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# GAS PRESSURES IN THE AIR CELL OF THE OSTRICH EGG PRIOR TO PIPPING AS RELATED TO OXYGEN CONSUMPTION, EGGSHELL GAS CONDUCTANCE, AND EGG TEMPERATURE[1]

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*Abstract.* It has been suggested that air cell oxygen partial pressure ($P_AO_2$) in avian eggs just prior to internal pipping (PreIp stage) resembles that of avian (and mammalian) alveolar partial pressure, e.g., $P_AO_2 \simeq 104$ torr. On the other hand, indirect evidence from water vapor eggshell conductance ($G_{H_2O}$) suggests that PreIp $P_AO_2$ is allometrically related to egg mass: large and small eggs would have high and low $P_AO_2$, respectively, where the calculated PreIp $P_AO_2$ of the Ostrich (*Struthio camelus*) egg, from those data, is about 125 torr.

The rate of egg mass specific oxygen consumption ($\dot{M}_{O_2}$), $P_AO_2$, and the partial pressure of $CO_2$ in the air cell ($P_ACO_2$) were measured; oxygen diffusive eggshell conductance ($G_{O_2}$), and air cell gas exchange ratio (R) were calculated; egg content surface temperature ($T_S$) and the rate of mass loss were measured in Ostrich eggs, all during the last stages of development at 35.5°C and 45% relative humidity. The mass loss was corrected for the effect of R to yield rate of water loss ($\dot{M}_{H_2O}$). This value and vapor saturation value at $T_S$ were used to calculate $G_{H_2O}$.

Mean ± standard deviation $P_AO_2$ and $P_ACO_2$ during PreIp stage were 103 ± 4.5 torr and 46 ± 6.0 torr, respectively. The $G_{O_2}$ found (129 ml [STPD]·(day·torr)$^{-1}$ ± 57) was lower than that predicted by allometric relationships or by calculation from $G_{H_2O}$ (185 ml [STPD]·(day·torr)$^{-1}$). The ratio $G_{O_2}/G_{H_2O}$ was 0.59 ± 0.15, significantly different from the expected 0.85 (using the respective diffusion coefficients). A temperature difference of 2.0 ± 0.5°C was measured between the egg content surface and the incubator. The higher temperature of the egg content surface, associated with an increase of water vapor pressure in the air cell, presumably decreases $G_{O_2}$ and increases $G_{H_2O}$. Values of R indicate that 1 day prior to external pipping the movements of the mature embryo influence the pattern of gas exchange by creating convective exchange.

*Key words: Ostrich; egg; oxygen consumption; air cell gas pressures; eggshell conductance; water loss; allometry.*

## INTRODUCTION

It has been argued that air cell oxygen and carbon dioxide partial pressures in avian eggs ($P_AO_2$ and $P_ACO_2$, respectively), just prior to the internal pipping stage (PreIp), are analogous to and resemble that of avian (and mammalian) alveolar gas partial pressures. A typical value of PreIp $P_AO_2$ and $P_ACO_2$ for all eggs is approximately 104 torr and 41 torr, respectively (Rahn et al. 1974, Paganelli and Rahn 1984). However, calculations of $O_2$ diffusive shell conductance ($G_{O_2}$) based on the measured water vapor eggshell conductance ($G_{H_2O}$) (Paganelli 1980), and the rate of oxygen consumption during the PreIp stage, made for many species, suggested that PreIp $P_AO_2$ and $P_ACO_2$ are allometrically related to egg mass. Thus, small and large eggs tend to have low and high PreIp $P_AO_2$, respectively (Hoyt et al. 1978b, Hoyt and Rahn 1980, Vleck et al. 1980). This has been supported by some direct measurements on small eggs (Bucher and Barnhart 1984). The expected range of PreIp $P_AO_2$ (following Hoyt et al. 1978b) was from about 72 torr for the small Zebra Finch (*Poephila guttata*) egg to 126 torr for the Ostrich (*Struthio camelus*) egg.

As PreIp $P_AO_2$ was not measured directly in Ostrich eggs, and since the solution to the above problem appears to have a bearing on the understanding of the role of eggshell conductance in avian eggs, we have chosen to measure directly and in the same Ostrich egg the rate of oxygen consumption, the rate of water loss ($\dot{M}_{H_2O}$), $P_AO_2$, $P_ACO_2$, and the temperature of the surface of the egg content from which water evaporation occurs ($T_S$) during the final stages of development.

