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Thermal emissivity of avian eggshells

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ABSTRACT

The hypothesis has been tested that evolution has resulted in lower thermal emissivity of eggs of birds breeding openly in cold climates than of eggs of birds that nest under protective covering or in warmer climates. Directional thermal emissivity has been estimated from directional–hemispherical reflectance spectra. Due to several methodological difficulties the absolute emissivity is not accurately determined, but differences between species are obvious. Most notably, small waders of the genus *Calidris*, breeding in cold climates on the tundra, and in most cases with uniparental nest attendance, have low directional emissivity of their eggshells, about 0.92 when integration is carried out for wavelengths up to 16 µm. Species belonging to Galloanserinae have the highest directional emissivity, about 0.96, of their eggs. No differences due to climate or breeding conditions were found within this group. Eggs of most other birds tested possess intermediate emissivity, but the values for *Pica pica* and *Corvus corone cornix* are as low as for *Calidris*. Large species-dependent differences in spectral reflectance were found at specific wavelengths. For instance, at 4.259 µm the directional–hemispherical reflectance for galliforms range from 0.05 to 0.09, while for *Fratercula arctica* and *Fulmarus glacialis* it is about 0.3. The reflection peaks at 6.5 and 11.3 µm due to calcite are differentially attenuated in different species.

In conclusion, the hypothesis that evolution has resulted in lower thermal emissivity of bird eggs being exposed in cold climates is not supported by our results. The emissivity is not clearly related to nesting habits or climate, and it is unlikely that the small differences observed are ecologically important. The spectral differences between eggs that nevertheless exist should be taken into account when using infrared thermometers for estimating the surface temperature of avian eggs.

1. Introduction

Most bird eggs are heated by the bodies of the parents during the development of the embryo, and keeping the eggs at a temperature much above ambient is important in cold climates. For various reasons parents may leave their nests unattended for shorter or longer periods, during which the eggs cool. In some bird species only one parent attends to the eggs, and has to leave the nest for feeding. The little stint (*Calidris minuta*) may leave its nest unattended for half an hour, during which the egg surface temperature can fall below 10 °C (Tulp and Schekkerman, 2006). During snowstorms eggs of sanderling (*Calidris alba*) may be abandoned for extended times (Reneerkens et al., 2011). In other cases the parents are forced to leave the nest due to predators. Thus common terns (*Sterna hirundo*) have been observed to leave nests for hours during night due to owls (Arnold et al., 2006). Even if embryos survive and eggs hatch, low incubation temperature has negative effects on hatchling development and survival (Olson et al., 2006; Hepp and Kennamer, 2012; Carter et al., 2014). Hepp and Kennamer (2012) found that the incubation time was increased from 30.1 to 37.9 days, i.e. by 26% when the temperature was lowered from 37.3 to 35.0 °C. Development in domestic fowl comes to a stop below 25 °C (Funk and Biellier, 1944) and hatching is seriously compromised already at a temperature four degrees below normal (Mortola, 2006). Clearly, it is of survival value for the embryo if the egg is constructed such that cooling takes place as

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slowly as possible during these periods. Cooling takes place mainly by radiation and air convection, and although other factors, such as nest construction, probably are more important (Rockweit et al., 2012). Björn et al. (2012) pointed to the importance of eggshell emissivity as a factor that could affect egg temperature and thus embryo or hatchling survival. These authors also list further references related to emissivity and bird egg temperature. A priori, it is likely that there is an evolutionary pressure towards a low emission of thermal radiation for birds nesting in cold climates, and the aim of this work is to test the hypothesis that this has affected emissivity.

Measurements of infrared reflectance spectra on eggs of domestic hens have been carried out before (Narushin et al., 2004), but these authors used a different measurement geometry and reported their result as transmission in arbitrary units and with an arbitrary zero line. Therefore these results cannot be compared with ours.

A note on terminology: some authors distinguish between emissivity of a substance and emittance of an object, for instance emissivity of tungsten as opposed to the (higher) emittance of a coiled tungsten filament of an incandescent lamp. This has been discouraged by others, since “emittance” is also used in other senses. We here use “emissivity” as recommended in the third edition of IUPS (2003) Glossary of terms for thermal physiology, and we distinguish between directional emissivity in a direction near normal to the surface, and hemispherical emissivity, over 2π steradians.

