Vol. 737: 147–160, 2024
https://doi.org/10.3354/meps14244

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 6[§]

Contribution to the Theme Section 'How do marine heatwaves impact seabirds?'

Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird

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ABSTRACT: Climate change research on seabirds has so far focused mainly on indirect effects acting via impacts at lower trophic levels. However, seabirds that breed in exposed sites may also be vulnerable to direct impacts from extreme weather events such as heatwaves, which are projected to increase in both severity and frequency with climate change. Yet there are relatively few field studies of how breeding seabirds respond to heatwaves. Here, we used video footage from a breeding colony of common guillemots *Uria aalge* in the Baltic Sea over 4 consecutive breeding seasons (2019–2022) to explore responses to air temperature and sun exposure. We found a positive relationship between temperature and 2 thermoregulatory behaviours: panting and postural changes. In addition, we show that as temperatures increase, breeding partners spend less time together at the colony. At the highest temperatures, some birds even temporarily abandon their eggs and chicks. Of 48 breeding failures recorded on video over 4 breeding seasons, we documented 13 cases directly associated with heat stress (corresponding to ca. 9% of all 150 breeding attempts recorded); 11 of these occurred during 2 periods with sunshine and particularly high temperatures in 2020 and 2022. Using a larger data set (>500 breeding attempts over 12 seasons), we also identified a clear increase in the probability of egg loss at higher temperatures. As such, the responses of breeding seabirds to heatwaves could have important demographic consequences in some populations, especially as heatwaves continue to increase in frequency and magnitude.

KEY WORDS: Heatwaves · Seabirds · Heat stress · Thermoregulation · Climate change

1. INTRODUCTION

Pervasive effects of global warming have been documented in marine organisms across the globe (e.g. Poloczanska et al. 2013, Sydeman et al. 2015). These effects can be divided into direct effects of increasing temperatures on physiology and behaviour, and indirect effects acting via interactions with other species affected by increasing temperatures (Ockendon et al. 2014). The relative importance of these pathways varies between taxa, with taxa that are ectothermic and/or at a low trophic level generally thought to be more sensitive to direct effects, while taxa that are endothermic and/or at a high trophic level are thought to be more sensitive to indirect effects (Ockendon et al. 2014, Sydeman et al. 2015).

However, endotherms are also likely to suffer from direct impacts as heatwaves become more frequent and severe (see Oliver et al. 2018, Perkins-Kirk-

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[§]Advance View was available February 16, 2023

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patrick & Lewis 2020, IPCC 2021). Here, we define heatwaves loosely as 'prolonged periods of excessive heat' (Perkins-Kirkpatrick & Lewis 2020) that can occur both in the ocean (marine heatwaves; see Hobday et al. 2016) and on land. At these extreme temperatures, endotherms may pass thermal limits over which they are not able to regulate their internal temperature, which can result in physiological damage (e.g. Alhenaky et al. 2017) or even death from overheating or dehydration (e.g. Welbergen et al. 2008, McKechnie & Wolf 2010). Even below these limits, thermoregulatory behaviours may be energetically costly (McNab 2002) and can take time away from other activities (Andreasson et al. 2020, Cunningham et al. 2021). As such, there may be a trade-off between maintaining the right temperature and, for example, foraging or caring for offspring (Andreasson et al. 2020, Cunningham et al. 2021), with possible knock-on effects on survival and reproduction (see e.g. Moses et al. 2012). However, we still know relatively little about sublethal impacts of extreme temperatures on endotherms and the possible pathways through which these effects could eventually impact demographic rates (Elmore et al. 2017, Cunningham et al. 2021).

As endotherms high up in the trophic web, seabirds are often assumed to be affected by climate change mainly via indirect effects, primarily in the form of changes in the prey base driven by increasing water temperatures (Oswald & Arnold 2012, Sydeman et al. 2015). These effects are relatively well studied and can be large. For example, the 2014–2016 Pacific marine heatwave resulted in widespread breeding failures and mortalities as a result of reduced prey availability and quality (e.g. Piatt et al. 2020, Schoen et al. 2024, this Theme Section). However, while most seabird species spend the majority of their time at sea, they all breed on land — often in exposed sites where they may also be subject to the direct effects of increasingly high air temperatures (see e.g. Holt & Boersma 2022, Quintana et al. 2022). In response to these high temperatures, seabirds have been documented to display several behavioural strategies, including adjusting their posture to increase convective heat loss (e.g. Hand et al. 1981, Gaston et al. 2002), panting or gular fluttering to increase evaporative heat loss (e.g. Lustick et al. 1978, Hand et al. 1981, Gaston et al. 2002, Cook et al. 2020), changing direction in relation to the sun (e.g. Lustick et al. 1978, AlRashidi 2016) and bathing (e.g. Hand et al. 1981, Oswald et al. 2008). These behaviours all have associated costs. For example, one study found that as temperatures increase, great skuas *Catharacta skua* spend more time cooling off by bathing, leading to lower nest attendance and a higher risk of nest predation (Oswald et al. 2008).

High-latitude seabird species may be particularly vulnerable to the direct effects of global warming, as they are adapted to conserve rather than lose heat and therefore show limited heat tolerance (Choy et al. 2021, O'Connor et al. 2021). One such high-latitude species is the common guillemot *Uria aalge*. The common guillemot is widely distributed in the Northern Hemisphere, showing a circumpolar distribution with latitudinal extremes in Portugal (39° N) and Svalbard (79° N) (Ainley et al. 2021). It is adapted to deep dives in cold waters with its high levels of metabolic heat production (Croll & McLaren 1993) and dense, dark back plumage, which warms rapidly in the sun (see Gaston et al. 2002). As such, common guillemots are likely to be sensitive to heat stress, especially since they tend to breed on highly exposed cliffs. This is also supported by studies of the closely related Brünnich's guillemot *U. lomvia*, which suggest that they show limited tolerance to high air temperatures (Choy et al. 2021).

However, to the best of our knowledge, no studies have yet explored behavioural responses to high nest-site temperatures in common guillemots or the consequences of these responses. In general, studies on the direct effects of increasing air temperatures on seabirds are scarce (Oswald & Arnold 2012, but see recent studies Cook et al. 2020, Choy et al. 2021, Holt & Boersma 2022, Quintana et al. 2022). An improved understanding of the direct effects of extreme temperatures on seabirds is crucial for predicting the impact of the increasing frequency and severity of heatwaves.

