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Mind the Wind: Microclimate Effects on Incubation Effort of an Arctic Seabird

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Abstract

1. The energetic costs of reproduction in birds strongly depend on the climate experienced during incubation. Climate change and increasing chance of extreme weather events may severely affect these costs, especially for species incubating in extreme environments.
2. In this three-year study, I used an experimental approach to investigate the effects of microclimate and nest-shelter on the incubation effort of female common eiders (*Somateria mollissima*) in a wild Arctic population. I added artificial shelters to a random selection of nesting females, and compared the body mass loss during incubation between females with and without shelter.
3. Non-sheltered females experienced a higher mass loss during incubation than females with artificial shelter. This manipulation allowed me to identify wind as the key climatic variable leading to an energetically challenging incubation and was positively correlated with mass loss for non-sheltered females. Increasing ambient temperatures tended to decrease mass loss, but this effect was negligible in absence of wind. Humidity had no effect on mass loss.
4. This study is one of few that clearly demonstrate a direct effect of climate on avian life-history. By showing that increasing wind speed counteracts the energetic benefits of a rising ambient temperature, this study emphasizes that climatic variables other than temperature may also affect wild populations and need to be taken into account when predicting the effects of climate change.

Samandrag

1. Energikostnaden ved reproduksjon hos fuglar er sterkt avhengig av klimaet dei er eksponert for under ruginga. Klimaforandringar og auka sjansar ekstremvær kan ha ein stor påverknad på desse kostnadane, spesielt for artar som hekkar i ekstreme miljø.
2. I denne treårige studia har eg brukt ei eksperimentell tilnærming for å undersøke effekten av mikroklima og reirdekke på energikostnadane ved ruging hos Ærfugl (*Somateria mollissima*) i ein vill arktisk populasjon. Eg plasserte leveggjar rundt reiret til eit tilfeldig utval av hekkande Ærfuglhoar (éa) og samanlikna kroppsmassetapet under ruginga mellom éa med og utan reirdekke.
3. Éa utan reirdekke hadde eit høgare kroppsmassetap under ruginga enn éa med kunstig reirdekke. Denne manipulasjonen tillet oss å identifisere vind som den klimatiske variabelen som førte til auka energikostnadar ved ruging og vind var positivt korrelert med kroppsmassetap hos éa utan reirdekke. Auke i lufttemperatur hadde ein tendens til å senke kroppsmassetapet, men den effekten var ubetydeleg i fråvær av vind. Fuktgrad hadde ingen effekt på kroppsmassetapet.
4. Denne studia er ein av få som på ein klar måte demonstrerar ein direkte effekt av klima på livshistorie hos fuglar. Ved å vise at auke i vindhastigheit motverkar energifordelen ved ei auke i lufttemperatur, så visar denne studia at andre klimavariablar enn temperatur óg kan påverke ville populasjonar og må reknast med når ein skal forutsjå effekten av klimaforandringar.

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Introduction

Most scenarios of future climate predict a further increase in ambient and sea water temperatures, precipitation and in the number of extreme weather events (Christensen *et al.* 2013). Although rising temperatures often have a negative effect on life-history traits and population dynamics (Both *et al.* 2006; Drever *et al.* 2012), some traits may benefit from increasing temperatures (McKinnon, Nol & Juillet 2013). Reproduction is an energetically demanding phase of avian life history, both in terms of egg production and incubation (Williams 2005). Because the energetic costs of reproduction strongly depend on the climate experienced during incubation, they are expected to be greater for birds incubating in extreme environments (Tulp & Schekkerman 2006). Accordingly, it has been shown that the daily energy expenditure of Arctic breeding shorebirds is about 50% higher than in temperate breeding areas, the energy expenditure being the highest during the incubation phase (Piersma *et al.* 2003). While increasing ambient temperature may reduce energy expenditure (D'Alba, Monaghan & Nager 2009), wind and humidity may have the opposite effect. Wind can increase the rate of heat loss by disrupting the plumage and reducing thermal insulation, leading to an increase in energy expenditure (Weimerskirch *et al.* 2002). Even small changes in wind speed can drastically increase the convection of heat from the incubating bird to the environment (Heenan & Seymour 2012). Similarly, optimal nest humidity is important for successful chick development and hatching (Ar & Rahn 1980), and rainfall can negatively affect both chick (Ancil, Franke & Bêty 2014) and parent survival (Öberg *et al.* 2015). However, to our knowledge, the effect of relative humidity in on the energetic cost of incubation has never been investigated for birds.

