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Thermal investigations of some bird nests

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Abstract

This paper presents results from cooling investigations on bird eggs run in nests of several songbird species with contact and contact-less infrared thermometry and with a false colour thermography demonstration of temperature fields on egg surfaces and of the protecting nests. All experiments were performed on single or on up to four (clutch situation) fresh quail eggs. Results indicate that typical cooling curves show a two-phase exponential behaviour consisting of an initial part of warming the still air and the inside surface of the nest and a second part of egg cooling itself. Single eggs lying open to environment may experience a reduction of the cooling rate to 32% when placed in an open nest and even down to 14% in a covered nest. This corresponds to a prolongation of the time to cool down to half of the initial temperature difference from 11 to 35 and 80 min, respectively. IR photos demonstrate the strong thermal gradients of about 10 K of clutch eggs from the inner contact zone to their blunt ends.

Keywords: Bird nests; Cooling curves; Insulation; IR thermography; Thermometry

1. Introduction

Nests are an important “facility” in surviving and breeding strategy of animals, invented several times during evolution. Insects like ants, termites or bees use them to create microclimates for their brood and to conquer geographical areas that would otherwise be forbidden to them due to thermal reasons. Fish rear their progeny in them and mark their territory, mammals like voles or squirrels have individual nests for the night or the cold, while beavers (*Castor fiber*) construct huge dams and castles to be protected against predators. Chimpanzees use simple one-night nests for sleeping and construct new ones in the next evening [1].

Although being extremely different among themselves, bird nests are more or less a synonym for all nests, from the very simple flat-bowl like scraping nests in the ground camouflaged with some natural products like grass, mosses or lichens not to attract the attention of predators over the well-known cup shaped nests of many songbirds to the ingenious hanging homes of the various types of weaverbirds [1]. Moreover, natural cavities in cliffs, rocks or trees or bird-made holes may serve as retreating places for birds during the night, cold or incubation period. Construction material of nests also differs considerably: rush, twigs, plant stalks for the nest wall, simply put together with less attention or carefully placed and inside lined with soft feathers and downs, hair, wool, moss or lichens. Some birds solidify their twig construction with their saliva secretions or take soil and clay as wall material.

In the present investigation aimed for the nest’s isolative capacity and the cooling rate of eggs in it, we concentrated—with one exception—on smaller European songbird nests. We investigated the cooling rates of eggs inside these nests either without insulation from above in order to simulate a situation when no adult bird is sitting on the eggs or with a well-insulating material simulating the breeding bird except for the active heat transfer to the clutch. As only a few empty egg shells of each investigated species would be at hand for our experiments, all investigations were run with commercially available fresh quail eggs. The size difference to the true eggs of the nests was accepted as of minor importance.

The eggs’ heating up in water applied here renders a more or less homogeneous temperature distribution in the egg and thus a situation where Fourier’s cooling law may be applied in a one-dimensional, radial way. Turner showed [2]

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that such a state is an idealisation since the usual "contact incubation", when the brood patch of the bird touches the egg and delivers heat only to its upper part, produces temperature gradients in the egg. Warming it completely relies on a further dissipation of the heat through it. Thus, temperature fields would be more correct to describe the thermal situation in an egg. But as the heat conductivity is much higher in the egg than through the layer of still air around it in the nest, the simple approximation chosen here might be correct for the typical intermittent incubation situation of many songbirds.

2. Experimental

2.1. Bird nests

All nests in the present investigations originated from the collection of zoological objects in the Zoological Institute of the Free University of Berlin. They were transferred to the laboratory and used at room temperature (23–25 °C) without further acclimatisation. As temperature differences between the inside of the nest or the eggs in the nest and the ambient air were more important than absolute values, ambient temperatures were monitored and taken as reference throughout the experiments.

All nests and their different properties are collected in Table 1 together with specific data about the corresponding birds: the popular names given in English, German and French followed by the scientific nomenclature, the approximate weight of the bird, the size of the clutch, the two axes of the eggs, the outer as well as the inner diameter of the nest, the thickness of its wall and its height. Finally, comments on the architecture and the insulation of the wall are added. Quail nests are included in the list because their eggs were used in the experiments.

Breeding birds do not cover their nests continuously but leave them periodically during daytime for own foraging and for regulation of the egg temperature. Therefore, they were simulated by adequately sized plastic bags filled with styropor flocks lying on top of the nest. The bags were without contact to the eggs and had of course no heat transfer to the egg like a breeding parent. All bird nests used in the present investigations were more or less cup-like shaped so that the top insulation was well defined. The only exception was the hanging, completely closed weaverbird nest with its entrance from below.