Under controlled incubation conditions and provided that air cell gas partial pressures represent the conditions anywhere under the egg-

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shell, such measurements allow for the calculation of both gas and water vapor eggshell conductances and may resolve the theoretical dilemma between the two approaches.

## MATERIALS AND METHODS

### EGGS AND INCUBATION

Ostrich eggs were obtained from the Safari Zoological Gardens, Ramat-Gan, Israel. A total of 14 eggs from three successive batches were received within 2 weeks. The eggs were incubated in a controlled temperature chamber (Tuttanauer, Israel) equipped with water pans at incubation temperature ($T_I$) of 35.5 ± 0.2°C ($\bar{x}$ ± SD). Eggs were turned manually twice a day throughout incubation. The relative humidity (RH) in the incubator was recorded continuously using a calibrated hair hygrometer (Cassela; ±2%) and averaged over the period between each weighing. The mean RH was 45 ± 5% (range). Mean $P_{O_2}$ and mean $P_{CO_2}$ of the incubator air were 146.6 ± 1.8 torr ($\bar{x}$ ± SD) and 2.1 ± 1.3 torr, respectively. Weighings were carried out with a mechanical balance (Ohaus, "Triple beam") to an accuracy of ±0.05 g.

Day of external pipping was noted as day 0 because laying day was not always certain and external pipping to hatching time is, in our experience, highly variable.

### WATER LOSS AND EGGSHELL WATER VAPOR CONDUCTANCE

During the last 10 days of incubation, eggs were weighed at intervals of 24 hr to determine their rate of water loss. The RH in the incubator was monitored continuously and converted to weighted absolute humidity ($P_IH_2O$) using $T_I$ and vapor saturation pressure tables.

The rate of mass loss used for the calculations of eggshell water vapor conductance was always measured for periods in the incubator only, i.e., periods when oxygen consumption was measured were excluded in order not to introduce an error in the $G_{H_2O}$ measurements because of the difference in the $P_IH_2O$ in the measuring system. Since the air cell exchange ratio (R) was different from 0.727, a value at which the net mass exchanges of $O_2$ and $CO_2$ are equal (Drent 1975), the measured mass loss was corrected to net water loss, taking into account the actual R which was calculated from $P_AO_2$ and $P_ACO_2$ (Wangensteen et al. 1970/71). The mass loss correction due to the R deviation from 0.727 amounted to about 0.4 g/day.

A 4-mm diameter hole was drilled into the eggshell above the air cell and a sawn syringe needle hub, which could be sealed with a plastic plug, was secured above it with epoxy glue. When needed, the plug was opened and a fine thermocouple thermometer (Omega Type T, copper/constantan, gauge 24, nylon coated) could be quickly inserted through the hole to touch the inner shell membrane at the edge of the air cell. The egg was then turned in such a way that the egg content "sandwiched" the probe tip between the membranes. It was presumed that the measurement was made at the surface of the egg content from which water evaporation occurred ($T_S$). The hole was kept plugged between measurements. The $T_S$ readings (±0.05°C) were used to estimate the absolute humidity under the shell, assuming full saturation at the egg content surface.

### OXYGEN CONSUMPTION RATE

Oxygen consumption rate was measured in a "closed" system. Individual eggs were placed inside a 7-l desiccator over a continuously stirred 30% KOH solution, giving a $P_IH_2O$ of about 40 torr. The desiccator was placed inside a controlled temperature chamber at $T_I = 35.5 \pm 0.2$°C. The sealed desiccator was connected via a Tygon tube to a volume meter (Brooks, model 1053) which was filled with pure oxygen. A water manometer was connected to the measuring system to allow corrections of the pressure exerted by the piston. The rate of oxygen consumption was measured with a stopwatch by following the time course of the down movement of the piston of the volume meter between volume lines. The measurements were repeated until a constant oxygen consumption rate was recorded. Barometric pressure was recorded daily. This procedure took about 1–2 hr/egg. Results were corrected to STPD conditions, and expressed per kilogram fresh egg mass for comparison since not all eggs were available every day for $O_2$ consumption measurements.

