experiment. We measured mass using a hanging Pesola scale (±0.5 g precision),

the lengths of the head, culmen, and tarsus using a caliper (±0.1 mm), and wing length

using a ruler (±1 mm). Females were recaptured and weighed towards the end of the

incubation period: on average, 10 days after the first capture. Only in 2017, 11 females

were captured as part of other protocols.

Mass loss models (P1)

We calculated a daily rate of mass loss for each incubating female by subtracting their

initial weight from their final weight and dividing the result by the number of days

between the two captures. Head, culmen, and tarsus lengths were correlated (Pearson's r

= 0.82, 0.59, and 0.49) and were combined by extracting the principal axis from their

PCA to obtain a metric of bird size. In all analyses, nest cover was converted into a

categorical variable with two levels: 0-10% and 20-40%. To test for evidence in support

of P1, we identified 8 fixed-effects linear models with mass loss as their response

variable and which comprised the main predictor (categorical; supplementation and

control) and different covariates (Table S1). To limit the complexity and number of

models, we defined concurrent models based on categories of covariates. Three models

used environmental covariates: soil humidity (categorical; dry and wet), and nest cover

(categorical; 0-10% and 20-40%). Two models used biological covariates: nest initiation

date (numeric; Julian days), initial weight (numeric; grams), and size (numeric; principal

axis of PCA, see above). We expected the supplementation's effects to be modulated by

soil humidity or initiation date, so we included their interaction terms. Finally, two

models contained no covariates.

Incubation models (P2, P3, and P4)

For each dataset of nest temperatures recorded by the thermistors, we computed a moving

median and considered that a bird had vacated its nest if temperatures were 3 °C below

this threshold. We then calculated the average number of recesses per day per nest over

the study period (hereafter recess frequency) by dividing the total number of recesses by

the total number of minutes of data and multiplying the result by 1,440 minutes/day. We

divided the total number of recess minutes by the total number of recesses to obtain the

average duration of recesses (hereafter recess duration). Finally, we calculated the

proportion of time spent incubating (hereafter nest attendance) by dividing the total

number of incubation minutes by the total number of minutes of data.

We investigated the relationships between recess frequency and recess duration

using type 2 linear regressions. Using type 1 linear models, we examined whether nest

attendance could be accurately predicted by either or both previous metrics. To test for

evidence in support of P2, P3, and P4, we identified three sets of 6 fixed-effects models

with recess frequency, recess duration, and nest attendance, respectively, as their

response variable (Tables S1-S2-S3, respectively). Aside from the null model, these

models comprised combinations of the main predictor (supplementation) with categories

of covariates. Three models contained environmental variables, soil humidity

(categorical; dry and wet) and nest cover (categorical; 0-10% and 20-40%), and one

model contained the biological variable, nest initiation date (numeric; Julian days). We

expected the supplementation's effects to be modulated by soil humidity or initiation

date, so we included their interaction terms. Finally, two models contained no covariates.

Nesting success models (P5)

Nesting success was treated as a binomial variable indicating success (at least one

hatched chick) or failure (no hatched chicks) of the incubation. We evaluated nesting

success using the RMark package (Laake 2013) to estimate daily survival probabilities

over time and compensate for apparent nesting success by considering exposure days

(Mayfield 1961, 1975). To test for evidence in support of P5, we identified 10 fixed-

effects models (Table S5) of daily nest survival with different combinations of the main

predictor (supplementation) and categories of covariates. We included the year variable

in all models because we observed a large increase in predator abundance in 2017

accompanied by widespread and frequent nest failures across most shorebird species

monitored. We also included the interaction between time and the supplementation in all

models because we expected that the effect of the latter would vary during the study

period. Four models included combinations of time (numeric; days), year (categorical;

2016 and 2017), and supplementation variables only. A single model included nest cover

(categorical; 0-10% and 20-40%) in addition to the previous variables, while four models

included biological variables, nest attendance (numeric), recess frequency (numeric), and

recess duration (numeric), instead. Only the null model contained no covariates. Due to a

lower sample size available for its analysis, we separately investigated the effect of mass

loss on nesting success through a fixed effect model of daily nest survival including mass

lost per day and time as covariates.