In this study, we explored the impact of air temperature and sun exposure on (1) the frequency of thermoregulatory behaviour and (2) nest attendance by common guillemots on Stora Karlsö, the largest guillemot colony in the Baltic Sea. We expected the frequency of thermoregulatory behaviour to increase with temperature and sun exposure, and nest attendance to decrease as the birds spend more time away from exposed nesting sites to drink and cool off in the water (see e.g. Oswald et al. 2008). In addition, we (3) explored whether breeding failures in long-term breeding data are associated with higher temperatures and used extensive video footage to explore when and how higher temperatures may eventually result in breeding failures. During the course of the study, air temperatures in the region showed some of the highest values recorded since measurements started (SMHI 2020a, 2022a). The study thus allows us to explore not only how the incidence of thermoregulatory behaviours by common guillemots changes with increasing temperatures but also how maintaining tolerable internal temperatures when outside their thermoneutral zone may come with costs in the form of reduced nest attendance and, possibly, breeding failure.

2. MATERIALS AND METHODS

2.1. Study site

Stora Karlsö (57° 17′ N, 17° 58′ E) hosts the largest colony of common guillemots in the Baltic Sea, with approximately 25 000 pairs in 2021 (O. Olsson & J. Hentati-Sundberg unpubl. data). The breeding season at Stora Karlsö begins in mid-May. The breeding pair lays one egg directly on a ledge of the island's limestone cliffs, and the parents take turns with incubation. The chick hatches after about 32 d (Hedgren & Linnman 1979), after which at least one parent is generally present at all times to brood and guard the chick (Ainley et al. 2021). The chicks stay at the nesting site for about 3 wk, after which they jump off the breeding cliff (before being able to fly) and swim out to join their fathers waiting for them in the water (Hedgren & Linnman 1979).

Stora Karlsö has an artificial construction known as the Auk Lab, built to be used as a supplementary breeding site for guillemots, which started breeding there in 2009 (Fig. 1a; see Hentati-Sundberg et al. 2012). Breeding numbers have increased each year, and in 2022, 82 guillemot pairs bred in the Auk Lab. The Auk Lab is a steel construction with walls of oak boards, an inside area for researchers and equipment and 9 levels of breeding ledges on the outside. The ledges are built to mimic natural ledges and are therefore covered with limestone. Ledge surface temperatures as well as breeding phenology and success are similar to surrounding natural ledges (see Tables S1–S3 in Supplement 1 at www.int-res.com/articles/suppl/m737p147_supp/).

In 2019, video cameras (2 megapixel resolution IP-cameras; Avtech AVM543P) were installed on some of the ledges of the Auk Lab (Fig. 1a), recording continuously throughout the breeding season (see Fig. 1b). These cameras were replaced by a larger camera system in 2022 (4 megapixel resolution IP-cameras; Provision ISR, models DAI-340IPE-MVF and DI-340IPS-28), covering all ledges with breeding guillemots (i.e. all named ledges in Fig. 1a). The footage from the cameras was used for studies of behaviour and attendance, described below.

To measure the thermal environment that the guillemots experience, we used a datalogger (COMET U0541) with 2 TG8 PT1000 temperature probes: one on the wall of a sun-exposed ledge and the other on the wall of a shaded ledge (see Fig. 1a). The logger measured the temperature every 2 min for the entire breeding season. As local air temperature data were only available from 2020 onwards, we used data from the nearby weather station Hoburg A (56° 55′ N, 18° 9′ E, ca. 40 km from Stora Karlsö; SMHI 2022b) for one of the analyses that included data collected before the installation of the local temperature log-

Fig. 1. (a) The Karlsö Auk Lab, an artificial breeding site for common guillemots on Stora Karlsö, Sweden. Ledges are named according to level (1–6) and side (A, B, C, D). Locations of the temperature probes are marked by crosses: blue: shaded probe; orange: sun-exposed probe. (b) Screenshot of video footage of a sun-exposed ledge used in the study. The temperature probe is visible in the lower right corner of the image (indicated by arrow)

ger (see Section 2.4). Temperatures recorded at Hoburg A and Stora Karlsö are strongly correlated, although temperatures recorded with the sun-exposed probe are highly sensitive to sun exposure (see Fig. S1). For this reason, we only used the birds' responses to temperatures measured using the shaded probe in the analyses.

2.2. Temperature and thermoregulatory behaviour

Based on exploratory analysis of video recordings of breeding and non-breeding guillemots (Karlsson 2020), 3 distinct temperature-related behaviours previously described in seabirds were identified and analysed: panting (e.g. Lustick et al. 1978, Gaston et al. 2002), wing spreading (e.g. Gaston et al. 2002) and changing orientation towards the sun (e.g. Lustick et al. 1978, AlRashidi 2016) (see Video S1 in the Supplement at www.int-res.com/articles/suppl/m737p147_supp/ for an example).

The occurrence of each behaviour was analysed across intervals of 30 s during the hottest part of the day (15:00–21:00 h) over 2 yr (2020 and 2021), using data from 3 ledges with consistent camera coverage (C3, A3, D3; see Fig. 1a). In order to sample a wide range of temperatures, we used stratified random sampling, where time intervals were selected from each of 5 temperature ranges (0–9.9, 10–19.9, 20–29.9, 30–39.9 and 40–50°C) based on measurements from the local, sun-exposed probe. The sun-exposed probe was used for selecting intervals to capture a range of sun exposure; however, the shaded probe was used in the actual analysis (see below). Up to ten 30 s intervals were sampled within each temperature range from each ledge–year combination. To avoid pseudoreplication, we sampled data randomly from different days. This meant that for some temperature ranges, we did not achieve our target of 10 samples, as the temperatures in the more extreme ranges were observed on fewer than 10 d during the breeding season. In total, our sampling scheme resulted in 222 analysed time intervals. For each individual in each interval, we noted whether they exhibited the behaviour or not and whether they were in the shade, in the sun, or a bit of both. In each interval, 1–12 birds were present on the ledge, including breeders and non-breeders (mean = 5.8 ind.). All observations were carried out by a single observer.

The effect of temperature on the probability of exhibiting a given behaviour in a given interval was analysed using generalised linear mixed models, assuming a binomial response distribution and using a logit link function. Temperature measurements were taken from the local, shaded probe at the start of the interval. The time interval was included as a random effect, accounting for the fact that the observations of multiple individuals in the same interval are not independent. As continuous 24 h observations would have been necessary to link individuals across intervals and would still fail to link non-breeders across intervals, 'individual' could unfortunately not be included as a random effect. However, individual variability was quite small; individuals in the same interval and at the same level of sun exposure all either displayed or did not display thermoregulatory behaviours in 74% of cases. Therefore, while omitting 'individual' as a random effect may affect the estimated confidence intervals, it is unlikely to be the driver of the observed patterns.

