Temperature dependent preening behaviour in common guillemots *Uria aalge*

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Temperaturberoende putsningsbeteende hos sillgrisslor Uria aalge

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Abstract

As global temperature increase, new thermal conditions may challenge the physiological limits of endotherms. Examining the direct effects of extreme temperatures is an important component in understanding how these physiological limits may impact an organism's behaviour, breeding success and survival. Breeding at high latitude, with nest sites exposed to the changing weather of the summer months, makes the common guillemot *Uria aalge* a good model to examine how these changing thermal conditions may impact an organism's behaviour. In this study, I examined the amount of time spent on two different preening behaviours, self-preening and allopreening, in relation to increasing air temperatures and sun exposure using video footage from a breeding colony of common guillemots in the Baltic Sea. Both preening behaviours function as ectoparasite control in addition to allopreening that may also have an important role in social interactions between neighbours and partners. The results demonstrate a negative relationship between increasing air temperatures and the amount of time birds spent on self-preening in sun exposed conditions. Additionally, birds spent less time on allopreening as temperature increase at intermediate sun exposure. These results illustrate a possible trade-off between the regulation of internal body temperature and preening behaviour in common guillemots. This re-allocation of time and energy away from preening could ultimately affect the social dynamics and health of the colony in addition to the quality of parental care as the birds spend more time and energy on maintaining thermal homeostasis as temperature and sun exposure increase.

Keywords: Common guillemot, common murre, seabirds, Stora Karlsö, heat-stress, temperature, preening, allopreening

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Abbreviations

TNZ   Thermoneutral zone

T_{uc} Upper critical temperature

T_{lc} Lower critical temperature

1. Introduction

Increasing global temperatures rank as the most dominant consequence of contemporary climatic change (Trenberth et al. 2007), posing new challenges across animal taxa (Parmesan 2006). The impact of global warming can be categorised into indirect effects mediated by biotic interactions (e.g., through trophic relations, species interactions, and habitat quality) (Ockendon et al. 2014; Pistorius et al. 2023; Sydeman et al. 2012) and direct effects on physiology and behaviour (Oswald & Arnold 2012). Endotherms, opposed to ectotherms, generate heat from internal metabolic processes, a mechanism that allows the animal to maintain thermal homeostasis under challenging environmental conditions and are therefore thought to be less impacted by the direct effects of global warming. Most studies on endothermic species have focused on the indirect effects of global warming as drivers of distribution, population, and behavioural changes (Crick 2004; Ockendon et al. 2014; Sydeman et al. 2015). However, in the wake of increasing temperatures (IPCC 2021), more effort has been directed into studying the direct effects of global warming (Boyles et al. 2011; Oswald et al. 2011). Despite being able to buffer challenging thermal environments, physiological limits exist. The thermoneutral zone (TNZ) is a range of ambient temperatures where the endothermic organism can maintain internal body temperatures with minimal metabolic regulation. Below lower critical temperatures (T_{lc}) and above upper critical temperatures (T_{uc}), the animal must expend more energy to maintain thermal homeostasis (fig. 1). As ambient temperatures go above their T_{uc}, the animal has to dissipate the extra heat load by physiological and behavioural thermoregulation e.g., perspiration, panting and seeking shade. The inability to regulate internal temperature can result in physiological damage or even death (Angilletta 2009; McKechnie & Wolf 2010). These physiological damages include but are not limited to oxidative damage, immunosuppression, increased inflammation, compromised gut health, and reduced growth performance (Akbarian 2016; Farag & Alagawany 2018; He et al. 2020; Mitchell & Goddard, 1990). Even below the risk for physiological damage, these thermoregulatory behaviours come at a time- and energy cost (McNab 2002) that limit the amount of available time and energy spent on other behaviours such as foraging, defending territories or caring for offspring (Cunningham et al. 2021) which could impact the breeding success (Bourne et al. 2020; Gaston et al 2002; Olin et al. 2023; Oswald et al. 2008; van de Ven et al.

2020) and ultimately the survival of a species. However, as to date, few studies have been exploring the impact of these thermoregulatory demands on the rest of the behavioural repertoire of an organism, and if certain behaviours are consequently avoided as they generate additional heat or simply do not have time to be expressed.
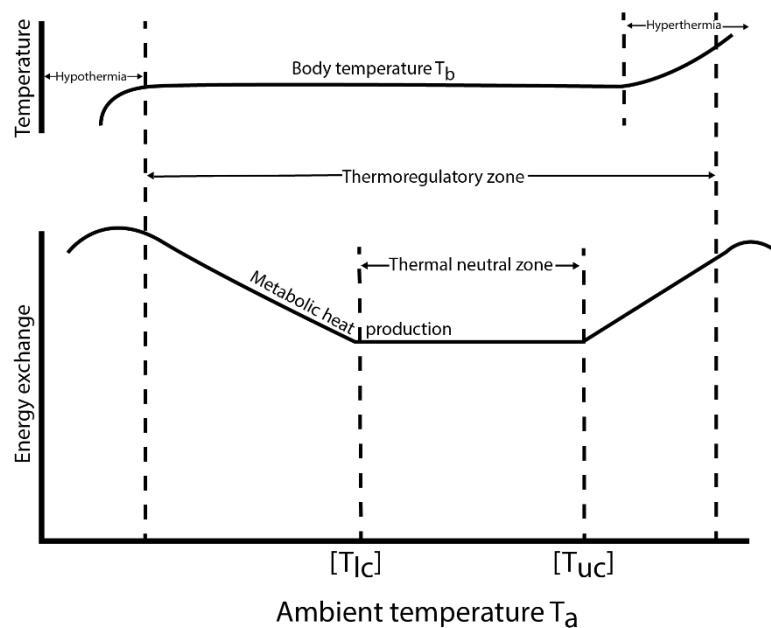
Figure 1. Thermoregulation and the thermal neutral zone: schematic relationships among ambient temperature (T_a), metabolic heat production and body temperature (T_b). T_{lc} = lower critical temperature, T_{uc} = upper critical temperature. Reproduced from Widowski (2010) with some alternations.

