Surface temperatures of albatross eggs and nests

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Abstract

Knowledge of thermal traits is essential for understanding and modelling physiological responses to environmental change. Egg temperatures are poorly studied in most tubenose species. We employed a contactless infrared thermometer to measure egg and nest surface temperatures throughout the incubation period for four albatross species at Bird Island, South Georgia. The observed mean warm-side temperature of 33.4°C for Wandering Albatross *Diomedea exulans* was similar to measurements obtained from this species using dummy eggs elsewhere. Observed mean warm-side temperatures for Black-browed Albatross *Thalassarche melanophris*, Grey-headed Albatross *Thalassarche chrysostoma*, and Light-mantled Albatross *Phoebetria palpebrata*, reported here for the first time, were 30.7-31.5°C, which is lower than egg

Please cite as:
Boersch-Supan et al. in press, Emu – Austral Ornithology, doi: 10.1080/01584197.2017.1406311

temperatures reported for most Procellariiformes. Temperature gradients across viable eggs declined by up to 9°C during incubation, reflecting increased embryonic circulation and metabolic heat production. This suggests bioenergetic models should not assume constant egg temperatures during embryo development. Non-viable (addled) eggs could be identified by large temperature gradients in late incubation, indicating that infrared thermometry can be used to determine whether the embryo has died or the egg is infertile in monitoring and managed breeding (e.g. translocation) programmes. Egg temperatures were correlated with ground temperatures, indicating that incubated eggs are vulnerable to environmental variability.

Keywords: Egg temperature, incubation, seabirds, *Thalassarche*, *Diomedea*

Introduction

Avian incubation is inextricably linked to temperature, and therefore sensitive to a changing climate (Mainwaring 2015). Thermal conditions during incubation influence hatchling phenotypes (DuRant *et al.* 2013), with non-optimal temperatures resulting in embryo mortality or nestlings with lower fitness. Changing environmental conditions have the potential to shape many aspects of avian biology, including through direct physiological impacts (Oswald and Arnold 2012). However, our understanding of seabird responses to direct impacts of global warming is incomplete (Grémillet *et al.* 2012). Quantifying thermal traits is an essential precursor for better understanding and modelling seabird physiological responses to a changing environment (Konarzewski *et al.* 1998; Teixeira *et al.* 2014).

Egg temperature governs the metabolic rate of developing embryos (Mueller *et al.* 2015), but the exact definition and determination of egg temperature is problematic. The incubated egg is a complex living system, and incubation is a thermal mutualism, mediated by the physiology of both parent and embryo, and heat exchanges with the environment; as a result, different parts of the eggs can be at very different temperatures (Turner 2002).

In early incubation, metabolic activity inside the egg is negligible, and heat flux from the incubating parent to the nest (which is usually colder than the parent's body) leads to a pronounced temperature gradient between the side of egg in contact with the brood patch and that in contact with the nest surface. This gradient declines as incubation progresses, reflecting increased embryonic circulation and metabolic heat production (Turner 1987).

Monitoring egg temperatures is difficult, not only because of the complex temperature field, but also methodologically. Previous studies on surface nesting tubenoses have relied on thermistors in dummy eggs, replacing the live egg at least temporarily (Brown and Adams 1988; Shaffer *et al.* 2014), or invasive sampling (Howell and Bartholomew 1961; Williams and Ricklefs 1984). Dummy eggs are problematic because temperature estimates may be biased downwards, in particular during late incubation, due to the absence of circulation and embryonic heat generation. Furthermore, material properties of dummy eggs (e.g. heat capacities) may differ from those of live eggs. The insertion or implantation of thermometers into the air cell or interior of live eggs yields more precise estimates of the temperature experienced by the embryo, but is associated with substantial increases in embryo mortality (Warham 1990; Pulikanti *et al.* 2011). This is undesirable, in particular when dealing with species of conservation concern, such as many seabirds.

