Thermal ecology of Trumpeter Swan *Cygnus buccinator* incubation

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Abstract

Trumpeter Swans *Cygnus buccinator*, North America's largest waterfowl, breed at high latitudes where they construct unusually large nest mounds and incubate from the top of the mound while experiencing daily ambient temperature fluctuations of 25°C or more, as well as substantial exposure to solar radiation, high winds, rain and snow. This study investigates how incubating swans accommodate the thermal flux in their environment. Swan incubation dynamics were measured at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA, a federally protected high-elevation marsh complex where the last breeding population of Trumpeter Swans in the contiguous United States persisted during the early 20th century, a period when they neared extinction. Using around-the-clock digital video imaging, environmental monitoring devices and thermal recording devices, which were placed within clutches and also within and upon nest mound material, thermal dynamics were modelled in relation to swan incubation behaviour. Swans maintained a mean (± s.e.) egg temperature of 35.7 ± 0.27°C during active incubation. Linear mixed models of thermal covariates evaluated using AICc values and model weights (ω) revealed an interactive association between nest attendance and: (1) deviation of ambient environmental temperature from average egg incubation temperature, (2) solar radiation and (3) vapour density. Ambient temperature deviations above and below average egg incubation temperature, elevated solar radiation and declining vapour density were interactively associated with swan presence on the nest. Egg temperature *per se* was associated with both ambient temperature (positive) and vapour density (positive). Nest mound temperature was positively associated with ambient temperature, solar radiation and vapour density. The nest mound acted as a thermal mass, moderating thermal flux. Nesting success depended on swans shielding their eggs from excessive daytime warming and desiccation, and on contact incubation when ambient temperature was below the average egg incubation temperature.

Key words: nest attendance, nesting behaviour, solar radiation, temperature, vapour density.

The Trumpeter Swan *Cygnus buccinator*, North America's largest waterfowl species, once faced near extinction but now is exhibiting a remarkable population rebound under concerted management. Trumpeter Swan life history, breeding biology and management was reviewed historically by Banko (1960) and more recently in detail by Mitchell and Eichholz (2020).

Formerly abundant and geographically widespread, Trumpeter Swan populations underwent a severe decline during Euro-American settlement of North America because of excessive commercial and subsistence hunting, along with habitat loss and degradation (Dahl & Allard 1996). By 1933, the last population of Trumpeter Swans known to western science consisted of < 100 swans persisting within the Greater Yellowstone Ecosystem of Montana, Wyoming and Idaho, USA (Hansen 1973), primarily within the large Red Rock Lakes marsh complex of the Centennial Valley in southwestern Montana, USA and nearby Yellowstone National Park. In addition to a hunting ban within Yellowstone National Park, swans in the surrounding ecosystem were partially protected from persecution by the remoteness and climatic harshness of the region. Swans used ice-free rivers and lakes during winter in areas of geothermal activity. The federal Red Rock Lakes National Wildlife Refuge (RRLNWR) in southwestern Montana, USA was established by the United States Congress in 1935 to protect the remaining Trumpeter Swan population. Following the establishment of RRLNWR and nearly a century of active conservation management, Trumpeter Swan populations have rebounded to *c.* 63,000 adults, with > 500 swans occurring within the Greater Yellowstone Ecosystem near the shared borders of Montana, Idaho and Wyoming (Groves 2017).

Trumpeter Swans breed in temperate lake and marsh habitats characterised by open, shallow water (Hansen *et al.* 1971; Gale *et al.* 1987). Pairs establish and aggressively defend territories of variable size (28–61 ha at RRLNWR; Banko 1960), where they construct large nests of mounded vegetation. Nests are 1.2–3.6 m in diameter and 0.3–0.9 m in height, with a nest bowl 25–40 cm in diameter and 10–20 cm deep (Hansen *et al.* 1971; Mitchell & Eichholz 2020). Nest mounds consist of piled emergent and submerged aquatic vegetation, with occasional grasses and sedges. Nest construction is performed by both sexes (De Vos 1964; Hansen *et al.* 1971; Cooper 1979), and nest maintenance and modification continues during egg-laying and incubation (Henson & Grant 1992). Nests are largely unsheltered (Mitchell & Eichholz 2020), meaning that they are exposed to variable weather conditions.

Trumpeter Swan nests are unusually large relative to other large-bodied waterfowl (*e.g.* the Canada Goose *Branta canadensis*; Mowbray *et al.* 2020) and nest construction is energetically expensive (Mainwaring & Hartley 2013; Deeming & Reynolds 2015). Nest size and materials are important characteristics that can influence the microhabitat experienced by the eggs (Deeming & Mainwaring 2015). Large nests consisting of mounded vegetation like those constructed by Trumpeter Swans are uncommon in birds but are observed in Megapodiidae (the megapodes) terrestrially and Crocodilia (the crocodiles, alligators and relatives) aquatically. The nests of megapodes and crocodilians have been shown to maintain relatively stable internal temperatures despite wide fluctuation in environmental temperatures (Frith 1959; Chabreck 1973; Staton & Dixon 1977). Stability of nest temperatures has been attributed to exogenous heat transfer from the environment to the nest throughout the day (Chabreck 1973) and to the release of endogenous heat resulting from decomposition of nest vegetation (Webb *et al.* 1977). In these animals, egg incubation is successful due in part to nest structure and consequent thermal attributes despite environmental temperature fluctuations.

Trumpeter Swans lay eggs at *c.* 36–48 h intervals (Cooper 1979; Lumsden 2002), forming a typical clutch size of 4–6 eggs (Mitchell & Eichholz 2020). Swans initiate incubation just prior to clutch completion (Banko 1960; Cooper 1979), as is common in birds, and incubate for 32–37 days (Banko 1960; Hansen *et al.* 1971) contacting eggs with their large, featherless webbed feet when incubating (Cooper 1979; Lumsden 2002). Males do not incubate eggs (De Vos 1964), nor do males provide females with food during the incubation phase of reproduction. Consequently, incubating females must allocate time for self-maintenance, including foraging and preening, during the incubation phase of reproduction. In this way, females face a trade-off between self-care and care of the eggs, seemingly mitigating risk of exposure to themselves and their eggs through the timing, frequency and duration of breaks from continuous incubation (*i.e.* recesses). These behavioural decisions are influenced by energy requirements, predation risk and environmental conditions (Conway & Martin 2000a). Energy requirements and predation risk during incubation may be reduced by nest-site selection in Trumpeter Swans (Mitchell & Eichholz 2020), but even selection of an excellent nest location may be insufficient to counteract unfavourable environmental conditions.

The relationship between incubation behaviour and the thermal environment for Trumpeter Swans is unclear. Many birds increase nest attentiveness in response to environmental characteristics that cause egg temperatures to deviate outside ideal thermal limits (Conway & Martin 2000b). Some species increase nest attentiveness at unfavourable temperatures through less frequent and shorter incubation recesses (Skutch 1962; Turner 2002), reducing exposure of eggs to undesirable temperatures for prolonged periods (Haftorn 1988; Conway & Martin 2000a,b). Previous studies of incubation in Trumpeter Swans show variable estimates of nest attentiveness ranging from 58–100% (Shea 1979; Henson & Cooper 1993; Bush 2018; Mitchell & Eichholz 2020), punctuated by daytime incubation recesses of variable length (Cooper 1979; Shea 1979; Bush 2018; Mitchell & Eichholz 2020). Daytime recesses are common (typically 2–3 per day; Bush 2018) although rare, short night-time recesses have been observed (typically 0–1 per night; Bush 2018).

The natural thermal environment of breeding Trumpeter Swans has received little study. Cooper (1979) found no correlation between incubation duration and average daily temperature, solar radiation or precipitation for a single pair of captive swans. Conversely, others have found that incubation recess timing and duration correlate with the time of day, increasing temperature and the stage of incubation (Bush 2018; Mitchell & Eichholz 2020). However, the thermal environment faced by nesting Trumpeter Swans is complex and multiple modes of heat transfer may be salient for Trumpeter Swans employing open nesting at high elevation in northern environments. Summary information on modes of heat exchange relevant to Trumpeter Swans is provided in Appendix 1.

The general objective of this study was to measure variation in the natural thermal environment experienced by Trumpeter Swans whilst nesting in the wild and to relate these fluctuations to the swans' incubation behaviour. Given the importance of behavioural adjustments and parental decisions in modulating environmental effects on nest microclimate, it would be valuable to understand how incubating swans respond to substantial thermal challenges throughout their long incubation period. A useful approach would be to measure the fluctuating ambient environmental conditions of a nesting marsh while simultaneously measuring the thermal dynamics of the microenvironment of the nest and the eggs within the nest bowl, as well as parental incubation behaviour influencing the nest and egg microenvironments. A better understanding of the capacity of swans to adjust incubation behaviour to accommodate thermal challenges could yield insight into factors that limit Trumpeter Swan nesting success and their breeding distribution, and thus help to guide ongoing swan conservation and restoration initiatives.