Models including a temperature effect and/or an effect of individual sun exposure (shaded/partially sun-exposed/fully sun-exposed) and a possible interaction between the 2 were compared to a null model using Akaike's information criterion for small sample sizes (AIC_C) (Hurvich & Tsai 1989). The behaviour 'orientation towards the sun' was only analysed for birds that were partially or fully sun-exposed. The models were fitted in R v.4.1.0 (R Core Team 2021), which was also used for all subsequent analyses and visualisations (see https://github.com/agnesolin/codeHEATpap for all data and code), using the function 'glmer' in the package 'lme4' (Bates et al. 2015). The R package 'DHARMa' (Hartig 2021) was used to assess model fit (see Fig. S2).

2.3. Temperature and nest-site attendance

To examine the relationship between nest attendance and temperature, we used observations of arrivals and departures of breeding pairs from 3 ledges in the Auk Lab (C3, D3, A3; see Fig. 1a) over 2 years (N_{2020} = 15 breeding pairs, N_{2021} = 16 breeding pairs). The observations were carried out by a single observer from 15:00–21:00 h on a subsample of days for each ledge and year (N_{2020} = 60 ledge-days, N_{2021} = 44 ledge-days). In total, 624 h of footage were analysed. The arrivals and departures were subsequently translated into presence data for each pair (0 = both absent, 1 = one partner present, 2 = both partners present) for every other minute to match up with the resolution of the temperature data. Temperature data were obtained from the local, shaded probe.

Presence at the nest site was modelled as a function of temperature, time of day and number of days since the pair laid their egg. There were no relays in the data set. We used generalised additive models with the family set to ordered categorical, and 0, 1 or 2 partners present as the response variable. Pair ID, which is unique across years and ledges, was included as a random effect. The models were fitted using the R package 'mgcv' (Wood 2017). Optimal smoothing parameters were selected using restricted maximum likelihood. We did not expect the effect of temperature and time of day to take on forms more complex than a quadratic relationship, and therefore we restricted the number of knots to 3, while we allowed more flexible shapes for the effect of number of days since egg-laying.

As samples taken from the same pair 2 min apart cannot be considered independent, we fitted the models using randomly sampled data of a single 2 min interval per hour and pair, repeating the process 100 times. For each fit, we compared models including a temperature effect and models not including a temperature effect using AIC_C (Hurvich & Tsai 1989). Time of day and days since egg-laying were always included in the model. The appropriateness of the model structure was evaluated using the function 'qq.gam' in 'mcgv' (see Fig. S3). There did not appear to be a problem with variable concurvity, with the average 'worst' estimate (see function 'concurvity' in 'mgcv') being below 0.75 for all variables.

2.4. Heat-induced breeding failures

To determine whether breeding failures were more likely to occur on hotter days, we applied a Cox proportional hazards regression model to long-term breeding data from the Auk Lab. We used data from 524 breeding attempts from 2011–2022, including 170 failed attempts. The data, which are based on daily field visits, included laying, hatching and fledging dates and the date on which failure was recorded if the breeding attempt failed. We translated this into daily survival (0 for every day the attempt 'survived'; 1 on the day it was recorded as failed), resulting in a total of 22 529 pair-observation days. To represent weather conditions, we used temperature (maximum between 15:00 and 21:00 h) and cloud cover (minimum between 15:00 and 21:00 h, translated into almost clear to cloudy [cloud cover > 25%] and mostly clear [cloud cover ≤ 25%], based on limits from SMHI 2020b) measured at the weather station Hoburg A. As recorded heat-related failures tend to occur later in the day (see Table S4), we used weather data from the day before, thus assuming that the field visit—which can occur at any time of the day—missed the failure on the day that it occurred. However, in 2022, we knew the exact day of the failure due to complete camera coverage so we used data from the same day that the failure was recorded. We also included which side of the Auk Lab the pair was nesting on, as this has a large effect on sun exposure. Finally, we included year as a factor to account for the potential influence of other variables (e.g. eagle disturbance; Hentati-Sundberg et al. 2021). Observations were clustered by pair ID to achieve robust variance estimates. The models were fitted using the R package 'survival' (Therneau 2021), fitting separate models for incubation and chick-rearing. Covariates were tested for proportional hazards using the function 'cox.zph', and if hazards were non-proportional, the relevant covariates were re-fitted with time-varying coefficients. Candidate models were compared using AIC_C (Hurvich & Tsai 1989).

To explore in more detail when and how high nest-site temperatures may eventually result in breeding failure, we examined all failed attempts that were recorded with our cameras. We excluded attempts that failed due to human disturbance (N = 4). In total, we examined 150 breeding attempts ($N_{2019} = 15$, $N_{2020} = 24$, $N_{2021} = 24$, $N_{2022} = 87$), with 48 of these attempts resulting in breeding failures ($N_{2019} = 3$, $N_{2020} = 9$, $N_{2021} = 7$, $N_{2022} = 29$). We assessed whether any of these failures appeared to be the result of thermal stress, and if so, through what mechanism, by recording the sequence of events that led to the egg or chick loss and combining this data with parallel observations of thermoregulatory behaviour and temperature.

3. RESULTS

3.1. Temperature and thermoregulatory behaviour

The probability that the birds were panting or spreading their wings increased with temperature and degree of sun exposure (Fig. 2, Table 1). These behaviours tended to co-occur (r = 0.79, p < 0.001), but the probability of wing spreading started increasing at lower temperatures, and wing spreading was also more likely to occur in shaded individuals (Fig. 2). While ca. 13% of sun-exposed or partially sun-exposed birds sat facing the sun, there was no effect of temperature or sun exposure on this behaviour (Table 1). The co-occurrence of facing the sun and panting/wing spreading was relatively low (r = 0.26 and r = 0.32, respectively, p < 0.001).