The amount of shelter generated by a nest could potentially reduce the energy required for maintaining body temperature at an optimal level as well as keeping a stable incubation temperature, and thus reduce the energy allocated to incubation. Consequently, by constructing or choosing suitable nest sites, incubating birds can reduce the energetic costs of incubation, potentially leading to fitness benefits (Kim & Monaghan 2005). Hence, parents occupying sheltered nest-sites may have better breeding performance than those occupying exposed nest sites, or similar breeding performance, but at a lower energetic cost. This effect likely depends on environmental conditions and should be more marked during harsh years (e.g. years with strong wind, cold temperature, and precipitation).

The common eider is a sea duck known to be sensitive to climatic conditions (Lehikoinen, Kilpi & Ost 2006; Descamps *et al.* 2010). It has a circumpolar distribution breeding mainly in Arctic

and Boreal marine areas. Female eiders lay eggs in small cup-shaped holes filled with down. They incubate without male aid, relying upon accumulated body reserves during the whole incubation period (ca. 24-26 days). On Svalbard, incubating females generally nest on small barren islands and lose approximately 35-40% of their initial body weight during incubation (Gabrielsen *et al.* 1991). This mass loss is a good proxy of the energetic reproductive effort of female eiders (Descamps *et al.* 2010). Furthermore, it has been shown that female eiders nesting on a windswept island lose body weight faster than those in more sheltered colonies (Kilpi & Lindstrom 1997), and that females with artificial shelters lose less mass during incubation (Fast, Gilchrist & Clark 2007) independently of their quality (D'Alba, Monaghan & Nager 2009). In the last two studies, the shelter effect was translated into a temperature effect, and the decrease in body mass loss has been explained by the less variable and milder ambient temperatures experienced by the females during incubation (Fast, Gilchrist & Clark 2007; D'Alba, Monaghan & Nager 2009). Although these studies confirm the important role of ambient temperature on the energetic costs of incubation, they did not investigate the specific effects of other microclimatic factors, such as wind and humidity, and their possible interaction effect on these costs.

In order to understand the causal relationships between microclimate and incubation effort, it is important to examine concurrently the direct effects of wind, humidity and ambient temperature on the mass loss during incubation. However, the effects of nest-site characteristics on incubation effort may be confounded by correlations between these characteristics and individual quality. For example, D'Alba, Monaghan and Nager (2009) found that common eider females with naturally sheltered nest-sites produced larger clutches than non-sheltered females, implying that females of better quality (Wilson & Nussey 2010) preferred naturally sheltered nest-sites. Therefore an experimental approach to control for individual heterogeneity in the population is strongly recommended for such a study.

I investigated the effects of wind, ambient temperature and humidity on incubation effort of nesting females in an Arctic population of common eiders (Kongsfjorden, Svalbard). I ran the study over three years, allowing me to test for inter-annual variations. In order to disentangle the specific effect of wind from the effects of other microclimatic variables on the incubation effort while controlling for variation in female quality, I experimentally manipulated the degree of wind protection of the nest by adding artificial shelters around a random selection of nests occupied by incubating females. I predicted that ambient temperature would be negatively correlated with incubation effort, while humidity and wind would be positively correlated with

this effort measured by the mass loss during incubation. Consequently, female eiders with a nest-shelter were expected to lose less body mass during incubation than those occupying non-sheltered nests.