Our specific objectives therefore were to: (1) describe the frequency, timing and duration of incubation recesses from the nest during incubation; (2) model the influences of the marsh thermal properties on swan nest attentiveness; and (3) model the thermal environment experienced by the swan egg. We hypothesised that females would increase nest attentiveness when environmental characteristics are unfavourable for egg development, consistent with Conway and Martin (2000a,b). Under unfavourable environmental circumstances, egg maintenance requires greater temporal and energy investment by the female to overcome environmental challenges. Conversely, we hypothesised that swans will decrease nest attentiveness when environmental characteristics are favourable for egg development. In this scenario, eggs do not require immediate care and females have an opportunity to recess from incubation behaviour for self-maintenance activities. Additionally, we measured behaviours performed by incubating adults while they were engaged in active incubation on the nest bowl, including resting with their heads down, monitoring their surroundings, maintaining the nest and themselves and interacting with the eggs or their mate. We recognised that swans breeding at high elevation in the Greater Yellowstone Ecosystem may experience an unusually challenging thermal environment for a species that incubates in an unprotected, open nest. Hence, we also sought to understand localised incubation patterns and thermal constraints, to develop management recommendations and to guide field protocols.

Methods

Study area and population

Thirteen Trumpeter Swan nests occupied by unmarked swans were monitored during the swan breeding season (April–July) of 2020 and 2021 at Red Rock Lakes National Wildlife Refuge (hereafter RRLNWR) located in the Centennial Valley of southwestern Montana, USA. RRLNWR is a *c.* 26,000 ha protected marsh and prairie complex with an average elevation of *c.* 2,000 m (Fischer 1976). The Centennial Valley sustains the longest winters in the continental USA (Fischer 1976). Snowfall can average > 170 cm annually, and frost can occur in every month of the year (NOAA National Data Center). Two large shallow lakes dominate the valley floor within refuge boundaries: Upper Red Rock Lake (*c.* 1,200 ha) and Lower Red Rock Lake (*c.* 800 ha). Both lakes consist of uniform basins with aquatic vegetation throughout and with substrates comprised of mud, detritus and peat. The primary emergent vegetation consists of Spikerush *Eleocharis macrotachya* and sedges *Carex* sp. (Banko 1960). Upper and Lower Red Rock Lakes are surrounded by meadows, marshes, smaller lakes and ponds. Water bodies of importance to nesting swans in 2020–2021 included Upper Red Rock Lake, Lower Red Rock Lake, Swan Lake (*c.* 240 ha), Widgeon Pond (*c.* 40 ha) and Shambow Pond (*c.* 3 ha). For logistical reasons and to minimise regional disturbance to nesting swans, research activities were limited to swans nesting on Lower Red Rock Lake and Widgeon Pond (Fig. 1). Muskrats *Ondatra zibethicus* are common within RRLNWR, particularly within Lower Red Rock Lake where Spikerush stands are abundant throughout. Consistent with Banko's (1960) observations, Muskrat structures (*e.g.* push-ups or lodges) comprised the foundation for most Trumpeter Swan nests, with few nests constructed on the shoreline itself. In both 2020 and 2021, egg-laying occurred in late April to mid-May, and cygnets hatched in late May to late June. The remaining Centennial Valley surrounding RRLNWR consists of sagebrush *Artemisia* sp. steppe and grassland, much of which is privately owned and used for Cattle *Bos taurus* grazing.

Data collection

Locating swan nests

Trumpeter Swan nests were located by searching areas known to hold established breeding pairs, and areas that contained potential swan nests described from aerial surveys conducted by the U.S. Fish and Wildlife Service (Kyle Cutting, USFWS, pers. comm.). When a nest was located, its coordinates were recorded on a handheld global positioning system (GPS) device (GPSMAP 65; Garmin International Inc., Olathe, Kansas, USA), and the clutch size was also recorded. All active nests containing ≥ 1 egg were included in this study.

Measuring incubation behaviour

At each nest in 2020 ($n = 8$), an around-the-clock videography system was placed, replicating the methods of Bush (2018), to record incubation behaviour. We did not

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Figure 1. Map of the Lower Red Rock Lake (map insert: Widgeon Pond) within the Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA. Locations of Trumpeter Swan nests monitored during the study are represented as blue stars (2020; *n* = 8) and orange stars (2021; *n* = 5).

employ videography in 2021 and this study only used 2021 nest data to estimate nesting success. The 2020 videography systems consisted of bullet cameras (ENC-102NRA; EZSpyCam, Los Angeles, California, USA) secured to 2 m PVC poles driven into marsh substrate. Cameras and poles were concealed with camouflage duct tape, paint and surrounding vegetation. To prevent swans from abandoning nests due to camera deployment, systems were placed at each nest only after egg-laying had been completed for that nest (Richardson *et al.* 2009). Batteries and digital video recorders (DVRs) were placed in waterproof containers resting on wooden stands 20–30 m from nests, and DVRs were connected to nest cameras via cables submerged in the marsh water. Containers and stands were concealed with camouflaged tarps and marsh vegetation. At 4 nests, wooden stands with batteries and DVRs eventually were relocated adjacent to cameras at nests after the connecting cables were destroyed, seemingly by Muskrats chewing through cables.

Nests were visited every 3–7 days to check nest status, replace batteries and DVR

SD cards, and undertake any maintenance required on the equipment. These research activities prompted swans to leave their nests temporarily. If the eggs were left uncovered by swans, we covered the eggs with ≥ 2 cm nest material to prevent exposure to solar radiation and to mask the presence of eggs until the parental swan returned to the nest. Videography equipment was removed from each nest after the cygnets hatched and left the nest mound.

Measuring thermal environment

An Onset HOBO® micro weather station (Onset, Melrose, Massachusetts, USA) with four smart sensors was used to measure prevailing weather conditions within the marsh: (1) air temperature and relative humidity (Model S-THB-M002 w/M RSA solar radiation shield), (2) wind and gust velocity (Model S-WCF-M003), (3) insolation (Model S-LIB-M003) and (4) precipitation (Model S-RGF-M002). All swan nests used in analytical models were located ≤ 2 km from the weather station, and a single weather station was sufficient to measure the weather conditions at this macro scale. As described below, we then looked at microhabitat features at the nest within the context of the macro scale measurements. The weather station was installed over water in a Spikerush stand at a location approximately central to all monitored nest locations on Lower Red Rock Lake except for one nest at Widgeon Pond. The nest at Widgeon Pond quickly failed following nest predation (Miller & Delehanty 2021a) so we did not install a weather station at Widgeon Pond. The weather station was visited every 1–2 weeks for battery replacement, data download and any necessary equipment maintenance. The weather station was retrieved after all swan nesting was complete.

Effective thermal environment of swan nests and eggs was measured using Thermochron iButton® temperature loggers (Model DS1922L; Maxim Integrated Products, Sunnyvale, California, USA; hereafter, iButtons). Manufacturing specifications included a temperature accuracy of ± 0.5°C between –10 to + 65°C, and an operating range of –40°C to + 85°C. iButtons were programmed to record at 10-min intervals, which represented our subjective decision to best optimise the trade-off between maximising resolution and usage of iButton memory (~64 kb) and minimising disturbance to swan nests by allowing iButtons to last the entire expected swan incubation period (*c.* 35 days).

After egg-laying was complete, three iButtons were placed at each nest monitored in 2020 ($n = 8$; Fig. 2). iButtons also were deployed into nests and mounds in 2021 but were placed to gain preliminary data on thermal attributes outside the scope of this study and those data are not reported here. In 2020, (1) The first iButton was placed within the natural clutch of eggs in the swan nest bowl. This iButton was mounted within a natural but evacuated egg from a Trumpeter or Mute Swan *Cygnus olor*. An iButton mounted within an eggshell represents a "hollow-body model" (Huey 1991). This is useful because, when mounted as a hollow-body, the iButton near-instantaneously records prevailing temperatures (in our case at 10 min intervals), without the temperature lags that would be introduced as a result of the

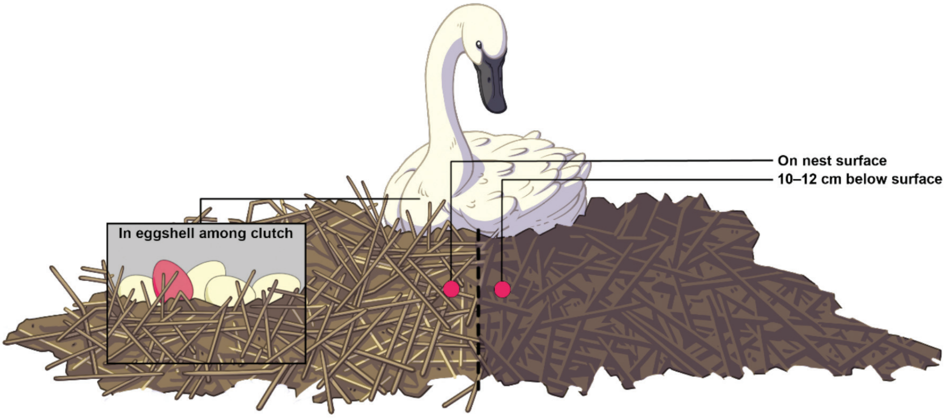

Figure 2. Generalised diagram of a Trumpeter Swan nest with incubating adult, indicating the deployment locations of iButton® temperature loggers in red. Right half of the dashed line represents a cross-section of the nest. iButton locations consisted of: (1) an iButton installed in an empty swan eggshell and deployed within the active clutch, (2) an iButton buried 10–12 cm within the nest vegetation, and (3) an iButton on the surface of the nest exposed to the external environment.

thermal mass of a fluid in a fluid-filled experimental egg. For consistency in measurements as eggs were turned by incubating swans, thin wooden dowels were used to suspend iButtons in the centre of the evacuated eggshells. The hole created to access an egg's interior was patched with a smooth putty and painted to match the colour of the eggshell. (2) The second iButton was placed at a *c.* 10–12 cm depth beneath the nest mound surface, 50–70 cm from the south edge of the nest bowl. This iButton was shielded from the immediate external environment by nest mound vegetation. (3) The third iButton was placed on the surface of the nest, *c.* 50–70 cm from the south edge of the nest bowl. This iButton was exposed to the immediate external environment.