### AIR CELL GAS PRESSURES

Air cell volume was 130–260 ml, depending on incubation day and the conductance of the egg. Air cell gas pressures were sampled using the syringe equilibrium method (Tazawa et al. 1980). During experiments the hole in the eggshell over

the air cell was unplugged, and a 20-ml plastic syringe with a pulled plunger was connected to the hub for equilibration. Equilibration time was checked by connecting similar syringes to a desiccator containing a known mixture of $O_2$, $CO_2$, and $N_2$ by the same method used for connection to the eggshell (Table 1). $O_2$ concentration was determined using a Dual Cell Oxygen Analyzer (Ametek model S-3A). Half of the contents of the 20-ml syringe were injected at a constant rate through a small column filled with drierite (W. H. Hammond Drierite Company) made from a 1-ml "tuberculin" syringe (for water vapor removal) into the first cell. The remaining gas sample was injected into the second cell through a similar Ascarite (Thomas Scientific) column (for $CO_2$ and water vapor removal). Preliminary tests showed that a 7-ml sample was sufficient to read the $O_2$ concentration correctly. From the reading of the two cells, the $CO_2$ fraction in the dried gas ($F_{CO_2}$) was calculated as:

$$F_{CO_2} = (\text{cell 2 reading} - \text{cell 1 reading}) \div \text{cell 2 reading}.$$

The method was checked against known concentrations of $CO_2$ and $O_2$ and found to be accurate in the range of $F_{CO_2}$ of 0.005–0.15 and $O_2$ fractions of 0.05–0.21 ± 0.001.

Assuming diffusive gas exchange, R for diffusion, $R_d$ was calculated according to Wangensteen et al., (1970/71) where $\Delta P_{CO_2}$ is divided by $\Delta P_{O_2}$ and multiplied by 0.78, the ratio of the diffusion coefficients of these gases in air (Paganelli et al. 1978, Paganelli 1980).

### TEMPERATURE MEASUREMENTS

All temperature measurements were made using a Wescor model TH-65 TC thermometer equipped with copper-constantan thermocouples accurate to ±0.05°C. The instrument was calibrated and checked periodically against a standard mercury thermometer.

### EXPERIMENTAL PROTOCOL

Every evening all eggs were turned. Three 20-ml syringes were connected to the air cells of three eggs and an extra syringe was placed inside the incubator near the eggs. The following day incubator temperature and humidity records were averaged, the incubator was opened, the incubator air sample syringe was sealed and the air cell sample syringe was disconnected from an egg and sealed. A fine thermocouple was quickly introduced into the air cell through the hole in the shell for reading $T_S$ as described above. The hole was plugged and the syringe was immediately taken for gas analyses. The egg was then candled to determine if internal pipping had occurred (the day before the beak of the embryo penetrated into the air cell was defined as the PreIp stage), weighed, and immediately placed in the $\dot{M}O_2$ measuring system. The procedure was repeated for the other two eggs. All other eggs in the incubator were turned again.

TABLE 1. Equilibration times (T ± SD) of the 20-ml syringes used for sampling air cell gases ($n$ = 6).

| Gas | $T_{50\%}$ (min) | $T_{99.9\%}$ (min) |
|---|---|---|
| $O_2$ | 15.5 ± 3.0 | 200.0 ± 7.0 |
| $CO_2$ | 19.9 ± 4.0 | 270.0 ± 22.8 |
| Ratio | 0.78 | 0.77 |

## RESULTS

### EGGS AND HATCHLINGS

Mean egg mass was 1,646 ± 166 g ($\bar{x}$ ± SD) ($n$ = 14). The mean fresh mass of 12 hatchlings (including yolk sac) was 1,018 ± 76 g and mean egg mass of the eggs from which they hatched was 1,586 ± 118 g, indicating a relative hatchling mass of 64.2 ± 3.1%. Incubation duration at 35.5°C was 44.6 ± 1.3 days. A significant difference of 2.0 ± 0.5°C was measured between $T_S$ and $T_I$ on days 7–4 before external pipping ($P < 0.01$).

### OXYGEN CONSUMPTION

Maximal mass specific oxygen consumption rate $\dot{M}O_2$ obtained for the period days 6–4 before external pipping was 126.3 ± 10.5 ml[STPD]·(kg·hr)$^{-1}$ ($n$ = 27). Values measured on days 7–4 before external pipping were not significantly different (Fig. 1, ANOVA). After day 4 before external pipping, $\dot{M}O_2$ decreased by 13.4% ($P < 0.05$) and increased again 1 day before external pipping. The PreIp $\dot{M}O_2$ was 115.3 ± 4.7 ml[STPD]·(kg·hr)$^{-1}$ ($n$ = 6).