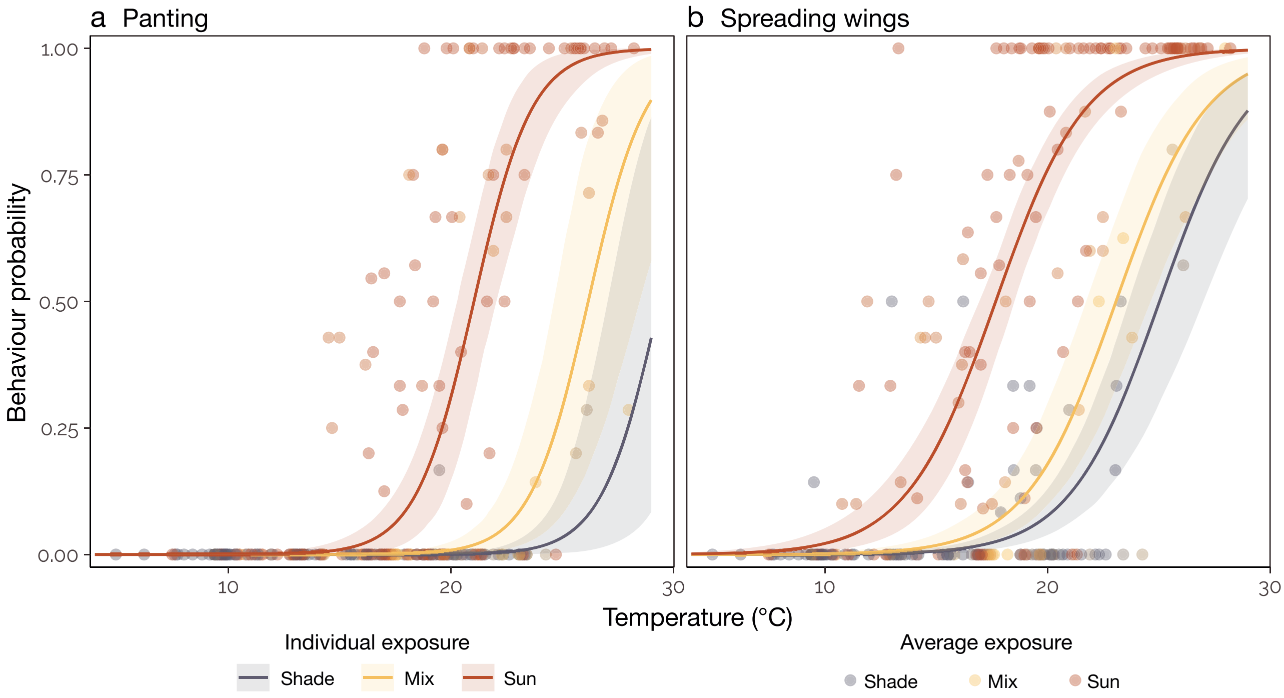

Fig. 2. Effect of nest-site temperature on the probability that the common guillemots at Stora Karlsö display the thermoregulatory behaviours (a) panting and (b) spreading wings. Lines and shaded areas: predictions from generalised linear mixed models with associated 95% bootstrap prediction intervals; points: proportion of birds that displayed each behaviour for each 30 s interval. Colours indicate degree of sun exposure. Temperatures are based on measurements from the local, shaded temperature probe

Table 1. Values of Akaike's information criterion adjusted for small sample sizes (ΔAIC_C) for alternative models of the 3 studied thermoregulatory behaviours (panting, spreading wings and orientation towards the sun) in common guillemots, in reference to the lowest AIC_C-value in the model set. We considered the simplest models within a ΔAIC_C of 4 to be the best model (see Burnham & Anderson 2002; highlighted in **bold**). R^2 of fixed effects are also included

Model terms	ΔAIC_C R^2 Panting	 Spreading wings	 Orientation
NULL	161.9 <0.01	238.9 <0.01	**1.0** **<0.01**
Temperature	103.6 0.27	102.4 0.30	1.2 <0.01
Sun exposure	89.4 0.20	120.5 0.26	1.8 <0.01
Temperature + sun exposure	**0** **0.48**	**0** **0.48**	1.8 <0.01
Temperature + sun exposure + temperature × sun exposure	2.7 0.48	3.1 0.48	0 0.01

3.2. Temperature and nest-site attendance

Temperature had a clear effect on attendance patterns; the occasions where both partners were completely absent — leaving the egg or chick unattended — only occurred above temperatures of 24.7°C (Fig. 3a). Models including an effect of temperature had an average (±SD) ΔAIC_C of −14.7 ± 5.3 compared to models not including a temperature effect (averaged across the models with randomly sampled data, ΔAIC_C below −4 suggests strong support; Burnham & Anderson 2002). While the fitted models only indicated a minor impact of temperature on the probability of both partners leaving the ledge, likely at least partly due to the combination of its rare occurrence and the subsampling, they clearly supported a decreasing probability that both partners were present at the same time (Fig. 3b). At 12°C, the predicted probability of both partners being present was ca. 0.17, while at the maximum measured temperatures (28.5°C), this probability declined to ca. 0.05 (based on predictions for 18:00 h around the time of hatching).