Initially, all iButtons were deployed within evacuated swan eggshells. However, swans proved to be sensitive to the presence of experimental swan eggs placed on the surface of the nest mound outside of the nest bowl as well as any experimental eggs placed within the nest mound that were discovered by swans during nest maintenance. Finding an experimental egg outside of the nest bowl prompted a rapid egg retrieval response by incubating swans (Miller & Delehanty 2021b), with swans persistently rolling experimental eggs containing iButtons into the nest bowl and incorporating them into the natural clutch of eggs. After recognising Trumpeter Swan egg retrieval, we instead coated iButtons for deployment at the nest surface and within the nest mound with a spray-on plastic protectant (Roznik & Alford 2012), and secured the otherwise exposed iButtons to a 20 cm length of wooden dowel to serve as an anchoring spike that was then inserted into the nest vegetation. During nest checks, made every 3–7 days, iButtons that were out of place were repositioned to their original locations. Despite these efforts, swans also persistently moved nest material to cover the iButton placed to measure nest mound surface temperature. Thus, temperatures from these iButtons could not reliably be included in our analyses. Instead, ambient temperature data recorded by the weather station were used to represent prevailing ambient temperature at the nest. iButtons were retrieved after swan cygnets had hatched and left the nest mound.

Treatment of the data

Video data processing

Videography footage was constrained to remove video of so-called "disturbance recesses" (Mitchell & Eichholz 2020) attributable to observer presence, in this case assumed to be from 1 h preceding to 1 h following observer visits. From the remaining videography, measurements were made of nest attendance, incubation recesses in which the swan covered eggs with nest vegetation and incubation recesses in which the swan left eggs exposed to the environment.

Nest attendance was defined as the time that incubating swans were actively interacting with the eggs. Active incubation consisted of swans occupying the nest bowl, either warming, cooling or shielding eggs, although the direction of heat transfer was not visibly indicated by the swans' posture. Nest attendance also included the swans turning eggs, covering and uncovering eggs, and adjusting their bodies during incubation. Incubation recess was defined as the time that incubating swans were not sitting on the nest or actively interacting with the eggs. The start of an incubation recess was defined as the moment when a parental swan left the nest mound and the end of a recess as when a parental swan returned to the nest mound (Bush 2018).

In order to compare nest attendance, and also the duration and frequency of incubation recesses, for successful *versus* unsuccessful nests, videography footage was analysed at 1 min intervals. For analysis with thermal data, videography footage was divided into 10 min intervals, because the thermal devices were logging data every 10 min. Despite this coarser resolution, the choice of 10 min intervals was justified by the longer incubation recesses and extended nest absences typical of Trumpeter Swans (Cooper 1979; Shea 1979; Bush 2018; Mitchell & Eichholz 2020). Within each 1- or 10-min interval, if the majority of time was characterised by nest attendance, that interval was correspondingly classed as nest attendance; otherwise, if the majority of time was characterised by the swan being absent from the nest, that interval was recorded as an incubation recess. There were no 10 min intervals with behavioural data in which nest attendance and incubation recess were equal. Incubation day was estimated by backdating from hatch date, when possible, using the average Trumpeter Swan incubation duration of 35 days.

More detailed measures of swan behaviour were also recorded when the swans were on their nests. These measurements included occurrences of swans incubating with their head down seemingly resting, incubating with their head up seemingly monitoring their surroundings, engaging in nest maintenance while incubating (*e.g.* adjusting or adding new vegetation), engaging in self-maintenance (*e.g.* preening or obtaining food or water during incubation), interacting with the eggs (*e.g.* turning the eggs, or adjusting position on the nest during incubation bouts), and pair-bond interactions (presumably with the male bird). These behaviours were measured as the number of seconds performed but were limited to daylight periods, because there was insufficient resolution in the night-time video footage.

Processing thermal data

Readings from the remote weather station were uploaded using HOBOware Pro software (Windows version 3.7.23; Onset, Melrose, Massachusetts, USA) and for each iButton using 1-wire software (Windows version 4.1.0; Maxim Integrated, Dallas, Texas, USA). Temperature data files were converted within these software packages to an appropriate file format (.cvs) for use with Excel (Windows version 2110; Microsoft, Redmond, Washington, USA) and RStudio (Windows version 2021.09.0-351; R Core Team 2023).

We appreciated that swan nest attendance could be positively associated with environmental temperature deviations either higher or lower than the mean egg temperature achieved during active incubation. To evaluate this, we first estimated the mean temperature of eggs under active incubation from successful nests. This value was derived directly from iButton thermal recorders mounted inside the evacuated swan eggs incorporated into the clutch by the females and incubated together with swan eggs containing live embryos destined to hatch. We considered that this temperature, 35.70°C, provided a representative incubation temperature for egg development. We then calculated the squared deviation of the ambient air temperature from this average egg incubation temperature (Equation 1), and used the squared deviation from average egg incubation temperature to model nest attendance in relation to ambient air temperature.

Equation 1:

$$\textit{Air Temperature Deviation} = \\ (35.70°C - \textit{Air Temperature}°C)^2$$

This process recognised that temperature deviations both below and above average egg incubation temperature could be positively associated with swan nest attendance and that the risk of eggs perishing due to deviations from the suitable temperature likely increases exponentially as deviation from an ideal incubation temperature increases (Scholander *et al.* 1950).

Thermal exchange between ambient air and the nest mound, as well as between ambient air and eggs that were unattended during incubation recess, could parsimoniously be approximated by a simple linear relationship in which heat passively transfers from warmer to cooler points. Hence, and in the absence of temperature measures recorded at the surface of the nest (for reasons described above), untransformed ambient air temperature measurements from the weather station were used to assess the relationships between air temperature and nest and unattended egg temperature.

Humidity in the air was expressed as vapour density, a quantification of the water content of air expressed as g/m^3. Vapour density differs from relative humidity in that vapour density quantifies the total water vapour present in the air independent of air temperature. This allowed examination of prevailing humidity and ambient temperature simultaneously in statistical models while maintaining independence among the predictor variables. Vapour density was calculated by multiplying the percentage relative humidity, recorded by the weather station, by the saturated vapour density (Equation 2), where saturated vapour density represents the maximum possible density of water vapour in air at a given temperature.

Equation 2:

$$\textit{Vapour Density} = \textit{Relative Humidity} \times \textit{Saturated Vapour Density}$$

To estimate saturated vapour density for Equation 2, the polynomial relation with air temperature used by LaBaugh and co-authors (Equation 3; from LaBaugh *et al.* 2018) was calculated:

Equation 3:

$$\textit{Saturated Vapour Density} = 5.018 + 0.32321 \times \textit{Air Temperature} + 0.00818147 \times (\textit{Air Temperature})^2 + 0.00031243 \times (\textit{Air Temperature})^3$$

Data analyses

Trumpeter Swan cygnets hatched successfully at four nests in 2020 and the thermal, environmental and behavioural data from these nests were used to model basic thermal relationships for Trumpeter Swan nesting. An additional four monitored nests failed in 2020. These nests were not included in models and could not be aged with the same reliability as successful nests because nest age could not be backdated from hatch date. Nevertheless, these nests allowed for behavioural and thermal comparisons between successful and unsuccessful swan nests.

Because night-time video observations were consistent with previous observations (Henson & Cooper 1994; Bush 2018) that Trumpeter Swans incubate continuously through the night, swan daytime nesting behaviour was modelled from 30 min prior to sunrise to 30 min following sunset. This prevented undue influence of night-time conditions such as air temperature (< 10°C) and insolation (= 0 W/m^2) when trying to understand the timing and environmental conditions influencing swan daytime incubation recess behaviour.

Generalized linear mixed models (GLMMs) with binomial distributions were generated to describe Trumpeter Swan nest attendance (presence or absence from nest). In addition, linear mixed models (LMMs) were generated to describe Trumpeter Swan nest mound temperature and temperature of eggs while parental swans were on incubation recess. Individual nest (nest ID) and incubation day were included as random factors within models. This allowed for consideration of additive and multiplicative fixed-effects of thermal covariates while accounting for repeated measures at individual nests within and across days. To avoid multicollinearity among model covariates, one correlated variable was removed from any pair of variables with a Pearson's correlation coefficient of $r > 0.65$

(Coates *et al.* 2014). Specifically, gust speed was removed due to its correlation with wind speed (r = 0.982, d.f. = 2146). Gust speed was selected for removal because the gust speed data comprised more values of 0 than the correlated wind speed values.

Fourteen mixed-effects models of swan nest attendance, 14 mixed-effects models of swan nest mound temperature and 14 mixed-effects models of swan egg temperature were constructed. Each set of competing models included a null model consisting only of random effects. For swan nest attendance, fixed effects consisted of air temperature deviation from average egg incubation temperature, vapour density, insolation, precipitation (rainfall and snowfall), wind speed and wind direction. For swan nest mound temperature and for swan egg temperature, fixed effects consisted of ambient air temperature, vapour density, insolation, precipitation, wind speed and wind direction. In all cases, model support was evaluated by using Akaike's Information Criterion with a second-order bias correction for small sample size (AIC_c; Akaike 1973; Anderson 2008). Model weights (ω) were calculated to identify the most explanatory model relative to other models within each model group (Anderson 2008). Additive and interactive (*i.e.* multiplicative) mixed-effects models were both considered, using combinations of two and three factors based on the fixed effects from single-factor models that outperformed the null model.