2. Materials

Most of the estimates were carried out with empty eggshells from a collection at Lund University. Since collecting eggs of wild birds has been illegal in many countries for a considerable time, most of the eggshells were several decades old, in some cases over one hundred years of age. To ascertain that infrared reflectance did not change with age some estimates were done using eggshells from fresh eggs, and some control estimates were also taken on intact eggs of quail and domestic hen.

3. Methods

Direct measurement of thermal emissivity requires heating of the sample above the surroundings and the measuring instrument, and this might result in changed properties, so an indirect method was used. This method depends on Kirchhoff's law, stating that the emissivity is one minus the reflectance measured in a certain way, if transmission of radiation through the sample is negligible. The reflectance that has been measured is the so-called directional–hemispherical reflectance: radiation is incident at near normal to the sample surface (10° to the normal), and the reflected radiation is measured over 2π steradians of solid angle. Subtraction of these values from 1, multiplication by a blackbody spectrum for 30 °C, integration over the spectrum, and division by the blackbody spectrum integrated over the same spectral range was used as a proxy for the total directional emissivity. The blackbody spectrum was calculated per wavenumber interval, since the instrument spectral step size is uniform on the wavenumber scale, not the wavelength scale. Using two instruments we could cover wavelengths from 2.5 to 22 μm, but for reasons discussed below we have only used values up to 16 μm. Some data for the instruments are shown in Supplementary Table ST1, and further details are available in Hecker et al. (2011). Various port sizes were used with each instrument, but for reasons given below, estimates with the smaller port sizes (10–17 mm diameter) are considered less reliable and conclusions are based on estimates with 19 and 20 mm ports.

To give an idea of reproducibility we compare reflectance spectra of the four eggs in a clutch of two *Calidris* species in Supplementary Fig. SF1. It is clear that the variability is greatest in the region around 1500 cm^{-1}.

4. Methodological concerns

1. The instruments used are primarily intended for measurements on flat surfaces. Eggs of different sizes have different curvatures. It was therefore important to investigate the effect of curvature on the results. We have done this in several ways:
 (a) by measuring paper balls of different sizes painted with the same paint.
 (b) By measuring the same eggs with differently sized apertures (instrument ports).
 (c) By measuring both the blunt and the pointed end of eggs for which the curvature at the two ends is very different.

 As expected for mostly specular surfaces, for the smallest eggs as well as the pointed end of small eggs, smaller ports give slightly higher emissivity values than 19 and 20 mm ports, because radiation is restricted to a smaller incidence angle. However, because beam intensity is not constant over the port aperture, an accurate correction for finite port size is not possible, and we have only included values for ports of 19 and 20 mm diameter, i.e. 9.5 and 10 mm radius, in our final computations, in order to make all results comparable. Likewise, although we have done estimates also of the pointed end, we have only included data for the blunt end of the eggs, except for the age comparison in Supplementary Table ST2. The strongest indication that there exist differences in emissivity, independently of any curvature artifact, is that eggs of similar curvature (such as those of quail, *Coturnix coturnix* on one hand, and sandpipers, *Calidris sp*. or magpie, *Pica pica* on the other) can have very different emissivity. The average blunt end radii of curvature in mm were for *Cournix coturnix* 11.5, *Lagopus muta* 13.4, *Lagopus lagopus* 12.3, *P. pica* 11.3, *C. coronae cornix* 13.1, and for *Calidris* species ranging from 10.1 (*Calidris temminckii*) to 13.1 (*Calidris melanotos*). These radii were determined from photographs of eggs against a background of mm-ruled paper. When the radius of curvature comes close to the radius of the entrance port of the instrument, below 11 mm in our case, the emissivity values obtained are likely to be lower than true directional (perpendicular) emissivity. This is the case here only for *C. minuta* and *C. temminckii*.

2. Most of the eggshells used are old museum specimens. It was therefore important to investigate if age would have an effect on the results. The conclusion from five species for which both old and new eggs were measured is that there is no significant age effect (Supplementary Table ST2). In addition a few full-spectra comparing reflectance of old and new eggs are shown in Supplementary Fig. SF2.
3. To rule out the possibility that the results in some way depend on the instrumentation, two different instruments were used. Fig. 1 shows, as an example, spectral emissivity for eggs of *C. alba* weighted by the 30 °C blackbody spectrum as measured using a 15 mm port for the instrument in Uppsala and a 20 mm port for the instrument in Enschede (also the blackbody spectrum itself is shown). The Uppsala curve is very noisy at the high-wavelength end, especially for this small port, and even extends above the blackbody curve. Therefore the estimates with the smaller ports are considered uncertain, and not