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# The white colour of the Ostrich (*Struthio camelus*) egg is a trade-off between predation and overheating

**Flora John Magige · Børge Moe · Eivin Røskaft**

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**Abstract** Most ground nesters lay pigmented eggs, and egg pigmentation generally matches the environment. Pigmentation of eggs has evolved as a protective device against predation, but dark-pigmented eggs can be susceptible to overheating when exposed to solar radiation. The Ostrich (*Struthio camelus*) lays white eggs that are unattended for the first few weeks before incubation, and are quite visible to predators. To evaluate the effect of colour on the surface and core temperatures, we painted some Ostrich eggs dark brown or white, and left some unpainted (control), and exposed all of them directly to the sun during the day. The surface and core temperatures of brown eggs were significantly higher than those of the white-painted and control eggs. In addition, the core temperature of brown eggs exceeded 37.5°C, which is the temperature at which embryo mortality starts to increase. In a second experiment, we placed eggs (brown-painted and control) in various types of vegetation to study their visibility to an observer walking towards them. The white eggs were discovered from a significantly longer distance than the brown eggs, indicating that the predation risk may be much higher for white eggs. The results thus suggest that white eggs minimise overheating and allow the Ostrich to leave its eggs unattended before incubation starts, but they are more susceptible to predation.

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F. J. Magige (✉) · B. Moe · E. Røskaft
Department of Biology, Norwegian University of Science and Technology (NTNU), Realfagbygget, 7491 Trondheim, Norway
e-mail: magigef@yahoo.co.uk

B. Moe
Division of Arctic Ecology, Norwegian Institute for Nature Research (NINA), 9296 Tromsø, Norway

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## Introduction

Most ground nesters have pigmented eggs, whereas species nesting in deep holes generally lack pigmentation and markings (Lack 1968; Kilner 2006). Pigmentation of eggs has evolved as a defence against brood parasitism (Rothstein 1990; Davies 2000), as a structural component of shell strength (Gosler et al. 2005), as protection against potentially harmful solar radiation (Gosler et al. 2005; Kilner 2006) or as an anti-predator strategy (Portmann 1959; Caro 2005; Kilner 2006). Ground nesters suffer more predation than birds nesting off the ground (Martin 1993). Egg crypsis is therefore a probable explanation in the case of ground-nesting birds, because the colour of the eggshell provides concealment and minimises nest predation (Bertram and Burger 1981; Götmark 1992, 1993; Lloyd et al. 2000).

Although egg pigmentation reduces predation risk, a dark surface generally absorbs more radiant heat than a white one. Since the ground-nesting Ostrich (*Struthio camelus*) lays white eggs on nests that are generally exposed on grass plains for almost 2 weeks before incubation starts (Bertram 1992; own observations), the eggs are exposed to intense solar radiation. The survival of unattended avian eggs depends on their thermal properties and on how resistant the embryos are to extreme temperatures. Avian embryos can be very tolerant to hypothermia, but are far less tolerant to hyperthermia (Webb 1987). The optimum temperature for Ostrich egg incubation is 36.0–36.5°C (e.g. Deeming 1993; Hassan et al. 2004), and incubation temperatures above 37.5°C increase the incidence of dead embryos (Hassan et al. 2004).

The white colour of the Ostrich egg is thought to reduce the risk of it overheating during the period when the eggs are unattended, but it is also believed to make it more visible to predators (Bertram and Burger 1981). Spotted hyenas (*Crocuta crocuta*), Egyptian Vultures (*Neophron percnopterus*) and lions (*Panthera leo*) are the main predators of Ostrich eggs (Bertram 1992), and visually locate nests by directly spotting unattended eggs and/or observing parental activity (Collias and Collias 1984; Martin et al. 2000).