Mean nest attendance between successful and unsuccessful nests was compared using a two-sample t-test. Incubation recess frequency, incubation recess duration and mean egg incubation temperature between successful and unsuccessful nests were compared using one-way nested ANOVAs to detect any strong associations despite the small sample sizes.

All calculations and statistical procedures were performed in RStudio (R Core Team 2023) using the packages "lme4" and "AICcmodavg" for functionality associated with mixed-effects modelling, and the package "dplyr" for functionality associated with nested analysis of variance.

Results

Thirteen Trumpeter Swan nests were monitored during the 2020 (n = 8) and 2021 (n = 5) breeding seasons. Eight nests (61.5%) were successful, with an average clutch size of 4.6 eggs and an average egg hatching rate of 76.4%. Five nests (38.5%) were unsuccessful, with an average clutch size of 4.0 eggs (Table 1). One unsuccessful nest in 2020 (Table 1: Nest 12) was abandoned by the adults following partial nest depredation by an unknown egg predator (Miller & Delehanty 2021a). This occurred prior to equipment installation, and behavioural data from this nest was excluded from all calculations. For the remaining 7 nests in 2020, > 4,100 h of simultaneous videography and thermal records were observed, with an average of 596.05 h (range = 345.60–869.52 h) per nest. Across 2020–2021, four nests were unsuccessful for unknown reasons.

In successful nests during active incubation, Trumpeter Swans maintained a daily average egg incubation temperature of 35.70 ± 0.27°C ($\bar{x}$ ± s.e., range = 35.22–36.43°C), as measured by thermal data from iButtons from within the clutch. This value

Table 1. Summary of Trumpeter Swan nesting attempts in 2020–2021 (n = 13), giving the outcome (fate), location, number of eggs laid, number of eggs hatched and percentage of eggs hatched. All nests were observed at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA.

Nest fate	Year	Location	No. eggs laid	No. eggs hatched	% Eggs hatched
Successful					
1	2020	Lower Red Rock Lake	4	3	75.0
2	2020	Lower Red Rock Lake	6	3	50.0
3	2020	Lower Red Rock Lake	5	3	60.0
4	2020	Lower Red Rock Lake	3	2	66.7
5	2021	Lower Red Rock Lake	4	4	100.0
6	2021	Lower Red Rock Lake	5	3	60.0
7	2021	Lower Red Rock Lake	3	3	100.0
8	2021	Wigeon Pond	7	7	100.0
Unsuccessful					
9	2020	Lower Red Rock Lake	3	0	0.0
10	2020	Lower Red Rock Lake	5	0	0.0
11	2020	Lower Red Rock Lake	4	0	0.0
12	2020	Wigeon Pond	7	0	0.0
13	2021	Lower Red Rock Lake	1	0	0.0

served as a reference temperature describing average egg incubation temperature in successful nests and was used for calculating ambient air temperature deviations from average incubation temperature. Interestingly, swans maintained night-time egg temperatures ($\bar{x} \pm$ s.e. = 35.41 ± 0.19°C, range = 35.12–36.48°C) similar to daytime egg temperatures, but these data were not included in further analyses due to established model parameters.

During the study period, 634 Trumpeter Swan incubation recesses were observed. Successful swans (n = 4) took 2.87 ± 1.60 recesses/day ($\bar{x} \pm$ s.e., range = 0–6 recesses/day) and unsuccessful swans (n = 3) took 3.48 ± 2.03 recesses/day ($\bar{x} \pm$ s.e.; range = 0–7 recesses/day) during incubation. Recesses lasted 52.16 ± 21.88 min ($\bar{x} \pm$ s.e., range = 10.02–137.46 min) for successful swans and 74.92 ± 60.99 min ($\bar{x} \pm$ s.e., range = 12.29–358.61 min) for unsuccessful swans. A majority (n = 623; 98.26%) of recesses occurred during the day, from 30 min prior to sunrise to 30 min following sunset. Eggs were covered with nest material during most (n = 621; 97.95%) recesses.

Mean nest attendance differed significantly between successful and unsuccessful swans with greater incubation constancy for successful nests (t_5 = 2.44, $P < 0.05$; Table 2). Recesses tended to be less frequent among successful nests than unsuccessful nests, but this was not significant ($F_{1,5}$ = 3.77, n.s.; Table 3). Recess duration was significantly shorter among successful nests than unsuccessful nests ($F_{1,5}$ = 37.28, $P < 0.05$; Table 3).

Eleven mixed-effects models explaining Trumpeter Swan nest attendance significantly outperformed the null model under the

Table 2. Mean (± s.e.) percentage nest attendance time recorded for Trumpeter Swans nesting at Red Rock Lakes National Wildlife Refuge in 2020. Differences in nest attendance were found between nests that failed and nests where one or more cygnets hatched successfully (two-sample t-test: $t = 3.42$, d.f. = 5, $P = 0.021$).

Nest attendance	**Mean (± s.e.)**	***n***
Successful	95.20 ± 0.64%	4
Unsuccessful	86.46 ± 3.53%	3
Total	**91.45 ± 2.22%**	**7**

Table 3. Mean (± s.e.) frequency and duration of incubation recesses by Trumpeter Swans nesting at Red Rock Lakes National Wildlife Refuge in 2020. Comparisons were made between nests that failed and nests where one or more cygnets hatched successfully. No differences in incubation recess frequency were observed, but differences in incubation recess duration were observed (one-way nested ANOVA, $\alpha = 0.05$).

	$\bar{x}$ ± s.e.	**$F_{1,5}$**	***P* value**
Recess Frequency			
Successful	2.87 ± 1.60 recesses/day		
Unsuccessful	3.48 ± 2.03 recesses/day		
Total	**3.08 ± 1.78 recesses/day**	3.77	0.056
Recess Duration			
Successful	52.16 ± 21.88 min		
Unsuccessful	74.92 ± 60.99 min		
Total	**60.12 ± 41.70 min**	37.28	< 0.001

criterion that AIC_c values two or more units less than the null demonstrated superior model performance (Table 4). The best performing model for nest attendance was a three-way interactive model consisting of air temperature deviation (positive association), insolation (positive association), and vapour density (slightly negative association; Table 4, Fig. 3). This model garnered 100.0% of the weight of evidence (*i.e.* $\omega = 1.00$).

For Trumpeter Swan nest mound temperature, eleven mixed-effects models significantly outperformed the null model. The best performing model consisted of

Table 4. General Linear Mixed Models (GLMMs; family = binomial) describing Trumpeter Swan nest attendance relative to thermal environmental covariates. The null model consists solely of random effects (swan nest, incubation day). K = number of parameters; AIC_c = Akaike's Information Criterion with second-order bias correction; ΔAIC_c = difference between AIC_c values of models; ω = model weight; and Cum. ω = cumulative weight of models.

Model	K	AIC_c	ΔAIC_c	ω	**Cum.** ω
Air Temp. Dev.[a] * Vapour Density[b] * Insolation[c]	10	3958.02	0.00	1.000	1.000
Air Temp. Dev. + Vapour Density + Insolation	6	4006.79	48.76	0.000	1.000
Air Temp. Dev. * Insolation	6	4015.58	57.55	0.000	1.000
Air Temp. Dev. + Insolation	5	4021.13	63.10	0.000	1.000
Air Temp. Dev. * Vapour Density	6	4021.57	63.55	0.000	1.000
Vapour Density * Insolation	6	4022.15	64.13	0.000	1.000
Vapour Density + Insolation	5	4024.24	66.22	0.000	1.000
Air Temp. Dev.	4	4030.25	72.22	0.000	1.000
Insolation	4	4038.98	80.96	0.000	1.000
Air Temp. Dev. + Vapour Density	5	4061.34	103.32	0.000	1.000
Vapour Density	4	4089.98	131.96	0.000	1.000
Null	3	4116.31	158.29	0.000	1.000
Precipitation[d]	4	4117.80	159.77	0.000	1.000
Wind Speed[e]	4	4120.84	162.82	0.000	1.000
Wind Direction[f]	4	4122.57	164.55	0.000	1.000

[a] Air Temp Dev. = square deviation of air temperature relative to mean incubation temperature (°C); [b] Vapour Density = relative mass of water relative to air; [c] Insolation = instantaneous solar radiation per unit area (W/m^2); [d] Precipitation = accumulated precipitation (rain and snow, mm); [e] Wind Speed = instantaneous wind speed (m/sec); [f] Wind Direction = polar coordinate relative to °N.

