ASPECTS OF INCUBATION IN OSTRICHES

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SUMMARY

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We studied incubation in domesticated Ostriches *Struthio camelus* in South Africa and wild Ostriches in Kenya. Although the eggs were large, with relatively high thermal capacities, unattended eggs exposed to the sun reached dangerously high temperatures (40,5°C). Experimental exposure of fresh eggs to the sun for seven days prior to incubation greatly reduced the percentage of embryos which developed, and no embryos survived 15 days of exposure. In the wild, Ostriches frequently shade their eggs in the pre-incubation period to prevent overheating.

During natural incubation, temperatures in the eggs (range 30,8–33,8°C) and of nest-air (31,9–34,6°C) were remarkably constant, despite the daily ambient fluctuations of air temperatures (17,8–38,9°C). Similarly the humidity of the nest-air (39–52%) was lower and less variable than the ambient air (39–72%). Water loss during 42 days of incubation was 11–12% of initial egg weight and, in addition, early laid eggs lost 3–4% during the 2½–3 week pre-incubation period. The water vapour conductivity and the daily water loss of Ostrich eggs were similar to those of other birds, in proportion to egg size, despite the arid environment inhabited by Ostriches. Some of the constraints on the feeding and breeding behaviour of Ostriches imposed by the physical requirements of their eggs are discussed.

INTRODUCTION

This investigation into aspects of the incubation of the Ostrich *Struthio camelus* arose to help link together three disparate lines of research. Firstly, field studies of the communal nesting system of Ostriches (Sauer & Sauer 1966a, b; Bertram 1979 a, b, c; Hurxthal 1979) suggest ways in which the evolution of the breeding system and social organization of Ostriches may be constrained by some of the physical requirements of their eggs. These ways need to be investigated.

Secondly, incubation research in the laboratory is leading to an understanding of many of the physical and biological requirements of developing avian embryos (Ar *et al.* 1974; Rahn & Ar 1974; Drent 1975; Ar & Rahn 1978). However, with few exceptions (Hoyt *et al.* 1978), such studies have dealt only with the eggs of much smaller birds.

Thirdly, several studies have concentrated on the adaptation of the Ostrich to its hot and sometimes arid environments. Cloudsley-Thompson & Mohamed (1967), Crawford & Schmidt-Nielsen (1967), Louw *et al.* (1969) and Louw (1972) have concentrated on the physiological adaptations of the adult birds. Siegfried & Frost (1974) considered some of the behavioural and physiological adaptations of incubating Ostriches, with emphasis on the energy budgets of the adults. More information was required on the environment, adaptations and treatment of the eggs themselves.

The unusual features of Ostrich incubation stem from the species' desert habitat and its large size: the two are probably correlated. The hot environment means that the danger of the eggs' overheating may be a greater problem than of their becoming too cool (Drent 1975). The arid envronment may, in evolutionary terms, influence the rate of water loss of the egg and the characteristics of its shell. The large size of the bird means that its egg is both very large (about 1500 g (Bertram 1979a)) yet proportionately small (Lack 1968), being only about 1,5% of the adult female's weight. The large size of the egg means that its temperature fluctuations will be slow, and also that there may be a considerable temperature gradient across it.

Because the eggs are proportionately small, the adult bird can incubate up to about 22 of them (Bertram 1979b). If one female laid them all at two-day intervals, it would take her 42 days. In practice, however, the nests of wild Ostriches usually contain the eggs of three or more birds (Bertram 1979a), the greatest contribution being laid by the "major" hen who, with the male, selects the nest and incubates the eggs. In general the early eggs in an Ostrich nest have to wait for 2½–3 weeks before the six-week incubation period begins. During this long pre-incubation period, the eggs are often left unattended and therefore completely exposed to the sun.

This paper describes the results of an investigation into the temperature and humidity conditions in Ostrich nests, and the water loss and hatchability of their eggs.

METHODS

Most data were collected on Ostrich farms at Oudtshoorn, Cape Province, South Africa, in January 1979 using domesticated South African Ostriches *S.c. australis*. Other data, on fully wild Masai Ostriches *S.c. massaicus*, were obtained by BCRB in Tsavo West National Park, Kenya, from July to October in 1977 and 1978 (Bertram 1979a, b, c).