### AIR CELL GAS PRESSURES

Mean $P_AO_2$ (Fig. 2) and $P_ACO_2$ during PreIp stage were 103.0 ± 4.5 torr and 46.0 ± 6.0 torr, respectively (67 measurements; 12 eggs; 10 days). The simultaneous individual measurements of $P_ACO_2$ and $P_AO_2$ are shown in Figure 3. These

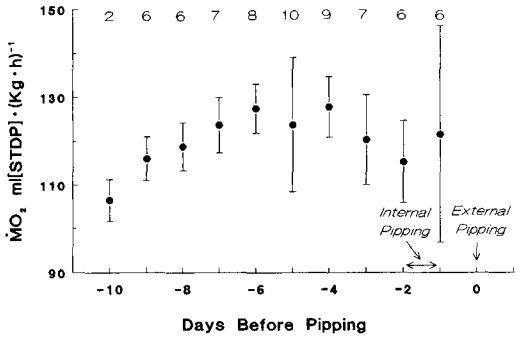


FIGURE 1. Mass specific oxygen consumption rate ($\dot{M}o_2$) of Ostrich eggs during the last days of incubation. Numbers above the data points are the number of eggs measured on each day. Internal and external pipping times are marked by arrows. Values are $\bar{x} \pm$ SD.

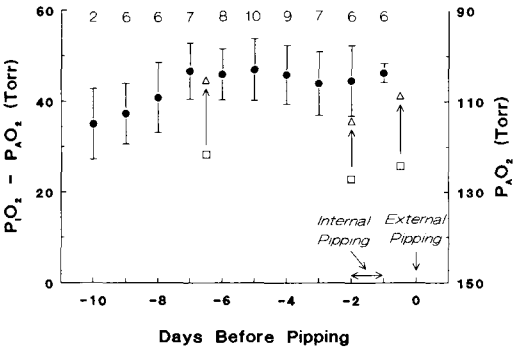


FIGURE 2. Air cell oxygen partial pressures ($P_AO_2$; right ordinate, and incubator to air cell $O_2$ partial pressure difference [$P_IO_2 - P_AO_2$] left ordinate) during the last days of incubation in Ostrich eggs. Internal and external pipping times are marked by arrows. Squares represent data given by Hoyt et al. (1978b); triangles represent the same values corrected according to the $Go_2/GH_2O$ ratio found in the present study (see text for details). Values are $\bar{x} \pm$ SD. The numbers above the data points are the number of eggs measured on each day.

values do not include externally pipped eggs. The overall $R_d$ value from these measurements is 0.79 $\pm$ 0.06 ($n$ = 61). The daily $R_d$ values are shown in Figure 4. A significant decrease in $R_d$ was noted 1 day before external pipping. The $R_d$ value for the day between internal and external pipping was significantly lower ($P < 0.05$) than all the other days and was calculated separately.

## OXYGEN AND WATER VAPOR CONDUCTANCE

The mean $GH_2O$ was measured from water loss and when corrected for $R_d$ at 35.5°C was 177.4 $\pm$ 34.5 mg·(day·torr)$^{-1}$. This value is equal to 174.8 mg·(day·torr)$^{-1}$ at 25°C (Paganelli et al. 1978). The calculation of $GH_2O$ is similar to that described by Meir et al. (1984b) and is based on the assumption that the space under the eggshell is saturated with water vapor at $T_S$. The $Go_2$ was calculated by dividing the rate of oxygen consumption by the difference between $P_AO_2$ and $P_IO_2$ and is based on the assumption that $P_AO_2$ under the shell is equal to the value measured in the air cell. Values for mean $Go_2$, mean $GH_2O$ expressed in milliliters (STPD), and their ratio are given in Table 2. The $Go_2/GH_2O$ ratio in the Ostrich egg is significantly lower ($P < 0.01$) than the theoretical value and that measured in hen eggs (Table 2).