In this study, we conducted experiments on the egg temperature and predation risk to test the hypothesis proposed by Bertram and Burger (1981) that the white colour of Ostrich eggs is a trade-off between overheating and predation risk. The egg temperature experiment followed the approach used by Bertram and Burger (1981), but differed in the temperature equipment, the site (Serengeti National Park vs Oudtshoorn, South Africa and Tsavo West National Park, Kenya), the experimental eggs (dark-brown painted, white-painted and unpainted control eggs vs medium-brown painted and unpainted control eggs), the sample size (6 vs 2 eggs), the number of days with egg-core temperature measurements (4 days vs 1 day), the statistical approach (mixed linear model vs descriptive statistics) and the predation experiment (visibility test vs natural predation).

We measured the surface and core temperatures of brown-painted, white-painted and control (natural colour) eggs on different days and at different times of the day to test whether brown eggs were more likely to overheat. Our predation experiment was conducted as a visibility test where we determined at what distance brown-painted and control eggs were discovered by a walking observer. We assumed that if the human observer discovered one egg colour from further away than the other, the predators would also discover this egg colour more easily.

## Methods

### Study area

The experiments were conducted in the Ikorongo (563 $km^2$) and Grumeti (416 $km^2$) Game Reserves, northwest of the Serengeti National Park, northern Tanzania, during the period 5–12 December 2006. Six eggs of almost identical volume (mean 1,299 $cm^3$, SE ± 14) were collected from different abandoned nests in the game reserves. We only collected six eggs because of the strict regulations in the protected areas, and for conservation purposes. Two of the eggs were painted dark brown and two white (oil-based Gold Star paint; Gold Star, Dar es Salaam, Tanzania), and the remaining two were left without paint as controls. The temperatures of the egg surface, the egg core and the ground surface were measured with copper–constantan thermocouples ( type 0.005; precision 0.1°C; California Fine Wire, Grover City, Calif., USA) and stored on a data logger (Squirrel 1200 series; Grant Instruments, Cambridge, UK). Since the data logger had four operative input ports, one of the two combinations was recorded at the same time: (1) three egg-surface temperatures and one ground-surface temperature, or (2) three egg-core temperatures and one ground-surface temperature. We measured the temperature of the eggs before exposing them to sunlight to make sure that their starting temperatures were similar. The eggs were then exposed in the sun for approximately 2 h before we started recording. Winds were not so strong as to influence the results, but we stopped the experiment immediately when it clouded over or started raining.

During the temperature measurements, the eggs were placed on a ground surface that was similar to that of a natural Ostrich nest location, and its temperature was measured by placing a thermocouple on it. One brown-painted, one white-painted and one control egg were always measured at the same time. Thermocouples attached with transparent tape on top of the eggs were used to measure the surface temperature of the eggs on 2 days (5 and 6 December) between 1450 and 1610 hours, and the eggs were switched every half an hour. Egg-core temperatures were measured on 4 days (7, 10, 11 and 12 December), between 1230 and 1630 hours. To do this, a hole was drilled right at the centre of the egg and a stiff polypropylene tube (length 68 mm, outer diameter 3 mm, inner diameter 0.8 mm) carrying the thermocouple was inserted into the egg. This tube was mounted firmly at a 90° angle onto a plastic base (60 mm in diameter and 4 mm thick) which was sealed to the surface of the egg with epoxy glue.

### Egg visibility

The visibility study was carried out on overcast afternoons so as to reduce any effect of sunshine reflecting from the painted eggs. Two eggs, one painted brown and one control, were placed beside a person, and the observer walked away from the eggs until they disappeared from her vision. Then she started walking towards them. When she saw the first egg, she immediately stopped and recorded the distance to the person beside the eggs using a Leica Geovid Rangefinder (7 × 42 BDA; accuracy: ± 1 m; Leica, Portugal). The observer then continued walking until she saw the second egg, and again recorded the distance to the person beside the eggs. The experiment was done repeatedly on different days and in different types of vegetation with different heights of grass.