The body temperatures of tubenoses are lower than those in other birds (Warham 1971), with a mean body temperature of 38.7±0.9°C across 54 species (Warham 1996). Much less is known about egg and incubation temperatures of tubenoses (Warham 1990; Warham 1996). Data for tropical and burrow-nesting species indicate that egg temperatures are on average 3.7°C lower than body or brood patch temperatures (Warham 1996). In albatrosses, thermal aspects of incubation have been studied for Laysan and Black-footed Albatross *Phoebastria immutabilis* and *P. nigripes*. Central temperatures of live eggs were close to adult brood patch temperatures, which were within 1.7°C of adult body temperatures (Howell and Bartholomew 1961). Further, central temperatures of live eggs increased by about 3°C between early and late incubation (Grant *et al.* 1982). Deployment of dummy eggs revealed diurnal variations of 1-2°C in adult body temperatures, and egg turning behaviour (Shaffer *et al.* 2014). Of the southern hemisphere albatrosses, data are only available for Wandering Albatross *Diomedea exulans* from Marion Island (Brown and Adams 1988), where thermistors in dummy eggs recorded an incubation temperature of 32.1±1.2°C, well below the body temperature of 39.2°C of this species (Warham 1971).

Infrared thermometry of the egg shell surface is a non-invasive temperature determination method routinely used in the poultry industry (Peebles *et al.* 2012). Egg shell temperatures correspond closely to internal temperatures under the egg surface (Sotherland *et al.* 1987; Peebles *et al.* 2012), making infrared thermometry an ideal method for field measurements of egg temperatures without compromising the integrity of the egg. We conducted this study to determine the utility of off-the-shelf infrared thermometers to measure egg and nest surface temperatures over the course of incubation for four albatross species breeding in the subantarctic: Wandering Albatross, Black-browed Albatross *Thalassarche melanophris*, Grey-headed Albatross *T. chrysostoma*, and Light-mantled Albatross *Phoebetria palpebrata*. No egg temperatures have been reported previously for the latter three species. We further wanted to determine whether the assumption of a constant egg temperature throughout incubation, made by some bioenergetic models (Konarzewski *et al.* 1998; Teixeira *et al.* 2014), was appropriate.

Materials and methods

Temperature measurements were collected at Bird Island, South Georgia (54°00'S 30°03'W) during the 2014/15 austral summer using a hand-held infrared thermometer (GM550, Benetech, Shenzhen, China). The device has a spectral range of 8-14 μm, and assumes an emissivity of 0.95, which is appropriate for most non-reflective surfaces including bird eggs (Björn *et al.* 2016).

Temperatures were collected during routine monitoring of nests (to determine failure or hatching dates) in long-term study colonies. Monitoring is approved by the Ethics Committee of the British Antarctic Survey, and conducted under permit from the Government of South Georgia and the South Sandwich Islands. Incubating birds were carefully approached, the egg was removed and egg temperature measurements were taken within 5-6s to minimize the effect of wind-driven cooling. Two measurements were taken along the egg equator - one on the side touching the nest, further termed 'egg bottom', and one on the opposite side, which would have been in contact with the brood patch, further termed 'egg top' (Fig. S1). When environmental temperatures are below brood patch temperatures, the egg top will be warmer than the egg bottom in an undisturbed, continually incubated egg. However, eggs are regularly and intentionally rotated by the parent, and eggs may be unintentionally rotated when the bird is approached. Therefore the in-situ egg top may not correspond to the warmer side of the egg. Because the across-egg temperature gradient was the biologically relevant quantity here, we further distinguished the 'warm side' and 'cold side' of each egg in our data analysis, irrespective of the in-situ orientation of eggs at the time of measurement. Two further temperature measurements, of the nest cup underneath the incubating parent, and the ground beside the nest, were taken within 10-12s of approaching the nest. Fieldwork took place on overcast days, reducing the effect of solar irradiance. Temperature measurements were collected on multiple occasions between 3 December 2014 and 14 March 2015, corresponding to incubation times of 20-82 days (c. 25-110% of mean incubation duration). Measurements were recorded on a single occasion at 97 nests and on two or three occasions at 17 nests.

