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Wild white-capped noddies keep a cool head in a heated situation

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ABSTRACT

Sunning, or sunbathing, is a behavior observed in diverse birds from at least 50 taxonomic families. While sunning, birds exhibit signs of heat stress, notably panting, indicating a risk of overheating. Given that even modest increases in brain temperature can impair brain function, sunning birds may have mechanisms that selectively cool the brain. Sunning birds could cool the brain using active physiological mechanisms (e.g., an ophthalmic rete or sleeping) or passive adaptations, such as light-colored plumage over the cranium. White-capped noddies are tropical seabirds that sunbathe in direct sunlight on cloudless days. Using infrared thermography on wild birds, we found that the white cap is 20 °C cooler than that of the black back while sunning. A deceased bird showed the same thermal profile, indicating that this difference arises from dichromatic coloration and not underlying physiology. Thus, the white cap may extend the duration of time noddies can sunbathe and keep the brain cool, near core body temperature, while allowing the rest of the body to heat up, perhaps to displace or kill parasites.

1. Introduction

Birds exhibit captivating diversity in coloration. Large-scale efforts have been made to understand the key evolutionary drivers responsible for maintaining inter-sexual and inter-specific variation in avian color (Delhey et al., 2023). For instance, many females are typically cryptic, whereas males are often the more elaborated sex to signal quality (Hill 1991) and attract mates (Dale et al., 2015; Delhey 2015). Coloration tends to be more elaborate in larger species, both males and females, suggesting that most smaller birds are less colorful to maximize crypsis (Delhey et al., 2023). A need for abrasion resistance (Bonser 1995), increased flight efficiency (Rogalla et al., 2021a), and especially thermoregulatory concerns (Dufour et al., 2020) also influence the color of avian plumage. Different colors reflect and absorb light differently (Rogalla et al., 2022). Darker plumage is typically associated with lower reflectance and higher surface heat absorption from solar radiation. Conversely, lighter-colored plumage reflects more radiation, generally keeping birds cooler (Hochscheid et al., 2002; Angelier 2020). Long-distance migrants are also lighter in color in an effort to absorb less solar radiation and prevent overheating as they have no refuge from ultraviolet light during diurnal movements (Delhey et al., 2021, see also Lindströ;m et al., 2021; Sjö;berg et al., 2021). This is why birds are generally expected to become lighter in a warming world (Delhey et al., 2020). However, some birds actually seek out heat from the midday sun.

Sunning, or sunbathing, is a common behavior observed across many avian groups (Simmons 1986). To do so, birds adopt postures aimed at maximizing surface area, and the interception of solar radiation, in direct sunlight (Fig. 1). Sunning can increase body temperature in cool environments, just as basking does in non-avian reptiles, but in hot environments, sunning can result in heat stress. Accordingly, behavioral signs of heat stress in sunning birds, such as panting, suggest that sunning serves functions other than thermoregulation (Cade 1973; Bush and Clayton 2018). Birds sun to expose parasites to ultraviolet radiation, or to promote their desiccation, in an effort to control parasite numbers (Blem and Blem 1993; Moyer and Wagenbach 1995); this idea could apply also to the control of feather-degrading bacteria (Saranathan and Burtt 2007). Sunning might also stimulate parasites to move, which could facilitate their removal through preening (Bush and Clayton 2018). Additionally, sunning could warm preen oil to reduce its viscosity and facilitate its incorporation onto feathers while preening. Preen oil has antimicrobial properties (Alt et al., 2020) and helps waterproof feathers, which is particularly important for birds that land on water (Moller and Laursen 2019). Whatever the specific functions served by sunbathing, the exposure to direct sunlight creates a risk of overheating.

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Fig. 1. Photograph of a sunning white-capped noddy showing the color dichromatism between head and back (credit J.A.L.).