The breeding Ostriches at Oudtshoorn are generally kept in monogamous pairs, in enclosures up to 1 ha in area, and planted with lucerne. These enclosures are on low ground so that they can be irrigated, and therefore the food quality and soil moisture content are probably higher than those encountered by wild birds.

Egg weights were measured using an Ohaus triple-beam balance. Weight loss before incubation was measured in two situations. Firstly, 19 fresh eggs were kept in an unattended artificial nest in full sunlight for periods of 15 days (10 eggs) and seven days (9 eggs), being turned twice a day through 180° (longitudinal axis) and 90° (vertical axis). On most of these days there was little or no cloud cover, night temperatures dropped 13–18°C, maximum daily temperatures averaged 32,1°C (maximum 40,6°C), and humidity at 14h00 averaged 30,5% (range 12–57%). Secondly, 28 fresh eggs were kept by A. P. Koen (pers. comm.) for periods of three to nine days while stored indoors at 20°C and turned twice daily.

Temperatures in eggs and nests were measured with thermistor probes connected to a Prelim 170 telethermometer. Nest humidity was measured with a Shaw minihygrometer with a 30-m extension lead, and ambient humidity with a Durotherm hygrometer. Temperature and humidity readings were taken at 10 min intervals and the hourly means and standard deviations calculated.

At an artificial nest before incubation, temperatures were measured at the centre of a fresh Ostrich egg in the middle of a clutch of 12, in the soil immediately under the egg, and in the air between the eggs; nest humidity was measured between the eggs. The ambient shade temperature and humidity were measured 1 m away from the eggs.

Similar measurements were made at a nest occupied by Ostriches. Internal egg temperatures were measured in the centre of an egg and at the bottom, just inside the shell. The ostriches pulled at probes and wires within their nests and displaced them with their feet, so it proved necessary to place the probes measuring nest temperature and humidity within a realistic fibreglass dummy egg which was well ventilated on its undersurface with large (2 cm) holes. Both the dummy egg and the probed Ostrich egg were pegged down so that their movements were restricted; both were immediately accepted by the Ostriches.

Ambient temperatures and humidity were measured at shaded spots 20 m from the occupied nest, and internal temperatures in an isolated, unshaded egg 20 m from the nest were also recorded. The birds were thoroughly habituated to humans and appeared to pay no attention to the observers who sat about 30 m from the nest outside the enclosure.

RESULTS

Weight loss before incubation

The mean weight loss of eggs in full sun was 2,88 g per day, or 0,21% per day of the mean fresh weight of 1 387 g (Table 1). By contrast, the mean daily weight loss of eggs stored in cool indoor conditions was 1,71 g per day, or 0,12% of fresh weight. Eggs in most natural nests would probably lose weight at a rate somewhere between these two extremes.

Individual eggs lost weight at different rates: the maximum rate of weight loss was 2,3 times as great as the minimum rate for eggs under the same conditions. The rate of loss did not change with the age of the egg, nor was it correlated with the size of the egg, nor did it show any clear relationship with surface characteristics of the shell. There was no difference between the rates of weight loss of fertile and infertile eggs.

Weight loss during incubation

Table 1 also shows the weight losses of eggs being incubated by Ostriches and by an incubator (Koen 1977). Birds moved eggs in their nests several times a day, apparently haphazardly, whereas the incubator eggs were turned systematically twice a day. The incubator was kept at 37°C air temperature and 62% relative humidity. The values of temperature and humidity in nests (where measured) were both somewhat lower.

TABLE 1
WEIGHT LOSS BY OSTRICH EGGS BEFORE AND DURING INCUBATION

Stage	Mean daily weight loss (g/day)	(± S.D.)	Number of eggs
Before incubation:			
Stored in unattended nest in full sun:	2,88	±0,70	19
Stored at 20°C:			
Fertile eggs	1,73	±0,32	14
Infertile eggs	1,69	±0,20	14
During incubation:			
Farmed birds incubating naturally			
Pair 1 (2nd & 3rd weeks)	2,99	±0,41	6
Pair 2 (3rd week)	3,51	±0,76	12
Pair 3 (5th week)	4,30	±0,34	14
Wild birds, East Africa, incubating naturally (2nd–5th weeks)	3,92	±0,48	26
Incubators:			
Fertile eggs (1st–6th weeks)	2,80	±0,39	19
Infertile eggs (1st–6th weeks)	2,82	±0,29	18