Laying dates were known for all eggs except for those of Light-mantled Albatross, for which only approximate hatching dates (±1 week) were known. Due to the uncertainty in egg age, Light-mantled Albatrosses were excluded from temporal analyses. Egg fate was known for all nests, and eggs that did not hatch were excluded from analyses, unless noted otherwise.

Statistical analyses were conducted in R 3.3.2 (R Core Team 2016). Species differences and temporal trends in egg temperatures, as well as differences between nest and ground temperatures were investigated using linear mixed models (LMMs), fitted using `nlme` (Pinheiro *et al.* 2017), with a nest-level random effect to account for repeated observations. Across-egg temperature gradients of late incubation eggs (>65 days, c. 85% of mean incubation time) were compared within species using Welch's t-test, to account for unequal sample sizes, since hatching outcomes were not experimentally controlled. This data subset did not contain repeated measurements.

Results

Mean values for egg temperatures, i.e. top (T_{top}), bottom (T_{bot}), warm-side (T_w) and cold-side (T_c), as well as nest and ground temperatures are given in Table 1. Egg top temperatures were generally, but not always, warmer than egg bottom temperatures (Table S1). The highest occurrence of eggs with a colder top than bottom (i.e. $T_{top} < T_{bot}$) was in Black-browed Albatross, and accounted for about a third of measurements in that species. Warm-side temperatures differed between species (LMM, $F_{4,14} = 5459, p < 0.001$). Model estimates revealed a 1.9-2.7°C higher temperature in Wandering Albatrosses (33.4°C, 95% CI 32.7-34.1) than the other three species, but no evidence for differences among Black-browed (30.7°C, 95% CI 30.0-31.4), Grey-headed (31.5°C, 95% CI 30.6-32.4), and Light-mantled Albatrosses (31.4°C, 95% CI 30.2-32.6). Nest temperatures were on average 5.1°C (95% CI 4.4-6.2) higher than ground temperatures. No temporal trends related to incubation duration were observed in warm-side temperatures (LMM, β=0.00, 95% CI -0.02-0.02) after accounting for the variation in ground temperatures (Table S2), but cold-side temperatures increased during incubation by 0.11°C per day (95% CI 0.07-0.14; Table S2), resulting in a decreasing across-egg temperature gradient (Fig. 1). During late incubation, temperature gradients across eggs (i.e. the difference between the warm and cold side ΔT_{wc}) of Black-browed and Grey-headed Albatrosses differed significantly between viable and addled eggs (Table S3), the latter exhibiting larger gradients, similar to those observed during early incubation (Fig. 1). ΔT_{wc} of viable and addled eggs did not overlap in Black-browed Albatross, and only a single addled egg in Grey-headed Albatross exhibited a temperature gradient within the range of viable eggs in this species. Only one Wandering Albatross egg in our sample did not hatch. This egg exhibited a temperature gradient 3.9°C larger than the mean for viable eggs of this species (Table S3).

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Boersch-Supan et al. in press, Emu – Austral Ornithology, doi: 10.1080/01584197.2017.1406311

Discussion

Our measurements revealed low egg top temperatures in all four species. Warm-side temperatures were 2-5°C lower than those reported for subtropical albatrosses (Howell and Bartholomew 1961; Grant *et al.* 1982; Shaffer *et al.* 2014), and Southern Giant Petrels *Macronectes giganteus* (Williams and Ricklefs 1984). The observed mean warm-side temperature of 33.3°C for Wandering Albatross is similar to measurements obtained with dummy eggs on Marion Island (32.1±1.2°C, Brown and Adams 1988). No reference values exist for the three smaller species. Their mean warm-side egg temperatures (30.7-31.1°C) are lower than those of most tubenoses (Warham 1996). Lower central egg temperatures have been reported for incubated eggs of Fork-tailed Storm Petrels *Oceanodroma furcata* (30.2±2.6°C, Boersma 1982), and for Scopoli's Shearwaters *Calonectris diomedea* using dummy eggs (29.6±0.6°C, Wink *et al.* 1987). Low egg temperatures may serve to minimize water loss during the long incubation period (Warham 1990). The observed egg temperature variability (SD 1.5-3.0°C) is consistent with observations in surface nesting tubenoses (Williams and Ricklefs 1984; Shaffer *et al.* 2014).