### Data analysis

The egg volume was calculated as volume ($cm^3$) = L × $B^2$ × 0.00051, where L is the length (mm) and B is the breadth (mm) of an egg (Hoyt 1979). Surface and core temperature data were recorded every minute during the experiments. In the subsequent analyses, we used only one value of temperature for every 0.5 h for each variable (eggs and ground). The 0.5 h temperature was calculated as the mean of the temperatures recorded during a 10-min interval (5 min before and after the 0.5 h time).

We measured the temperatures of six eggs (two brown-painted, two white-painted and two controls). To control for repeated measurements of each egg in the subsequent statistical analyses, we used a mixed linear model and entered egg identity as a random factor (Crawley 2002). The mixed linear model analysing the surface temperature of the egg was entered with the egg colour (factor: brown, white, control) and date (factor: 5, 6 December) and time of day (covariate) as explanatory variables. The model analysing the egg-core temperature was entered with the egg colour (factor: brown, white, control), date (factor: 7, 10, 11, 12 December), time of day (covariate) and the quadratic term of time of day (covariate). The model analysing the egg-core temperature was specified as an autoregressive model to control for the temporal autocorrelation within the time series of temperature measurements. Visibility between brown-painted and control eggs was compared using a paired sample *t* test. Statistical analyses were performed with S-PLUS v7.0 (Insightful, Seattle, Wash., USA). Means are reported with ± standard error.

## Results

### Egg-surface temperatures

The egg-surface temperature was significantly influenced by the colour and the date ($P \leq 0.001$; Table 1, Fig. 1). However, time of day had no significant effect as a covariate ($P = 0.12$; Table 1) because the experiment was conducted during a very short period of the day (between 1450 and 1610 hours). The surface temperature of the brown eggs was significantly higher than that of the white and control eggs ($P = 0.001$; Table 1, Fig. 1). The mean surface temperatures of the white and control eggs were 11.5°C (±0.78) and 10.8°C (±0.63) lower than the brown eggs, respectively. Since 6 December was significantly warmer than 5 December ($P < 0.001$; Table 1, Fig. 1), considerable variation is likely between different days.

**Table 1** Summary of a mixed linear model analysing the surface temperature of Ostrich (*Struthio camelus*) eggs as a function of egg colour (brown, white or control), date and time of day on 5 and 6 December 2006

| | Num *df* | Den *df* | *F* | *P* |
|---|---|---|---|---|
| Final model | | | | |
| Intercept | 1 | 15 | 15,391 | <0.001 |
| Egg colour | 2 | 3 | 148 | 0.001 |
| Date | 1 | 15 | 182 | <0.001 |
| Rejected terms | | | | |
| Time of day | 1 | 15 | 2.7 | 0.12 |

Num *df* and Den *df* represent the numerator and denominator degrees of freedom, respectively

### Egg-core temperatures

The core temperature of the eggs was found to be significantly influenced by egg colour, date, time of day, the quadratic term of time of day, and the interactions between egg colour × date, egg colour × time of day, and egg colour × quadratic term of time of day (Table 2). The mean core temperatures of the brown eggs were 11.3 and 10.1°C warmer at the hottest part of the day than the white and control eggs, respectively, . The core temperature of the brown eggs was significantly higher than that of the white and the control eggs ($P < 0.001$; Table 2). There was a tendency of gradual increase in the egg-core temperatures as a function of time, following a quadratic curve with an increasing difference between brown eggs and white and control eggs as the day progressed (Fig. 2). We have presented the predicted core temperatures of the