There was considerable variation both between nests and between eggs in the rate of weight loss. For eggs in nests it averaged 3,85 g per day, or 0,28% of fresh egg weight. In incubators, the rate of weight loss was lower than in natural nests. There was no significant change in weight loss over time, and no difference in weight loss between fertile and infertile eggs, indicating that the weight loss was not due to the metabolism of the egg. The overall total weight loss during incubation of eggs in an Ostrich nest would therefore be 162 g, or 11–12% of the total weight. In addition, eggs laid several days before incubation started in a natural nest would have lost between 0 and 55 g, depending on their position in the laying order. Thus the maximum weight loss between laying and hatching would be about 15%.

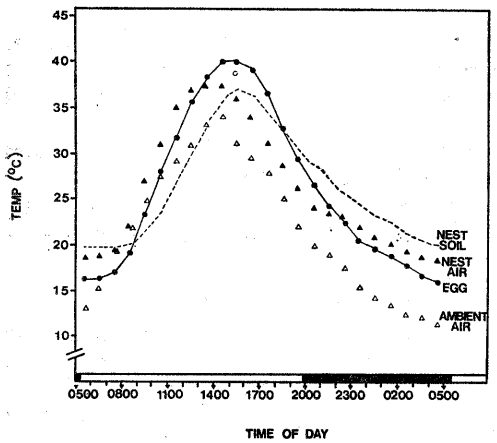

FIGURE 1
Temperatures in an unattended Ostrich nest over a 24-hour period.

Temperatures before incubation

Fig. 1 shows the results of a 24-hour series of recordings of temperatures in an unattended Ostrich nest. Standard deviations of the hourly means have been omitted since only 10% were greater than 1,0°C and the greatest was 2,0°C; the high deviations occurred during hours when the ambient temperatures were rising or falling steeply in the early morning and evening.

The eggs in the unattended nest reached high internal temperatures. The maximum central temperature was 40,5°C, which was considerably higher than the ambient air temperature. The increased egg temperature was due to solar radiation, although much of the radiation was reflected off the shiny white surface. Artificially coloured dark eggs reached even higher temperatures than normal eggs (Bertram & Burger, in prep.). Eggs reached their maximum temperatures almost two hours after the peak ambient temperatures. Thus the large thermal capacity of the large eggs tends to reduce the risk of overheating. The soil under the egg heated and cooled more slowly than the egg itself, and would also tend to dampen the egg's temperature oscillations.

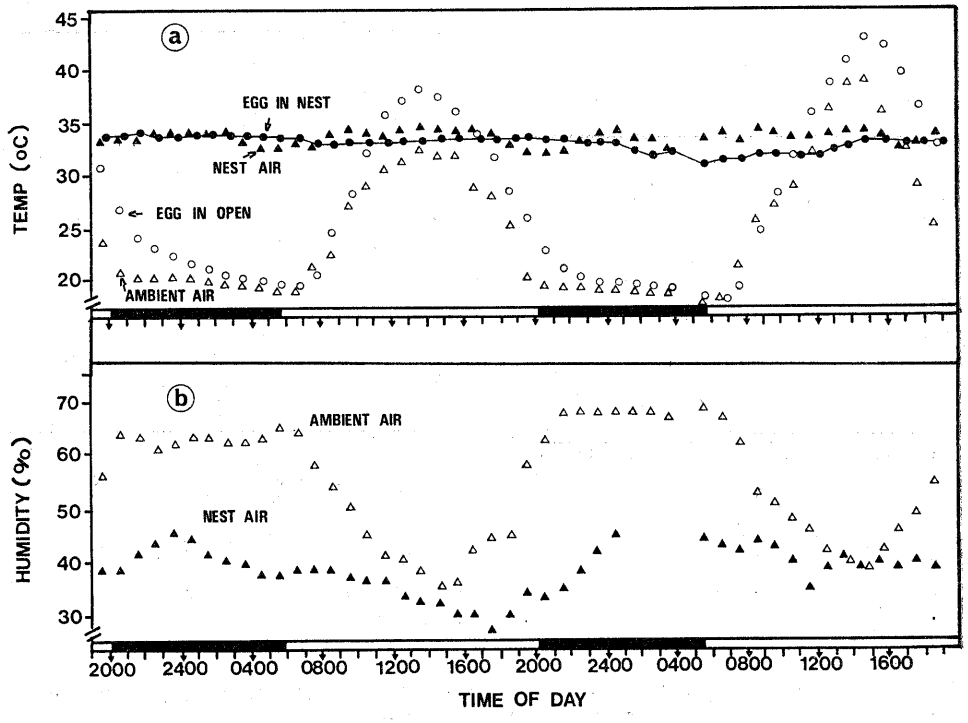

FIGURE 2
Temperatures and relative humidities over a 48-hour period at an incubated Ostrich nest.