In Black-browed Albatross there was a large proportion of "cold-top" eggs, which may indicate higher intentional or unintentional (i.e. disturbance related) egg turning frequencies in this species. In albatrosses, egg turning has only been quantified in Laysan Albatross (2.1±0.7 turns/hour, Shaffer *et al.* 2014), but nest ventilation frequencies differ between sympatric Laysan and Black-footed Albatross (Grant *et al.* 1982). As we did not observe differences among species in their disturbance response to the approaching investigator, we suggest that this finding may also reflect species-specific differences in egg turning behaviour.

Temperature gradients across eggs have not been determined previously for tubenoses. Cold-side temperatures increased during incubation for the three species with precisely known egg ages, reflecting increasing circulation and embryonic heat production. Observed gradients are similar in magnitude and temporal dynamics to those found across European Herring Gull *Larus argentatus* eggs (Drent 1970). Central egg temperature in Black-footed and Laysan Albatrosses increases by about 3°C between early and late incubation, and a similar temperature difference has been observed between viable and non-viable late-stage eggs (Grant *et al.* 1982). Our results are consistent with both observations. Viable and addled eggs can therefore be distinguished in late incubation (>65 days, c. 85% of mean incubation time) using infrared thermometry, an across-egg temperature gradient ≥3.0°C being indicative of a dead or non-viable embryo. The large change in across-egg temperature gradients indicates the importance of including temperature dynamics in bioenergetic models of eggs. There was no indication that rates of temperature increase during incubation varied among species, which is consistent with theoretical predictions that temperature gradients are independent of egg size for eggs > c. 50g (Turner 1987).

Temperatures within the nest cup were consistently higher than those of the ground adjacent to the nest, indicating an insulatory role of the nest floor in all species. This is consistent with nest temperature observations in Wandering Albatross on Marion Island (Haupt *et al.* 2016). However, both warm-side and cold-side egg temperatures were correlated with ground temperatures, indicating that incubated eggs are not fully decoupled from environmental conditions, and are therefore vulnerable to changing environmental temperatures.

Internal egg temperatures are the least biased measure of embryonic temperatures, but come at the expense of substantially increased embryo mortality (Grant *et al.* 1982; Williams and

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Ricklefs 1984; Warham 1990; Pulikanti *et al.* 2011). Infrared measurements of egg shell temperatures correspond closely to air cell temperatures (Peebles *et al.* 2012), thus providing a non-invasive means to determine egg temperatures and thermal dynamics of embryonic development. We cannot exclude the possibility that our measurements were biased downwards because of cooling of the egg surface during handling. However, the similarity between egg temperatures of Wandering Albatross in our study, and those measured at Marion Island (Brown and Adams 1988), suggest any bias is small.

We demonstrate that infrared thermometry is a viable, non-invasive approach to studying thermal aspects of albatross breeding biology under field conditions. Our approach necessitates a brief disturbance of the incubating parent, making it less suitable for studying thermal phenomena at diel or daily scales, but it provides physiological trait data on the scale of the incubation period that is suitable as inputs for biophysical models, and demonstrates that it is possible to thermally distinguish viable and non-viable albatross eggs during late incubation. Infrared thermometry therefore is a useful tool for assessing egg status in monitoring or managed breeding (e.g. translocation) programmes.

Acknowledgements

We thank Lucy Quinn and Jessica Walkup for assistance in the field, and the editors and reviewers for constructive comments. PHBS, LRJ, and SJR were supported by US National Science Foundation Grant PLR-1341649. This study contributes to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by the UK Natural Environment Research Council.

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Please cite as:
Boersch-Supan et al. in press, Emu – Austral Ornithology, doi: 10.1080/01584197.2017.1406311

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Display Items

Table 1: Wandering Albatross (*Diomedea exulans*) incubated eggs at higher temperatures (°C, mean ± SD, where available) than the other albatrosses. Nest temperatures were consistently higher than ground temperatures. Egg top and bottom refer to the orientation of the egg in the nest, warm and cold side to the warmer and colder side of the egg irrespective of egg orientation. Non-viable eggs were excluded here. [a] Warham (1996).