Hyperthermia impacts the normal physiological functioning of many bodily systems (Leon and Bouchama 2015). Acute heat stress causes vasodilation of the cutaneous vasculature, resulting in a faster heart rate; respiratory rate increases in an attempt to reduce core body temperature (Crandall 2008). But hyperthermia is of particular concern for the central nervous system (Khan and Brown 2002). The brain is a thermally-sensitive organ for which even modest increases (>1 °C) in temperature impair brain function in humans (Walter and Carraretto 2016). Disrupted neurological processes can manifest as impaired attention, motivation, and short-term memory (Walter and Carraretto 2016) and likely arise from disrupted cellular signalling and neuronal function (Kiyatkin 2005; White et al., 2007). In birds, chronic heat stress damages hypothalamic vasculature and neurons (He et al., 2019; Bohler et al., 2021), which could intimate a mechanism for the reduced motor control and impaired cognitive performance of hyperthermic zebra finches (*Taeniopygia guttata*) (Danner et al., 2021).

How could sunning birds prevent overheating? Sunning birds could cool down using active mechanisms, such as panting (Ellis et al., 1995). More broadly, birds could also shift their posture to change the exposed area, erect feathers to retard heat gain (Lustick, 1984, Wolf and Walsberg 2000; Rogalla et al., 2022), or vasodilate vessels in the bill (Tattersall et al., 2017), legs (Steen and Steen 1965), or other structures (Eastick et al., 2019). Other adaptations might function to specifically cool the brain, including the counter-current heat exchange found in the avian ophthalmic rete (Arad and Midtgard 1990; Fuller et al., 2003), engaging in slow-wave sleep (Ungurean et al., 2020), or light-colored plumage over the cranium.

The white-capped noddy, also known as the black noddy, (*Anous minutus*) is a tropical and subtropical seabird with a worldwide distribution. Noddies are so named because they nod (or bow) near conspecifics. Doing so displays their white cap, suggesting this plumage serves a role in communication (Fisk 1977). However, the cap might also serve a thermoregulatory role. On hot, sunny days, white-capped noddies can be seen sunbathing on reflective surfaces, such as open patches of sand, or on sheet-metal rooves (Cannon 1979; Moyer and Wagenbach 1995) (Fig. 1). Here, they maintain a posture with the wings partly outstretched and the tail feathers splayed, and the birds intermittently pant. The purpose of their sun-loving behavior may be to either kill, or displace, lice (Moyer and Wagenbach 1995) and perhaps mites (Hernandes and Brito 2022). Using infrared thermography, we measured the heat reflected from the white cap and black back of noddies sunning or nesting to test the hypothesis that the adaptive significance of the white cap is to passively keep the brain cool, near core body temperature, while allowing the rest of the surface of the body to heat up, perhaps to deter parasites.

2. Material and methods

This study was conducted on Heron Island, Australia (23.4423°S, 151.9148°E) at the southern end of the Great Barrier Reef in the austral summers of 2016–2018. White-capped noddies are the most common bird on Heron Island, with numbers in the tens of thousands (Barnes and Hill 1989; Ogden 1993). Here, they commonly nest in *Pisonia* trees (*Pisonia grandis*), with dozens of nests per tree. *Pisonia* trees have broad leaves that offer inconsistent shade to nesting birds.

To better understand the sunning behavior, we first timed how long individual birds spent sunning (n = 725 birds). To do so, we timed from when a bird started sunning to when they departed (without provocation) at a distance of 10 m or more. These data allowed us to characterize the histogram of sunning duration. In 2017, we collected infrared thermal images of sunning (and one nesting) birds (n = 43). We photographed and measured instantaneous surface temperature from the white cap and black back of noddies using a hand-held thermal imager (Testo 875i, Testo Ag, Lenzkirch, Germany). Thermal imaging can provide new insight into the function of different parts of the body and might even estimate the internal body temperature of birds (McCafferty 2013; Tattersall et al., 2017; Eastick et al., 2019). These island-living birds do not appear to be bothered by human presence; as such, we were able to take photographs over each bird, no more than 2 m away and occasionally much closer. For this cohort of birds, we did not record how long they had been sunning.