1.1 Preening Behaviours in Birds

Birds spend on average 9.2% of the day in maintenance activities, with the major part being spent on preening (Cotgreave & Clayton 1994). Preening involves the bird pulling feathers between the mandibles of the beak or using the tips of the mandibles to nibble on the feathers. The activity of preening serves several functions, both as a way of socialising and in maintaining the plumage in good condition and free from ectoparasites (Hart 1997, 1992). Many ectoparasites have become highly specialized on their hosts ecology, synchronizing their life cycles with their hosts breeding season (e.g., Barton 1996; Clifford 1979; Hoberg 1996). Studies have demonstrated that birds with impaired preening ability are subjected to an increase of ectoparasites that subsequently reduce fitness (Clayton 1990;

Booth et al. 1993). Ectoparasites have been the reason of nest desertion (Feare 1976; Duffy 1991), and the cause of egg loss and increased chick mortality (Bergström et al. 1999; Gaston et al. 2002; Mangin et al. 2003) as shown by several studies of birds. Although birds have a wide variety of defences to combat ectoparasites, preening has been shown to be the most important (Clayton et al. 2010).

In addition to its function as ectoparasite control, preening may also have a social purpose. Mutual preening, also called allopreening (Harrison 1965), may be an important component of social interactions between partners and neighbours. In colony-breeding species, cooperation among neighbours is important. As the group size of the colony increases, allopreening has been shown to become more prevalent (Lewis et al. 2007; Radford & Du Plessis 2006). This positive correlation between allopreening and group size could be a way to keep good relations between neighbours as studies suggest that allopreening may function as a reciprocal stress reducer (Kober & Gaston 2003), decreasing the probability of fights and associated breeding failure in high-density colonies (Lewis et al. 2007). In addition to its social function among neighbours, allopreening may also have an important role in pair bonding and parental cooperation in offspring care (Kenny et al. 2017). In some species, allopreening may stimulate the production of the pituitary hormone prolactin which, in turn, promotes parental care (Buntin 1986). A decline in allopreening could therefore have a possible negative impact on the formation and maintenance of pair bonds, parental care and subsequently their breeding success.

As studies demonstrate, preening is an important behaviour for both the health, social interactions, and breeding success in many birds. Preening is, however, an energy-intensive activity (Croll & McLaren, 1993) that, to the best of my knowledge, have not yet been studied in relation to extreme temperatures. Furthermore, whether preening will be de-prioritised when more pressing behaviours, such as thermoregulation is required in increasing temperatures.

1.2 Study Species

Breeding in exposed sites at high latitudes during the summer months, some species of seabirds are subjected to extensive weather and temperature changes. Their nesting conditions in addition with their adaptation to cold environments makes seabirds model bioindicators of changing thermal conditions (Oswald & Arnold 2012). This study will focus on the common guillemot *Uria aalge*, a high-latitude, high-density colony breeding seabird distributed circumpolar in the Northern Hemisphere. Equipped with a dense plumage and a high metabolic rate (Croll & McLaren 1993), the common guillemot is adapted to cold environments (Choy et al. 2021), diving to great depths in the frigid sea (Piatt & Nettleship 1984). Due to its adaptation to colder environments in addition to the exposed nature of their

nesting site, the common guillemot is as a good model species for examining an organism's scope of responses to its upper thermal limits. Studies on the closely related Brünnich's guillemot have observed thermoregulatory behaviour and death as a result of mosquito parasitism and heat stress on days with maximum air temperatures as low as 22 °C (Gaston & Elliott 2013; Gaston et al. 2002). The common guillemot has exhibited similar vulnerability against higher temperatures, exhibiting two thermoregulatory behaviours, panting, and spreading of wings, as temperatures increased (Olin et al. 2023). In addition, as temperatures reached their thermal limits, breeding partners spent less time together at the colony. Heat stress even resulted in breeding common guillemots leaving their nest site to cool off in the sea, subjecting their egg or chick to the elements and possible predation (Olin et al. 2023).

As the common guillemot is a long-lived species, breeding in large, high-density colonies, aspects that can favour the maintenance of parasites within populations (McCoy et al. 2016), preening may be crucial in maintaining a healthy plumage. Additionally, studies have shown that allopreening is important for communication within pairs, where the absence of allopreening delayed the exchange of brooding duties (Takahashi 2013). As heatwaves becomes more frequent, examining the direct effects of thermal extremes on preening behaviour may broaden our understanding of the common guillemot's physiological limits, and in extension how these limits will affect their health, social dynamics, and breeding success in a future of increasing global temperatures.

