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

OPINION PIECE

Challenges of quantifying direct heat stress effects of climate change on seabirds

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ABSTRACT: The importance of heat stress as a consequence of climate climate change is often overlooked for seabirds. As endotherms, seabirds must actively thermoregulate at temperatures above their thermoneutral zone, or risk lethal hyperthermia. Although essential activities (e.g. foraging, breeding) may be traded off for thermoregulatory behaviors during periods of heat stress, a recent report by Olin et al. (2024; Mar Ecol Prog Ser 737:147–160 in this Theme Section) is one of very few that directly link this to demography. We argue that heat stress effects, which have strong theoretical support, are underreported directly because large-scale mortality events are rare, and small-scale events are hard to identify and easily obscured by indirect trophic effects. Quantifying heat stress effects on seabirds is necessary to understand fully the threats from climate change but requires prioritizing research in the following areas: developing methods to attribute heat mortality, determining baseline levels of heat mortality, elucidating ecological and organismal differences that underlie heat stress sensitivity, investigating the importance of possible sublethal mechanisms, and separating heat stress trade-offs from indirect effects of climate.

KEY WORDS: Climate change · Heat stress · Seabirds · Trade-offs

1. INTRODUCTION

Recent climatic changes have had pervasive ecological effects on seabirds, and climate projections indicate that these changes will intensify (Dias et al. 2019, Pistorius et al. 2023). Seabirds are often considered bellwethers of climate change (Hazen et al. 2019, Xavier et al. 2022) because they are well studied and have exhibited dramatic, climate-driven changes in mortality, productivity, and distribution (Sydeman et al. 2012, Pistorius et al. 2023). Climate change can affect seabirds directly, by the action of climatic variables (e.g. wind, precipitation, thermal changes) on bird physiology or behavior, or indirectly through trophic relations, species interactions, and habitat quality (Oswald & Arnold 2012, Sydeman et al. 2012, Pistorius et al. 2023). Marine heatwaves have been shown to have strong indirect effects on seabirds through drastically reduced food availability (e.g. Piatt et al. 2020), but since marine and terrestrial heatwaves can co-occur (Rodrigues et al. 2019, Pathmeswaran et al. 2022), there is also potential for direct heat stress effects on breeding seabirds, especially at exposed colonies in coastal areas where extreme air temperatures could arise during the convergence of marine and terrestrial heatwaves (Rodrigues et al. 2019, Pathmeswaran et al. 2022).

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Despite strong theoretical support for heat stress as a direct effect of climatic change for endotherms (Oswald & Arnold 2012, McKechnie & Wolf 2019, Levesque & Marshall 2021), there is relatively little empirical research, and indirect effects of climate dominate the marine biology literature (Sydeman et al. 2012, Jenouvrier 2013, Pistorius et al. 2023). Here, we provide an up-to-date synopsis of lethal and sublethal heat stress effects for seabirds. We examine why these direct effects are generally overlooked, highlight known mechanisms and some key incidences reported since our last review (Oswald & Arnold 2012), and outline research required to quantify these effects.

2. THEORETICAL SUPPORT FOR PERVASIVE HEAT STRESS EFFECTS

As endotherms, seabirds generate heat from internal metabolic processes that facilitate activity in cold environments. However, this creates an extra heat load to dissipate by physiological and behavioral thermoregulation once ambient temperatures rise above a fairly limited range (their thermoneutral zone). If ambient temperatures surpass thermoregulatory abilities, body temperature rises to the critical thermal maxima, at which tissue injury begins (estimated as 43–46°C for birds; McKechnie & Wolf 2019) and prolonged exposure is lethal. Lethal body temperature ranges from 48 to 62°C for arid-zone terrestrial birds (McKechnie & Wolf 2019) that live where ambient temperatures range from 45 to 50°C in the shade but are effectively much higher in full sun (e.g. 65°C operative temperature; Cunningham et al. 2021). Thus, for these species, potentially lethal thermal maxima are often encountered. Although niche theory implies that lethal ambient temperatures should be lower for species in cooler areas (Porter & Kearney 2009), empirical evidence indicates that upper thermal tolerance may be evolutionarily conserved (Araújo et al. 2013). It is therefore currently unclear which species might be most sensitive to heat stress (although see Cook et al. 2020 and Choy et al. 2021 for examples), but high-latitude species that possess adaptations to reduce heat loss and face disproportionate rates of climatic warming are good candidates (Nudds & Oswald 2007, Oswald & Arnold 2012). The importance of heat stress also depends on the abilities of birds to limit thermal loading through behaviors that minimize radiative heat gain; increase convective and conductive heat loss; and/or replenish water lost through evaporative cooling (Oswald & Arnold 2012).