Temperatures during incubation

Fig. 2a shows the temperatures during a 48-hour period of observations made at a nest containing 16 eggs in their fifth week of incubation. Less complete recordings at another incubated nest produced results very similar to those illustrated. The standard deviations have again been omitted for clarity: the greatest were 0,3°C for the egg centre, 0,8°C for the nest air, 1,5°C for the egg in the open, and 2,1°C for the ambient air.

The Ostriches maintained a remarkably constant egg temperature, ranging through only 3,0°C (30,8–33,8°C) while the ambient air temperature ranged through 21,1°C (17,8–38,9°C). The mean temperature at the centre of the egg was 32,9 ± 0,7°C while the mean temperature just inside the bottom of the egg was 1,9°C lower. On one occasion the external egg temperature of the under

surface of seven eggs was measured with a Barnes PRT 10L infrared radiation thermometer, and averaged 29,5°C for central eggs and 28,2°C for outer eggs.

The nest air temperature averaged 0,7°C higher (33,6 ± 0,7°C) than the central egg temperature, the greatest difference being 2,8°C. At another nest, however, the mean nest air temperature over a 24-hour period was 32,2 ± 0,8°C.

The skin temperature of the groin of the incubating (tame) male Ostrich was measured twice on the same occasion and was 37,1–37,4°C.

Humidity before incubation

Fig. 3 shows the humidity at an unattended nest over a 24-hour period. Standard deviations are omitted because they were small. The humidity of the nest air rose and fell in the same way as the humidity of the ambient air outside the nest, but it varied less. Thus the mere presence of the nest and eggs was sufficient to effect some stablizing of the daily oscillations in humidity. The means were very similar: 52% for the nest and 55% for the ambient air.

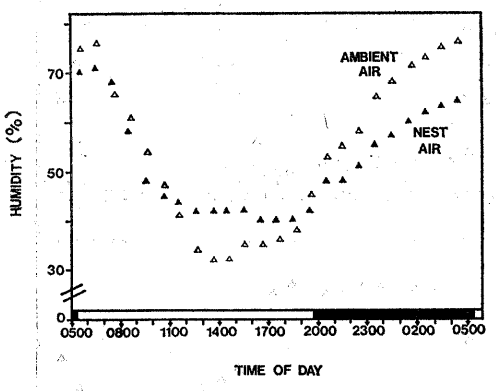

FIGURE 3
Relative humidities in an unattended Ostrich nest over a 24-hour period.

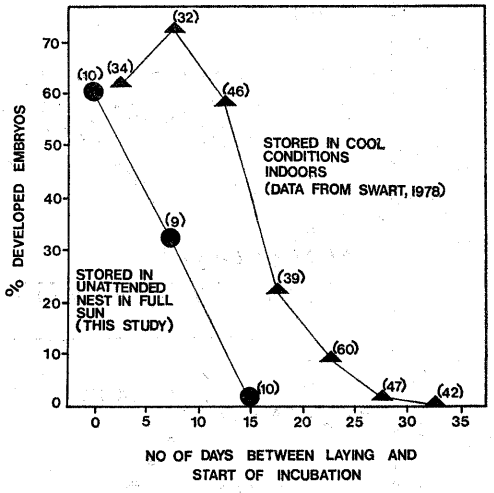

FIGURE 4
Viability of Ostrich eggs after storage for different periods and under different conditions. (Sample sizes shown in parentheses.)