1.3 Aims and Objectives

This study aims at exploring the relationship between temperature and preening behaviour in common guillemots at Stora Karlsö. To address this aim, I will examine the amount of time spent separately on the two preening behaviours, allopreening and self-preening in relation to increasing temperatures and sun exposure to determine if an association between thermal conditions and preening behaviour exist. The expectation is that, as sun exposure increases and temperature rises, the amount of time spent on both preening behaviours will decrease.

2. Materials and Methods

2.1 Study Site

The study was performed at Stora Karlsö (57° 17' N, 17° 58' E), an island situated in the Baltic Sea, west of Gotland. The island supports the largest colony of common guillemots in the Baltic Sea with a breeding population estimated to ca. 25 000 pairs in 2021 (O. Olsson & J. Hentati-Sundberg unpubl. data). The breeding pair lay one egg directly on the bare rock ledge in mid-May to early June. The common guillemot practice biparental care with male and female parents taking turns incubating the egg for approximately 32 days (Hedgren & Linnman 1979) and thereafter feeding, brooding, and guarding the chick from predators and the elements. After around 3 weeks on the ledge, the chick will promptly leave the nest accompanied by their father, thereby concluding the breeding season (Hedgren & Linnman 1979).

Karlsö Auk Lab is a hollow steel- and oak construction situated on Stora Karlsö´s west facing cliffs (Hentati-Sundberg et al. 2012). The inside space of Auk Lab facilitates researchers and equipment while the exterior is equipped with 9 levels of limestone covered ledges, making an artificial breeding site for common guillemots (fig. 2) and razor bills. Since its construction in 2008, the number of breeding guillemots on Auk Lab has steadily increased to 82 pairs in 2022 (P. A Berglund pers. comm.). Video cameras (4 megapixel resolution IP-cameras; Provision ISR, models DAI-340IPE-MVF and DI-340IPS-28) continuously record the breeding season. This study utilized pre-recorded video footage from 2022.

Figure 2. Screenshot of video footage from an Auk Lab breeding ledge used in this study. The sun-exposed probe is marked by an orange arrow. An individual self-preening behind its wing marked by a blue arrow.

2.2 Temperature Data

Air temperature data were recorded from a weather station located 15 m from Auk Lab, Stora Karlsö. The air temperature was recorded every 15 min. In addition, temperature at the breeding ledges was measured with 2 TG8 PT1000 temperature probes placed on the walls of a sun-exposed ledge and a shaded ledge, respectively. Ledge temperatures was recorded every 2 min. It should be noted that ledge surface temperatures are similar to surrounding natural ledges (Olin et al. 2023). Air temperature data from the weather station was used during the analysis of both preening behaviours (see 2.3).

2.3 Behavioural Data

Only preening behaviour of individuals who were incubating an egg or brooding a chick were studied. This limitation guarantee that the individuals studied would be present during the whole observation time. Independently collected breeding data was used to verify the identity of the breeding individuals throughout the breeding season. Collected preening data would be discarded for the specific individual and time interval if an exchange of breeding partner occurred during the observation time.

Preening behaviour was subdivided into two categories: self-preening and allopreening. Allopreening included preening of partner and/or neighbours. Preening of chick was not included as the chick is only present during a specific portion of the breeding season. All observations were carried out by me. Behaviours

was recorded during 15 min intervals, selected through the procedure described in the next section (see 2.4). Based on the video footage, the number of seconds spent on the two preening behaviours was recorded for each interval. The amount of time spent on each preening behaviour was recorded collectively for all breeding individuals on the ledge due to time constraints, as individual preening data would take longer time to record. The mean of each preening behaviour is then calculated by dividing the total time spent on each behaviour summed across all tracked individuals on the breeding ledge by the total number of tracked individuals. Preening behaviour was recorded on two breeding ledges, using the same time intervals. The two breeding ledges were selected based on the sun probes position (fig. 2) in addition to the homogeneity of sun exposure across the ledge. In each interval 3–6 birds were present on the breeding ledge, only including the ones tracked in the study,

In addition, the exposure of each bird i.e., whether they were in the shade, in the sun, or a bit of both were noted after half the time interval. A conclusive category for the specific time interval was noted based on the exposure of 2/3 or more of the group. If neither 2/3 of the group was exposed to sun or shade, the specific time interval would be categorized as having "mixed" exposure. Overcast weather during the entire time interval would be categorized as "shade".

2.4 Sampling Design

To examine the relationship between temperature and preening behaviour, time intervals was obtained through a stratified random sampling with measurement from the sun exposed probe (fig. 2). The measurements from the sun-exposed probe were used in order to represent a wide spectrum of temperatures and variation in sun exposure as the sun-exposed probe is affected by both sun and air temperature. The time intervals were selected from 5 temperature ranges ($0-9.9$, $10-19.9$, $20-29.9$, $30-39.9$ and $40-50$°C) and from hours during the day ($15:00-19:00$ h) when similar type of activity is exhibited in order to minimize variation due to the animal's daily rhythm. All the selected time intervals where within the breeding season ($20/5-5/7$) of the selected ledges i.e., when the majority of individuals were incubating an egg or rearing a chick. Up to eight intervals were sampled in each temperature range. No date was sampled twice as to avoid pseudoreplication. This resulted in fewer samples for the extreme ranges as these temperatures where not observed enough days during the breeding season to generate eight independent samples per ledge. As the same time intervals is analysed twice, once per breeding ledge, the random sampling generated 70 time intervals of 15 min each. Four of these time intervals, one from each temperature range had missing video footage. As a result, in total 66 time intervals was used in this study, 32 and 35 time intervals per breeding ledge, respectively, due to missing video footage.