Methods

Study-site

The study was conducted on Prins Heinrich island outside Ny-Ålesund in Kongsfjorden (78°55'N, 12°00'E), Svalbard, during three subsequent breeding seasons (2012-2014). This island (2.43 hectares) is covered with tundra vegetation and soil, with a surrounding shoreline of small rocks. Between 200 and 400 eiders nest on the island (N = 218, 271 and 362 in 2012, 2013 and 2014 respectively), as well as a few pairs of Barnacle geese (*Branta leucopsis*), Glaucous gulls (*Larus hyperboreus*) and Arctic terns (*Sterna paradisaea*). The main predator of common eider eggs is the Glaucous gull, of which three pairs were nesting on the island each year. Females started laying eggs in early June (4 June in 2012 and 2013 and 3 June in 2014). All nests on the island were marked and numbered with a wooden stick placed into the ground close to the nest. Nesting birds were monitored every second day until incubation started and the number of eggs per nest was recorded at each visit. Female eiders may start incubating after the first egg is laid until after the clutch is completed, and the incubation period is about 25 days (Hanssen, Engebretsen & Erikstad 2002). Nest-sites sometimes provided some degree of shelter when placed close to rocks, driftwood or natural cavities. However, preliminary analyses showed no effect of natural shelter on mass loss (ANOVA with daily body mass loss as response variable and year and shelter category – with vs. without shelter – as predictors; $F_{1, 59} = 0.037$, $P = 0.848$), and I thus pooled data from all non-manipulated nests into a single category, referred to as “non-sheltered” for further analyses.

Nest-shelter experiment

To remove the effect of the wind on body mass loss during incubation while controlling for possible female differences and keeping humidity and ambient temperature unchanged, I randomly assigned artificial shelters to females with non-sheltered nests. The artificial shelters were placed during the first capture and consisted of three wooden planks (approx. 15 cm height, 50 cm length) protecting three sides around the nest (Fig. 1). A total of 11 and 17 nests were provided with such shelters in 2013 and 2014, respectively. No artificial shelters were added in 2012. Preliminary analyses, using an ANOVA with either ambient temperature or

humidity as response variable and shelter category as predictor, showed no effect of artificial shelters on neither ambient temperature ($F_{1, 65} = 2.057$, $P = 0.156$) nor humidity ($F_{1, 65} = 1.801$, $P = 0.184$). The wind-shield effect of the artificial shelters was confirmed by using a handheld anemometer (Mastech, Guangdong, China). After placing a shelter around a nest, the female was observed from a distance until she returned to the nest to make sure the shelter was accepted and the nest wasn't predated. All females returned to the nest within approx. 10 minutes.

Recorded variables

Females which had finished egg-laying and started incubating were captured using a fishing rod with a nylon loop at the end. Birds were weighed to the nearest 5g using a Pesola scale and their tarsus length, wing length and head-bill length were measured using a calliper to the nearest mm. The mean dates for the first captures were the 12th of June in 2012 and 2013, and the 14th of June in 2014. After 15 (min 13, max 17) days, the birds were recaptured and weighed. From these two measurements of body mass, I calculated the percentage decrease in body mass per day as:

$$\% \text{ daily mass loss} = 100 \times \frac{(\text{Initial mass} - \text{final mass})}{(\text{Initial mass} \times \text{number of days})}$$

where number of days refers to the period between the first and last capture. Body mass has been shown to be a good proxy of body condition in eider ducks (Descamps *et al.* 2010) and correcting for structural size did not affect the results in this study (not shown).

At first capture, a temperature and humidity logger (iButton Hydrocron DS1921 - Maxim Integrated Products, Sunnyvale, California) was placed approx. 10 cm from the nest edge at eider head height (Fig. 1). Ambient temperature and humidity were logged every 10 minutes until the logger was retrieved at the second capture. In 2014 an anemometer (Davis Instruments, Hayward, California), logging wind speed and direction, was placed on the island and the wind data were recorded during the whole study period. Mean wind speed measured on the island in 2014 was 2.77 m/s (SD = 0.29) with a mean wind direction of 203.4 degrees (SD = 79.1). Wind speed measurements on the island were highly correlated with those logged by the Ny-Ålesund weather station located approx. 1.3 km from the study site ($r = 0.98$). Hence, I used the wind speed data from Ny-Ålesund to estimate the wind on the island during the three years of the study.

Statistical analyses

I first tested whether females with artificial shelter differed from the non-sheltered females using an ANOVA where the clutch size or body mass at first capture were the response variables, while years and shelter category were predictor variables. Data from 2012 were excluded from these analyses since no artificial shelters were used during this season.