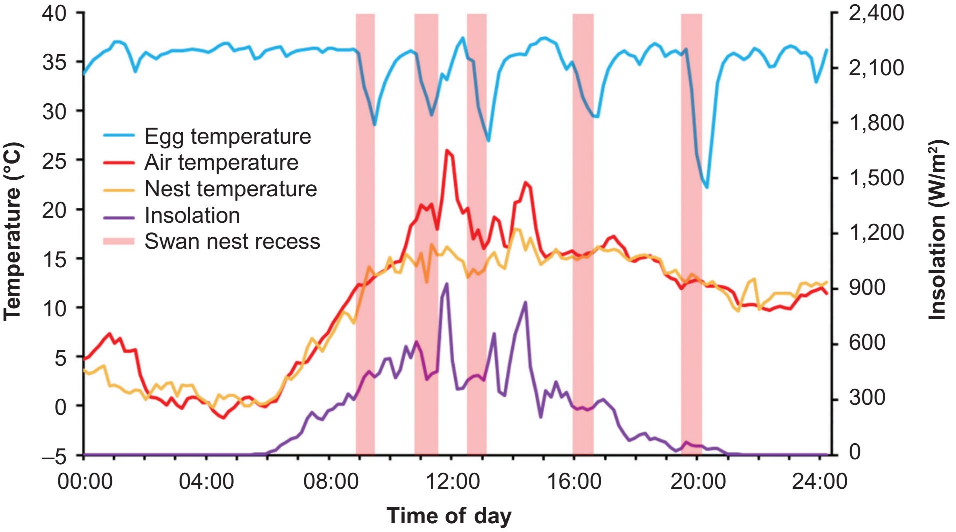

Figure 3. Temperature (°C) and insolation (W/m^2) relative to time elapsed across 24 h (00:00–24:00 h) at an active Trumpeter Swan nest at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA in May 2020. Vertical pink bars indicate periods where the incubating swan was on an incubation recess.

the 3-way interaction of air temperature (positive association), insolation (positive association) and vapour density (positive association) garnering a model weight of $\omega = 0.672$ (Table 5). The remainder of the weight of evidence (32.8%) was carried by a model consisting of the interaction between air temperature (positive) and insolation (positive).

For Trumpeter Swan egg temperature during incubation recesses, eleven mixed-effects models significantly outperformed the null model. The best performing model, with weight of evidence $\omega = 1.000$, consisted of the interactions between air temperature (positive association) and vapour density (slightly positive association; Table 6). Contrary to the models explaining nest attendance and nest temperature, the least explanatory covariate for egg temperature during incubation recesses was insolation.

Swans engaged in many behaviours while actively incubating, as described by the percentage of the daytime period engaged in secondary behaviours while simultaneously incubating. Specifically, swans rested with their heads down ($\bar{x}$ = 34.61% ± 2.11 s.e.), engaged in nest maintenance ($\bar{x}$ = 25.13% ± 2.91 s.e.), monitored their surroundings ($\bar{x}$ = 21.71% ± 4.59 s.e.), performed self-maintenance ($\bar{x}$ = 12.41% ± 2.89 s.e.), interacted with eggs ($\bar{x}$ = 6.10% ± 1.42 s.e.), and engaged in pair bonding postures and movement with the presumed male swan ($\bar{x}$ ± s.e. < 0.01%; Fig. 4).

Discussion

Daytime incubation behaviour in Trumpeter Swans was strongly influenced by

Table 5. Linear Mixed Models (LMMs) describing Trumpeter Swan nest temperature relative to thermal environmental covariates. The null model consists solely of random effects (swan nest, incubation day). K = number of parameters; AIC_c = Akaike's Information Criterion with second-order bias correction; ΔAIC_c = difference between AIC_c values of models; ω = model weight; and Cum. ω = cumulative weight of models.

Model	K	AIC_c	ΔAIC_c	ω	Cum. ω
Air Temp.[a] * Vapour Density[b] * Insolation[c]	10	44400.99	0.00	0.672	0.672
Air Temp. * Insolation	6	44402.42	1.43	0.328	1.000
Air Temp. + Insolation	6	44436.42	35.43	0.000	1.000
Air Temp. + Vapour Density + Insolation	6	44470.98	69.99	0.000	1.000
Air Temp. * Vapour Density	5	44479.43	78.44	0.000	1.000
Air Temp. + Vapour Density	5	44492.99	92.00	0.000	1.000
Air Temp.	4	44505.27	104.28	0.000	1.000
Insolation * Vapour Density	6	44531.22	130.23	0.000	1.000
Insolation	6	44542.52	141.53	0.000	1.000
Insolation + Vapour Density	5	44551.73	150.74	0.000	1.000
Vapour Density	6	44623.55	222.56	0.000	1.000
Null	5	44629.83	228.84	0.000	1.000
Wind Speed[d]	4	44635.50	234.51	0.000	1.000
Precipitation[e]	4	44665.95	264.96	0.000	1.000
Wind Direction[f]	4	44665.95	264.96	0.000	1.000

[a] Air Temp. = instantaneous air temperature (°C); [b] Vapour Density = relative mass of water relative to air; [c] Insolation = instantaneous solar radiation per unit area (W/m^2); [d] Wind Speed = instantaneous wind speed (m/sec); [e] Precipitation = accumulated precipitation (rain and snow, mm); [f] Wind Direction = polar coordinate relative to °N.

environmental thermal factors. Model results provided strong evidence that three environmental thermal factors were associated with swan incubation: ambient temperature, insolation and vapour density. Considered as a three-way interaction, these three covariates accounted for 100% of the model weight when evaluating nest attendance relative to the thermal environment. This three-way interaction means that all three covariates can be acting simultaneously and that the influence of any one covariate at a given moment is contingent on the prevailing values of the other two covariates at that moment. This makes biological sense because the egg is

Table 6. Linear Mixed Models (LMMs) describing Trumpeter Swan egg temperature relative to different thermal environmental covariates. The null model consists solely of random effects (swan nest, incubation day). K = number of parameters; $\mathrm{AIC_c}$ = Akaike's Information Criterion with second-order bias correction; $\Delta\mathrm{AIC_c}$ = difference between $\mathrm{AIC_c}$ values of models, ω = model weight; and Cum. ω = cumulative weight of models.

Model	K	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	ω	Cum. ω
Air Temp.[a] * Vapour Density[b]	6	21888.34	0.00	1.000	1.000
Air Temp. * Vapour Density * Precipitation[c]	10	21905.06	16.72	0.000	1.000
Air Temp. + Vapour Density + Precipitation	6	21939.19	50.85	0.000	1.000
Air Temp. + Vapour Density	5	21944.16	55.83	0.000	1.000
Air Temp. + Precipitation	5	21989.15	100.81	0.000	1.000
Air Temp. * Precipitation	6	21995.04	106.71	0.000	1.000
Air Temp.	4	21998.30	109.97	0.000	1.000
Vapour Density + Precipitation	5	22006.28	117.95	0.000	1.000
Vapour Density * Precipitation	6	22007.85	119.52	0.000	1.000
Vapour Density	4	22048.54	160.20	0.000	1.000
Precipitation	4	22050.11	161.77	0.000	1.000
Null	3	22059.28	170.94	0.000	1.000
Wind Speed[d]	4	22073.99	185.65	0.000	1.000
Wind Direction[e]	4	22076.66	188.33	0.000	1.000
Insolation[f]	4	22083.52	195.18	0.000	1.000

[a]Air Temp. = instantaneous air temperature (°C); [b]Vapour Density = relative mass of water relative to air; [c]Precipitation = accumulated precipitation (rain and snow, mm); [d]Wind Speed = instantaneous wind speed (m/sec); [e]Wind Direction = polar coordinate relative to °N; [f]Insolation = instantaneous solar radiation per unit area (W/m^2).

subject to the totality of the thermal environment at all times and, adaptively, the adult swan's responsiveness must be to the eggs' total thermal exposure.

Within the context of a three-way interaction, the magnitude of the effect of one covariate on incubation behaviour at any moment can only be understood relative to the values of the other covariates at that moment; however, the sign (positive or negative) of the one covariate within the linear model indicates the direction of influence of that covariate. This gives important biological insight into environmental effects on swan incubation behaviour. For example, we found that the degree of deviation of ambient temperature from average egg incubation temperature was positively associated with incubation. Swans incubated more under cool daytime

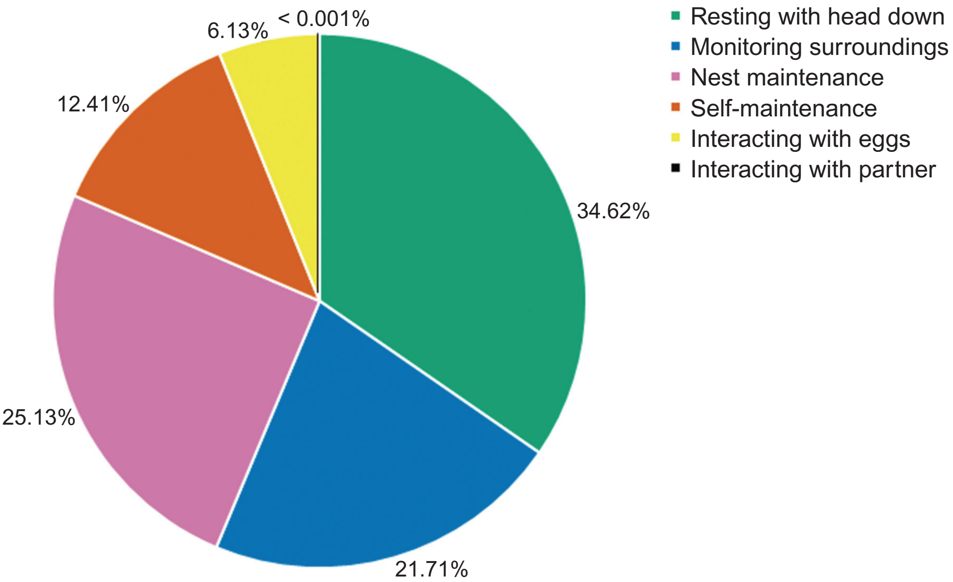

Figure 4. Percentage of time spent by Trumpeter Swans (x̄; *n* = 7 birds) on different behaviours during active incubation at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA. Behaviours observed included occurrences of swans resting with their heads down, monitoring their surroundings, nest maintenance (*e.g.* adjusting or adding new vegetation), self-maintenance (*e.g.* preening or obtaining food or water during incubation), interacting with eggs (*e.g.* turning the eggs or adjusting their position in the nest during incubation bouts) and pair-bond interactions with the presumed male.

conditions. Similarly, insolation showed a positive relationship with incubation. Swans incubated more under high sun exposure, physically protecting eggs by shading them with their bodies. Lastly, vapour density was negatively associated with incubation. When air was drier, swans incubated more, perhaps protecting eggs from undue water loss by creating still and humid air within the nest cup microenvironment.