Next, we collected time-series data on individual birds to gain insight into the kinetics of any temperature changes by measuring heat reflectance from the head and back at the top of every minute, from when the birds landed until they flushed (n = 12). Photographs were taken between 1100 and 1600 h on cloudless days, during which ambient temperature (24.8–26.1 °C) and humidity (69.6–81.3%) varied within narrow ranges (Fig. 2). Out on Heron Reef, breezes varied between light (6.9 km/h) to fresh (35.6 km/h), but in the interior of Heron Island, where noddies sun, wind was calm (<1 km/h). Surface temperature of the plumage was extracted from the photographs of sunning noddies using IRSoft 3.1 (Testo Ag, Lenzkirch, Germany). Average temperature of the white cap and black back were calculated, assuming an emissivity of 0.96, by tracing the area (Eastick et al., 2019). Tracing was done by one person. Importantly, because the thermal imager had a double lens which produced both a thermal image and a digital image at a resolution of 160 × 120 pixels, it was possible to use anatomical landmarks for the tracing, and not heat signatures. A subset of photographs were scored by a second person to minimize any scorer bias, but the values obtained were not distinguishable.

Statistical analyses were performed in SYSTAT 13 version 13.2 (Systat Software Inc., U.S.A.). We used a two-tailed paired *t*-test to compare the surface temperature of the cap to that of the back for sunning birds of unknown history (n = 43). Although we could not

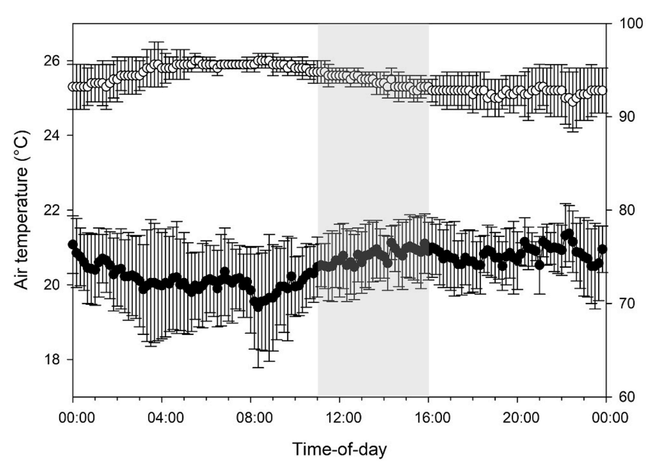

Fig. 2. Weather on Heron Island for dates on which thermal images of sunning noddies were taken. Specifically, ambient temperature (*open circles*) and humidity (*closed circles*) is shown over the day. Grey shading denotes the temporal window for photography. Values are plotted as mean ± S.D.; data was provided by the Australian Institute of Marine Science (2020).

identify individual birds, given the large number of birds on the island, we assumed that these "one-off" measurements were made on different birds. For the time-series data (n = 12), we used a general linear mixed model to look for changes in cap and back temperature over time; individual was set as a random effect, and 'minute' was a fixed effect.

3. Results

Of the 725 focal observations of sunning noddies, we found that 96.6% did not sun longer than 9 min, and only one bird did so more than 14 min (Fig. 3AB). Using the thermal imagery, we found that the plumage of the white cap (mean ± S.E.: 43.9 ± 0.5 °C) was significantly cooler than that of the black back (63.5 ± 0.6 °C) of sunning noddies ($t = -32.68$, df = 42, $p < 0.001$; Fig. 3C). The hottest temperature observed on the back was a hotspot reaching 83.0 °C. When following specific birds from the time they started sunning up to 9 min, we found that surface temperature of the white cap did not change ($F = 0.81$, df = 1,74; $p = 0.372$; Fig. 3D). In contrast, the black back became significantly hotter with sunning duration ($F = 12.53$, df = 1,74, $p = 0.001$); the increase in back temperature primarily occurred in the first 2 min. Variant temperatures arose purely from dichromatic coloration and solar radiation, as evidenced by (*1*) a similar thermal profile of a deceased noddy put in the sun (white cap: 45.3 °C; black back: 70.5 °C), and (*2*) a homogenously low profile of a living bird nesting in the shade (surface temperatures below 34 °C) (Fig. 4).