2.2. Bird eggs

Empty egg shells of all investigated nests were available in the zoological collection, but because of fragility they were not used in the thermal investigations. To be in a more or less realistic state they should have been filled with a liquid or semi-solid material of comparable heat capacity. Moreover, thermosensors had to be inserted into them and secured with some sort of glue or cement. Therefore, we decided to use commercially available quail eggs. In most experiments, two or three quail eggs were placed in the nests so that their egg mass amounted to about the same value as a typical four to five egg clutch of the original bird.

The eggs were heated up in a water bath to temperatures (about 40 °C) slightly above the usual breeding temperature, taken out of the water with a spoon, quickly dried with paper towels and transferred into the nests. Attention was paid that the temperature sensors did not loose contact to the egg.

2.3. Data logger thermometry

For continuous monitoring of temperatures 10 kΩ NTC resistors (accuracy ±0.7 K at 20 °C) were inserted through the blunt end into the egg or distributed at special points in the nest (inside and outside surface of the wall, bottom, a few centimetres above the centre of the nest in the open air). The resistors were connected to data loggers (type HOBO Temp, Series 01, Onset Computer Corporation, Pocasset, MA, USA). These loggers store up to 1800 data points at an eight bit digitalizing, so that a resolution of 0.3–0.4 °C can be obtained in the chosen temperature range of 50 °C. The stored data are read out and transferred by a special software (BoxCar 3.5) to a PC for further treatment in a Microsoft Excel programme. The body of experimental information was obtained via this set-up.

2.4. IR thermometry

A hand-held infrared thermometer (THI-300, Tasco, Japan) was additionally used for contactless temperature determination. It works in a temperature range of 0–300 °C and a spectral range from 6 to 12 μm. Its field of view is so small that a good temperature resolution was obtained along the surface of an egg. The repeatability amounts to ±0.8 K, the accuracy to ±1%.

2.5. Thermography

To obtain an impression of the temperature distribution in a bird nest or along the surface of a cooling egg and to locate "hot spots" in a clutch situation, a hand-held infrared camera (AGEMA 570 PRO, Darmstadt/Germany) was applied. It uses an uncooled microbolometer with 320 × 240 pixels that resolves temperature differences of ±0.2 K and local distances of 2 mm and renders an absolute accuracy of 2 K which is sufficient for the present experiments where temperature changes with time and space are of interest and not absolute values. The taken IR pictures were processed and analysed with the software Irwin 5.0 working under Microsoft Windows 95 (for details see [3–6]).

Quail eggs as used in the thermometric part of the present investigations were heated up in a water bath to unnaturally high 55 °C. This temperature was chosen to make the effects more clear and to have a longer time period for observations.

Table 1
Bird nests used in the present investigation, popular names given in English, German, French

				S/W (cm g^{-1})	N	Egg (cm)	$\varnothing_a$ (cm)	$\varnothing_i$ (cm)	d (cm)	h (cm)	Comments
Blackbird	Amsel	Merle noir	*Turdus merula*	25/90	4–5	2.9 × 2.1	13–15	10–12	2.0	6.0	Roots, moss, earth, lined with blades
Song trush	Singdrossel	Grive musicienne	*Turdus philomelus*	25/90	4–5	2.7 × 2.0	12–15	9.0	1.5	6.0	Moss, grass, thin-walled
Serin	Girlitz	Serin cini	*Serinus serinus*	12/30	4–5	1.6 × 1.2	7.5	4.0	1.7	6.0	Well-lined: hair, feathers
Greenfinch	Grünling	Verdier d'Europe	*Carduelis chloris*	15/30	4–5	1.9 × 1.4	10.0	5.5	1.7	5.5	Thick-walled, warm, lined: feather, hair
Yellowhammer	Goldammer	Bruant jaune	*Emberiza citrinella*	17/30	4–5	2.1 × l.6	10–11	6.0	2.0	4.0	Strong, thick-walled, lined with hair
Chaffinch	Buchfink	Pinson des arbres	*Fringilla coelebs*	16/30	4–5	1.9 × 1.5	10.0	4–5	–	6–7	Skilful, thick-walled, inside smooth, moss
Brambling	Bergfink	Pinson du nord	*Fringilla montifringilla*	16/30	3–5	–	7.5	4.0	2.0	5.0	Loose, lined with moss, lichens
Dunnock	Heckenbraunelle	Accenteur mouchet	*Prunella modularis*	15/30	4–5	2.0 × 1.5	9–11	4–7	1.5	4.0	Pretty cub, carefully lined with hair
Swallow	Rauchschwalbe	Hirondelle de cheminée	*Hirundo rustica*	<15/30	4–6	2.0 × l.4	16 × 9	8 × 7	–	9.0	Glued to the wall, fat soil including twigs
House Martin	Mehlschwalbe	Hirondelle de fenetre	*Delichon urbica*	<15/30	4–6	2.0 × 1.4	9–13	10	2.0	4.0	Glued to the wall, closed hemisphere
Weaverbird[a]	Webervogel	Tisserin	*Ploceus cucullatus*	13/30	2	1.9 × 1.3	10–15	7–12	1.5	16	Artificially woven
Quail[b]	Wachtel	Caille des bles	*Coturnix coturnix*	25/90	8–13	3.0 × 2.3	–	–	–	–	Shallow scrape