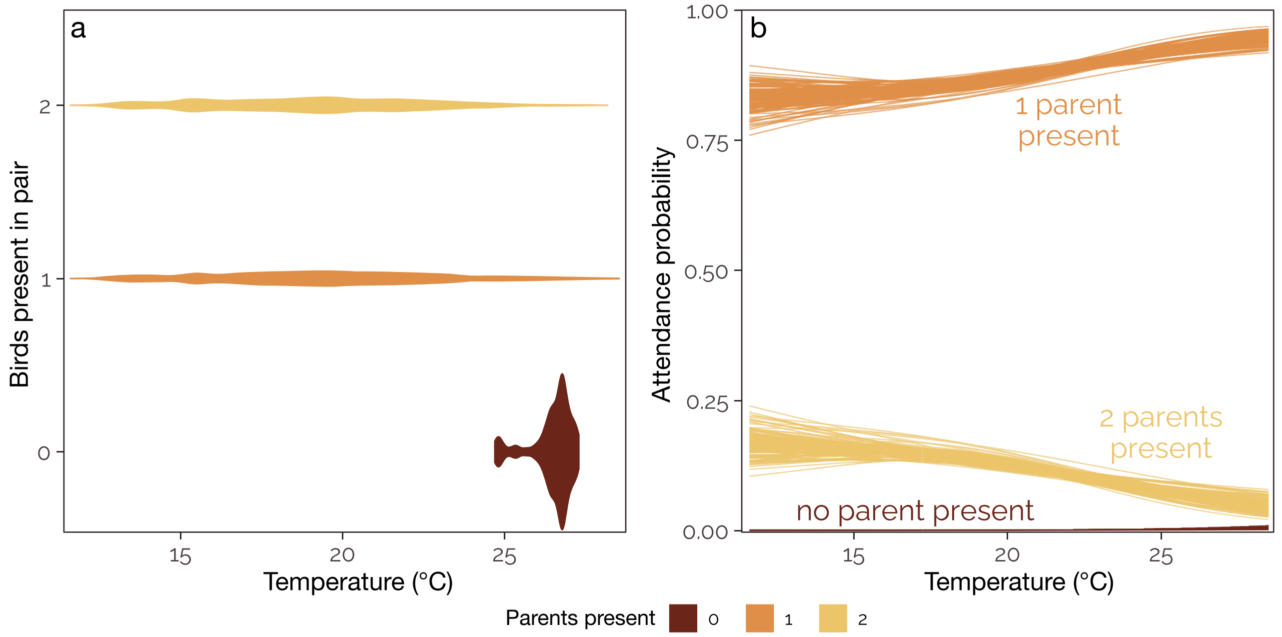

Fig. 3. Observed nest-site attendance patterns for the studied common guillemot pairs at Stora Karlsö based on 624 h of observations. (a) Density plot of observations of birds in a pair present at the nest site across temperatures. (b) Predicted probabilities of attendance based on the fitted generalised additive model. Lines represent model predictions from models re-fit 100 times with randomly sampled data (one sample per hour and pair). The models also include effects of time of day (set to 18:00 h) and days since egg-laying (set to 32, roughly at hatching). Temperatures are based on measurements from the local, shaded temperature probe

3.3. Heat-induced breeding failures

We saw strong support for an effect of temperature on the probability of egg loss in our time series of breeding attempts from 2011–2022 (Fig. 4, Table S5). The relationship between temperature and the risk of failure during incubation was nonlinear, with a sharp increase in failure risk above 20°C. There was no support for any other effects on the risk of failure during incubation, nor was there any support for relationships between the examined covariates and risk of failure during chick-rearing (Tables S5 & S6).

Of the 48 breeding failures recorded on video, 13 failures (ca. 27 %) were interpreted as being the result of high temperatures (Table 2; see Videos S1–S4 for a few example video clips). Other failures were due to, for example, eggs rolling off the ledge during fights or being crushed by incubating parents (see Table S4 for a full list of descriptions of breeding failures and Table 2 for a summary). Of the losses that were judged to be heat-related, several happened when both parents were absent, leaving the egg or chick unattended. These losses included 1 unattended egg that was preyed on by a gull and 2 eggs and 1 chick that were accidentally knocked off the ledge by other guillemots. In 4 cases, chicks appeared to die from

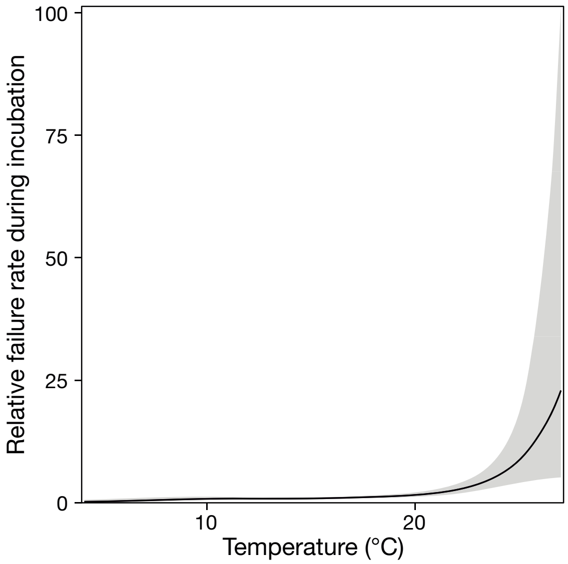

Fig. 4. Effect of air temperature on relative failure rate during incubation (relative to a reference failure rate of 1 at the mean temperature in the data set [16.4°C]). Black line shows predictions based on a Cox proportional hazards model fit to a data set of 524 common guillemot breeding attempts from 2011–2022 at Stora Karlsö. Shaded areas: 95 % CI. The model includes no other predictors (see Table S5 in the Supplement for model selection results, www.int-res.com/articles/suppl/m737p147_supp/). Temperatures are taken from the weather station Hoburg A

Table 2. Causes of nesting failures of common guillemots observed from video footage 2019–2022 (N = 48). A detailed list is provided in Table S4 in the Supplement www.int-res.com/articles/suppl/m737p147_supp/). The category 'other' includes one egg that was neglected, one chick that was dead at hatching and one accidental loss during an attack by a razorbill

Cause of failure	N	N heat-related
Egg/chick accidentally knocked down during fight	10	0
Egg/chick accidentally knocked down (not during fight)	16	8
Egg crushed by parent	4	0
Egg/chick predated when unguarded	7	1
Chick dies on ledge	5	4
Chick falls off ledge by itself	3	0
Other	3	0

heat stress after being left unprotected in the sun. In the remaining 5 cases, the incubating parent shifted its position to face the sun — which is a known thermoregulatory behaviour in other species, as described above — and moved closer to the edge, accidentally knocking its own egg off the ledge. All losses associated with heat were preceded by thermoregulatory behaviours such as panting.

The majority of the identified heat-associated losses (11 out of 13) occurred during 2 periods: (1) 2 d at the end of June 2020 when 1 chick and 3 eggs were lost, and (2) 2 d at the end of June 2022 when 3 eggs and 4 chicks were lost (see Table S4). On both occasions, air temperatures measured at Hoburg A were at a maximum for the season (peaking at 25.5 and 25.1°C in 2020 and 2022, respectively) and skies were clear (Fig. 5). Corresponding maximum temperatures measured with the sun-exposed probe were 48.3 and 45.6°C.

4. DISCUSSION

In this study, we found clear evidence that common guillemots are subject to direct negative effects of high nest-site temperatures. Over the last 12 yr, egg losses were more likely to occur during periods of warmer temperatures, and we made direct observations of 13 breeding failures that were judged to be directly heat-related, corresponding to ca. 27% of failures recorded on video and ca. 9% of the breeding attempts. We also observed clear behavioural responses of adult guillemots to higher temperatures, both in the form of thermoregulatory behaviours (panting, changing posture) and reduced nest attendance, which is likely to have consequences for energy and water budgets, social dynamics and, ultimately, breeding success.