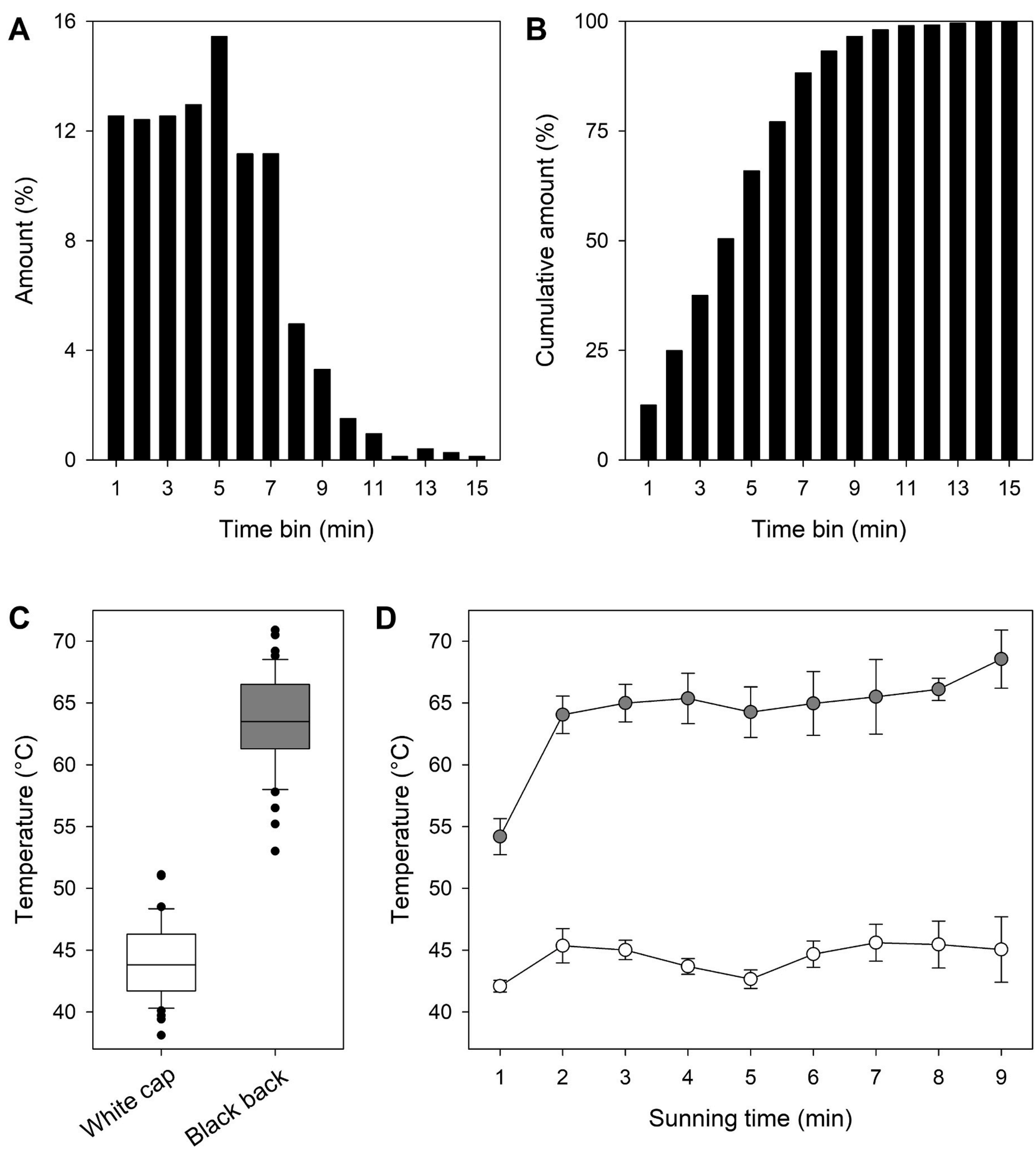

Fig. 3. (**A**) Histogram of the duration of sunning episodes organized in 1-min time bins (n = 725) and (**B**) the cumulative plot showing that of 725 observations of sunning noddies, birds rarely sun longer than 9 min (and none longer than 15 min). (**C**) Instantaneous temperatures from birds of unknown history showing that the black back is 20 °C hotter (on average) than the white cap (n = 43). (**D**) Time-series of sunning duration on cap (*open circles*) and back (*grey circles*) temperatures revealing that the cap does not change temperature over time, whereas the back increased quickly in sunlight (n = 12).