3. EMPIRICAL REPORTS OF LETHAL HEAT STRESS

Despite these theoretical indications that seabirds could experience lethal heat stress from climatic warming, few incidences have been reported. A recent report of heat mortality for Magellanic penguins *Spheniscus magellanicus* in Argentina (Holt & Boersma 2022) is one of very few published records of large-scale, heat-related deaths for adult seabirds. However, this report of 264 dead adults is dwarfed by the mortality caused by indirect effects of climate change, such as marine heatwaves (e.g. Piatt et al. 2020 estimated 1 million dead or dying common murres *Uria aalge* from the 'Blob'). Thus, either heat stress has not yet exceeded the buffering capacities of seabirds, or research efforts are currently insufficient to detect it. Here, we argue the latter view.

Direct heat stress effects of climate (Fig. 1) are underreported for 2 reasons: they are difficult to identify and are easily obscured. Obvious, large-scale, heat-related mortality events for seabirds are comparatively rare and more common for chicks than adults (e.g. Salzman 1982), but may be on the rise (e.g. Holt & Boersma 2022, Quintana et al. 2022). Adult mortality need not be on a large scale to have population-level repercussions, as population growth is generally most sensitive to this rate (Jenouvrier 2013). One problem is that there is currently no benchmark, baseline level of heat mortality against which to measure any increase from climate change. For little penguins *Eudyptula minor* in subtropical zones, incidence of heat mortality is variable but has been reported as averaging 1.7–5.0% of dead birds (Dann & Chambers 2013, Cannell et al. 2016). How such estimates might change across populations and species (both within and outside the breeding season) is unknown, but is vital for the detection of heat stress effects of climate change. A second challenge is that although attributing indirect climatic effects, such as starvation, competition, or predation, is relatively straightforward, there are no general biochemical or histopathological markers for avian heat mortality (Xie et al. 2020). Thus, attributing heat mortality (Fig. 1) necessarily requires exclusion of all other likely causes (e.g. Holt & Boersma 2022, Quintana et al. 2022).

4. EMPIRICAL REPORTS OF SUBLETHAL HEAT STRESS

Unfortunately, similar challenges hold for detecting sublethal heat stress impacts, and these can easily be lost among indirect climatic effects. Thermo-

