

Egg temperature and incubation behaviour of the ostrich

by

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ABSTRACT

The paper reports on aspects of the physiology and behaviour of incubation in the Ostrich *Struthio camelus*. Temperatures of eggs, nest and ambient, in relation to the parent birds' incubation rhythms, and provisional estimates of the cost of energy and water to the incubating bird point up functional features of the division of labour between the parents.

I INTRODUCTION

Large birds can inhabit warm areas only by adaptations to increase capacity for heat loss in relation to heat production (Kendeigh 1972). The Ostrich *Struthio camelus*, in addition to being the world's largest living bird, is a successful inhabitant of hot, arid country, including true deserts. Many animals living in deserts are able to do so only because of their ability to escape to protective microclimates. This strategy is denied the Ostrich — it is of too large a size.

The Ostrich employs a number of physiological adaptations in overcoming its thermoregulatory problems (Cloudsley-Thompson and El Mohamed 1967, Crawford and Schmidt-Nielsen 1967, Louw, Belonje and Coetzee 1969, Louw 1972). Significantly, these physiological mechanisms, enhanced by behavioural strategies, operate to save water; and it is clear that conservation of water is crucial to the bird's ability to survive in deserts. Ostriches are highly adaptable in responding to unpredictable local environmental conditions, and, in the desert, have been recorded breeding at all times of the year (Sauer and Sauer 1966). When sitting on their nests, Ostriches are isolated from water-holes and are directly exposed to cycling extremes in ambient temperature, wind and solar radiation.

There is little published information on the functional significance of the Ostrich's incubation performance, as an extension of its adaptations to successful desert survival. This paper presents data on aspects of the physiology and behaviour of incubation in the Ostrich.

II METHODS

A blind was used to observe undisturbed feral Ostriches in the Mossel Bay district, South Africa. Following Drent's (1970) method, ambient, nest-air and egg temperatures were measured continuously by means of thermistor probes and telemetry during 24-hour watches on one pair of incubating birds. The air cell of one egg in a clutch of 10 was implanted with a thermistor probe. The tip of the probe rested against the inner cell membrane. The hole in the egg was sealed with epoxy resin. Temperatures were recorded at five-minute intervals. Cooling rates of eggs were measured in accordance with the procedure and precautions advocated by Kendeigh (1973).

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III RESULTS

3.1 Incubation rhythm

It has long been known that the male Ostrich tends the eggs and incubates at night, whereas the female is on the nest during the day (le Vaillant 1790). However, the shares of the sexes are not equal. Normally, in undisturbed steady incubation, each monogamous parent takes one complete shift, which is an unbroken sitting spell, every 24 hours. During a continuous 24-hour watch on one nest the male's sitting spell amounted to 14,75 hours and that of the female 9,25 hours. Thus, in this case, the male tended the eggs for about 61 per cent of the 24-hour period. Normally, the male relieves the female at the nest in the late afternoon and sits through the night until well after sunrise. Times of morning and afternoon change-overs, expressed respectively in hours after and before times of local sunrise and sunset, were recorded as 2,1 and 2,0 hours after sunrise, and 2,5, 2,5 and 2,7 hours before sunset. Change-overs took place quickly, and the eggs were uncovered for no more than a few minutes.

Aside from moving their necks and heads, it is remarkable how little the parents change position when on the nest. It appears as if the eggs are shifted relatively seldom. An undisturbed male observed incubating for 10 hours did not change position on the nest, nor did he attempt to shift the eggs. A female was observed to change position once in 10 hours of undisturbed incubation, and once, just before change-over, to use her beak in attempting to shift the eggs. According to Sauer and Sauer (1966) the parents turn and displace the eggs daily once steady incubation has started.

3.2 Nest-air and egg temperatures

The data are summarised in Table 1, and derive from a nest that contained 10 eggs which the parents had been incubating steadily for seven days (i.e., seven days after completion of laying). Under equilibrium conditions of undisturbed steady incubation, the temperature values reported here for Ostrich eggs fall within the range of temperatures at which avian eggs are held normally during incubation (cf. Drent 1973). It is remarkable how constant are the temperature regimes of the eggs and nest; and this is an expression of the parents' high degree of attentiveness, relatively stable body-temperature (see Bligh and Hartley 1965, Crawford and Schmidt-Nielsen 1967), relative lack of movement on the nest and

Table 1. Average egg, nest-air and ambient temperatures during natural incubation in the Ostrich.