The effect of nest shelter on incubation effort was analysed using an ANOVA with daily body mass loss as response variable and shelter category and year as predictor variables. I then tested the effects of microclimate variables (average wind speed, ambient temperature and humidity between the two captures) on incubation effort with multiple linear regressions where the body mass loss was the response variable and the microclimatic variables, their interactions and year were the predictor variables (see Appendix 1 for correlations between the microclimate variables). I ran separate models for each shelter category (artificial shelter vs. no shelter). Indeed, artificially sheltered nest-sites are protected from the wind and the model for this nest category only included humidity and ambient temperature as predictor variables. All covariates were mean centred in both analyses. Model selection was performed using the Akaike's Information criterion corrected for small sample size (AICc, Burnham and Anderson (2002)). All statistical analyses were done using R v.3.1.2 (R Core Team 2013).

Results

Neither the mean body weight of incubating eiders at first capture nor their clutch size differed between years (body weight: $F_{1, 64} = 0.04$, $P = 0.84$, clutch size: $F_{1, 62} = 3.17$, $P = 0.08$; Table 1) or between shelter categories (body weight: $F_{1, 64} = 0.43$, $P = 0.51$, clutch size: $F_{1, 62} = 0.95$, $P = 0.33$; Table 1).

Females without artificial shelter breeding in 2013 had a significantly higher body mass loss compared to 2014 (Table 2a&b). This was most likely due to the more challenging conditions encountered by the birds in 2013, with stronger wind, colder temperature and higher humidity (Table 1). Females with an artificial shelter lost significantly less body mass in 2013 compared to those without shelter (Table 2b). In 2014, the difference between the two shelter categories was smaller, as shown by the interaction between year and artificial shelter (Table 2b). Nevertheless, artificially sheltered females lost less body mass than non-sheltered females.

In non-sheltered nests, body mass loss of females during incubation was mostly affected by the wind (Table 3a&b). Although wind and temperature were negatively correlated (Appendix 1)

results from the multiple regression suggest that differences in ambient temperature had little effect on the body mass loss at low wind speeds, but became important when wind speed increased (Table 3b; Fig. 2). In artificially sheltered females neither ambient temperature nor humidity had a statistically significant effect on body mass loss (Table 4), and the average mass loss was similar in 2013 and 2014 despite differences in ambient temperature and humidity. These results confirm the importance of the wind as microclimatic factor affecting incubation effort in common eider females (Fig 3). When protected from the wind, the influence of other microclimatic variables on the incubation effort was limited.

Discussion

In this study I have shown that the microclimate during incubation has a strong effect on the body mass loss of female common eiders, but only for females incubating on nests unprotected from the wind. For these females, an increase of 1 m/s in the average wind speed increased the total mass loss by 11% during the incubation period. Increasing ambient temperatures tended to counteract this effect (Fig 2), while relative humidity had no effect on incubation effort over the range of humidity observed. Artificially sheltered females lost on average 0.25% less mass each day in 2013 (ca. 111g in total during 25 days of incubation) and their body mass loss was not affected by either ambient temperature or humidity. The shelter effect on incubation costs is also confirmed by the absence of inter-annual difference in mass loss in sheltered females while non-sheltered females had a higher body mass loss in 2013 than in 2014, the former being the year with the worst conditions (Table 1).

Unlike a previous study (D'Alba, Monaghan & Nager 2009), I was unable to detect any differences in body mass loss during incubation between females differing in the degree of natural shelter. A likely explanation is that the natural shelters included in our study offered very limited protection from the wind. A few nest sites with an apparently higher degree of shelter were available on the island, but I was unable to capture the females occupying these nest sites and thus I could not include them in the study. Nevertheless, our results indicate that by choosing a well sheltered nest site, female common eiders could reduce a large part of the negative impact of wind on incubation energetics. Still, naturally sheltered nest-sites were not preferred over non-sheltered nest sites by early laying females (CHH, personal observation), and the majority of the incubating females chose non-sheltered nest sites even if sheltered ones were available. This suggests that breeding in a sheltered nest may also have some costs. Predation is often the main cause of reproductive failure in birds (Martin 1993) and nest-site

selection may represent a trade-off between predation and appropriate microclimate for incubation (Amat & Masero 2004). Accordingly, Öst & Steele (2010) have reported that predation risk in common eiders increased with nest shelter, providing a plausible explanation for the observed lack of selection for sheltered nest-sites by the females in our study. Moreover, some sheltered nest-sites in our study area were close to the shore where the risk of being flooded was high. The energetic benefit from a sheltered nest-site may thus be counterbalanced by a higher fitness cost, in terms of nest predation and/or flood risk (Viera *et al.* 2006).