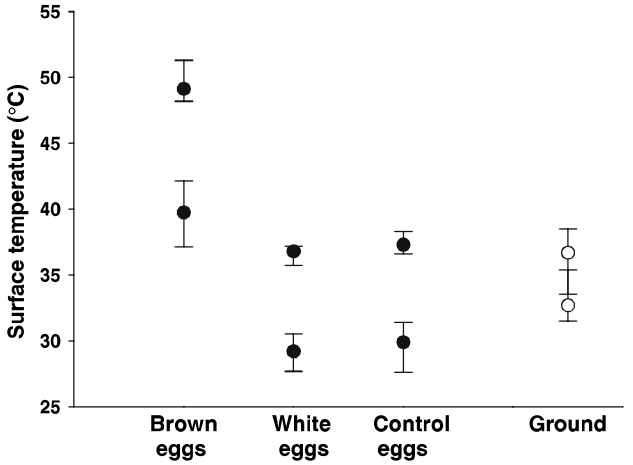



**Fig. 1** Surface temperature (°C) of brown-painted, white-painted and control Ostrich (*Struthio camelus*) eggs, and the ground, measured between 1450 and 1610 hours on 2 days (5 and 6 December 2006). The *circles* represent the two mean surface temperatures of the 2 days, respectively, and the *error bars* represent the maximum and minimum temperatures recorded on the 2 days, respectively

**Table 2** Summary of a mixed linear model analysing the core temperature of Ostrich eggs as a function of egg colour (brown, white or controls), date and time of day, on 7, 10, 11 and 12 December 2006

| | Num *df* | Den *df* | *F* | *P* |
|---|---|---|---|---|
| Intercept | 1 | 39 | 386,801 | <0.001 |
| Egg colour | 2 | 3 | 2,490.9 | <0.001 |
| Date | 3 | 39 | 428.4 | <0.001 |
| Time of day | 1 | 39 | 4,240.8 | <0.001 |
| Time of day (quadratic) | 1 | 39 | 168.4 | <0.001 |
| Egg colour × date | 6 | 39 | 40.7 | <0.001 |
| Egg colour × time of day | 2 | 39 | 133.8 | <0.001 |
| Egg colour × time of day (quadratic) | 2 | 39 | 8.3 | 0.001 |

Num *df* and Den *df* represent the numerator and denominator degrees of freedom, respectively

experimental eggs (along with the predicted ground-surface temperature) for the warmest day (12 December) to illustrate the great effects of egg colour and to show the temporal pattern (Fig. 2). The predicted egg-core temperatures are derived from the parameter estimates obtained from the analysis in Table 2, whereas the predicted ground-surface temperatures are derived from parameter estimates from a linear model including "date" as factor and with "time of day" and the quadratic term of time of day as covariates. The core temperatures of the brown eggs exceeded 37.5°C, which is the temperature at which the mortality of Ostrich embryos starts to increase, whereas the core temperature of white or control eggs was below 37.5°C. The ground-surface temperature was highest at 1440 hours, whereas the egg-core temperatures were highest at 1655 hours, indicating a time lag for the core temperature of the eggs to be raised to the peak temperature.

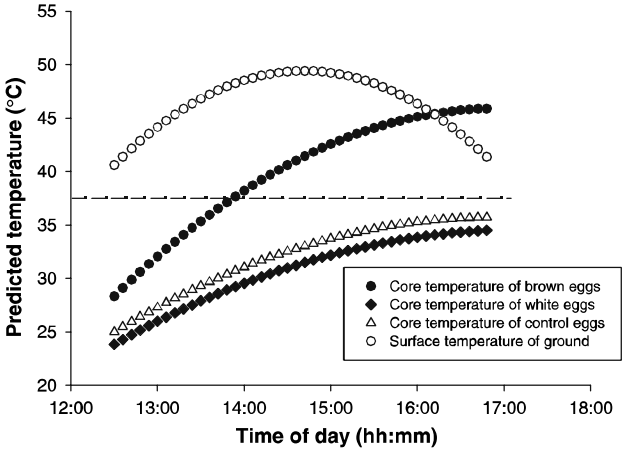



**Fig. 2** Predicted core temperatures (°C) of brown-painted, white-painted and control eggs, and predicted surface temperature of the ground, as a function of the time of day on the warmest day of the measurements (12 December 2006). The predicted core temperatures for the warmest day are derived from the parameter estimates obtained from the analysis in Table 2. For the warmest day, the ground temperature = 53.5 × time of day −1.82 × (time of day × time of day) −343.6. The *dashed horizontal line* represents the egg-core temperature (37.5°C) at which embryo mortality starts to increase