S/W: size/weight of the bird; N: number of eggs per clutch; $\varnothing_a$: outer nest diameter; $\varnothing_i$: inner nest diameter; d: wall thickness; h: height (data taken from ornithological textbooks and from avian field-guides).

[a] Construct completely closed, hanging nests with entrance from below.

[b] Construct flat scraped nests in the ground with some insulation by feathers and plant material.

The eggs were dried and transferred to the chosen nest as quick as possible. In some experiments the cup-shaped nests were kept open on top to follow the temperature decrease of the eggs thermographically, in other ones they were closed to have a more natural breeding condition. Although the IR camera only discriminates the surface temperatures, it is nevertheless possible to look slightly through the walls into the nest or just into the upper layers of the nest walls due to their light construction. In this way, nest inner temperatures and their changes could be estimated also for covered nests.

3. Results

3.1. Quail eggs

The quail (*Coturnix coturnix*) eggs used had a fresh mass of 11.2 ± 0.8 g (mean standard deviation, $n = 12$) with a range from 10.6 to 13.1 g. Their geometrical size was 3.0 cm × 2.3 cm, comparable to that of the blackbird (*Turdus merula*) or the song trush (*Turdus philomelus*) but larger than the eggs of many of those birds whose nests were investigated (see Table 1). The egg surface amounted to $\sim 20\,\text{cm}^2$, its heat capacity to $37.5\,\text{J deg}^{-1}$.

3.2. Cooling rates

Examining cooling curves it is essential to use the temperature difference between the egg and ambient and not the absolute values as obtained by the data logger. Most statistic programmes (like Excel, e.g.) offer exponential regression lines without an additive term in their equation for the ambient temperature and render completely wrong exponents and low correlation coefficients as seen in Fig. 1 (compared with Fig. 2a and b). The step-wise cooling curve is due to the eight bit-resolution in the experimental temperature range.

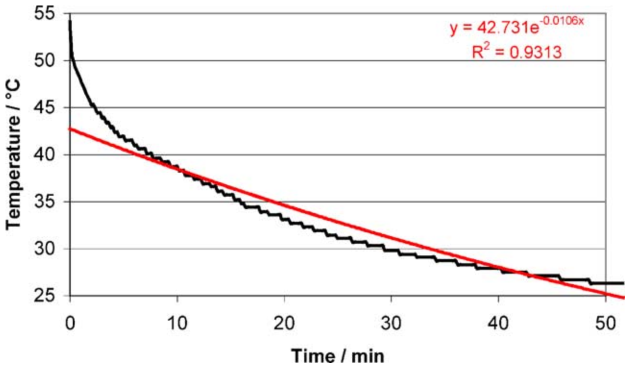

Fig. 1. Cooling curve of a quail egg (12.6 g) lying open on a table at 24.2 °C ambient temperature. The sensor of the data logger was inserted into the blunt end of the egg. Two further sensors determined the temperature in the direct vicinity of the egg. The curve presents the egg temperature proper (in °C) and not the temperature difference (in K). For further information see text.