We retained the top-ranked model from each set of models (mass loss, recess

frequency, recess duration, nest attendance, and nest survival) using model selection via

AIC with second-order bias correction (Burnham and Anderson 2002). We also closely

inspected other models that obtained similar AICc scores while checking for potential

pretending variables (variables that do not improve the fit of the model and whose

estimates overlap 0; Anderson 2008). All statistical analyses were performed with R

version 3.2.2 (R Development Core Team 2015), and AICc model selection was

conducted using the AICcmodavg package (Mazerolle, 2017).

RESULTS

General results

During the summer of 2016, we found 55 white-rumped sandpiper nests that were in their

laying or incubation stages, versus 45 in 2017. Within our 9 randomly located nest

searching plots, this equates to 23 and 16 nests/km^2 in 2016 and 2017, respectively. A

total of 57 nests were used in our experiment (29 in 2016 and 28 in 2017), as the others

were either part of other projects or were empty before we could set up the experiment.

Monitored nests were generally initiated during the final week of June.

Mass loss analyses (P1)

White-rumped sandpipers weighed 46.0g (SD = 3.5g, CV = 0.08) and 44.8g (SD = 2.7g,

CV = 0.06) on average at the beginning and end of the experiment, respectively. Changes

in mass were variable during the experiment: while some females lost up to 12.5 g, others

gained up to 6.0 g across the studied period. The top-ranked model explaining variation

in mass loss per day ($R^2_{adjusted}$ = 0.44, Table S1) included the supplementation, initial

weight, and their interaction (Table 1). We found no support for P1 since the resource

supplementation had no impact on the rate of mass loss of incubating females (95% CI =

[-0.10, 0.32], Fig. 3a) regardless of initial weight. However, we found that birds lost

weight proportionally to their initial weight (95% CI = [0.06, 0.43], Fig. 3b), regardless

of whether they received a resource supplementation (95% CI = [-0.24, 0.21]). Heavier

birds at the start of the experiment lost more weight per day: for example, our model

predicts that a 41g female will gain 0.29g/day while a 51g female will lose 0.41g/day. We

also found that an extreme value in our dataset (a 57g female that lost 1g/day) was not a

leverage point (Cook 1979) as it did not substantially change the outcome of the analysis.

Incubation analyses (P2, P3, and P4)

Over the course of our experiment, we found that female white-rumped sandpipers

incubated for 85.5% of the time (SD = 2.5). On average, they left their nests 27.4 times

per 24 hours (SD = 5.7). Such recesses lasted 7 minutes and 48 seconds on average (SD =

1.4). Among incubating females, nest attendance displayed very little variability (CV =

0.03) compared to recess frequency (CV = 0.21) and duration (CV = 0.18, Fig. S1).

Recess frequency and duration were negatively correlated and shared 37.5% of

variability. Unsurprisingly, recess frequency and recess duration together explained

95.1% (F-statistic = 490.8) of the variability in nest attendance. Separately, they only

explained respectively 27.4% (F-statistic = 20.35) and 8.2% (F-statistic = 5.5). We found

no support for P2 or P3 because the top-ranked models for recess frequency and recess

duration were the null models which contained no variables (Tables F-G). The top-ranked

model explaining variation in nest attendance ($R^2_{adjusted}$ = 0.10, Table S4) included

treatment, nest initiation date, and their interaction (Table 1). We found no support for P4

since the resource supplementation had no impact on nest attendance of incubating

females (95% CI = [-0.018, 0.008], Fig. 3c). However, we found that nest attendance

decreased with the initiation date of nests (95% CI = [-0.023, - 0.003], Fig. 3d),

regardless of whether they received a resource supplementation (95% CI = [-0.005,

0.023]). According to this model, a 10-day difference in the beginning of incubation

would result in a 3% difference in the time spent incubating. Extrapolated over a 21-day

long incubation period, this would equate to a difference of 15 hours and 7 minutes of

incubation.

Nesting success analyses (P5)

We successfully determined the fate of 50 of the 57 nests used in our experiment. In

2016, 19 nests were successful while 7 failed. In 2017, only 5 nests were successful and

19 failed for a total of 24 successful clutches out of 50 across both years. On average,

nests were initiated around June 23rd, hatched around July 15th, and failed around July

11th. Among nests that received the mealworm supplementation, 15 failed and 12

hatched, as compared to 14 failed and 14 hatched control nests. The top-ranked model

explaining variation in daily nest survival included time (days since the first nest) and the

year of the experiment (Tables 1 and S5). We found no support for P5 since the resource

supplementation variable was not included in this model. However, we found that daily

nest survival was lower in 2017 compared to 2016 (95% CI = [-2.75, -0.91], Fig. 4a) and

decreased over time (95% CI = [-2.75, -1.07], Fig. 4b).