2.5 Data Analysis

For the relationship between temperature and the two preening behaviours, assuming normal distribution, Generalised Additive Models were fitted using the R package 'mgcv'. Temperature and exposure were used as the explanatory variables in the models. As preening behaviour can vary as a function of breeding stage (Maxson & Oring 1980), the different breeding stages (e.g., incubation of egg or rearing of chick) should be regarded in the models. However, as temperature and date are strongly correlated ($p = 0.001$, appx. 1), these two variables cannot be incorporated in the same model as it reduces the precision of the estimated coefficients and p-values, making the results difficult to interpret. I will therefore focus on the effect of temperature on preening behaviour but, for context, seasonal variation will be examined separately (see discussion). Mann-Whitney tests were used to examine the relationship between the two preening behaviours and the two breeding stages (incubation of egg and chick-rearing). The mean date for chick hatching was calculated from dividing the hatching dates from the two studied ledges summed across all tracked individuals in order to split the breeding season into a pre- and post-hatching period. R v. 4.3.0 (R Core Team 2023) was used for all data analysis and visualisation.

3. Results

3.1 The Effect of Temperature and Sun Exposure

For birds exposed to the sun, time spent on self-preening decreased as temperatures increased (F = 12.04, p = $2.58 \cdot 10^{-5}$). A decline of self-preening behaviour in sun exposed birds can be observed at ~15 °C, reaching a plateau at ~23 °C where little to no self-preening is being expressed (fig. 3c). However, it should be noted that 15 °C is the lowest recorded temperature in sun exposed conditions. Self-preening behaviour increase as temperature increase (F = 6.21, p = 0.016) for birds in shaded conditions (fig. 3a). The self-preening behaviour remained independent of temperature for birds in mixed sun exposed conditions (fig. 3b), demonstrating no correlation between the two variables (F = 0.001, p = 0.97).
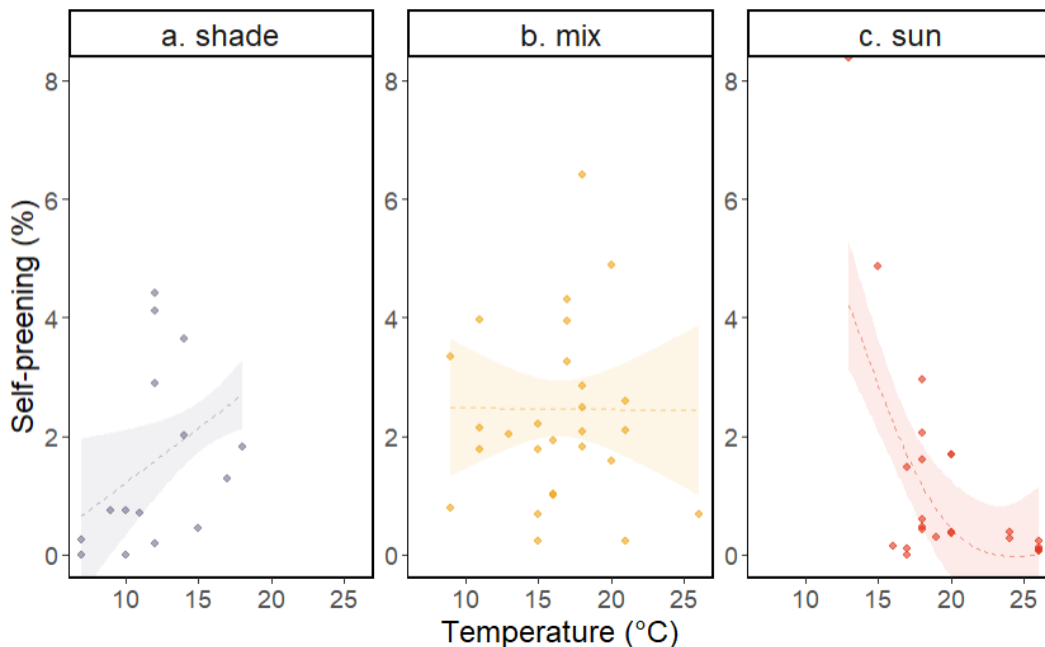

Figure 3. Effect of temperature and sun exposure on the self-preening behaviour of common guillemots at Stora Karlsö. Temperature (°C) is based on air temperatures recorded by the weather station from the start of the interval. Sun exposure i.e., shade, mix or sun, represent the sun exposure on the breeding ledge after half the time interval. Preening behaviour is represented in the percentage (%) of seconds spent on self-preening during a 15 min interval. Lines and shaded areas represent nonlinear models with associated 95% confidence intervals.