The IUCN red list found that 35% of all bird species are vulnerable to climate change. Seabird families are particularly susceptible to such changes (Foden *et al.* 2009), and 40% of all seabird species are affected by climate change (Croxall *et al.* 2012). Most documented effects of climate change on seabirds have been indirect, for example through changes in food resources or foraging performance (Jenouvrier 2013). However, direct effects of climate change on life-history traits, such as timing of breeding (Visser, Holleman & Caro 2009), nest-survival (Descamps *et al.* 2015), or reproductive effort (this study) should not be overlooked.

Our study suggests that increase in wind speed may counteract the energetic gain from the rising ambient temperature predicted from climate change, and possibly increase the energetic costs of incubation. These results emphasize the importance of wind as a key environmental factor when predicting the effects of a changing climate on breeding populations of ground nesting birds in the Arctic. They suggest that increasingly demanding environmental conditions during incubation resulting from a changing climate may affect species differently, depending on, for example, breeding strategy. More specifically, cavity nesting birds may be less affected by a changing climate during the breeding season than ground nesting birds, such as the common eider. To fully understand the consequences of climate change on the life-histories of breeding birds in the Arctic, future studies are needed to investigate whether wind patterns in the Arctic are likely to change, and how such changes may affect bird species with different breeding strategies.

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Figures



Figure 1. Female common eider with an artificial shelter and the temperature/humidity logger inside. A white plastic ball with air vents was placed around the logger to prevent exposure to direct sunlight. Photo: Elise Skottene.

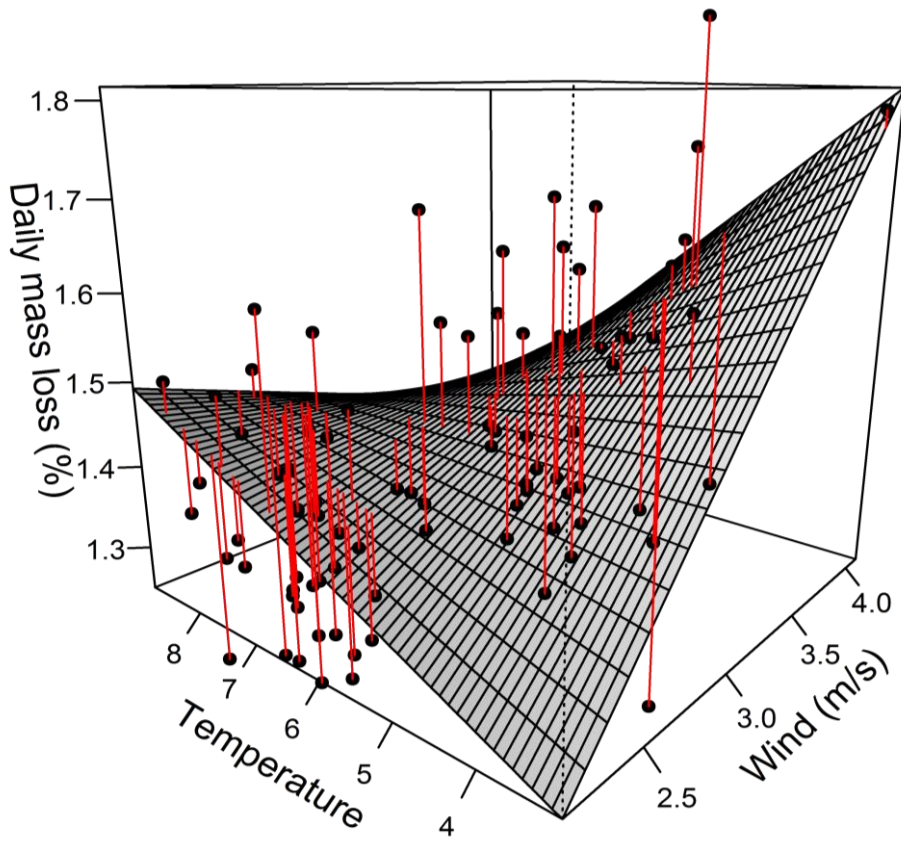


Figure 2. Estimated effects of ambient temperature and wind speed on the daily mass loss of non-sheltered females. The figure was made using parameter estimates from the model presented in Table 3b and considering the mean humidity value (78% RH).