DISCUSSION

We carried out a supplementation experiment mimicking an increased abundance of

arthropods in the Canadian Arctic and found no evidence that white-rumped sandpipers

should be affected by additional resources while nesting. Contrary to our predictions, the

rate of mass loss per day, nest attendance, and nesting success of incubating females were

all unaffected by resource supplementation. This does not support our hypothesis that

increases in arthropod productivity during incubation could increase the nesting success

of female white-rumped sandpipers by improving their body condition and/or by allowing

them to spend more time incubating. However, we found that mass loss per day, nest

attendance, and nesting success were likely linked to the initial reproductive traits of

incubating females. This suggests that *in situ* resources may not be limiting for white-

rumped sandpipers during incubation, yet the strategies that they employ during this

period, and the successfulness of the latter, seem to be driven by inter-individual traits

upon the initiation of incubation. We will explore how these traits impact breeding as

well as why our supplementation experiment had no detectable effects in the following

sections.

Mass loss (P1)

In an experiment carried out on the tropical wintering site of a migratory bird, Cooper *et*

al. (2015) observed that diminished abundances of arthropod prey had no effect on body

mass. However, birds that were exposed to food reduction deposited more fat and lost

more pectoral muscle mass, leading to delayed departure dates for spring migration

(Cooper et al. 2015). Similarly, it is possible that our supplementation, while leaving

mass loss unchanged, had an effect on the body composition of white-rumped sandpipers

(Gloutney et al. 1999). Compared to the control group, females that had access to

additional resources may have been able to develop to a greater extent their flight

muscles in preparation for their fall migration starting only a few days after chicks have

hatched. This could then lead to positive carry over effects on adult survival during

migration or even wintering. Although authors have addressed the possibility of carry-

over effects of resource abundance affecting migrating birds on their breeding grounds

(Marra et al. 1998, Robb et al. 2008, Harrison et al. 2011, Legagneux et al. 2012), to our

knowledge, no studies have considered effects originating in the Arctic and whose

repercussions would be observed during other stages of the life history of birds.

The positive linear relationship between weight loss and weight has already been

shown in birds (Monaghan et al. 1989) and suggests that mass loss of smaller birds is

more constrained physiologically than that of larger birds. Because weight loss increased

with initial weight and was unaffected by the size of birds, it is likely that heavier

females, who lost up to 1g/day, had more body reserves and did not need to feed as much.

On the other hand, leaner females gained weight (up to 0.7g/day) during the incubation

period, suggesting that they prioritized feeding.

Incubation (P2, P3, and P4)

We observed a strong negative relationship between recess frequency and recess

duration, with a similar negative effects of recess frequency and duration on nest

attendance; we also measured a high inter-individual variability in recess frequency and

duration while nest attendance among individuals remained relatively constant. These

analyses reveal that white-rumped sandpipers can have variable strategies to maintain the

balance between the frequency of recesses and their duration. However, because the

increase of frequency was generally accompanied by a reduction in duration (and vice

versa), the resulting outcome, total nest attendance, varied very little among different

individuals (CV = 0.03). In contrast, recess duration and frequency showed larger

variability (CV = 0.18 and 0.21 respectively), yet we could not detect any major

biological drivers (including the supplementation) of this variability. Because we found

no evidence of an effect of the resource supplementation on nest attendance, we suggest

that the latter is not dependent on the abundance of resources during the incubation

period. Individual characteristics and various predation pressures could be at play and

warrant further investigations.

Despite its low variability, nest attendance decreased when delays in nest

initiation increased (-0.3% per day). Because early nest initiation is associated with high

body condition (Blums et al. 2002, 2005), nest attendance may in fact be driven by the

physical state of white-rumped sandpipers at the beginning of incubation. Females that

initiated early likely spent more time incubating at the expense of feeding time; their

better body condition allowing them to use previously accumulated body stores. Females

that initiated later in the season would have spent less time incubating and more time

feeding to compensate for their poorer body condition. As it was the case for mass loss,

we found evidence that the trade-off between incubation and feeding is unaffected by

supplementation, suggesting that this trade-off is rather driven by a parameter linked to

the body condition of females at the beginning of incubation.