Humidity during incubation

Fig. 2b shows the mean hourly humidities over the same 48-hour watch at an incubated nest as in Fig. 2a. The humidity of the nest air ranged only between 32 and 52% (mean 41 ± 5%) while that of the ambient air fluctuated between 39 and 72% (mean 59 ± 11%). At another nest during a 20-hour period, nest humidity averaged 43 ± 3% (range 39 to 49%, mean nest temperature 32,2 ± 0,8°C) while the ambient air humidity averaged 59 ± 8% (range 46 to 72%, air temperature 22,3 ± 7,3°C). Fluctuations of nest air humidity were roughly in phase with those of the ambient air, the two values being closest around the middle of the day when the temperature of ambient air was close to that of the nest air.

The effects of delay before incubation on embryo development

The eggs in the unattended nest were incubated in an incubator. Eggs which did not hatch were examined; Fig. 4 shows the decline in the viability of the unattended eggs with increasing length of time between laying and the start of incubation. The failure of some fully developed embryos to hatch appears to be an artifact of the artificial incubation process (Burger & Bertram in prep.), and therefore the percentages of developed embryos are shown in Fig. 4, rather than the

percentages of hatched chicks. It can be seen that a 15-day storage period exposed to full sunlight caused 100% mortality, and that as little as 7 days exposure halved the proportion of eggs which reached complete development. Also shown in Fig. 4 are data from Swart (1978) which show that the percentage embryo development of eggs stored indoors in cool conditions was better than those exposed to the sun, but that nonetheless it started to decline sharply with storage periods longer than 15 days.

DISCUSSION

Ostrich eggs exposed to the sun reached lethally high temperatures. The centre of the egg reached a maximum of 40,5°C, and the upper part of the egg where the embryo blastoderm floats (Drent 1975) felt hotter than the sides and bottom. The upper lethal temperature of birds' eggs is between 42 and 48°C, depending on the age, and in eggs of the domestic fowl no embryos survive prolonged temperatures above 40,5°C (Drent 1975). Excessive heating of the Ostrich eggs probably contributed to the steep reduction in embryonic survival caused by several days of exposure to the sun (Fig. 4). The high temperatures in the eggs occurred when the ambient temperature was maximally 35°C, which would occur quite frequently in many parts of the Ostrich's range.

The hatching success of eggs in wild nests is appreciably higher than those in Fig. 4 (Hurxthal 1979). It is noticeable that in the wild the parent birds frequently guard the nest during the daytime during the pre-incubation phase (unpublished observations), protecting the eggs both from the sun and from depredation by Egyptian Vultures *Neophron percnopterus* (Brooke 1979; Boswall 1977; Bertram & Burger in prep.). This obviously prevents the bird from feeding at that time, and so may impose an additional limitation on the number of eggs she can lay (Bertram in prep.). Protecting the eggs by covering them with vegetation is probably not a viable method in an arid, windy environment.

The presence of a clutch of eggs dampened the daily oscillations in humidity. It is likely, although not yet demonstrated, that the temperature rise experienced by an Ostrich egg in an unattended nest would also be influenced by the presence or absence of other eggs in the nest (Frost & Siegfried 1977). The presence of surrounding eggs would partially shade a central egg for much of the day, would reduce radiation onto the lower sides of the egg from the heated soil nearby, but would probably reduce the airflow past the egg. Thus, an early egg's hatchability might well be enhanced by being surrounded by other eggs.

The mean central egg temperatures recorded in eggs in nests being incubated was 32,9°C, which is lower than the 36°C recorded by Siegfried & Frost (1974), and lower than those recorded for most other bird species (Drent 1975). It should be noted, however, that we were recording the temperature of a fresh egg among a clutch of eggs containing large embryos, which would by then have been producing an appreciable quantity of their own heat (Drent 1970). More recent recordings of temperatures inside fibreglass dummy eggs at the start of incubation by wild Ostriches in East Africa have shown central temperatures remaining between 32 and 36°C (Bertram in prep.).

Clearly there are considerable problems in recording incubating egg temperatures. Some are due to feedback from heat produced by the embryo influencing the adult bird's incubation behaviour (Franks 1967). Others are caused by the high temperature gradient across the eggs, which is especially large across large eggs. The central temperature is probably lower than that experienced by the early developing embryo. The temperature measured by a thermistor placed in the air sac fluctuates considerably faster than does the central temperature (Simkiss 1974).