Parent	Per cent attentiveness	Temperatures °C						No. records
		Egg		Nest-air		Ambient		
		mean	S.D.	mean	S.D.	mean	S.D.	
Male	100	33,85	0,48	31,88	0,25	19,48	2,33	177
Female	100	36,07	0,88	31,55	0,13	25,19	1,97	111

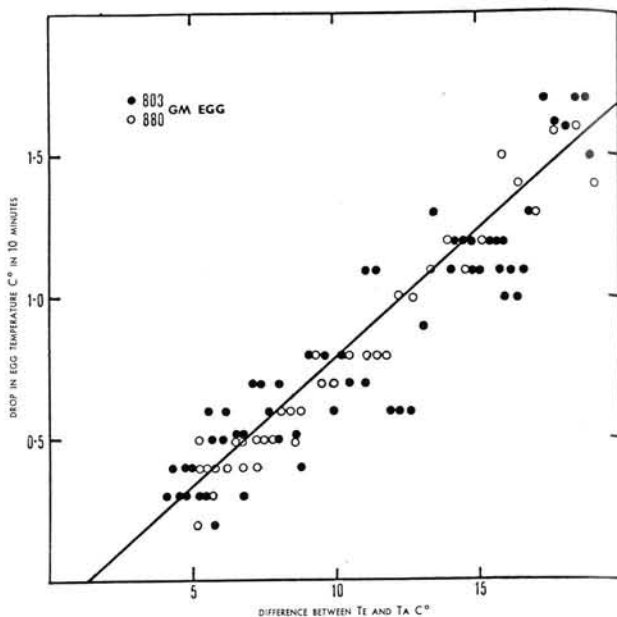


Figure 1. Relationship between fall in egg temperature and difference between egg and ambient temperature in the Ostrich.

shifting of the eggs, and the relatively slow rate at which the large eggs lose and gain heat.

The laboratory determined cooling rates of two fresh (unincubated) eggs weighing 880,6 and 803,0 g are shown in Figure 1; a cooling rate of $0,53^{\circ}\text{C}/^{\circ}\text{C}/\text{h}$ was calculated from the combined data. This figure agrees well with the expected constant extrapolated from known cooling constants for eggs of other species (Drent in prep.).

During a more or less constant ambient temperature of 25°C , an Ostrich egg, stationary in the centre of a 10-egg clutch, cooled at the rate of $2,27^{\circ}\text{C}/\text{h}$ and gained heat at $0,94^{\circ}\text{C}/\text{h}$ during a total period of two hours, involving the absence and presence of a parent with concomitant egg temperature changes of $1,4^{\circ}\text{C}$ between $32,0^{\circ}$ and $33,4^{\circ}\text{C}$.

3.3 Energy cost of incubation

The parameters set out below for the Ostrich have been applied to Kendeigh's (1963) equation for the calculation of the energy cost of incubation.

- n = no. eggs in clutch = 10
 w = mean weight of eggs = 1 000 g
 h = specific heat of egg = $0,80 \text{ g-cal}/^{\circ}\text{C}$
 b = cooling rate of eggs = $0,5^{\circ}\text{C}/^{\circ}\text{C}/\text{h}$
 t_e = egg temp. maintained in nest = $35,9^{\circ}\text{C}$ (male) = $36,1^{\circ}\text{C}$ (female)
 t_{na} = nest-air temp. surrounding eggs = $31,9^{\circ}\text{C}$ (male) = $31,6^{\circ}\text{C}$ (female)
 i = interval in hours = 14,75 (male) = 9,25 (female)
 c = % total surface egg covered by parent = 30%
 a = % of time interval parent sitting on eggs = 100%

$$\text{k cal/bird-day} = \frac{n \cdot w \cdot h \cdot b \cdot (t_e - t_{na}) \cdot i \cdot (1 - c \cdot a)}{1000}$$

On this basis, the male Ostrich parent expends 165.2 k cal/bird-day, whereas the cost to the female is 116.6 k cal/bird-day. Hence, the female saves about nine per cent of the energy she would have to expend if the energy cost were to be equally divided between the parents.

IV DISCUSSION

The data reported here derive from feral, monogamous Ostriches living in a relatively serene environment. Nevertheless, they are indicative of aspects of the functional significance of the Ostrich's incubation performance, as an extension of its adaptations to successful survival in hot and arid country.

Desert nights generally are cool (because of radiational loss to space), and heat flow from the incubating parent to and through the eggs is relatively high. In the Ostrich the male is responsible for this extra-energy demanding phase of incubation. Production of the clutch (approximately 10% of the Ostrich's body weight) must tax the female's energy reserves, and presumably any energy saved after that could promote quicker production of a subsequent clutch should the first one be lost. This may be important in the desert where conditions favourable for breeding occur erratically and are short-lived.