Nesting success (P5)

Although recess frequency and nest attendance can partially predict nesting success in

shorebirds (e.g. Smith *et al.* 2012, Meyer et al. 2020), we found no evidence of these

relationships in our experiment. Declines in nesting success have been linked with

increased predation pressure in temperate systems (Patnode and White 1992, Sloan et al.

1998). In the Arctic, nest survival has been suggested to decline due to increasing risks of

nest abandonment while predation pressure remains stable throughout the summer

(Weiser et al. 2017). Generally, long-lived species favour their survival and may abandon

the nest when breeding costs reach critical energy demands (Williams 1966, Weiser et al.

2017). Our results suggest that nest abandonment became more prevalent as the season

progressed even though sandpipers had access to resource supplements. This implies that

the quantity of resources during incubation is unlikely a signal to leave the nest before

hatching. However, shorebirds face unpredictable abiotic (Tulp and Schekkerman 2006,

Smith and Wilson 2010) and biotic (Smith et al. 2012) conditions that may raise

incubation costs beyond their limit, forcing them to abandon. The fact that our

supplementation had no effect on nest survival indicates that white-rumped sandpipers

cannot compensate for these unexpected incubation costs with increased nutritional

intake. For the future scenarios of increased productivity in the Arctic, we suggest that an

increased peak of arthropods during incubation may not necessarily translate into higher

nesting success of these sandpipers. However, they could benefit before (increased

fueling) and after (prior to migration, chick survival) incubation.

By noting that nest survival declines as the short Arctic summer progresses, we

add support to other studies that early initiation favors higher nest survival in birds

(Blums et al. 2005, Weiser et al. 2017). As early initiation is often displayed by the birds

possessing the best body condition (Blums *et al.* 2002, 2005), we can once again

highlight the positive relationship between the state of females at the beginning of

incubation and nesting success. Body conditions at the start of incubation can be

determined in part during the pre-laying stage when shorebirds reconstitute their body

stores post-migration (Drent & Daan 1980; Morrison & Hobson 2004). The pre-laying

stage is then likely more critical than the incubation stage in terms of energy gains and

repercussions on incubation. We can thus expect additional resources to affect shorebirds

during this period. Considering that the decision of whether or not to breed often relies on

reaching a threshold of body condition (Rowe et al. 1994, Legagneux et al. 2016),

additional resources on the breeding grounds could increase the number of individuals

whose body condition reaches such theoretical threshold (Legagneux et al. 2012). In turn,

more individuals could invest in breeding (Prevedello et al. 2013) rather than skip

reproduction (Legagneux *et al.* 2016).

Conclusion

We found no evidence of an effect of our resource supplementation on mass loss,

incubation, and nesting success of female white-rumped sandpipers during their

incubation period in the Canadian Arctic. It is important to highlight that those

methodological limitations of this study may contribute to explaining the lack of detected

effects. It is possible that the number of mealworms consumed varied from one female to

another, reducing our ability to draw conclusions on the effects of the supplementation.

While we attempted to quantify the number of mealworms consumed, disturbances such

as rain, wind, and flooding made this very difficult. It is also frequent for incubating

sandpipers to fly up to 200m away from their nest to feed. With this in mind, it is possible

that females only fed upon the supplementary resources when walking to and from their

nest, even though the food supplement was always available *ad libitum.*

429   Other authors have suggested that supplementation experiments tend to have

insignificant effects on individuals when they naturally have access to good or moderate

amounts of resources (Boutin 1990, Nager et al. 1997, Ruffino et al. 2014). Although this

would be difficult to quantify, it is possible that the abundance of arthropods in the Arctic

may be above the saturation point of shorebirds during part of the summer. Studies that

quantify arthropod abundance systematically as a resource for shorebirds (Schekkerman

et al. 2003) could eventually verify whether arctic-breeding shorebirds have access to

sufficient, non-limiting resources during incubation. Also, it seems that predation, rather

than resource availability, is the leading cause of nest failure in shorebirds (Weiser et al.