Species	*n*	Body[a]	Egg Top	Egg Warm	Egg Bottom	Egg Cold	Nest	Ground
Thalassarche melanophris	41	38.7	29.7±2.3	30.7±1.6	29.3±2.5	28.4±2.5	7.1±4.0	3.0±2.6
Thalassarche chrysostoma	26	39.7	31.1±3.2	31.5±3.1	30.6±3.2	30.2±3.1	8.1±5.9	3.1±4.2
Phoebetria palpebrata	14	38.1	31.1±3.7	31.4±3.1	29.6±3.1	29.3±3.6	5.4±5.0	2.7±4.7
Diomedea exulans	39	39.2	33.4±2.2	33.4±2.1	28.4±3.2	28.4±3.2	9.5±5.5	2.5±2.7

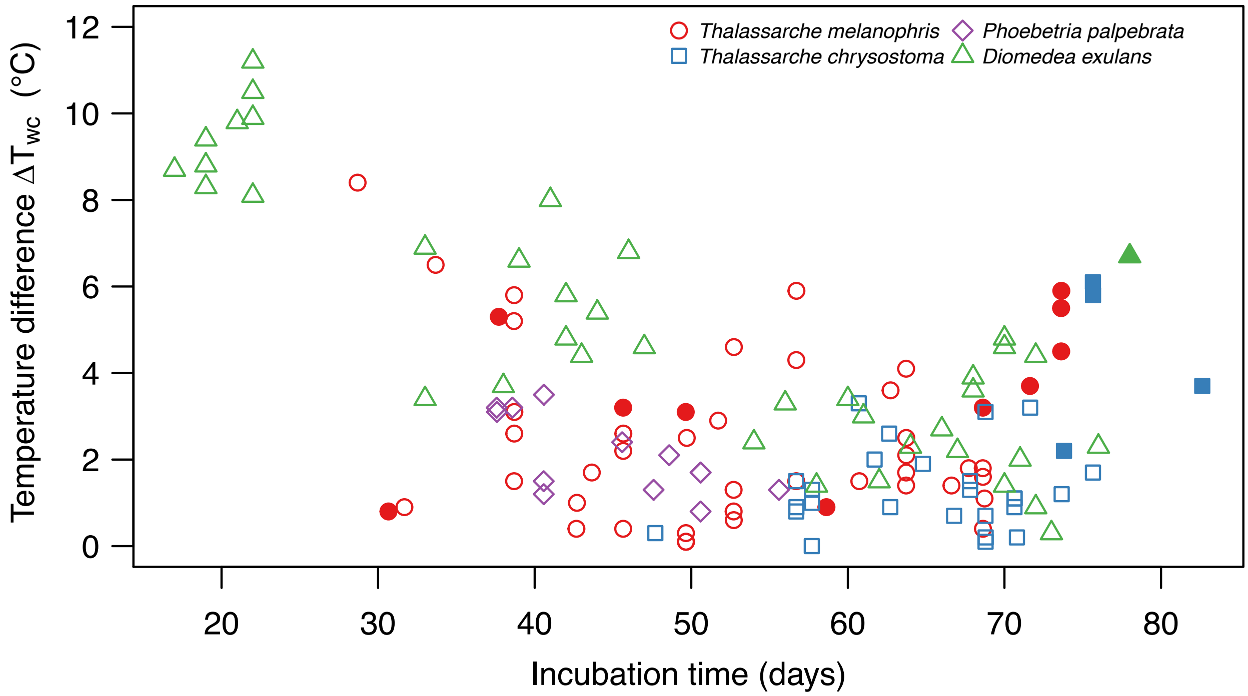

Figure 1: Absolute temperature differences across eggs declined during incubation in four albatross species. Open symbols indicate eggs that hatched. Solid symbols indicate eggs that ultimately did not hatch, but that may have been alive earlier in the season. Egg age is approximate (±1 week) for *Phoebetria palpebrata*.

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