Data on productive energy (=maximum energy available minus energy required to sustain essential body processes) are not available for the Ostrich. Thus it is not possible, at this stage, to estimate the proportion of productive energy devoted to incubation. However, productive energy is related to body weight, as is basal metabolism. Crawford and Schmidt-Nielsen (1967) obtained a figure of 2 350 k cal/day for basal metabolism in a 100 kg Ostrich. This value is considerably in excess of one predicted from body size, and it is probable that 1 800 k cal/day is more realistic (see Crawford and Schmidt-Nielsen *op.cit.*). On this basis, the fractions of the parents' energy for basal metabolism devoted to incubation amount to nine and six per cent in the male and female respectively. These proportions are relatively low when measured against comparable values for a number of smaller birds (see Lasiewski and Dawson 1967, Drent 1973). The main conclusion here is that the daily energetic cost of incubation is relatively low in the Ostrich, though points to be considered are: (a) the long incubation period of 42 days, and (b) the demands of relatively low ambient temperatures typical of the desert night. Under natural conditions, birds' eggs exposed upon departure of the parent lose heat faster than their rate of heating when the parents return (Drent 1973). Ostrich eggs are no exception to this. Clearly, therefore, during relatively cool ambient temperature constant attentiveness would be advantageous in saving the Ostrich energy in addition to functioning as an anti-predator strategy.

Although the Ostrich can store large amounts of subcutaneous fat during a relatively short period

when on a high nutritional plane, it cannot store water and efficient economical use of water is crucial to the species' survival in the desert (Louw, *et al* 1969). Nesting Ostriches are often isolated and cannot visit water-holes (Sauer and Sauer 1966). By relieving the female well before sunset and by remaining on the nest until well after sunrise, the male, in addition to spending most time on the nest, permits the female two foraging spells, one during early morning and one during evening — Ostriches locate their food by sight. Louw (1972) has pointed up the importance of condensing fog and the comparatively high relative humidity of the air at night in the Namib desert, and their effects on the feeding habits of Ostriches. When grazing in the early hours of the morning the Ostriches favoured those grasses which had a high moisture content (the moisture content of these grasses had dropped by about 20 per cent at noon); direct intake of moisture, deposited as condensing fog or dew, would also have been high during the early hours of morning. The Ostrich's parental rhythm of incubation appears to be adapted to permitting the female to exploit the relatively greater availability of moisture present during early morning in hot and arid country.

Louw *et al* (1969) have demonstrated that convective and radiant cooling, through feather erection and wing drooping, is important to the Ostrich, especially in respect of water-saving. According to these authors only as a last resort, when the ambient temperature approaches 34°C, and when there is no wind, will the birds employ evaporative cooling by increasing the rate of respiration.

Crawford and Schmidt-Nielsen (1967) estimated that the critical threshold for change in respiratory rate was 25°C. Louw *et al* (*op.cit.*) pointed out that this figure (25°C) was obtained for birds kept in an artificially heated room where apparently opportunity for convective cooling was minimal. A somewhat similar condition applies to an incubating Ostrich: the bird's body is close to the ground, where wind effect is minimal, solar effect maximal and postural and ptilomotor constraints militate against efficient exposure of large areas of bare skin. We have recorded the high respiratory rate (45/min, see Crawford and Schmidt-Nielsen 1967) in females incubating in full sunlight, under still air conditions and ambient temperature at 25°C. During moderate ambient temperatures of this magnitude females have been observed to occasionally leave the care of warming the eggs to the sun, while standing guard nearby and employing convective cooling behaviour. During the night, early morning and evening, when ambient temperatures are relatively low, in the sitting male water loss due to pulmocutaneous evaporation should be minimal.

We have found very obviously heat-stressed parents sitting on their nests when surface soil temperature was greater than 55°C and air temperature 49°C at 50 cm above ground level. At these temperatures it is the heat flow from the environment to the eggs that is important, and it is necessary for the parent to sit closely to withdraw heat from the eggs. Under these conditions, we have observed a male to take over egg-tending duties in the middle of the day; the

female moved to the shade of a nearby thorn bush (*Acacia karroo*) and took up a posture designed to maximise convective and radiant cooling. After 15 minutes her respiration decreased to the normal low rate. The frequency and extent of this deviation from the usual parental rhythm of incubation are not known, but the adjustment appears functionally significant resulting in a saving of water to the female. Crawford and Schmidt-Nielsen (1967) have shown that at an ambient temperature of 45°C the Ostrich dissipates by respiratory evaporation about 100 per cent of its metabolic heat production, and in the process of doing so loses water at the high rate of 4.5 g per minute.

In conclusion, the Ostrich's incubation regime appears to be flexible and functionally well adapted to relatively severe demands caused by limited availability of water and energy, generally imposed by the desert environment. Many of the details attending the species' physiological and behavioural adaptations for successful incubation, however, remain to be worked out. While there obviously is cooperation between the members of a breeding unit, there must be also competition between the interests and investments of males and females (see Trivers 1972). For instance, very little is known about incubation in polygynous breeding Ostriches. Polygyny is common in the Ostrich, and as many as five females can lay in one nest. According to Sauer and Sauer (1966) polygynous Ostrich parents may actively help to synchronize the time of hatching of the brood through separating the eggs with the most advanced embryos; these eggs are rolled into especially dug pits surrounding the edge of the nest. Further field observations and experiments are needed to identify the relationships between egg and ambient temperatures and other cues that influence parental behaviour in incubating Ostriches.

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