## Egg visibility

The mean discovery distance to the control egg from the observer was significantly longer than that of the brown-painted egg (control: 28.1 ± 3.9 m; brown: 17.3 ± 2.0 m: $t_{15} = -4.85$, $P < 0.001$). The scatter plot shows a linear relationship between the visibility of the white and brown eggs (linear regression: distance to brown-painted egg = 0.47 (± 0.06) × distance to control egg + 4.16 (± 1.8), $r^2 = 0.83$, $n = 16$, $P < 0.001$; Fig. 3), and the slope of this relationship was significantly different from 1 (the upper 95% confidence limit for the slope was 0.59), demonstrating a higher visibility of white eggs.

## Discussion

There was a significant effect of egg colour on both the surface and core temperatures of the Ostrich eggs during exposure to direct sunlight, and egg temperatures varied substantially between different days. The effect of time of

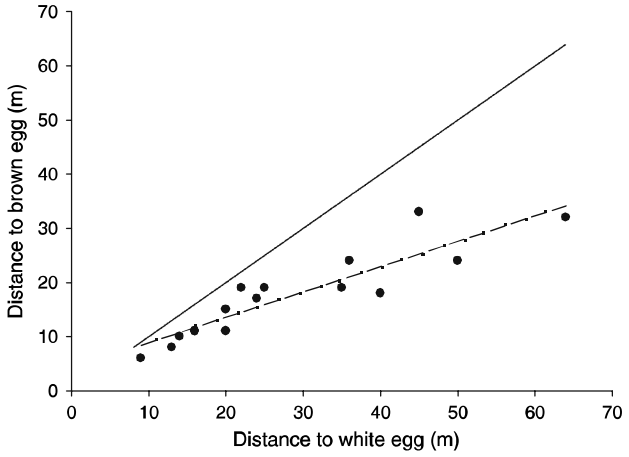



**Fig. 3** Relationship between the visibility of brown-painted and control eggs for an observer walking towards the eggs. The *thick line* represents the 1:1 relationship between the distances to the brown-painted and control eggs. The *dashed line* represents the real relationship observed during the experiment in which the control egg was observed first

day with respect to surface temperature was not seen due to the short period of time in which the experiment was conducted (Table 1), but we assume that it follows the same temporal pattern as shown for the ground-surface temperature in Fig. 2. The egg-core and ground-surface temperatures showed a significant quadratic temporal pattern, with peak temperatures being obtained in the late afternoon (Fig. 2). Moreover, the significant interactions between egg colour × time of day, egg colour × quadratic term of time of day and egg colour × date demonstrate that the difference in core temperature between the different egg colours varied with the time of day and between dates. Thus, the core temperature of brown eggs was significantly higher than that of white-painted and control eggs, and the difference was highest in late afternoon and on the warmest day (Table 2; Fig. 2).

Since some types of egg pigments cause higher solar reflectance than others (Bakken et al. 1978), we regard the brown-painted eggs as crude representatives rather than perfect representatives for cryptic brown eggs in nature. However, the substantial differences in temperature between white- and brown-painted eggs demonstrated in this experiment suggest that egg coloration may have significant fitness consequences. On the warm and sunny days, the core temperature of the brown eggs was well above 40°C, whereas the white-painted and the control eggs were below 37.5°C. An estimate of the upper thermal tolerance for short-time exposure in most species is 41°C, and for exposures lasting several hours it is 39°C (Webb 1987). In Ostriches, increased embryo mortality is reported at temperatures above 37.5°C (Hassan et al. 2004; Ipek et al. 2003) and reduced hatching success is reported at temperatures above 40°C (Deeming et al. 1993). The high core temperatures of brown-painted eggs observed in this experiment (Fig. 2) would be lethal to Ostrich embryos given the Ostrich's habit of leaving the nests exposed to solar radiation during the day before the start of incubation. The warmest day on which we conducted the experiment had a maximum air temperature of only 30°C (G. Mwakalebe, Serengeti Meteorological Centre, personal communication), suggesting that the selection pressure against unattended brown eggs would be very high in excessive temperatures if brown Ostrich eggs existed in this environment. Therefore, white seems to be the adaptive Ostrich egg colour to prevent overheating (Bertram and Burger 1981).