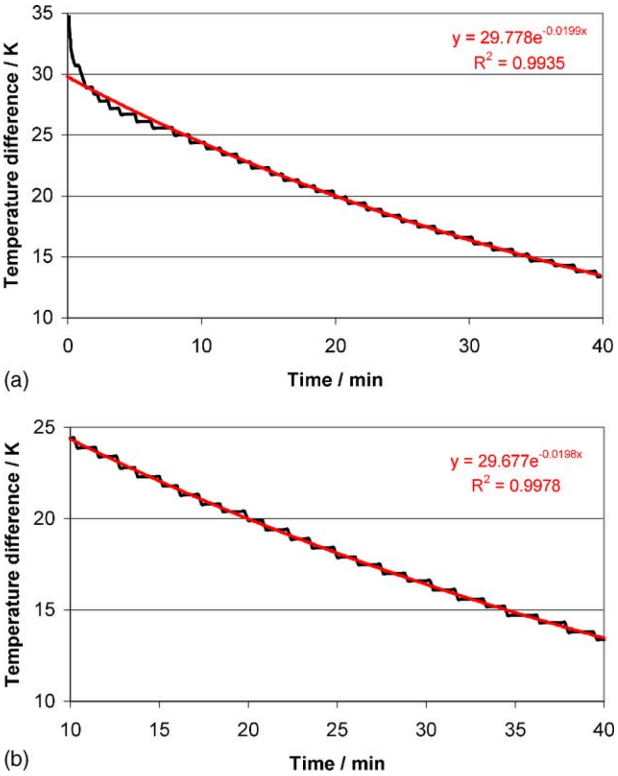

Fig. 2. (a) Total cooling curve of a fresh quail egg (13.1 g) in an open chaffinch nest. The slope shows the temperature difference between the egg and the room (24.0 °C). The three parts of (i) handling, (ii) warming the surrounding air, and (iii) of egg cooling together with the exponential regression line (grey) are shown. (b) Third part of the slope in Fig. 2a together with the exponential regression line, the fitting equation and the correlation coefficient.

Cooling of eggs inside or outside the nest follows Newton's law of cooling and thus an exponential time course. In the present experiments this course is split in three parts (Fig. 1): a first very steep descend that is due to handling of the eggs directly after heating them up in a water bath and transporting them to the nest. It is coined by conductive heat transfer to the transporting medium (spoon, forceps, fingers) and by evaporation of residual water from the egg surface. This part was eliminated from the evaluation. The second part originates from warming a layer of air around the eggs when lying unprotected on a table or of the still air inside the nest under "natural" conditions [7,8]. Both parts endure for less than 10 min and lead to the final proper part of cooling, which corresponds to those daily periods when the breeding parent leaves the nest because of own feeding or temperature regulation.

This three-fold splitting is easily seen in Fig. 2a for a quail egg of 13.1 g in the open nest of a chaffinch (*Fringilla coelebs*, see Table 1). The exponential regression line for the whole period with an exponent of $-0.0199\,\text{min}^{-1}$ describes the final part correctly, but under- and overestimates the first minutes. Taking only the last part renders a perfect description with an exponent of $-0.0198\,\text{min}^{-1}$, a drop of temperature difference to the 1/*e*-part (36.8% of

Table 2
Some data concerning the total cooling process and the subdivision in two periods (as described in the text)

Bird's nest/Eggs	Total rate (min^{-1})	R^2	Time (min)	Rate 1 (min^{-1})	R^2	Time (min)	Rate 2 (min^{-1})	R^2	Time (min)
Blackbird/four eggs[a]	−0.0164	0.9965	0–140	−0.0279	0.9865	0–12	−0.0161	0.9967	15–140
Weaverbird/three eggs	−0.0319	0.9978	0–47	−0.0366	0.9928	0–8	−0.031	0.9976	10–47
Table/one egg	−0.0474	0.9974	0–55	−0.1019	0.9813	0.2–3	−0.0474	0.997	10–55
Table/one egg	−0.0557	0.996	0–65	−0.0756	0.9944	0.6–5	−0.0542	0.9953	10–65
Table/one egg	−0.0849	0.9780	0–40	−0.0944	0.9976	0–6	−0.0878	0.9731	5–40

The rate is given as exponent of an exponential trend line together with its regression coefficient R^2. Time indicates the duration of the evaluated period.

[a] In this experiment the blackbird's nest was covered with a "breeding bird".

the initial value) in 50.5 min and a correlation coefficient $R^2 = 0.9978$ (Fig. 2b). Corresponding data are collected in Table 2.