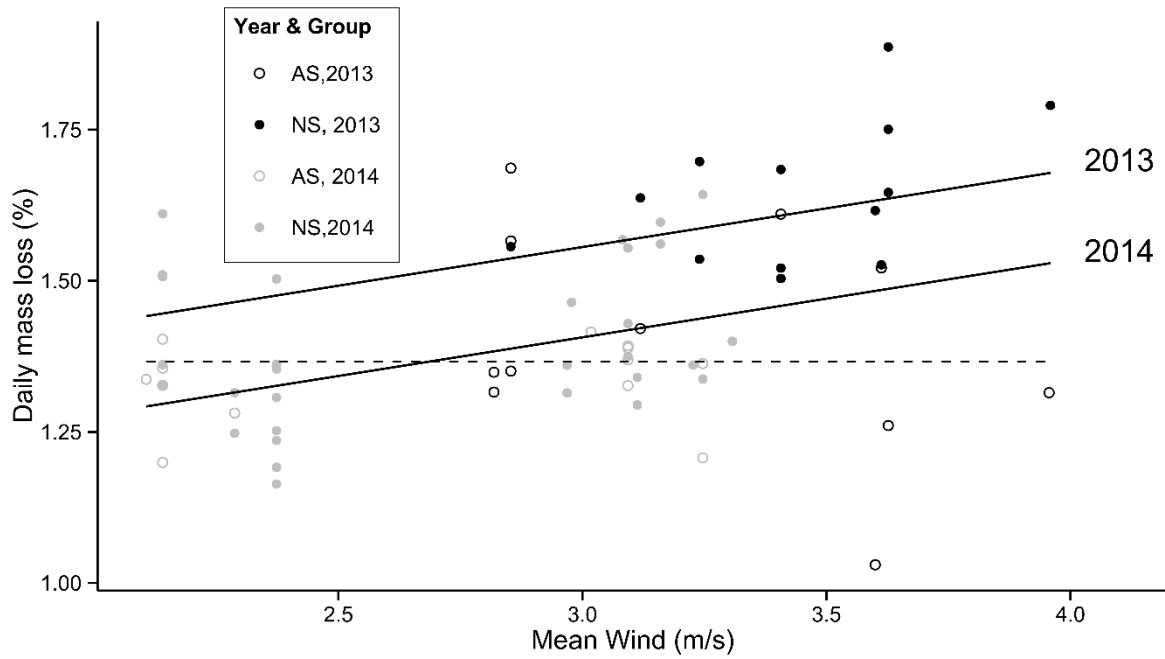


Figure 3. Estimated effects of wind on the daily mass loss of non-sheltered females (NS) (solid dots and lines) and artificially sheltered females (AS) (open dots, dashed line) during incubation with the average ambient temperature (6.47 °C). The figure has been made using parameter estimates from the model presented in Table 3b (non-sheltered) and the mean mass loss for artificially sheltered.

Tables

Table 1. Mean (\pm SE) values of female mass (%) and clutch size at the start of the incubation, and the yearly average for three microclimate variables.

| | Mass (g) | Clutch Size | Wind (m/s) | Temp ($^{\circ}$C) | Humidity (%RH) |
|----------------------|-----------------|--------------------|-------------------|--------------------------------------|-----------------------|
| 2012 (N = 20) | 1823 \pm 19.1 | 4.2 \pm 0.06 | 2.63 \pm 0.016 | 8.31 \pm 0.10 | 74.97 \pm 0.91 |
| 2013 (N = 24) | 1828 \pm 19.9 | 3.5 \pm 0.21 | 3.35 \pm 0.074 | 5.11 \pm 0.18 | 80.9 \pm 0.53 |
| 2014 (N = 43) | 1813 \pm 14.6 | 3.0 \pm 0.18 | 2.59 \pm 0.069 | 6.92 \pm 0.15 | 77.5 \pm 0.57 |