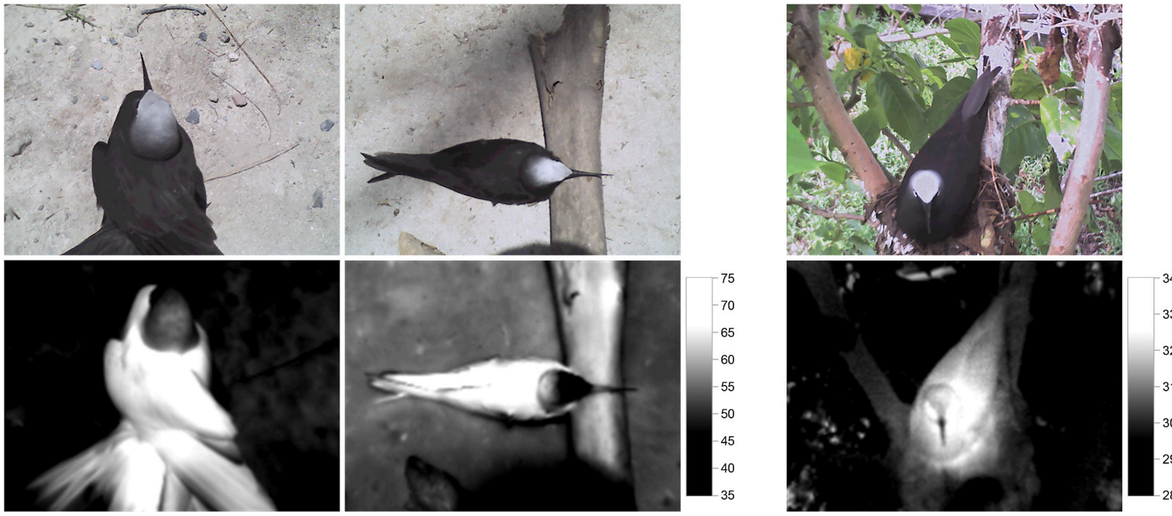

Fig. 4. Visible-light images (*top row*) and thermal images (*bottom row*) of a (living) noddy, sunning with wings akimbo (*left*), a deceased noddy placed on sand in direct sunlight (*middle*), and a nesting noddy in the shade (*right*). The thermal scale was the same for the two left-most photographs; another scale, with a much narrower range spanning only 6 °C, was used for the right-most image. These comparisons reveal that the difference in temperature between the cap and back is dependent on sunlight *per se*, and not a functioning cardiorespiratory system.

4. Discussion

Sunning white-capped noddies maintain their white cap *c.* 20 °C lower than that of their black back. This difference does not arise from physiological changes occurring only in the head, such as the presence of an ophthalmic rete (Arad and Midtgard 1990; Fuller et al., 2003) or cutaneous evaporation (Rogalla et al., 2021b) as a dead noddy showed the same thermal profile when placed in direct sunlight. Furthermore, the cooler temperature of the white cap did not arise because of wet feathers after hunting at sea, since none of the birds were visibly wet and the temperature profile of the dead specimen was similar to living birds. Instead, the 20 °C difference arises because darker plumage absorbs more solar radiation relative to lighter-colored plumage (Wolf and Walsberg 2000; Hochscheid et al., 2002; Angelier 2020; Rogalla et al., 2022). A similar pattern, albeit of a much smaller magnitude, has been reported in other endotherms, including black-and-white Holstein dairy cattle (*Bos taurus*) (Isola et al., 2020) and in different color morphs of springbok (*Antidorcas marsupialis*) (Hetem et al., 2009). The thermal effects of color depend on the absorbance of both visible and near-infrared wavelengths of sunlight. Near-infrared is rarely measured, and visible reflectance is often a poor predictor of total reflectance (Stuart-Fox et al., 2017). Higher near-infrared reflectivity is common for species inhabiting hotter, drier environments with increased solar irradiance (Medina et al., 2018). Fortunately, Medina et al. (2018) report both visible and near-infrared reflectivity for white-capped noddies. In support of our thermal imaging findings, the plumage of the white cap has a higher total reflectance (mean ± S.D.: 42.8 ± 3.7%) compared to the black back (28.5 ± 5.5%).