It is well understood that egg cooling can dampen embryonic development, but it is also true that unregulated environmental heat inputs jeopardise embryos within unattended eggs through potentially lethal overheating. Swans consistently incubated through cold night-time temperatures, as others have observed (Bush 2018), then tended to delay taking daytime incubation recesses until ambient temperature warmed in the morning, also observed by others (Bush 2018). Similarly, warm ambient temperatures during late afternoon also have been associated with incubation recesses (Bush 2018), and we noted but did not quantify a similar pattern in this study. Importantly, swans also actively incubated during hot periods of the day and showed a strong propensity to return quickly to the nest upon abrupt increases in solar radiation such as occurs when the sun appeared from behind moving clouds. As an example, this can be seen in Fig. 3, which presents a representative day in which thermal conditions change and swans make behavioural adjustments. Solar radiation spikes, for example, are quickly followed by cessation of incubation recesses. We interpret this as parental swans returning to nests to protect eggs from excessive radiative warming by the parent shielding their eggs with their bodies. This effect is quantified more universally by the inclusion of a positive insolation effect in the most explanatory models describing swan incubation patterns.

Further evidence that incubating swans are sensitive to insolation can be seen in two ways. When modelling egg temperature during recesses, insolation was not predictive even though the nest mound warmed under solar radiation. This superficially puzzling result is explained by the fact that swans virtually always covered their eggs, shading them, prior to incubation recess. Secondly, swans returned to their nests if insolation increased while on recess. In other words, solar radiation warms the nest mound, in general, but swans use behaviour to shield their eggs from excessive solar radiation through a combination of covering their eggs while on recess and shielding their eggs with their own body when actively incubating.

Perhaps surprisingly, swans exhibited a measurable sensitivity to vapour density. Swans were more likely to incubate when vapour density was lower, which is to say that the air was dryer. We do not fully understand this relationship. However, dry air would tend to be associated with more rapid water loss from eggs. By incubating when vapour density is low, swans likely are creating a more humid microenvironment for the eggs beneath their bodies, perhaps conserving the eggs' water contents to last through the prolonged incubation period. We appreciated that with daily warming, local air movements may have tended to bring warmer and dryer terrestrial air over the marsh surface. In fact, a negative association between vapour density and wind speed ($r^2 = 0.213$, d.f. = 1, $P < 0.001$; Supporting Materials Fig. S1) was detected in a *post hoc* analysis. This implies that dry air tended to move over the marsh. However, vapour density, not wind speed, was retained in the models because vapour density was more explanatory. A small portion of the variation in wind speed could be predicted by time of day ($r^2 = 0.105$, d.f. = 1, $P < 0.05$) in *post hoc* analysis. The valley air usually warmed as the day progressed, generating afternoon winds. Nevertheless, swan incubation appeared to be negatively associated with vapour density *per se* rather than the speed of moving air.

Trumpeter Swans maintained eggs at an average temperature of 35.70 ± 0.27°C, a temperature consistent with observations of other bird species (Rahn 1991). To our knowledge, this is the first report of the Trumpeter Swan egg incubation temperature. Ambient air temperature exceeding the average incubation temperature was never observed in 2020. While parental swans were on incubation recess, the temperature of the unattended eggs in the clutch decreased (Fig. 3) and did so relative to ambient air temperature. Importantly, peaks in insolation could result in substantial increase in egg temperature independent of ambient air temperature. This is supported empirically by a pilot study that we conducted in 2019, where two swan egg models were deployed into a swan nest mound after swans completed nesting. One egg was placed on the surface of the nest bowl exposed to the external environment; another was buried in the nest vegetation, shielded from the external environment. The exposed egg consistently reached temperatures much greater than average ambient temperatures (Fig. 5), attributable to significant radiative heat gain. This reinforces our conclusions that swan eggs are susceptible to lethal overheating without females covering eggs during recesses and shielding eggs with their bodies when actively incubating. Swan egg temperature also showed some propensity to increase with increasing vapour density. With greater moisture in the air, the potential for evaporative heat loss decreases, resulting in a higher heat retention within the swan egg.

Nest thermal patterns provided insight into how parental swans generally cope with competing demands during incubation. Trumpeter Swans incubate eggs by covering them with their large, webbed feet (Cooper 1979; Lumsden 2002), which leaves the eggs exposed to the nest bowl floor as a secondary conductive surface. In general, nest mound temperatures were much less variable than air temperature (Fig. 3). Nest mound temperature flux was positively associated with air temperature and solar radiation. Typically, nests would moderate

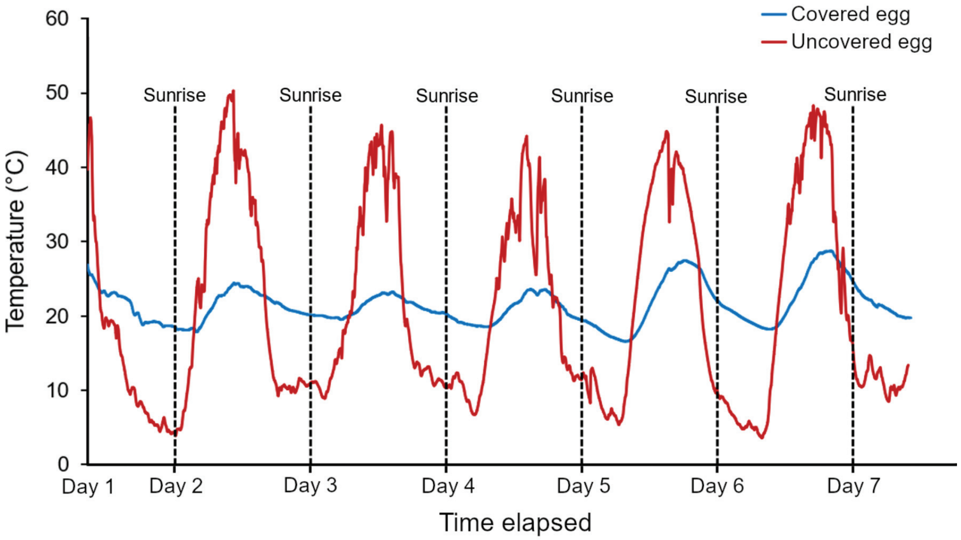

Figure 5. Egg temperature (°C) relative to time elapsed (min) at Grays Lake National Wildlife Refuge, southeast Idaho, USA between 1–7 July 2019, depicting an unattended Trumpeter Swan egg model covered with nest vegetation during recess and an unattended egg model uncovered in the nest bowl. Vertical dashed lines indicate daily sunrise.

spikes in temperature and insolation and would retain warmth gained during the day well into the night. The swan nest bowl appeared to be an important source of conductive heat exchange to the eggs, providing a more stable microenvironment than the environment immediately surrounding the nest. The act of swans covering their eggs with nest vegetation prior to recess would further stabilise the rate of heat loss or gain from eggs during recess. Swan nest temperature also showed some propensity to increase with increasing vapour density. Similar to egg temperature, with greater moisture in the air, the potential for evaporative heat loss decreases, resulting in a higher heat retention within the swan nest mound.

Trumpeter Swans in this study had an average nest attendance (91.45% ± 2.22%) similar to previously reported values for wild swans (Shea 1979; Henson & Cooper 1993; Bush 2018; Mitchell & Eichholz 2020). In successful nests, swans engaged in daytime recesses of variable length but engaged in fewer and shorter recesses than unsuccessful swans. More frequent and longer incubation recesses signalled forthcoming nest failure. This pattern has two reasonable interpretations. Inability to sustain high incubation constancy may have caused nest failure. Alternatively, if nest failure somehow was more likely, swans may have reduced their investment in the clutch. Distinguishing between these mechanisms will require further research.

Following nest failure, all remaining unhatched eggs from this study in 2020 were collected by U.S. Fish and Wildlife Service personnel for an unrelated study. They found that within all unhatched Trumpeter Swan eggs from failed nests (*n* = 15), no significant development had taken place (Andrea Kristof, USFWS, pers. comm.). Future investigation is needed to understand what female characteristics may contribute to nest failure. For example, age, experience and female body condition may contribute to a swan's inability to complete incubation.

Nest predation has been suggested as a primary influence on incubation patterns in birds (Conway & Martin 2000a), but this seems unlikely for Trumpeter Swans. Species whose incubation strategies are characterised by predator avoidance tend to construct discreet, sheltered nests and take consistent, often crepuscular incubation recesses (Wiebe & Martin 1997; Coates & Delehanty 2008). Trumpeter Swans by contrast are conspicuous white birds that construct large, exposed nests. Paired swans engage in social displays from the nest platform. We posit that incubating swans select for daytime recesses in response to the thermal environment rather than predator avoidance. Incubating adults may optimise their energy expenditures by leaving the nest to engage in necessary self-maintenance when conditions are moderate, optimising embryo development (Drent 1973; Turner 1994), while quickly returning to active incubation to rewarm eggs or to prevent overheating.