The guillemots showed remarkably predictable thermoregulatory responses to increasing temperatures. The birds began to pant and spread their wings at around 20°C if partly or fully shaded (Fig. 2). This corresponds relatively well with the observation that Brünnich's guillemots start panting at an air temperature of 25.9°C in experimental, shaded conditions (Choy et al. 2021). The probability that the birds were panting or spreading their wings then increased as a function of temperature, with virtually all birds displaying these behaviours when temperatures approached 25°C if they were exposed to the sun. Degree of sun exposure had a very strong effect on thermoregulatory behaviours; being fully shaded allowed the birds an extra 10°C temperature increase before panting was required, and the probability of panting at even the highest temperatures remained low if the bird was completely shaded (Fig. 2). It appears that the birds start spreading their wings at lower temperatures, while beginning to pant only at slightly higher temperatures (compare Fig. 2a & b). This makes sense because, while an effective cooling mechanism, panting is costly in terms of both energy and water (e.g. McKechnie et al. 2016, Andreasson et al. 2020). In line with this finding, Choy et al. (2021) showed that the metabolic rate of Brünnich's guillemots increased clearly beyond an air temperature of ca. 30°C and that they lose around 1.5 ml of water h^{-1} at 25°C through evaporative heat loss. However, it should be noted that this rate of water loss is modest compared to their body mass, and Choy et al. (2021) thus argued that dehydration is unlikely to be a large issue for guillemots.

In contrast, we did not see a consistent tendency in the birds to shift their position to face the sun at higher temperatures. As the guillemots' dark back plumage warms rapidly in the sun (Gaston et al. 2002), exposing their bright white chest to the sun could help to limit absorbed radiation. This behaviour has been observed in, for example, herring gulls *Larus argentatus* (Lustick et al. 1978), indicating a large effect of solar radiation on heat gain in seabirds (see also Rogalla et al. 2022). However, the orientation of guillemots is less flexible than that of the ground-nesting herring gulls, as facing the cliff, away from the sun, will be a better strategy for keeping the egg or chick safe. Indeed, we observed several individuals accidentally kicking their own egg

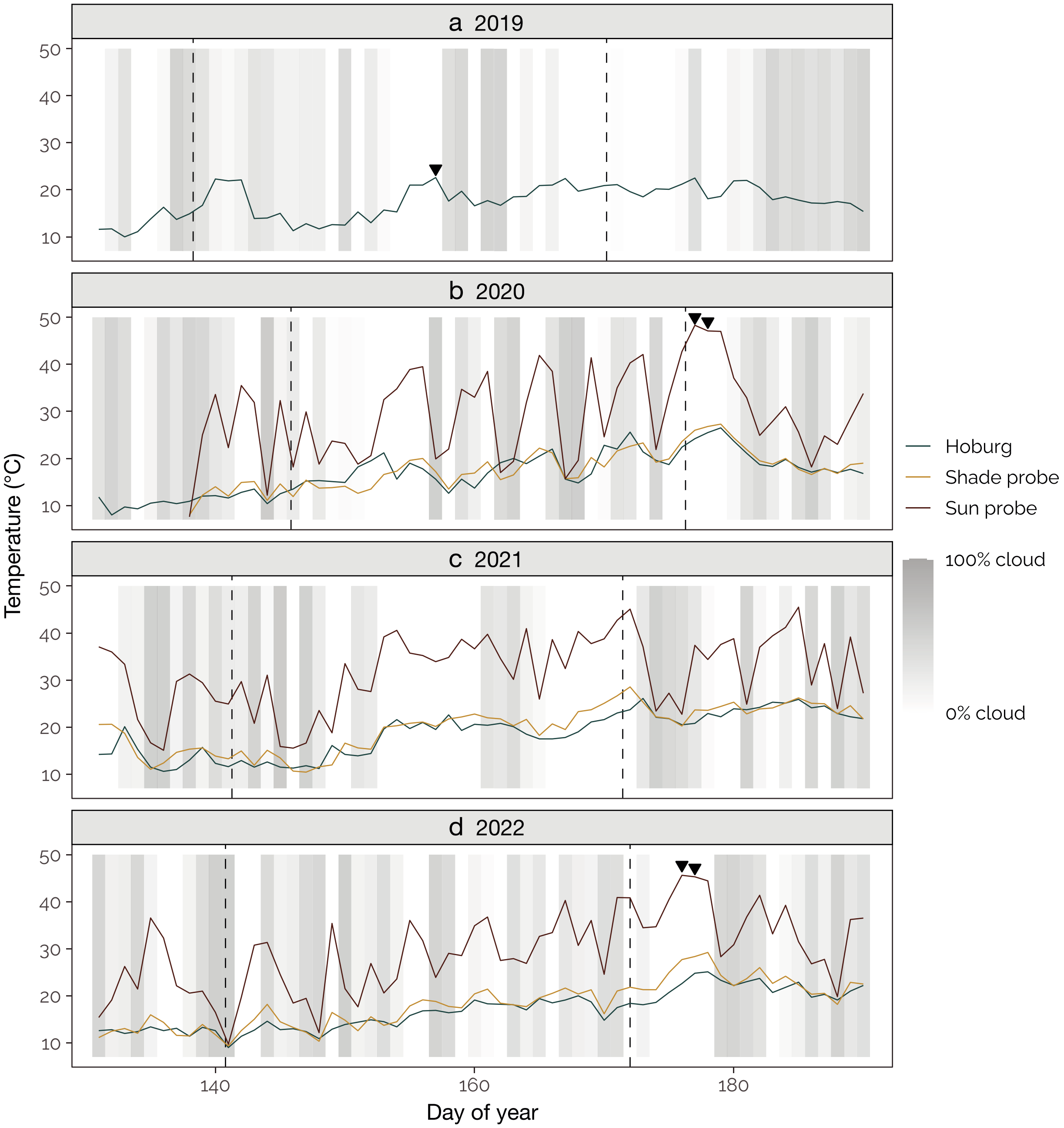

Fig. 5. Measured daily maximum temperatures using temperature probes on the common guillemot breeding ledges at Stora Karlsö (local probe data not available for 2019) and from the Hoburg A weather station for (a) 2019, (b) 2020, (c) 2021 and (d) 2022. Level of cloudiness as measured at the Hoburg A weather station is indicated by grey shading. Black triangles: days on which heat-associated breeding failures occurred; dashed black lines: average laying and hatching dates

off the ledge after shifting position to face the sun on a particularly hot day (see Table S4). The behaviour thus constitutes a trade-off in terms of risk, which likely at least partly explains why there was no effect of temperature on the probability of facing the sun. Further, the effect of plumage colouration on heat gain is complex and may depend on, for example, wind speed (see Rogalla et al. 2022 for a review), meaning that the optimal direction in relation to the sun may not be constant.