Table 2a). Model selection for the effects of nest-shelter (no shelter vs. artificial shelter) and year (2013 and 2014) on the daily mass loss (%) of incubating female eiders. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, Δ AICc is the difference in AICc compared to the model with lowest AICc, wAICc is the AICc weights and R^2 is the fraction of variance explained by the model ($R^2 = 1 - SS_{resid}/SS_{tot}$).

| Effect of nest-shelter and year on daily mass loss (%) | | | | | |
|---|----------|-------------|--------------------------------|--------------|-------------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R^2 |
| Shelter category:Year | 6 | -77.1 | 0 | 0.916 | 0.41 |
| Shelter category + Year | 5 | -72.3 | 4.78 | 0.084 | 0.35 |
| Year | 3 | -61.3 | 15.83 | 0.000 | 0.21 |
| Shelter category | 4 | -52.2 | 24.9 | 0.000 | 0.09 |

Table 2b). Effects of shelter and year on the daily mass loss (%) of common eider females at Prins Heinrich Island, Svalbard. The year 2012 is excluded from the analysis (see Methods for details).

| Parameter | Estimate \pm SE |
|-------------------------------------|-------------------------------------|
| Intercept (2013, No shelter) | 1.642 \pm 0.036 |
| Year 2014 | -0.248 \pm 0.043 |
| Artificial shelter | -0.24 \pm 0.053 |
| Artificial Shelter : 2014 | 0.181 \pm 0.068 |

Table 3a). Model selection for the effects of microclimate and year (2012, 2013 and 2014) on the daily mass loss (%) of non-sheltered females.

| Effect of microclimate and year on daily mass loss (%) of non-sheltered females | | | | | |
|--|----------|-------------|--------------------------------|--------------|----------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R² |
| Wind + Year | 5 | -81.2 | 0 | 0.37 | 0.53 |
| Wind:Temp + Year | 7 | -80.9 | 0.29 | 0.32 | 0.57 |
| Temp + Year | 5 | -79.6 | 1.57 | 0.17 | 0.52 |
| Humidity + Temp + Year | 6 | -79.4 | 1.82 | 0.15 | 0.54 |

Table 3b). Effects of microclimate and year on daily mass loss for non-sheltered females. All explanatory variables are mean centred. Model corresponds to the best model selected (see Appendix 2 for complete model selection).

| Parameter | Estimate \pm SE |
|-------------------------|-------------------------------------|
| Intercept (2012) | 1.310 \pm 0.046 |
| 2013 | 0.227 \pm 0.067 |
| 2014 | 0.078 \pm 0.061 |
| Wind | 0.074 \pm 0.068 |
| Temp | -0.005 \pm 0.027 |
| Temp : Wind | -0.062 \pm 0.029 |

Table 4. Model selection for the effects of microclimate and year (2013 and 2014) on the daily mass loss (%) of sheltered females.

| Effect of microclimate and year on daily mass loss (%) of artificially sheltered females | | | | | |
|---|----------|-------------|--------------------------------|--------------|----------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R² |
| Intercept | 2 | -23.9 | 0 | 0.48 | 0.00 |
| Year | 3 | -22.8 | 1.1 | 0.27 | 0.06 |
| Humidity | 3 | -22.6 | 1.32 | 0.25 | 0.05 |

Appendix 1

Microclimate

| | | |
|--------------|--------------|--------------|
| Wind | 0.53 | -0.89 |
| 0.45 | Humidity | -0.24 |
| -0.71 | -0.45 | Temp |

Body measurements

| | | | |
|-------------|-------------|-------------|-------------|
| Mass | 0.41 | 0.34 | 0.12 |
| 0.41 | Bill | 0.37 | 0.4 |
| 0.34 | 0.37 | Wing | 0.27 |
| 0.12 | 0.4 | 0.27 | Tarsus |

Figure 1. Pearson correlations between i) microclimate variables (upper right values are between non-sheltered females and lower left is between artificially sheltered females) and ii) body measurements.