Swans at RRLNWR typically select nest locations within lake and marsh habitat. One instance of nest depredation was observed during the two-year study, but this occurred prior to equipment installation at the nest. Possible egg predators based on previous reports include Common Raven *Corvus* *corax*, Raccoon *Procyon lotor*, Wolverine *Gulo luscus*, Black Bear *Ursus americanus*, Brown Bear *Ursus arctos*, Coyote *Canis latrans*, Grey Wolf *Canis lupus* or North American River Otter *Lontra canadensis* (Mitchell & Eichholz 2020). The nest at Widgeon Pond that was depredated was close to forest edge habitat with greater vegetation coverage, including willow stands, making the occurrence of possible nest predators more likely.

Trumpeter Swan management recommendations

One outcome of our monitoring and measurements is that we were able to identify ways in which thermal considerations can be incorporated into management recommendations. We recommend that visits to swan nests by wildlife managers and researchers are timed to minimise exposure of eggs to environmental thermal extremes including heat stressors. Nest visits should be timed to occur during somewhat thermally neutral periods as might occur during mid-morning and late afternoon, when weather is favourable. Trumpeter Swans should not be disturbed at night, during precipitation, or under extreme sunny, hot conditions. Investigators should always cover swan eggs with nest vegetation prior to leaving a nest, recognising disturbance recesses (Mitchell & Eichholz 2020) in which parental swans leave the nest rapidly without covering eggs to avoid human encounters. Investigators should approach nests slowly and conspicuously to give the swans a chance to cover their eggs before departing the nests. When possible, duration of nest visits should not exceed normal recess duration, approximately 1 h. Artificial nest structures placed in marshes to assist swans should include sufficient vegetation or other material to serve as a thermal mass that moderates nest temperature fluctuation as does a natural nest. Additionally, because Trumpeter Swans in the future may encounter increased exposure to unfavourable thermal conditions during the breeding season, concordant with global climate warming of 3.0°C or more over the next century (Girvetz *et al.* 2009), managers should give renewed attention to the thermal environment available to breeding swans.

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References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle, *In* B.N. Petrov & F. Csaksi, (eds.), *Second International Symposium on Information Theory,* pp. 267–281. Akademiai Kiado, Budapest, Hungary.

Anderson, D.R. 2008. *Model Based Inferences in the Life Sciences*. Springer Science, New York, USA.

Banko, W.E. 1960. *The Trumpeter Swan: Its History, Habits, and Population in the United States.* North

American Fauna, 63. United States Fish and Wildlife Service, Washington, United States.

Bush, D.A. 2018. Incubation behavior and genetic attributes of Trumpeter Swans restored to Grays Lake National Wildlife Refuge. M.Sc. thesis, Idaho State University, Pocatello, USA.

Chabreck, R.H. 1973. Temperature variation in nests of the American Alligator. *Herpetologica* 29: 48–51.

Coates P.S. & Delehanty D.J. 2008. Effects of environmental factors on incubation patterns of Greater Sage-Grouse. *Condor* 110: 627–638.

Coates, P.S., Casazza, M.L., Brussee, B.E., Ricca, M.A., Gustafson, K.B., Overton, C.T., Sanchez-Chopitea, E., Kroger, T., Mauch, K., Niell, L., Howe, K, Gardner, S., Espinos, S. & Delehanty, D.J. 2014. Spatially explicit modeling of Greater Sage-grouse (*Centrocercus Urophasianus*) habitat in Nevada and northeastern California: a decision-support tool for management. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia, USA.

Cooper, J.A. 1979. Trumpeter Swan nesting behaviour. *Wildfowl* 30: 55–71.

Conway, C.J. & Martin, T.E. 2000a. Evolution of passerine incubation behavior: influence of food, temperature, & nest predation. *Evolution* 54: 670–685.

Conway, C.J. & Martin, T.E. 2000b. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* 11: 178–188.

Dahl, T.E. & Allord, G.J. 1996. *History of Wetlands in the Conterminous United States*. U.S. Geological Survey Water Supply Paper No. 2425. USGS, Reston, Virginia, USA. Available at https://water.usgs.gov/nwsum/WSP2425/history.html (last accessed 9 August 2024).

Deeming, D.C. 2002. Behaviour patterns during incubation. *In* D.C. Deeming (ed.), *Avian Incubation: Behaviour, Environment, and Evolution,* pp. 63–87. Oxford University Press, Oxford, UK.

Deeming, D.C. & Ferguson, M.J.W. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. *In* D.C. Deeming & M.J. Ferguson (eds.), *Egg Incubation*, pp. 147–172. Cambridge University Press, Cambridge, UK.

Deeming, D.C. & Mainwaring, M.C. 2015. Functional properties of nests. *In* D.C. Deeming & S.J. Reynolds (eds.), *Nests, Eggs, and Incubation: New Ideas about Avian Reproduction*, pp. 29–49. Oxford University Press, Oxford, UK.

Deeming, D.C. & Reynolds, S.J. (eds.). 2015. *Nests, Eggs, and Incubation: New Ideas About Avian Reproduction*. Oxford University Press, Oxford, UK.

De Vos, A. 1964. Observations on the behaviour of captive Trumpeter Swans during the breeding season. *Ardea* 52: 166–189.

Drent, R.H. 1973. The natural history of incubation. *In* D.S. Farner (ed.), *Breeding Biology of Birds*, pp. 262–311. National Academy of Sciences, Washington D.C., USA.

DuRant, S.E., Hopkins, W.A., Hawley, D.M. & Hepp, G.R. 2012. Incubation temperature affects multiple measures of immunocompetence in young wood ducks (*Aix sponsa*). *Biology Letters* 8: 108–111.

Fischer, H. 1976. Red Rocks Refuge, valley of the swans. *Montana Outdoors* (Jan/Feb): 35–41. Montana Fish, Wildlife & Parks, Montana, USA.

French, N.A. 1997. Modeling incubation temperature; the effects of incubator design, embryonic development, & egg size. *Poultry Science* 76: 124–133.

Frith, H.J. 1959. Breeding of the mallee-fowl, *Leipoa ocellata* Gould (Megapodiidae). *CSIRO Wildlife Research* 4: 31–60.

Gale, R.S., Garton, E.O. & Ball, I.J. 1987. *The History, Ecology, and Management of the Rocky Mountain Population of Trumpeter Swans.* U.S. Fish and Wildlife Service, Montana Cooperative Wildlife Research Unit, Missoula, USA.

Girvetz, E.H., Zganjar, C., Raber, G.T., Maurer, E.P., Kareiva, P. & Lawler, J.J. 2009. Applied climate-change analysis: the climate wizard tool. *PLoS One* 4: e8320.

Groves, D.J. 2017. *The 2015 North American Swan Survey. A Cooperative North American Survey*. U.S. Fish & Wildlife Service, Office of Migratory Bird Management, Juneau, Alaska, USA.

Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scandinavica* 19: 97–110.

Hansen, H.A. 1973. Trumpeter Swan management. *Wildfowl* 24: 27–32.

Hansen, H.A., Shepard, P.E.K., King, J.G. & Troyer, W.A. 1971. The Trumpeter Swan in Alaska. *Wildlife Monographs* 26: 1–83.

Henson, P. & Cooper, J.A. 1993. Trumpeter Swan incubation in areas of differing food quality. *Journal of Wildlife Management*, 57: 709–716.

Henson, P. & Cooper, J.A. 1994. Nocturnal behavior of breeding Trumpeter Swans. *The Auk* 111: 1013–1018.

Henson, P. & Grant, T.A. 1992. Brown Bear, *Ursus arctos middendorfi*, predation on a Trumpeter Swan, *Cygnus buccinator*, nest. *Canadian Field-Naturalist* 106: 128–130.

Hepp, G.R., Kennamer, R.A. & Johnson, M.H. 2006. Maternal effects in Wood Ducks: incubation temperature influences incubation period and neonate phenotype. *Functional Ecology* 20: 308–314.

Huey, R.B. 1991. Physiological consequences of habitat selection. *The American Naturalist* 137: S91–S115.

LaBaugh, J.W., Rosenberry, D.O., Mushet, D.M., Neff, B.P., Nelson, R.D. & Euliss, Jr., N.H. 2018. Long-term changes in pond permanence, size, & salinity in Prairie Pothole Region wetlands: the role of groundwater-pond interaction. *Journal of Hydrology: Regional Studies* 17: 1–23.

Lumsden, H.G. 2002. Laying and incubation behavior of captive Trumpeter Swans. *Waterbirds*: 293–295.

Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. *In* T.C. Carter & B.M. Freeman (eds.)*, The Fertility and Hatchability of the Hen's Egg*, pp. 143–176. Oliver & Boyd, Edinburgh, Scotland.

Mainwaring, M.C. & Hartley, I.R. 2013. The energetic costs of nest building birds. *Avian Biology Research* 6: 12–7.

Martin, T.E., Scott, J. & Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267: 2287–2293.

Meijerhof, R. & Van Beek, G. 1993. Mathematical modelling of temperature & moisture loss of hatching eggs. *Journal of Theoretical Biology* 165: 27–41.

Miller, P.C. & Delehanty, D.J. 2021a. Active Trumpeter Swan nest on an active muskrat lodge. *Western North American Naturalist* 81: 462–465.