In our noddies, the dark feathers on the back heat to over 60 °C. The hottest spot observed on the back reached 83.0 °C, not unlike the 83.9 °C observed in brown-necked ravens (*Corvus ruficollis*) under intense solar radiation (Marder 1973). Such hot temperatures are needed to kill chewing lice (*Quadraceps hopkinsi*) found on noddies (Moyer and Wagenbach 1995, see also Hernandes and Brito 2022), but could also facilitate incorporation of preen oil as sunning noddies intermittently preen (pers. obs.). In contrast, while other factors might influence sunning duration, the white feathers over the skull might increase the time noddies can tolerate direct sunlight while sunning, or nesting in direct sunlight (Buttemer and Astheimer 1990), relative to species that sunbathe without heat-reflecting white plumage on their head. In accordance with this idea, three species of swallow, all with dark feathers atop their head, sunbathe, yet no individual did so more than 2 min (Blem and Blem 1993). Similarly, white-rumped vultures (*Gyps bengalensis*) with their unfeathered head, sun no more than 5 min (Houston 1980), not unlike the hooded vulture (*Necrosyrtes monachus*) which sun for no longer than 3.4 min (Gutiérrez et al., 2020). Conversely, some white-capped noddies could tolerate sunning four times as long, for up to 15 min, a maximum value that is congruent with other reports of sunning noddies (Moyer and Wagenbach 1995).

The white cap might keep the brain cooler than it might otherwise be with darker plumage. Wild-caught brown noddies (*A. stolidus*) maintain a core body temperature at 40.3 °C when housed under thermoneutral conditions (Mathiu et al., 1991; Ellis et al., 1995). When the ambient temperature inside the environmental chamber was increased above 35 °C, their body temperature likewise increased to 42–44 °C (Ellis et al., 1995). Such temperatures are remarkably similar to those reported here for the white feathers on the head of sunning white-capped noddies. Subcutaneous temperature measurements, or perhaps thermal imaging of the eye, are needed to determine the relationship between surface and subcranial temperatures.

In addition to the white cap, noddies have other mechanisms to cool down. Although noddies do not engage in gular fluttering in hot conditions, they nonetheless pant (Ellis et al., 1995). While panting, the respiratory rate can reach 192 breathes per minute, such that noddies lose heat primarily through evaporative cooling (Ellis et al., 1995). A possible, complementary mechanism that could selectively cool the brain in a hot environment would be to engage in slow-wave sleep. Unlike most mammals, birds can have hundreds or even thousands of sleep episodes per 24-h day, each just seconds or tens of seconds long (Lesku and Rattenborg 2014). During slow-wave sleep, the avian brain cools as the sleep episode lengthens (Ungurean et al., 2020). Although the reduction in brain temperature during slow-wave sleep in birds is less than 1 °C relative to preceding wakefulness (Szymczak et al., 1989; Pastukhov et al., 2001; Ungurean et al., 2020), this drop may be physiologically meaningful under the extreme heat of the tropical midday sun. Consistent with this idea, birds that have newly alighted on the sand flush readily and at far (multi-meter) distances; however, once settled and sunning, birds can be approached to within a hand's grasp (pers. obs.). Thus, sunning birds may be less aware of the surrounding environment, and actually be asleep. In the future, electrophysiological recordings of brain activity, and brain temperature, of sunning noddies would be insightful.

Recent findings that long-distance migrant birds are lighter in color to reduce thermal load (Delhey et al., 2021), along with the prediction that darker birds will be disadvantaged should climate change scenarios come to pass (Delhey et al., 2020), have consequences for sunning birds. Over the coming years, we expect to see noddies sunning for less time on extreme heat days. Over evolutionary time, we might see the expansion of light plumage on noddies (Clapp 1974) and other sunning birds, or feathers with greater near-infrared reflectivity on the head (Shawkey et al., 2017; Medina et al., 2018). In doing so, birds sunbathing in the 22nd century and beyond will continue to keep a cool head in a heated situation.

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CRediT authorship contribution statement

John A. Lesku: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Robert G. Barker:** Investigation, Writing – review & editing. **Hannah Elmes:** Formal analysis, Writing – original draft, Writing – review & editing. **Kylie A. Robert:** Investigation, Writing – review & editing. **Lauren Tworkowski:** Investigation, Writing – review & editing. **Travis L. Dutka:** Conceptualization, Methodology, Investigation, Writing – review & editing.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

The data required to reproduce our findings is available to download from figshare data repository at https://doi.org/10.26181/23796633.v1.

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