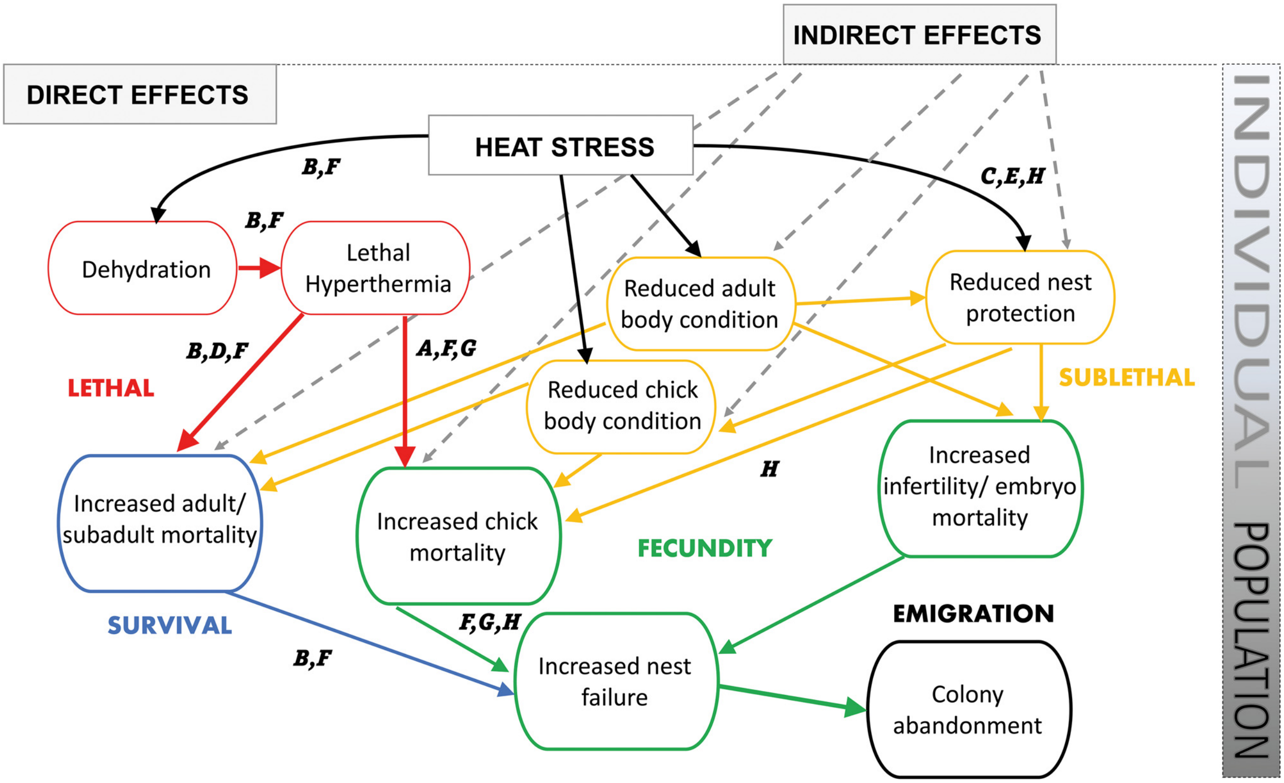

Fig. 1. Proposed lethal and sublethal mechanisms commonly linking (direct) heat stress effects on individual seabirds to population demographics. Dashed grey arrows represent indirect effects of climate (e.g. resource access, biotic interactions) on these mechanisms, which can have synergistic, antagonistic, or additive effects with heat stress. Letters represent mechanisms demonstrated by direct observation or causal studies (not just correlations) in the following publications: A: Salzman (1982); B: Gaston et al. (2002) and Choy et al. (2021); C: Oswald et al. (2008); D: Dann & Chambers (2013); E: Cook et al. (2020); F: Holt & Boersma (2022); G: Quintana et al. (2022); H: Olin et al. (2024)

regulatory behaviors to ameliorate heat stress, such as bathing or drinking, may require trade-offs with other activities, such as foraging or defending territories (Oswald et al. 2008, Oswald & Arnold 2012, Cunningham et al. 2021). Thus, sublethal heat stress exposure could have fitness consequences (Fig. 1). Ground-nesting seabirds are often directly exposed to thermal stress from solar radiation, so they use panting or gular-fluttering to maximize evaporative cooling (e.g. Hochscheid et al. 2002). However, breeding adults must usually leave nests to replace lost water, exposing chicks and eggs to heat stress, conspecific aggression, and predation (Oswald et al. 2008). Heat stress can therefore compound any indirect effect of climate that constrains time budgets or body condition (Fig. 1), such as food availability (Oswald et al. 2008) or parasitism (Gaston et al. 2002), and its importance may easily be overlooked.

Although sublethal trade-offs have been suggested for seabirds based on evidence from distributions (Oswald et al. 2011), behavioral manipulations (Oswald et al. 2008), remote observations (Cook et al. 2020), and respirometry (Choy et al. 2021), because of the challenges of attributing heat stress effects, observations connecting thermal stress directly to demography are lacking (Fig. 1). However, Olin et al. (2024 in this Theme Section) finally provide this evidence, linking heat stress to reduced fecundity of breeding common murres *Uria aalge* (see 'H' in Fig. 1). By using video surveillance in multiple years, they document desertion during intensive behavioral thermoregulation on hot days and subsequent loss of eggs or chicks. Incidences of egg/chick loss from heat stress comprised ~9% of breeding attempts, indicating that in this case, heat stress effects are wide-ranging and demographically important.

5. RESEARCH PRIORITIES

From the available evidence, climate-driven heat stress effects are already occurring for seabirds (Fig. 1), particularly at high latitudes (Gaston et al. 2002, Oswald et al. 2008, Olin et al. 2023), and are not insignificant (e.g. Holt & Boersma 2022, Olin et al. 2024). They are likely additive to other direct effects (e.g. wind or precipitation) and also indirect consequences of climate that can have important survival and sublethal implications. As these heat stress effects are likely underreported for the reasons outlined above, we suggest that research priorities should include developing indices to attribute heat mortality, quantifying baselines for heat mortality within populations, and disentangling the potential complexity of heat stress sensitivity and trade-offs and their interaction with indirect effects of climate. Heat shock proteins, which are thought to confer protection against protein denaturation at high temperatures (McKechnie & Wolf 2019), or the increased mRNA expression of their genes, may offer one potential avenue to develop a way to screen for heat mortality, although there is much natural variation both within and between individuals and species (Xie et al. 2018, Woodruff et al. 2022). Investigating heat stress as a possible cause of observed mortality and reporting its incidence (e.g. Dann & Chambers 2013, Cannell et al. 2016) is vital to compile baseline estimates of heat mortality and understand ecological differences that might underly heat stress sensitivities (e.g. body size, foraging mode, nest site selection, coastal/inland location, migration routes, availability of fresh water). Sublethal impacts can be explored using advancing technologies, such as biologging approaches (Arnold & Oswald 2018, Chmura et al. 2018), mini weather stations or temperature arrays (Oswald et al. 2008, Cunningham et al. 2015), or thermal imaging (Tattersall et al. 2018). Finally, even small changes to existing research programs, such as more investigators recording and analyzing video surveillance of nests during crucial parts of the breeding season (sensu Olin et al. 2024), perhaps using inexpensive trail cameras, could go a long way to distinguishing heat stress from indirect effects of climate.

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