Cryptic egg coloration could be explained as an adaptive anti-predator strategy in ground-nesting birds (Montevecchi 1976; Solís and de Lope 1995; Lloyd et al. 2000), although coloured eggs may impose a predation risk to some bird species, an idea for which there is support (Montevecchi 1976; Götmark 1992; Weidinger 2001). It has been argued that Ostriches lay white eggs because they are powerful enough to defend their nests (Wallace 1889). However, when nests are unattended, such big eggs are quite visible on the ground to both mammalian and avian predators. In our visibility study, a naturally white egg was seen first by the observer, suggesting that the brown eggs are better concealed. Ostriches would therefore have derived a selective advantage in the face of predators by having brown eggs. Our results therefore are consistent with the prediction, and support Bertram and Burger's (1981) conclusion, that white Ostrich eggs minimise overheating, but are prone to predation.

In conclusion, brown Ostrich eggs, if they had evolved, would have been less easily detected by predators than white eggs, as demonstrated by our visibility experiment. On the other hand, unattended brown eggs would be overheated on sunny and hot days, imposing a strong selection against brown eggs. Although some types of natural egg pigments may modify the degree of overheating, parent Ostriches could probably only leave brown eggs unattended on cold days or for very short periods of time (<1 h) on sunny and hot days without risking overheating. Hence, the strategy to leave the eggs unattended for several days before incubation starts only seems possible with white eggs.

## Zusammenfassung

Die weiße Farbe der Eier vom Strauß (*Struthio camelus*) ist ein trade-off zwischen Prädation und Überhitzung

Die meisten Bodenbrüter legen pigmentierte Eier, und die Eipigmentierung ist generell der Umwelt angepasst. Pigmentierung von Eiern hat sich als Schutzmaßnahme gegen Prädation entwickelt, aber dunkel pigmentierte Eier können anfällig für Überhitzung sein, wenn sie der Sonnenstrahlung ausgesetzt sind. Der Strauß legt weiße Eier, die während der ersten Wochen vor Bebrütungsbeginn unbeaufsichtigt und recht gut sichtbar für Prädatoren sind. Um die Effekte der Farbe auf die Temperaturen an der Oberfläche und im Inneren der Eier abschätzen zu können, haben wir einige Straußeneier dunkelbraun oder weiß angemalt und einige als Kontrolle unangemalt gelassen und alle tagsüber direkt der Sonne ausgesetzt. Die Oberflächen- und Kerntemperaturen der braunen Eier waren signifikant höher als die der weiß angemalten Eier und Kontrolleier. Außerdem überstieg die Kerntemperatur der braunen Eier 37.5°C, diejenige Temperatur, bei der die embryonale Sterblichkeit zuzunehmen beginnt. In einem zweiten Experiment haben wir Eier (braun angemalte und Kontrolleier) in verschiedenen Vegetationstypen platziert, um ihre Sichtbarkeit für einen auf sie zugehenden Beobachter

zu untersuchen. Die weißen Eier wurden aus signifikant größerer Entfernung entdeckt als die braunen Eier, was darauf hindeutet, dass das Prädationsrisiko für weiße Eier deutlich höher sein dürfte. Die Ergebnisse lassen daher darauf schließen, dass weiße Eier Überhitzung minimieren und es dem Strauß erlauben, seine Eier vor Bebrütungsbeginn unbeaufsichtigt zu lassen, jedoch sind sie anfälliger für Prädation.

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