The amount of time birds spent on allopreening decreased as temperatures increased in mixed sun exposed (fig. 4b) conditions (F = 9.39, p = 0.003). No significant relationship between the amount of time the birds spent on allopreening, and temperature could be observed for birds in shaded- (F = 0. 33, p = 0.57) (fig. 4a) and sun exposed (F = 3.26, p = 0.07) (fig. 4c) conditions.
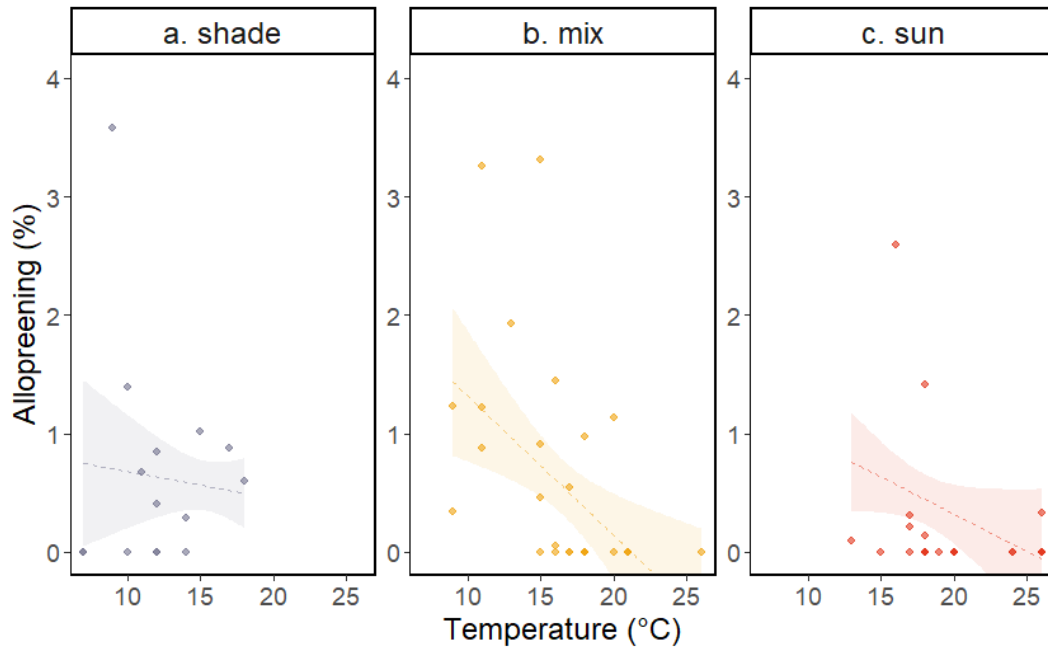

Figure 4. Effect of temperature and sun exposure on the allopreening behaviour of common guillemots at Stora Karlsö. Temperature (°C) is based on air temperatures recorded by the weather station from the start of the interval. Sun exposure i.e., shade, mix or sun, represent the sun exposure on the breeding ledge after half the time interval. Preening behaviour is represented in the percentage (%) seconds spent on allopreening during a 15 min interval. Lines and shaded areas represent nonlinear models with associated 95% confidence intervals.

3.2 Seasonal Patterns in Preening

There was no support for a relationship between breeding stages and the amount of time birds spent on self-preening (fig. 5), showing no significant change in the amount of time spent on self-preening before and after hatching (U = 654, p = 0.06). A significant change in the amount of time birds spent on allopreening before and after hatching could however be observed (U = 769, p = 0.0002), where birds spent less time on allopreening after the chick hatched (fig. 6).
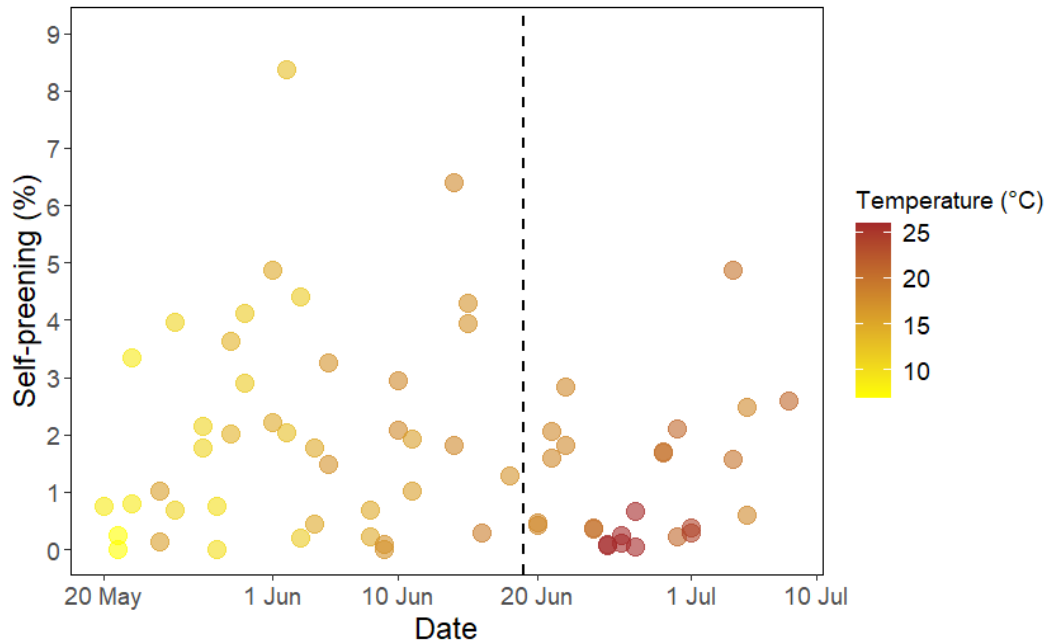
Figure 5. Relationship between self-preening behaviour and the breeding season of common guillemots at Stora Karlsö. Preening behaviour is represented in the percentage (%) of seconds spent on self-preening during a 15 min interval. The black dashed line represents the mean date (19/6) of chick hatching based on data from the individuals on the two studied breeding ledges. The colour of each data point represents the air temperature (°C) on that given date recorded by the weather station from the start of the interval.