2017). The fact that our supplementation experiment had no effects on white-rumped

sandpiper females during their incubation adds to the evidence that *in situ* resources are

not the principal limiting factor for animals living at high latitudes (Schoech and Hahn

2007, Ruffino et al. 2014). This would limit how the warming of the Arctic could

indirectly benefit shorebirds during their incubation through increased abundances of

arthropods. Further investigation of the carry-over effects of increased resources in the

Arctic on shorebirds will help determine whether some declining populations can find

relief in climate warming.

ETHICS

Our work was approved by the Animal Care Committee of the Université of Moncton.

DATA ACCESSIBILITY

The data, the video, and the code used in this study are available at

https://figshare.com/s/6af0f26709ee8a4b4134.

AUTHORS' CONTRIBUTIONS

LM: data curation, formal analysis, writing—original draft, writing—review and editing;

NL: conceptualization, funding acquisition, project administration, supervision, analysis,

writing—review and editing.

COMPETING INTERESTS

We have no competing interests.

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Table 1. Parameter estimates from the top-ranked multivariate fixed-effects linear models

examining the impact of a resource supplementation on mass loss, nest attendance, and

nesting success of incubating white-rumped sandpiper females using the information-

theoretical approach.

	Estimate	CI (lb)	CI (ub)	SD
Mass loss model (P1)				
Intercept	0.06	-0.09	0.20	0.07
Supplementation	0.11	-0.10	0.32	0.10
Weight	0.25	0.06	0.43	0.09
Supplementation x Weight	-0.02	-0.24	0.21	0.11
Recess frequency model (P2)				
Intercept	27.4	25.8	29.0	0.8
Recess duration model (P3)				
Intercept	7.8	7.4	8.2	0.2
Nest attendance model (P4)				
Intercept	0.858	0.848	0.867	0.005
Supplementation	-0.005	-0.018	0.008	0.007
Initiation	-0.013	-0.023	-0.003	0.005
Supplementation x Initiation	0.009	-0.005	0.023	0.007
Nesting success model (P5)				
Intercept	4.68	3.78	5.59	0.46
Year	-1.83	-2.75	-0.91	0.47
Time	-1.91	-2.75	-1.07	0.43

<u>Subscripts.</u> Supplementation: experimental addition of resources near the nest; Weight:

weight of the incubating female at the beginning of the experiment (standardized);

Initiation: Julian date at incubation started (standardized); Year: 2017 compared to

2016 (reference level); Time: number of days since the start of the experiment

(standardized); Estimate: predictor's estimate; CI (lb): lower bounds of the

confidence interval; CI (ub): upper bounds of the confidence interval; SD: standard

deviation.

Figure 1. Predictions derived from the hypothesis that increases in arthropod productivity

will improve the nesting success of female white-rumped sandpipers by improving their

body condition and/or by allowing them to spend more time incubating.

Figure 2. Location of the study area on Igloolik Island (Nunavut, Canada, 69.39 N; 81.55

W). Location of the study area (white circle in [B]) on Igloolik Island (Nunavut, Canada,

69.39 N; 81.55 W); (A and B)). (C) Cross-sectional view of the design of the

supplementation experiment conducted during the summers of 2016 and 2017 on and

around white-rumped sandpiper nests. We placed a small thermistor (C1) attached to a

thin wooden stick (C2) in the middle of the nest. We buried or covered the data logger

(C3) and wire. We placed a small cup (full of mealworms or empty) in a hole 5 meters

away from the nest.

Figure 3. Effect of a resource supplementation (mealworms) and of other covariates on mass loss and nest attendance of incubating white-rumped sandpiper females. Effect of the resource supplementation on mass loss per day (a). Effects of initial weight of incubating females on mass loss per day (b). Effect of resource supplementation on nest attendance (c). Effects of the date at which females started incubating on nest attendance (d). The "whiskers" of the box extend from the hinge to the largest and smallest values at most 1.5 x the inter-quartile range of the hinge. Dotted curves represent 95% CI.

664 **Figure 4.** Effects of a resource supplementation (mealworms; a) and time (b) on the daily

665 survival rate of white-rumped sandpiper nests. Groups sharing the same letter are not

666 different according to our top-ranked fixed-effects model (see Table 3). Error bars

667 represent 95% confidence intervals. Grey areas represent the standard error.