The impact of temperature on nest attendance behaviour also clearly illustrates the trade-offs associated with coping with thermal constraints. Here, we observed 2 effects. (1) A gradually decreasing probability of both parents being present on the ledge as temperatures increased. As one partner arrives back at the nesting site from a foraging trip, both partners usually spend some time together before the other (or, more rarely, the same) partner departs (Österblom & Olsson 2002). However, our observations suggest that at high temperatures, the partner that is not currently incubating or guarding the chick may instead leave very shortly after the arrival of their partner. This behaviour could impact future breeding success, as time present together may be important for strengthening the pair bond and maintaining the nest site. For example, more time at the nest allows for more time allopreening, which could act to both reduce parasite loads and strengthen social bonds (Lewis et al. 2007). This effect may be exacerbated by the fact that preening is an energetically costly behaviour that generates heat (Croll & McLaren 1993), which means that the birds may limit this behaviour at high temperatures (in line with the 'heat dissipation theory'; Grémillet et al. 2012, Nord & Nilsson 2019). Further, as the partner that is not incubating or guarding the chick is more likely to engage in aggressive interactions with other birds (Birkhead 1978), the reduced probability of the partner being present may affect the ability of the pair to defend their nest site. An absent partner also increases the risk that partners that are currently incubating or guarding their chick have to actively engage in fights, which increases the risk of egg/chick loss (see Tables 2 & S4).

(2) In addition to the gradual effect of temperature on the probability of both parents being present at the same time, we also observed that at peak temperatures (above 25°C), there were occasions where both parents were absent, leaving their egg or chick alone. While this behaviour was observed only on 2 days, it was seen in several pairs and was also observed on days not included in the analysis of attendance behaviour (see e.g. Table S4). Common guillemots very rarely leave eggs or chicks unattended, as this increases the risk of predation and attacks from neighbouring pairs (Ashbrook et al. 2010), and it is thus generally observed only in cases of severe food shortages (Birkhead & Nettleship 1984, Ashbrook et al. 2010). However, Brünnich's guillemots have previously been observed to leave their egg or chick in the case of heat stress (Gaston et al. 1995), as have other seabird species (e.g. Hand et al. 1981, Oswald et al. 2008). It seems likely that the effect observed here was indeed the result of the high temperatures, as there were no signs of food shortages in these years (no unusually long foraging trips, for example), and no observations of predators or other disturbances in association with the parents leaving the ledge. In addition, the parents displayed thermoregulatory behaviours, as described in this paper, well before leaving the ledge. With the parents thus prioritising cooling off and/or rehydrating over protecting their offspring, the observation can be considered an illustration of the trade-off that exists between reproductive success and survival (see e.g. Stearns 1989, Cunningham et al. 2021).

We also saw clear associations between temperature and breeding success, where the risk of losing an egg at a temperature of 27°C was 23 times higher than losing it at 16°C. We did not see an effect of temperature on the probability of losing a chick, however. This could potentially be because, compared to eggs, chicks left alone on the ledge are less vulnerable to predation or being accidentally knocked off the edge, and the chicks may also be able to seek shade and protection independently.

Of the 13 direct observations of breeding failures that we judged were directly related to heat stress, 11 failures coincided with 2 particularly severe periods of hot weather in late June 2020 and 2022 (Figs. 5 & 6), with local temperature measurements in the sun reaching >45°C. Based on long-term measurements from another island 140 km north-east of Stora Karlsö, 2020 brought the highest June temperatures recorded for more than a century (SMHI 2020a), while 2022 even broke existing records (SMHI 2022a). In 2020, another 4 breeding failures (3 eggs and 1 chick) occurred during this hot period on ledges that were not monitored by cameras. Total losses during these 2 periods correspond to ca. 17 and 10% of the breeding attempts active at the start of the heat wave in 2020 and 2022, respectively. For a sense of scale, making the simplifying assumption that estimates from the Auk Lab are representative of all 25000 breeding pairs on Stora Karlsö, this is equal to a loss of 4250 eggs or chicks throughout the colony in 2020 and 2500 eggs or chicks in 2022. Still, it should be noted that even in 2020 and 2022, breeding success in the Auk Lab remained relatively high (0.61 and 0.67, respectively) in comparison with, for example, the widespread complete breeding failures of common guillemots that have been linked to the 2014–2016 Pacific marine heatwave and its effects on prey availability and quality (e.g. Piatt et al. 2020, Schoen et al. 2024).

While, to our knowledge, our study is the first to reliably document the whole process leading to heat-related mortality in seabirds, high nest-site temperatures have also been associated with direct mortality of seabirds at other colonies. For example, western gulls *Larus occidentalis* experienced up to 90% chick