Figure 6. Relationship between allopreening behaviour and the breeding season of common guillemots at Stora Karlsö. Preening behaviour is represented in the percentage (%) of seconds spent on allopreening during a 15 min interval. The black dashed line represents the mean date (19/6) of chick hatching based on data from the individuals on the two studied breeding ledges. The colour of each data point represents the air temperature (°C) on that given date recorded by the weather station from the start of the interval.
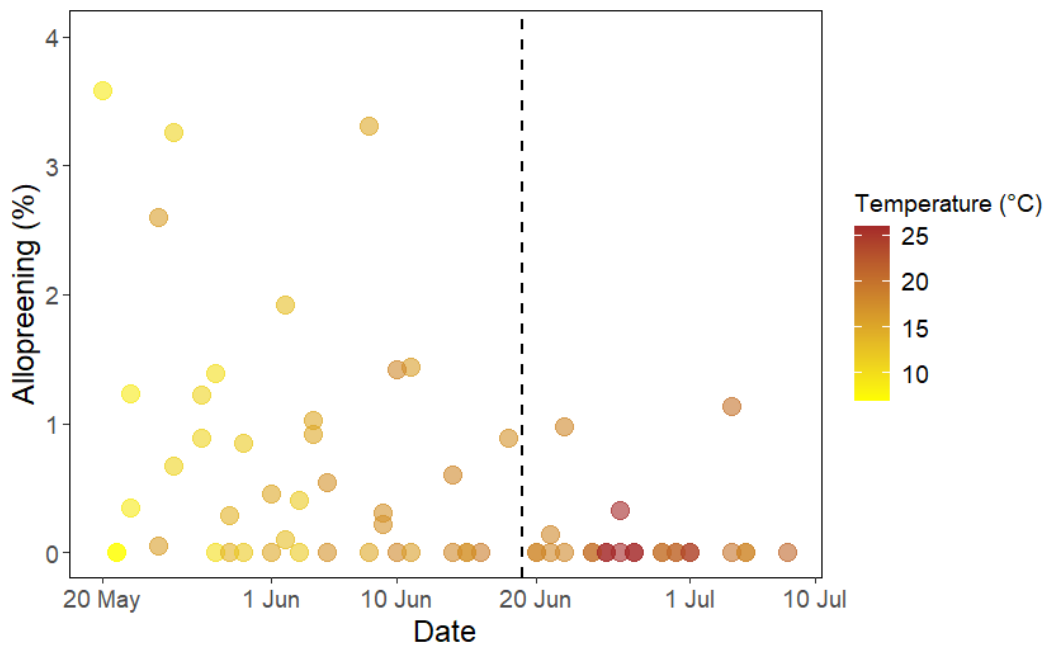
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4. Discussion

This study demonstrates that increasing temperature may have a direct negative effect on the self-preening and, possible allopreening, behaviour in common guillemots. Sun exposed birds spent less amount of time on self-preening behaviour as temperatures increased (fig. 3c). This decline in self-preening behaviour starts at ~15 °C, reaching a plateau at ~23 °C when little to no amount of time is spent on self-preening (fig. 3c). However, as stated earlier, 15 °C is the lowest recorded temperature in sun exposed conditions. Self-preening behaviour could therefore decrease at even lower temperatures that are not recorded in this study. In similarity, birds spent less time on allopreening as temperatures increased in mixed sun exposed conditions (fig. 4b). There was however no significant support for a relationship between increasing temperatures and allopreening in sun exposed conditions. This is in contrasts with the results on self-preening that found no significant support for a relationship between increasing temperatures and a decrease self-preening in mixed sun exposed conditions (fig. 3b) but could demonstrate a significant relationship between the two variables in sun exposed conditions (fig. 3c). Why the results from the two preening behaviours differ is not fully deduced, however this study could demonstrate that the amount of time spent on allopreening differ significantly before and after hatching, where birds spent less time on allopreening after the chick was hatched (fig. 6). Because of this correlation between allopreening and the breeding season, how and to what extent the results are affected by temperature versus the different breeding stages remains unclear (see 4.1). The amount of time birds spent on self-preening appear however to be constant throughout the breeding season (fig. 5) which argues that the effect of temperature on self-preening is not a by-product of the breeding season.