Miller, P.C. & Delehanty, D.J. 2021b. Egg retrieval by Trumpeter Swans. *Western Birds* 52: 266–286.

Mitchell, C.D. 2011. Trumpeter Swan (*Cygnus buccinator*) cygnet survivorship at Grays Lake National Wildlife Refuge, Idaho: pilot study report. U.S. Fish and Wildlife Service, Wayan, Idaho, USA.

Mitchell, C.D. & Eichholz, M.W. 2020. Trumpeter Swan (*Cygnus buccinator*), version

1.0. *In* S.M. Billerman, B.K. Keeney, P.G. Rodewald & T.S. Schulenberg (eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA.

Moreno, J. & Carlson, A. 1989. Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavia* 20: 123–128.

Mowbray, T.B., Ely, C.R., Sedinger, J.S. & Trost, R.E. 2020. Canada Goose (*Branta canadensis*), version 1.0. *In* P.G. Rodewald (ed.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA.

Rahn, H.E. 1991. Why birds lay eggs. *In* D.C. Deeming & M.W.J. Ferguson (eds.), *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*, pp. 345–360. Cambridge University Press, Cambridge, UK.

Reid, J.M., Monaghan, P. & Ruxton, G.D. 2002. Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). *Behavioral Ecology and Sociobiology* 51: 255–261.

Richardson, T.W., Gardali, T. & Jenkins, S.H. 2009. Review and meta analysis of camera effects on avian nest success. *Journal of Wildlife Management* 73: 287–293.

Roznik, E.A. & Alford, R.A. 2012. Does waterproofing Thermochron iButton dataloggers influence temperature readings? *Journal of Thermal Biology* 37: 260–264.

R Core Team 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria

Scholander, P.F., Hock, R., Walters, V. & Irving, L. 1950. Adaptation to cold in arctic and tropical mammals in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin* 99: 259–271.

Shea, R.E. 1979. The ecology of Trumpeter Swans in Yellowstone National Park and vicinity. M.Sc. thesis, University of Montana, Missoula, USA.

Skutch, A.F. 1962. The constancy of incubation. *Wilson Bulletin* 74: 115–152.

Smith, H.G. & Montgomerie, R.D. 1992. Male incubation in barn swallows: the influence of nest temperature and sexual selection. *Condor* 94: 750–759.

Staton, M.A. & Dixon, J.R. 1977. Breeding biology of the Spectacled Caiman, *Caiman crocodilus crocodilus* in the Venezuelan Llanos. U.S. Fish & Wildlife Service, Wildlife Research Report No. 5. U.S. Fish & Wildlife Service, Washington DC, USA.

Tinbergen, J.M. & Williams, J.B. 2002. Energetics of incubation. *In* D.C. Deeming (ed.), *Avian Incubation: Behaviour, Environment, and Evolution*, pp. 299–313. Oxford University Press, Oxford, UK.

Turner, J.S. 1994. Time and energy in the intermittent incubation of birds' eggs. *Israel Journal of Ecology and Evolution* 40: 519–540.

Turner, J.S. 2002. Maintenance of egg temperature. *In* D.C. Deeming (ed.), *Avian Incubation: Behaviour, Environment, and Evolution,* pp. 119–142. Oxford University Press, Oxford, UK.

Webb, D.R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89: 874–898.

Webb, G.J., Messel, W.H. & Magnusson, W.E. 1977. The nesting of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* (1977): 238–250.

Wiebe K.L. & Martin K. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. *Wildlife Biology* 3: 219–227.

Winkler, D.W., Billerman, S.M. & Lovette, I.J. 2020. Ducks, geese, and waterfowl (Anatidae), version 1.0. *In* S.M. Billerman, B.K. Keeney, P.G. Rodewald & T.S. Schulenberg (eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA.

Appendix 1. Swan incubation and avian egg heat exchange.

A freshly laid, fertile avian egg contains all the necessary nutrients and material components for the zygote to develop into a chick. However, adequate import of environmental oxygen (O_2), export of carbon dioxide (CO_2), appropriate microenvironment humidity for the passive exchange of these gases, and an external source of heat are required for successful development (Drent 1973). These external requirements are met through avian nesting and incubation behaviour (Deeming & Ferguson 1991; Deeming 2002; Turner 2002). With the exception of the avian family Megapodiidae in which breeding birds use environmental heat sources exclusively (Frith 1959), all birds regulate the temperatures of developing eggs through active incubation. Active incubation involves birds, usually the parents but sometimes other mature individuals, behaviourally regulating the microclimate experienced by eggs. Generally, this involves making direct contact with eggs and using internally derived metabolic heat to warm eggs to appropriate temperatures (Turner 2002), but active incubation also entails regulating other heat exchange pathways while simultaneously allowing for gas exchange between the embryo and the environment.

Most birds have similar thermal requirements for successful incubation. The importance of precise egg thermal regulation during incubation has been demonstrated in detail for Chickens *Gallus gallus domesticus* for which no embryos survived continuous incubation at temperatures > 40.5°C or < 35.0°C (Lundy 1969). Similar thermal constraints have been observed for 80 species representing 15 orders ($\bar{x}$ = 35.7°C, range = 31.4–42.5°C; Rahn 1991). Temperature limits both above and below mean incubation temperatures emphasise the thermal challenge presented to parental birds. In species that breed in environments with substantial daily thermal flux, capacity to warm eggs during cool periods and to prevent egg overheating during warm periods likely is a necessary adaptation to achieve reproductive success.

Eggs continuously exchange thermal energy with their environments through four mechanisms of heat transfer: conduction, convection, radiation and evaporation (Meijerhof & Van Beek 1993; French 1997). Conductive heat transfer occurs through contact between two surfaces. Thermal energy moves from the relatively warmer surface to the relatively cooler surface. Eggs can gain or lose heat through contact with the incubating parent but also through contact with the nest structure. Conductive warming of eggs by incubating birds making contact with eggs is widely appreciated, but warming through contact incubation is not the exclusive mechanism determining egg temperature.

Convective heat transfer occurs between a surface and a moving fluid. For example, warm eggs lose heat to cool air that moves across the egg surface. In this case, the moving air acts as a fluid and thermal energy moves from the relatively warm egg to the cooler air and is carried away from the nest environment by the air movement. Under a constant temperature differential between the egg surface and the fluid, the rate of convective heat loss from a warm egg to cool air increases with increasing air velocity such as increasing wind. Presumably, incubating birds have some capacity to regulate convective heat exchange by regulating their degree of contact with the eggs beneath them.

Radiative heat transfer occurs when the surface of a warm body emits energy as electromagnetic waves that propagate through air. When radiant energy such as solar radiation (insolation) is absorbed by an egg, it warms the egg. However, the radiant environment of eggs in a clutch is complex. Like all objects at temperatures greater than 0 K, eggs emit energy as long wavelength photon emissions.

Appendix 1 (*continued*).

Simultaneously, eggs receive energy emitted from other thermal bodies in their environment such as neighbouring eggs in the clutch, the nest mass and the mass of the incubating parent. However, two radiant heat exchange pathways are especially relevant to avian incubation. The first is cooling through uncompensated exposure to the open sky when eggs are uncovered. Essentially, eggs lose thermal energy by radiating it into the sky, a loss that is especially significant at night when there is little or no insolation to compensate for the egg's thermal emissions. The second critical exchange of radiant energy is daytime heat gain from insolation when eggs are exposed to sunlight. In daylight, solar energy from visible and near visible wavelengths are absorbed by eggs, warming them. Active incubation at night prevents excessive radiant heat loss to the night sky whereas active incubation during the day prevents excessive radiant heat gain from sunlight.

Evaporative heat transfer occurs through water vapourization, a reaction requiring heat. Eggs unavoidably lose heat by evaporation via the diffusion of water through the eggshell pores as a result of the higher water vapour pressure inside the eggs relative to the outside. As the embryo respires, evaporative heat loss occurs during passive gas exchange across the moist membrane surface at the base of eggshell pores that separates the inner egg from the external environment. Secondarily, eggs that are wetted by precipitation would cool as water evaporates from the external surface of the egg to the environment. Active incubation may provide eggs with a microenvironment characterised by a relative humidity that allows for gas exchange without excessive egg dehydration and simultaneously protect the egg from environmental precipitation.

Patterns of parental attentiveness to eggs (Skutch 1962; Deeming 2002), throughout incubation are central to hatching success (Webb 1987; Shea 1979), affect offspring phenotype (Webb 1987; Hepp *et al.* 2006; DuRant *et al.* 2012), and influence the risk of nest predation (Martin *et al.* 2000). Incubation represents a costly energetic investment for incubating adults, with increased attentiveness necessarily trading off with other essential behaviours, such as foraging (Moreno & Carlson 1989; Tinbergen & Williams 2002; Turner 2002). Birds have evolved a variety of incubation strategies to mitigate this trade-off. For example, around 50% of avian families employ biparental incubation, where both the male and female adults attend the nest and incubate the eggs (Deeming 2002). Shared incubation can minimise detrimental effects of inclement weather (Smith & Montgomerie 1992) and help achieve consistent attainment of optimal egg temperature (Reid *et al.* 2002). However, nearly 37% of avian families, including Anatidae (the ducks, geese and swans), are characterised by maternal incubation, where only the female contributes meaningfully to incubation (Deeming 2002; Winkler *et al.* 2020). In the Trumpeter Swan, the female contributes essentially all of the incubation (Banko 1960; Cooper 1979; Mitchell & Eichholz 2020).