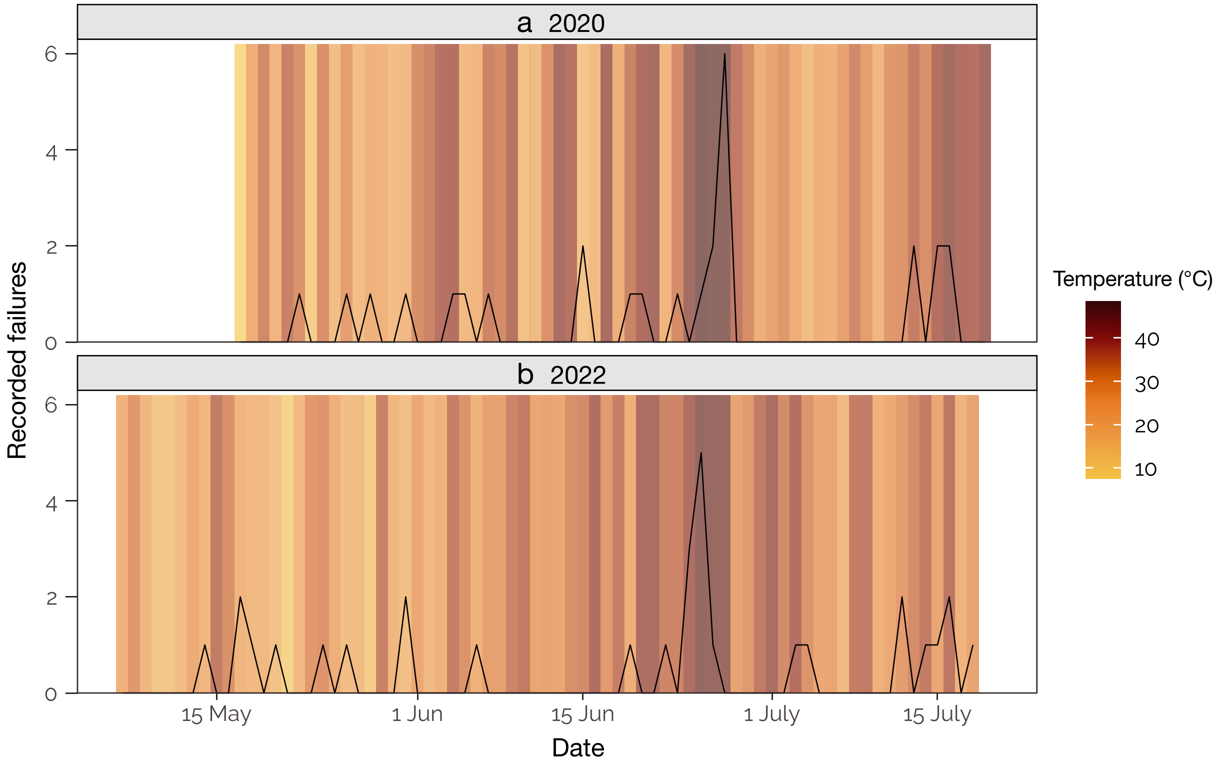

Fig. 6. Recorded common guillemot breeding failures per day in (a) 2020 and (b) 2022 at Stora Karlsö. Black lines: number of recorded failures for the day on which they were recorded; shading: maximum temperature measured using the local, sun-exposed probe

mortality in parts of the colony during a heatwave (Salzman 1982), 5% of adult Magellanic penguins *Spheniscus magellanicus* perished during a single day of high temperatures in one subsection of a colony (Holt & Boersma 2022) and 87% of monitored chicks in a colony of imperial cormorants *Leucocarbo atriceps* died during a particularly hot 2 d period (Quintana et al. 2022). Even individual extreme events such as these can have substantial impacts on population dynamics (see e.g. Frederiksen et al. 2008, Descamps et al. 2015), highlighting the need for a more complete understanding of the demographic consequences of heatwaves for seabirds. While air temperatures along the southern Baltic Sea coast were at a historical high in late June 2022, they were still completely in line with local and global trends, where large positive temperature anomalies are the new norm (Perkins-Kirkpatrick & Lewis 2020, SMHI 2020a, IPCC 2021). In this context, our results suggest that the direct effects of high nest-site temperatures are very likely to constitute an important and growing threat to seabirds.

In addition to these very direct effects of heatwaves on breeding success, there could also be harder-to-detect effects on fitness. For example, the declining probability of both partners being present at the same time could have consequences for social bonds and parasite loads as described above, which in turn could affect future breeding success. In addition, studies of other bird species have shown that high temperatures may also result in increased metabolic rates (Choy et al. 2021, O'Connor et al. 2021) and lower foraging success (du Plessis et al. 2012, Wiley & Ridley 2016, Andreasson et al. 2020), which could eventually result in reduced body condition. Further, as we did not measure the body temperature of the guillemots, we do not know whether they were able to successfully regulate their core body temperature; failure to do so may result in, for example, suppressed immune system functioning, as shown by studies of domestic fowl (e.g. Alhenaky et al. 2017). As such, much work remains in investigating the cumulative impacts of direct but sublethal impacts of heatwaves on seabirds.

Another important line of investigation with direct implications for conservation is the role of microclimate in determining how well the birds cope with extreme nest-site temperatures. The large difference in temperature between sunny and shaded ledges (Fig. 5) and the large effect of sun exposure on thermoregulatory behaviour (Fig. 2) both point to the importance of nest site choice. As such, the aspect and morphology of the cliff may be important in determining whether a given nesting spot will remain viable in a warming climate. For other seabird species, proximity to water (see e.g. Hand et al. 1981, Holt & Boersma 2022) or availability of shading vegetation (Yorio et al. 1995, Hart et al. 2016) will be similarly important. An improved understanding of which habitat characteristics facilitate the ability of seabirds to deal with extreme temperatures could provide crucial information for a move towards management strategies that consider the animals' thermal environment in the designation and design of protected areas (see Elmore et al. 2017), as well as for the construction of artificial nest sites with a cooler microclimate (e.g. Clitheroe 2021).

5. CONCLUSIONS

Our results clearly show that the Stora Karlsö guillemots are struggling to cope with heatwaves, and point to the importance of considering the direct effects of climate change on seabirds and other endotherms. While there is a growing body of work on small desert birds and domestic fowl (e.g. McKechnie & Wolf 2010, McKechnie et al. 2016, Alhenaky et al. 2017), this knowledge is not necessarily directly transferable to seabirds, many of which are adapted to conserve heat rather than lose it in order to cope with deep dives in cold waters and extended periods of incubation in freezing temperatures (e.g. Croll & McLaren 1993, Choy et al. 2021). As such, a taxon-specific understanding of the direct effects of heatwaves on seabirds is necessary.

These direct effects need to be considered in parallel with indirect effects, which can be substantial (e.g. Piatt et al. 2020, Schoen et al. 2024) and may result in the seabirds being doubly hit by increasing temperatures, both in water and on land. For example, parental absences at the nest site due to heat stress may, in years of poor food availability, be compounded by longer foraging times (see e.g. Oswald et al. 2008). In addition to food availability, other factors may also interact with heat stress, such as the presence of mosquitoes and other parasites (e.g. Gaston et al. 2002), the impact of which may be exacerbated by a potential reduction in allopreening (see above). As such, as heatwaves become more frequent and seabirds start to push the upper boundaries of their thermal niche, an improved mechanistic understanding of the direct effects, and how they interact with indirect effects, is crucial for better predicting, and possibly mitigating, future effects.

Acknowledgements. We are very grateful to Ruedi Nager for helpful comments on earlier versions of the manuscript, as well as to Sarah Schoen, Emily Choy and Steve Oswald for useful and encouraging feedback. We also thank WWF Sweden and Karlsö Jagt- och Djurskyddsförenings AB for economic and logistic support as well as Aron Hejdström for help in the field. J.H.S. and O.O. were supported by Marcus and Marianne Wallenbergs stiftelse (grant number 2018-0093). J.H.S. was also supported by Vetenskapsrådet (grant number 2021-03892) and FORMAS (grant number 2021-02639).

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Editorial responsibility: Mayumi L. Arimitsu (Guest Editor), Juneau, Alaska, USA
Reviewed by: S. K. Schoen, E. S. Choy, S. Oswald

Submitted: September 2, 2022
Accepted: January 4, 2023
Proofs received from author(s): February 9, 2022