As previous studies have demonstrated (Cunningham et al. 2021; Olin et al. 2023; Oswald & Arnold 2012; Oswald et al. 2008), thermoregulatory behaviour to mitigate heat stress may lead to less time and energy to spend on other important behaviour such as preening. Olin and colleagues (2023) have demonstrated that the probability for common guillemots to express thermoregulatory behaviours increase at air temperatures of 10–15 °C in sun exposed environments. The probability for thermoregulatory behaviours to be expressed was near 1 at ~25 °C (Olin et al. 2023), illustrating a possible T_{uc} in sun exposed conditions. Studies on the closely related Brünnich guillemot have in similarity observed an increasing

resting metabolic rate at ambient temperature of 16.4 °C (Choy et al. 2021). This study observed that common guillemots spent almost no time on self-preening and allopreening at ~23 °C, in similarity to the ~25 °C temperature limit previous mentioned (Olin et al. 2023), illustrating a possible trade-off between regulation of internal body temperature and preening behaviour in common guillemots. As previously stated, preening is an energy-intensive activity. Croll and McLaren (1993) measured an increase of 107% above the resting metabolic in common guillemot during preening. This increase in metabolic rate due to preening is thought to help the guillemot maintain internal body temperatures in cold conditions (Croll & McLaren 1993). However, as temperatures near their T_{uc}, preening might be an activity birds avoid not to generate additional heat. This study did in contrast find that birds in shaded conditions spent less time on self-preening at the lowest temperatures, only increasing in the amount of time spent on self-preening as temperatures increased (fig. 3a). While preening produces heat, the activity is, as stated earlier, also very energy intensive (Croll & McLaren 1993) a lack thereof could be a mean of preserving energy in an already energy demanding environment. Even within their TNZ, guillemots conserve heat, a physiological mechanism that proves less favourable in increasing ambient temperatures as guillemots produce heat at a faster rate than they can dissipate it (Choy et al. 2021). Meaning that they have to be metabolically cost-effective regarding which behaviour they express. Additionally, as time and energy are spent on panting, spreading their wings, and seeking shade or water in order to cool off, less time and energy can be allocated on preening. This effect is exacerbated by less birds being present at the breeding ledge during higher temperatures (Olin et al 2023), resulting in less neighbours and partners to allopreen.

This absence of preening behaviour could ultimately affect the social dynamics and health of the colony. Preening help in maintaining the plumage in good condition and free from ectoparasites (Hart 1997, 1992). Birds with impaired preening ability have been demonstrated to be subjected to an increase of ectoparasite that reduce fitness (Clayton 1990; Booth et al. 1993). Individuals that allocating less time to preening may therefore experience a higher ectoparasite load. Increasing temperature due to global warming can accelerate biochemical processes of many parasites, stimulate parasite development, and shorten generation time (Harvell et al. 2002, Kutz et al. 2009). In addition, heat stress can increase host susceptibility to parasites by weakening the host immune defences (Martínez-de la Puente et al. 2011). This could be detrimental for the bird's health as increasing temperatures could benefit ectoparasites and simultaneously decrease the amount of time the bird spends on preening, subsequently increasing their ectoparasite load. Consequently, a removal of a substantial amount of feathers mass due to ectoparasites can require the host to raise its metabolic rate to compensate for the loss of insulation (Booth et al. 1993). In the long-term, ineffective management of

ectoparasites could well mean the difference between breeding success and failure as parasites impose a physiological cost (de Lope & Møller 1993; Gaston et al. 2013; Martínez-de la Puente et al. 2011). In addition, allopreening seem to decrease at lower temperatures than self-preening (fig. 4) which could have more impact on the birds ectoparasite load as studies have suggested that allopreening is more important than self-preening in the means of ectoparasite control (Villa et al. 2016). Allopreening appears to help control ectoparasites on the head and neck which is regions that cannot be reached while self-preening (Barton et al. 1996). As the transmission and abundance of parasites often increase with group size (Brown & Brown 1986), allopreening may be a mutually beneficial behaviour for birds living in larger groups such as the common guillemot. Radford and Du Plessis (2006) demonstrated this importance when documenting a positive relationship between group size and allopreening.

In addition to its function as ectoparasites control, allopreening may also enable birds to live in larger social groups by forming bonds and establish hierarchies among group members (Lewis et al. 2007). Guillemots are long-lived and exhibit a high level of fidelity both to its mate and breeding site (Kokko et al. 2004). A study on allopreening in common guillemots found no evidence that increased allopreening between pairs led to increased fitness, however allopreening between neighbours was linked to increased fitness in the current breeding attempt (Lewis et al. 2007). Egg or chick loss due to fights is one of the most common causes of breeding failure in common guillemots (Olin et al. 2023). A possible explanation to this biased allopreening behaviour towards neighbours may be the objective to minimize egg or chick losses. This hypothesis is supported by the negative correlation between fight rates and allopreening rates, where aggression between neighbours was lower in pairs which were successful in their breeding attempt (Lewis et al. 2007). Studies have also demonstrated that higher levels of the stress hormone corticosterone, which can be induced by heat stress (Quinteiro-Filho et al. 2010), delay social interactions such as allopreening between pairs. This delay of allopreening can in turn further increase corticosterone levels, creating a cycle of increased stress levels and delayed social interactions (Takahashi, 2013). The breeding success could therefore be negatively affected as temperatures increase and allopreening between neighbours decrease, a possibility that could further exacerbate the risk of breeding failure in common guillemots due to heat stress (Olin et al. 2023).