Appendix 2

Table 1). Model selection for the effects of nest-shelter (no shelter vs. artificial shelter) and year (2013 and 2014) on the daily mass loss (%) of incubating female eiders. K is the number of parameters estimated, AICc the Aikake information criterion corrected for small sample size, Δ AICc is the difference in AICc compared to the model with lowest AICc, wAICc is the AICc weights and R^2 is the fraction of variance explained by the model ($R^2 = 1 - SS_{resid}/SS_{tot}$).

| Effect of nest-shelter and year on daily mass loss (%) | | | | | |
|---|----------|-------------|--------------------------------|--------------|-------------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R^2 |
| Shelter category*Year | 6 | -77.1 | 0 | 0.916 | 0.41 |
| Shelter category + Year | 5 | -72.3 | 4.78 | 0.084 | 0.35 |
| Year | 3 | -61.3 | 15.83 | 0.000 | 0.21 |
| Shelter category | 4 | -52.2 | 24.9 | 0.000 | 0.09 |

Table 2). Model selection for the effects of microclimate and year (2012, 2013 and 2014) on the daily mass loss (%) of non-sheltered females.

| Effect of microclimate and year on daily mass loss (%) of non-sheltered females | | | | | |
|--|----------|-------------|--------------|--------------|----------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R² |
| Wind + Year | 5 | -81.2 | 0 | 0.37 | 0.53 |
| Wind:Temp + Year | 7 | -80.9 | 0.29 | 0.32 | 0.57 |
| Temp + Year | 5 | -79.6 | 1.57 | 0.17 | 0.52 |
| Humidity + Temp + Year | 6 | -79.4 | 1.82 | 0.15 | 0.54 |
| Humidity + Wind + Year | 6 | -79.4 | 2.16 | 0.07 | 0.53 |
| Wind + Temp + Year | 6 | -78.8 | 2.35 | 0.06 | 0.53 |
| Year | 4 | -78.5 | 2.64 | 0.05 | 0.49 |
| Wind + Temp + Humidity + Wind:Temp + Year | 8 | -78.3 | 2.84 | 0.05 | 0.57 |
| Temp:Humidity + Year | 7 | -77.3 | 3.85 | 0.03 | 0.54 |
| Humidity + Year | 5 | -77.1 | 4.03 | 0.03 | 0.50 |
| Wind + Temp + Humidity + Year | 7 | -77.1 | 4.08 | 0.03 | 0.54 |
| Wind + Temp + Humidity + Wind:Humidity + Wind:Temp + Year | 9 | -76.8 | 4.40 | 0.02 | 0.58 |
| Wind : Humidity + Year | 7 | -76.5 | 4.70 | 0.02 | 0.54 |
| Wind + Temp + Humidity + Wind:Temp | 6 | -75.7 | 5.47 | 0.01 | 0.51 |

Table 3. Model selection for the effects of microclimate and year (2013 and 2014) on the daily mass loss (%) of sheltered females.

| Effect of microclimate and year on daily mass loss (%) of artificially sheltered females | | | | | |
|---|----------|-------------|--------------------------------|--------------|----------------------|
| Predictors | K | AICc | ΔAICc | wAICc | R² |
| Intercept | 2 | -23.9 | 0 | 0.48 | 0.00 |
| Year | 3 | -22.8 | 1.1 | 0.27 | 0.06 |
| Humidity | 3 | -22.6 | 1.32 | 0.25 | 0.05 |
| Temp | 3 | -21.6 | 2.35 | 0.1 | 0.01 |
| Temp + Year | 4 | -20.7 | 3.23 | 0.06 | 0.09 |
| Temp + Humidity | 4 | -20.4 | 3.5 | 0.06 | 0.08 |
| Temp : Humidity | 5 | -20.2 | 3.68 | 0.05 | 0.19 |
| Humidity + Year | 4 | -19.9 | 4.00 | 0.04 | 0.06 |
| Temp:Humidity + Year | 6 | -18.2 | 5.73 | 0.02 | 0.24 |
| Temp + Humidity + Year | 5 | -17.5 | 6.45 | 0.01 | 0.09 |