To evaluate the insulating facilities of a nest, cooling-rates of eggs were determined in three different categories: lying (i) single on a table in still air on paper towels (to reduce conductive heat loss to the support); (ii) single or as clutch in an open nest; and (iii) in a nest covered on top. Cooling rates change considerably in the three categories. Tables 2 and 3 present the corresponding results for quail eggs. Rate 2 in Table 2 (the long-term cooling rate without the initial steep descend) varies from $-0.0161\,\text{min}^{-1}$ (62.1 min) for a four-egg clutch in a covered blackbird nest over a three-egg clutch in a weaverbird nest with $-0.0310\,\text{min}^{-1}$ (32.3 min) to rates of up to $-0.0878\,\text{min}^{-1}$ (11.4 min) for single eggs in still air on a table. These values are expanded down to $-0.0125\,\text{min}^{-1}$ (80.0 min) for a single egg in a closed blackbird nest (Table 3). Taking the extremes of this compilation, one obtains an insulation gain in a closed blackbird nest of 80 min/11.4 min = 7.0 or 600%.

Table 3 compares the cooling rates of some nests open or covered and presents the energy gain as "ratio". This varies from 2.3 for a deep lying egg in a or for the bottom of a blackbird nest to just 1.3 for an egg in a serin (*Serinus serinus*) nest or the inside wall of a chaffinch nest. Both are deep, well-insulated cups with strong walls (Table 1). Depending on the structure and the architecture of the nest the influence of the insulating top layer is of varying importance. Some nests consist of strong upright walls of twigs and grasses, fortified with clay or similar solid material and lined with feathers, moss or lichens for further insulation. Here, irradiative heat loss to the top plays an important role, in contrast to simple, careless constructions with rather open walls. Nevertheless, variations also occur within one specific nest (see blackbird nest in Table 3).

Moreover, an open blackbird nest was investigated with four quail eggs, two of them with sensors in their blunt end and a further sensor at the bottom of the nest. Additionally, their surface temperatures were monitored contact-free with an IR-thermometer. Four quail eggs are too large to lie flat in one level in the nest so that they were partly covering one another. This resulted in highest rates for the upper two eggs ($-0.029\,\text{min}^{-1}$), a reduced one ($-0.026\,\text{min}^{-1}$) for the intermediate egg and a small one ($-0.023\,\text{min}^{-1}$) for the lowest egg. The bottom of the nest cup cooled most slowly ($-0.021\,\text{min}^{-1}$). When the nest was covered with a styrofoam cap, the rates became more homogenous at a level of $-0.016\,\text{min}^{-1}$.

3.3. IR thermographic pictures

Calibrated infrared false colour thermography renders contact-free information about temperature itself and temperature distribution on the surface of an object. In the present investigations IR thermography was applied to discriminate the local temperatures and thus their gradients inside the nests, between the egg(s) and the nestwall and across the nestwall itself. Besides this it was interesting to determine the temperature field [2] along the egg surface and the mutual influence of eggs in the contact zone. Moreover, short IR video clips showed cooling of eggs as well as of nests as function of time.

Table 3
Cooling rates and times of decrease to the 1/*e*-value (36.8%) for quail eggs and still air inside some nests, open or covered by an artificial breeding bird, and the ratio of the two rates

Object	Latin name	Open nest		Closed nest		Ratio
		Rate (min^{-1})	Time (min)	Rate (min^{-1})	Time (min)	
Blackbird nest, one egg	*Turdus merula*	−0.0295	33.9	−0.0125	80.0	2.36
Blackbird nest, one egg	*Turdus merula*	−0.0245	40.8	−0.0146	68.5	1.68
Blackbird nest, one egg	*Turdus merula*	−0.0315	31.7	−0.0159	62.9	1.98
Blackbird nest, four eggs	*Turdus merula*	−0.0295	33.9	−0.0161	62.1	1.83
Blackbird nest bottom	*Turdus merula*	−0.0212	47.2	−0.0091	109.9	2.33
Serin nest, one egg	*Serinus serinus*	−0.0310	32.3	−0.0250	40.0	1.24
Chaffinch nestwall inside	*Fringilla coelebs*	−0.0196	51.0	−0.0143	69.9	1.37

The mean of the correlation coefficients of all rates amounts to $R^2 = 0.992 + 0.015$.