4.1 Study Limitations

Due to time constraints, the mean of the two preening behaviours was noted for each time interval and breeding ledge. This results in the omission of individual variation in regard to both preening behaviours and the level of sun exposure. The level of sun exposure was based on the exposure of 2/3 of the group. Some of the time intervals during different periods of the breeding season exhibited greater variation in individual sun exposure. To assign a combined label for sun exposure could therefore be misleading to the different conditions the individuals was exposed to. Additionally, limitations of time intervals in the extreme temperature ranges may result in an inadequate representation of data distribution in the population, making one-time or limited occurrences seem more common than they are.

As previously stated, temperature and the progression of the breeding season are strongly correlated ($p = 0.001$, appx. 1) and could thus not be incorporated into the same model as the other variables as it would make the results difficult to interpret. A possible solution to mitigate this problem can be to analyse the temperature and preening behaviour in regards to the individual birds egg laying-, chick hatching- and fledging date. Analysing temperature in relation to the individual breeding progression could demonstrate any possible correlation between the two variables as the dates of the different breeding stages varies between individuals. Additionally, shaded breeding ledges with little to no sun exposure throughout the breeding season could be used as a control group to examine the relation between breeding stages and preening behaviour.

4.2 Concluding Remarks

Due the nature of their nesting site, high latitudes seabirds are subjected to extensive weather and temperature changes, making them more susceptible to changing climate (Choy et al. 2021; Gaston et al. 2002; Olin et al. 2023). Although the population of common guillemots are on a steady rise in the Baltic Sea (Olsson & Hentati-Sundberg 2017), increasing temperatures may create new physiological challenges in the near future. As previous research has demonstrated, thermoregulatory behaviour to maintain thermal homeostasis may require trade-offs with other activities (Cunningham et al. 2021; Oswald & Arnold 2012; Oswald et al. 2011). In this study, a decrease in self-preening behaviour, and possible allopreening, is demonstrated as temperatures and sun exposure increase. This re-allocation of time and energy away from preening behaviour could ultimately affect the social dynamics and health of the colony as birds spend more time and energy regulating their internal body temperature instead of interacting with group members, care for their offspring (Olin et al. 2023) and controlling ectoparasite load

(Gaston et al. 2002). As the consequences of global warming becomes more prominent, examining the direct effects of extreme temperatures may broaden our understanding of an organism's physiological limits and how these limits may impact their behaviour, breeding success and, ultimately, their longevity as a population.

Future studies on the relationship between temperature and preening behaviour should examine the behaviour on an individual level to capture the range of responses to thermal extremes. In addition, individual sun exposure should be considered when recording and analysing data as both this study and previous studies (Olin et al. 2023) have demonstrated that sun exposure effect the timing and extent of behaviours. The individual egg laying- and chick hatching date should be considered in order to separate the effects of temperature and the different stages of the breeding season. As sun exposure proved to have a great impact on birds' behavioural response to temperature, measuring the individual birds body temperature may provide further insight on how sun exposure creates different thermal microclimates on the breeding ledges and if these different conditions will influence where the common guillemot choose to nest in the future.

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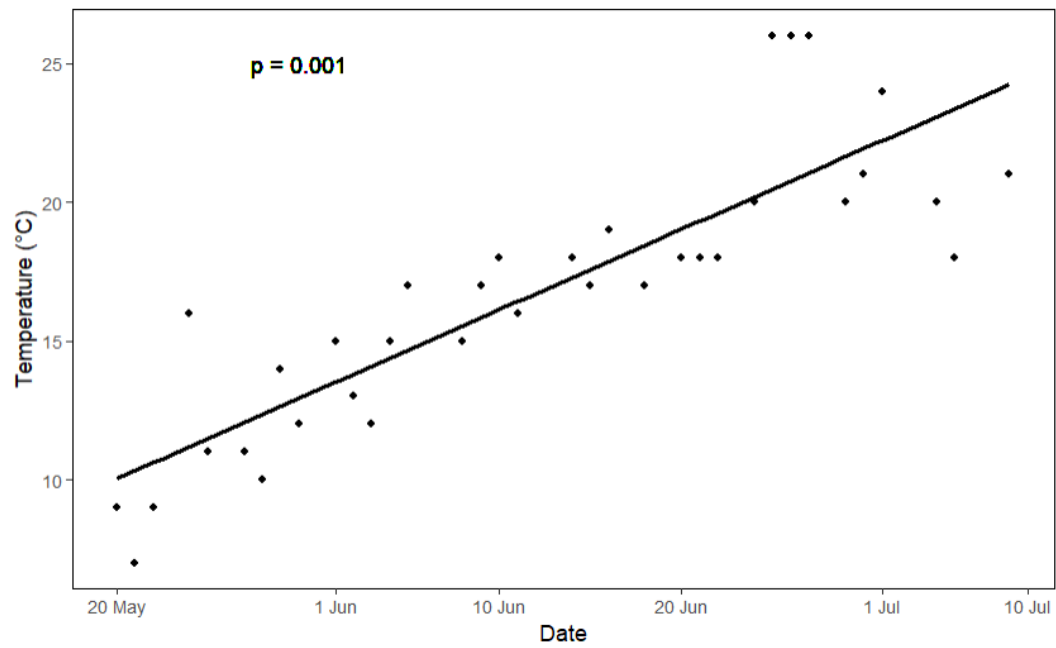
Acknowledgement

Appendix 1

Figure A1. Relationship between air temperature and date during the breeding season. Temperatures are based on measurements from the local weather station. A Mann-Kendall test was used to obtain the relationship between temperature and date.

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