Immediately after the Ostrich left its nest at the observer's close approach, it could be felt that some eggs were warmer than others, and that there were marked temperature differences between different parts of the same egg. There are no data on brood patches in Ostriches, but it is difficult to envisage close contact between the incubating bird's skin and all the eggs in the nest. It would appear that the large size of the Ostrich and of its eggs liberates it from some of the problems associated with maintaining suitable incubation temperatures. Clearly the temperature gradient between the outside air and the centre of the nest must be only a shallow one, since the distances involved are large and the temperature differences often small. The nest floor, 70–90 cm across, consists of a deep layer of finely-ground dusty soil, which must be an excellent insulator, and which also becomes warm once incubation has started, since one parent is almost always sitting at the nest. This fine dust is in contact with an estimated 25–33% of the egg's surface. The incubat-

ing bird scuffs its feathers into this dust and probably produces an effective seal, inside which the bird's bare skin areas probably heat the nest air as much as the eggs. The large size of the eggs means that any which are not properly covered will change in temperature only slowly. In the daytime, undisturbed wild Ostriches stand briefly at intervals of 1–2 hours and move their eggs, but the eggs are large enough, and during the daytime the ambient air temperatures are high enough, that no change in egg temperatures can be detected from these movements, although brief fluctuations in nest air temperature result.

The mean daily water loss of all 58 Ostrich eggs re-weighed during natural incubation (3,83 g/day) is close to the value of 3,41 g/day predicted by the equation derived by Drent (1975) for all birds studied:

daily water loss (mg/day) $= 15{,}2W^{0{,}74}$

where W is the fresh weight of the egg (1500 g). Water loss from the egg is dependent on the vapour conductance and the differences in vapour pressures between the inside of the egg and its microhabitat, and can be expressed by the following formula (Ar *et al.* 1974):

$$\dot{M}_{H_2O} = G_{H_2O} : \triangle P_{H_2O}$$

where $\dot{M}_{H_2O}$ is the water loss from the egg (mg/day), G_{H_2O} is the water vapour conductance (mg/day/torr) and $\triangle P_{H_2O}$ is the water vapour pressure difference between the middle of the egg and the microclimate outside the egg (torr). Using the methods of Ar *et al.* (1974), we calculated G_{H_2O} for Ostrich eggs from our data. This came to 135 mg/day/torr for eggs in natural nests with egg temperature 36°C (Siegfried & Frost 1974), nest air temperature 33,6°C, and nest relative humidity 41%; this compares with 156 mg/day/torr in incubators where egg and microclimate temperature is 37°C, and relative humidity 62%. Hoyt *et al.* (1978) obtained a value of 187 ± 29 mg/day/torr from eight eggs, presumably using a desiccator in the manner of Ar *et al.* (1974). These calculated values all lie between the values predicted from regressions using egg weight only (126 mg/day/torr) and egg weight and incubation period together (197 mg/day/torr) (Hoyt *et al.* 1978).

Thus despite their arid natural environment, Ostrich eggs exhibited a daily weight loss and water vapour conductivity similar to the eggs of other species, in proportion to their size. It is possible that the porosity of the eggs could not be reduced to limit water loss, without impairing the rates of exchange of O_2 and CO_2 (Ar *et al.* 1974). The total amount of water lost during the incubation period (11–12%) is, however, less than the average of 16% found in most bird species (Drent 1975). This is partly because the incubation period of the Ostrich (42 days) is far less than the 58 days expected from the size of the egg (Hoyt *et al.* 1978). A shortened incubation period might be partly an adaptation in the Ostrich reducing water loss from eggs in an arid environment. In addition to water lost during incubation, early-laid Ostrich eggs lose 3–4% of their weight during the long pre-incubation period.

It would be rewarding to carry out more complete and continuous series of recordings of weight loss, temperatures and humidities at Ostrich nests, especially in more arid conditions than those in this pilot study. The effects of different egg sizes on the chicks' ability to withstand environmental extremes before, during and after incubation would be well worth studying.

In a number of bird species it has been shown that synchronization of hatching occurs by auditory communication between embryos inside the eggs (Vince 1969). Among ratites, this has been demonstrated by Bruning (1974) in Rheas *Rhea americana*. It seems probable that the same phenomenon would occur with Ostriches, but this has not yet been shown.

The Ostrich farms at Oudtshoorn provide the material and the opportunity for investigating many of these points and the results of such investigations could well prove beneficial to the domestic Ostrich industry there (Burger & Bertram in prep.). At present, hatching success in incubators is considerably below what wild Ostriches achieve.

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