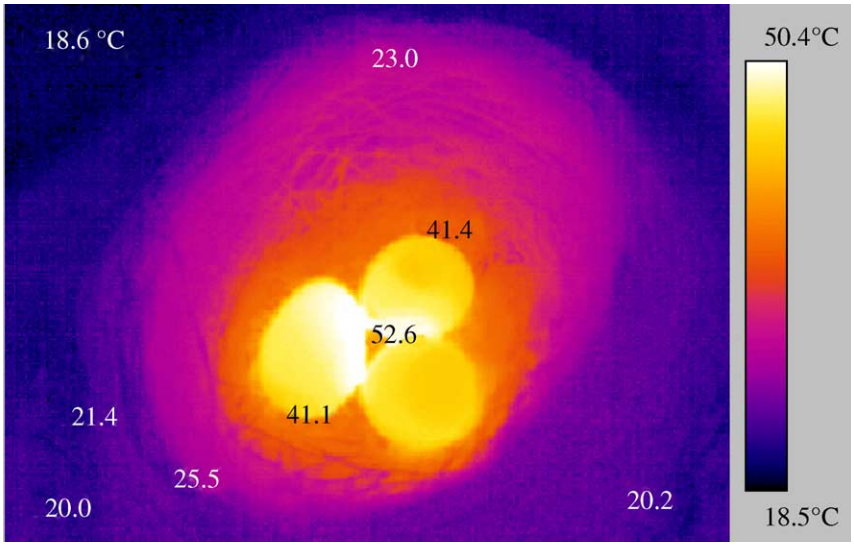

Fig. 3. Infrared false colour photograph of the temperature distribution inside a blackbird (*Turdus merula*) nest with three eggs. Temperatures at some special points are indicated, others can be found by means of the right-hand scale.

Temperature differences across the nest wall varied from 1 to 3 K depending on the used material, the structure of the wall and the care taken by the bird during the construction. Well-formed cup-like nests of chaffinch (*F. coelebs*), dunnock (*Prunella modularis*) or yellowharnmer (*Emberiza citrinella*) (Table 1) show high gradients and thus good insulation while less well-structured nests like those of song trush (*T. philomelus*) and brambling (*Fringilla montifringilla*) (Table 1) have temperature gradients near to zero. Monitoring egg temperatures by thermography was of course possible only with open nests. But also nests covered with a "breeding bird" or closed liked that of the weaverbird rendered essential information concerning the different insulation degrees along the walls and the bottom. Greenfinch (*Carduelis chloris*) nests, e.g. have a very poor insulation at the bottom but thick walls lined with feathers or hair.

Fig. 3 shows a look into a blackbird (*T. merula*) nest with three eggs. The photo was taken in a dark room at 18.6 °C some minutes after the eggs were heated up and placed in the nest. They already cooled down to around 41.1 °C at the remote ends but only to 52.6 °C in the central part where the eggs contact or face one another. Such an inhomogeneity or temperature field in the egg was also observed by other authors [2,9]. The inner surface of the nest remains for a longer time at 25.5 °C, the upper outside at 21.4 °C and the lower part of the nest at 20 °C.

A nest of the African weaverbird (*Ploceus cucculatus*) is presented in the thermographic mode in Fig. 4. Three heated eggs were placed inside the nest a few minutes before

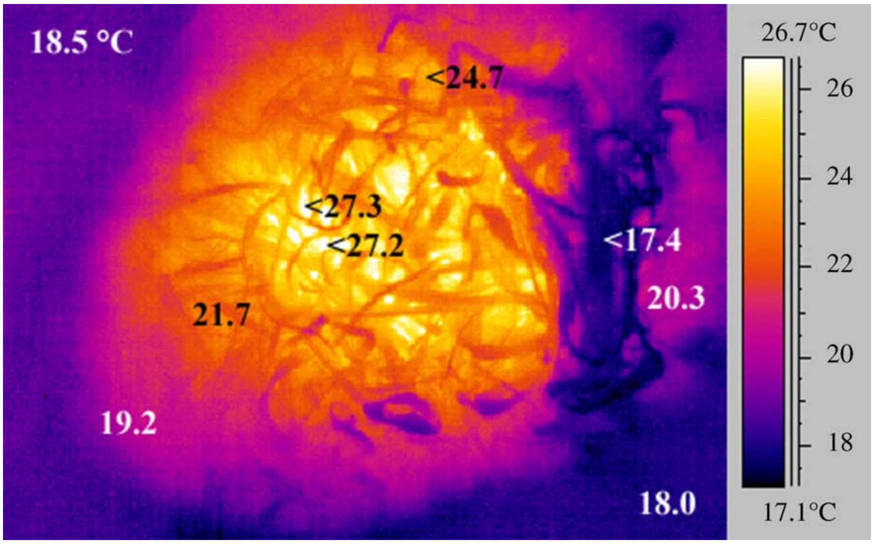

Fig. 4. Infrared false colour photograph of a weaverbird (*Ploceus cucullatus*) nest containing three eggs from the outside. The "<" sign is marking a special point and not used in a mathematical sense.

this photo was taken. The temperature span is significantly smaller than in Fig. 3 as the nest can be seen from outside only. At a microenvironment of about 18.5 °C, some structures (stalks extending far off the surface) are even below 17.4 °C, and the nest inner temperatures above 27 °C. The pictures show the light but strong woven structure of this hanging nest with an entrance from below and a breeding chamber aside of it. This picture confirms the high cooling rate of $-0.0319\,\text{min}^{-1}$ in the closed weaver nest presented in Table 2.

Although the original pictures are given in false colours that facilitate the temperature reading on the right hand scale, even in grey tones one gets a good impression of the temperature distribution inside the nest. Moreover, it is possible to make a rough temperature estimation for points of special interest.

4. Discussion

Bird nests are ingenious constructions in the animal kingdom. They may not only serve for incubating the eggs and rearing the brood but also to shelter the bird in cold periods. A bird nest compensates for the unfavourable surface-to-volume ratio of small eggs. They are better protected in cup-shaped nests against direct sun radiation, wind and rain when the breeding parent is away. Due to their high own metabolic demand smaller songbirds are less attentive for their eggs and sometimes out for foraging. Between two-third and three-fourth of the daylight time is dedicated to incubation, the rest to feeding [10]. But at the same time, sitting on the clutch reduces the parental energy dissipation between 15 and 65% for the bird. Thus, the nest may be understood as a well-fitting cloth to both, bird and egg, with an insulation in the same order of magnitude as the bird plumage itself [10].

The present investigations were dedicated to determine to which extent heat loss from eggs to the environment can be reduced by different songbird nests. Their cooling rates are often presented in the literature as temperature change per temperature difference and time ($\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$) and not as the exponent (min^{-1}) of an exponential approximation as in this paper. But our data can easily be transformed to the other measure rendering values from $5.27\,\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$ for a single quail egg on a table to $0.75\,\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$ for a single egg in a covered blackbird nest. This corresponds to an 86%-reduction in energy consumption for the breeding bird. Frost and Siegfried [7] published a rate of $2.58\,\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$ for a single moorhen (*Gallinula* chloropus) egg of 20.2 g in a draught-free box that corresponds well with the present quail egg data of 2.63 and $2.84\,\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$ under similar conditions. Using their regression equation with a quail egg mass of 11.3 g one arrives at $2.16\,\text{K}\,\text{K}^{-1}\,\text{h}^{-1}$. Such values can be only taken as a first approximation to the natural conditions since eggs—and thus clutches—have no uniform temperature but are characterised by a temperature field ([2,9], see also Fig. 3).

Kendeigh [11] proposed an equation to estimate the energy cost for incubation of a clutch of eggs. This equation contains the number of eggs, egg mass and specific heat, cooling constant, temperature difference and the fraction of the egg surface in contact with the bird's brood patch (usually <20%). Using a cooling rate of $-0.0161\,\text{min}^{-1}$ for a four-egg clutch in a covered blackbird nest (Table 2), a typical temperature difference of 3 K between egg and still nest air [9] as well as a specific heat capacity of $3.3\,\text{J}\,\text{g}^{-1}\,\text{K}^{-1}$ one arrives at a heat flow of 0.12 W. This has to be compensated by the breeding parent to keep the egg temperature constant. Standard metabolism of passerine birds scales by mass to a power of 0.75 [12]. Looking for a blackbird of 90 g, its metabolic rate comes to 1.01 W, which has to be dissipated through the bird's surface. Only 16% of this surface are in contact with the clutch [7,8] so that the $0.16 \times 1.01 = 0.16\,\text{W}$ leaving the bird through the contact area (brood patch) are enough to compensate for the calculated loss of 0.12 W. Such estimations are only approximations since intermittent breeding, clutch size and nest insulation may change the picture. But they support the often presented idea that the additional energy consumption for incubation is small or even zero [7–9].

Birds instinctively know how to construct their nests and which material to use. Closed nests are typical for small birds and become more open for larger ones [10]. Finer material like needles, leaves, reeds or mosses, but also hair, fur and feathers including downs are often used to further insulate and to cushion the eggs [13]. Redman et al. [14] showed for voles (*Microtus agrestis*) as nest-building mammals that wall thickness is the most important factor for insulation but that it conflicts with the energy consumption for constructing the nest. When the obtained size guarantees a temperature within the thermoneutral zone (where no additional energy is necessary to keep the body temperature) a further increase in thickness is useless. Empty nests are always near to the ambient temperature. Only the incubating bird produces the essential microclimate [10].

Good insulation, moreover, involves the danger of overheating the clutch by direct sun irradiation. Lethal temperatures start at about 40.5 °C, only a few degrees above the usual incubation temperatures (37–38 °C) so that "death through overheating is uncomfortably close at all times" [9]. Birds developed strategies to cope with this problem but they are not so easy to practise as to protect the clutch against cold. Undercooling is physiologically less dangerous for the brood, more simple to avoid and in its onset considerably away (25–27 °C) from brood temperature [9].

Romijn and Lokhorst [15] showed for chicken eggs that in the first half of the embryo development the heat production rate is very small, less than 10% of the final value [12]. Thus, it may be neglected for the present investigations. In the second half the heat production rate follows a sigmoid curve with a plateau value of about 130 mW (ca.

7 mW g^{-1}) comparable to the 0.12 W heat flow calculated above for the four-egg clutch of nearly the same mass. Thus, the embryo contributes significantly to the thermal balance in the nest. Its metabolism is high enough to increase the egg temperature by 2–3 K against ambient [2]. Eggs even have the possibility to regulate their temperature and to communicate with the parent bird about its breeding activity [10]. Drent [9] underlines such observations with the statement: "The heat-transfer relation between the parent and its eggs ... can be thought of as though the parent treats the eggs as an extension of its own body core".

It was mentioned above that bird nests not only serve for insulation of eggs and hatchlings but also for the adults. Buttemer found for verdins (*Auriparus flaviceps*) (see [14]) that their metabolic rates at 5 °C ambient temperature are 52% higher outside than inside the nest. Social weaver birds (*Philetairus socius*) roost in cold winter nights of the Kalahari desert with temperatures down to −10 °C in huge pending nests of many chambers with entrance tubes pointing to the ground. Even empty nests show temperatures 4–6 K higher than ambient, while occupied ones are up to 18 K warmer and grant energy savings of about 40% or 7 kJ per day. These reductions are essential for surviving since seeds and insects as food are scarce in the winter season [16–18].

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References

[1] K. von Frisch, Animal Architecture, Harcourt Brace Jovanovich, New York, 1974.
[2] J.S. Turner, in: D.C. Deeming, (Ed.), Avian Incubation—Behaviour, Environment, and Evolution, Oxford University Press, 2002, p. 119.
[3] I. Lamprecht, E. Schmolz, S. Hilsberg, S. Schlegel, Thermochim. Acta 382 (2002) 199.
[4] I. Lamprecht, E. Schmolz, L. Blanco, C.M. Romero, Thermochim. Acta 391 (2002) 107.
[5] D.P. DeWitt, G.D. Nutter, Theory and Practice of Radiation Thermometry, Wiley, New York, 1989.
[6] G. Gaussorgues, Infrared Thermography, Chapman and Hall, London, 1994.
[7] P.G.H. Frost, W.R. Siegfried, Ibis 119 (1977) 77.
[8] W.R. Siegfried, P.G.H. Frost, Ibis 117 (1975) 102.
[9] R. Drent, in: D.S. Farner, J.R. King, K.C. Parkers (Eds.), Avian Biology, vol. V, Academic Press, New York, San Francisco, London, 1975, p. 333 (Chapter 6).
[10] A. Ar, Y. Sidis, in: D.C. Deeming (Ed.), Avian Incubation—Behaviour, Environment, and Evolution, Oxford University Press, 2002, p. 143.
[11] C.S. Kendeigh, in: Proceedings of the 13th International Ornithology Congress, 1962, p. 884.
[12] A.I. Zotin, Thermodynamic Bases of Biological Processes—Physiological Reactions and Adaptations, De Gruyter, Berlin, New York, 1990, p. 293.
[13] http://www.stanfordalumni.org/birdsite/text/essays/.
[14] P. Redman, C. Selman, J.R. Speakman, J. Comp. Physiol. B 169 (1999) 581.
[15] C. Romijn, W. Lokhorst, J. Physiol. (Lond.) 145 (1960) 239.
[16] F.N. White, G.A. Bartholomew, T.R. Howell, Ibis 117 (1975) 171.
[17] G.A. Bartholomew, F.N. White, T.R. Howell, Ibis 118 (1976) 402.
[18] J.W.H. Ferguson, M.J.M. Nijland, N.C. Bennett, J. Comp. Physiol. B 172 (2002) 137.