## DISCUSSION

The $\dot{M}o_2$ values measured in the Ostrich eggs in this study are not different from those calculated from Hoyt et al. (1978b). The pattern of $\dot{M}o_2$ over the final days of incubation is also similar but we found a somewhat smaller decline in $\dot{M}o_2$ toward external pipping. $\dot{M}o_2$ increases again just prior to external pipping and we assume that this is associated with the changes in $O_2$ uptake mode during the transition from chorioallantoic to pulmonary respiration and with the active movements of the embryo at this stage. This assumption is indirectly confirmed by our observations on the changes in the $R_d$ 1 day before pipping (Fig. 4). If this R value is calculated according

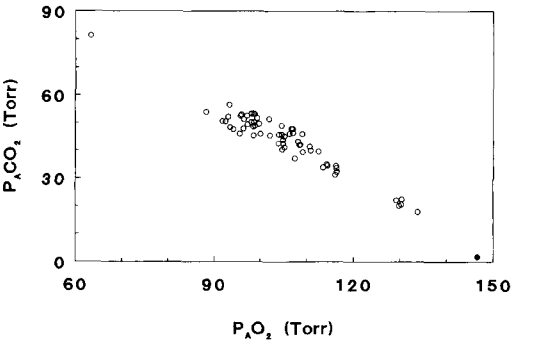


FIGURE 3. Air cell partial pressures of $CO_2$ and $O_2$ ($P_ACO_2$ and $P_AO_2$, respectively) during the last days of incubation in Ostrich eggs. The filled circle represents incubator partial pressure of $CO_2$ and $O_2$ ($P_AO_2$ and $P_ACO_2$, respectively). Mean ($\pm$SD) diffusive gas exchange ratio, $R_d$, is 0.79 $\pm$ 0.06.

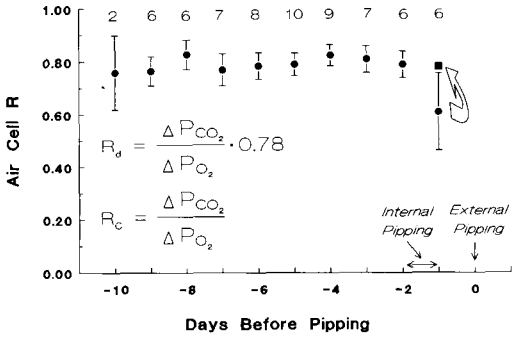


FIGURE 4. The air cell gas exchange ratio (R) of Ostrich eggs during the last days of incubation computed as $R_d$, where $R_d$ represents the R calculation in a diffusive system, and $R_c$ represents the R calculation in a convective system (equations in the figure, Wangensteen et al. 1970/71). The square at day −1 (between internal and external pipping) represents the same R calculated assuming convection (see text for details). Values are $\bar{x} \pm$ SD. The numbers above the data points are the number of eggs measured on each day.

to the convective equation (as $R_c$) and not as $R_d$ (Wangensteen et al. 1970–1), the corrected value is similar to those measured in the previous days (square at 1 day before pipping; Fig. 4). This indicates that pressure changes caused by pulmonary ventilation and embryo movements enable convection of air through the eggshell pores. The overall $R_d$ which is higher than 0.727 may be explained in two different ways: it may indicate utilization of nutrients in addition to lipids (Brody 1945) or a high diffusion to perfusion ratio over the air cell (Paganelli et al. 1988).

It has been suggested that the partial pressures of $O_2$ and $CO_2$ in the air cell just prior to pipping provide the embryo with a pipping stimulus (Visschedijk 1968). Rahn et al. (1974) and Paganelli and Rahn (1984) have proposed that these air cell partial pressures are similar in all species (ca. $P_AO_2$ = 104 torr and $P_ACO_2$ = 37 torr). However, Hoyt et al. (1978b) suggested that air cell oxygen pressure may be related allometrically to fresh egg mass. This is because $G_{H_2O}$ is proportional to the 0.81 power of fresh egg mass (Ar and Rahn 1978), and PreIp $\dot{M}_{O_2}$ is proportional to the 0.73 power of egg mass only (Hoyt et al. 1978a). Thus, the $O_2$ pressure difference across the shell ($P_IO_2 - P_AO_2$) should decrease in proportion to the −0.08 power of fresh egg mass, causing $P_AO_2$ to increase with fresh egg mass at comparable developmental stages of different species. Accordingly, the calculated $P_AO_2$ of the Ostrich egg during PreIp stage is 126 torr. Nevertheless, our direct measurements during the PreIp stage of mean $P_AO_2$ = 103 torr and mean $P_ACO_2$ = 46 torr confirm the proposition of Rahn et al. (1974). Data presented by Bucher and Barnhart (1984) on the eggs of small altricial *Agapornis roseicollis* contradict this proposition (Rahn et al. 1974), which is based mainly on data from precocial species. It now appears essential that direct $P_AO_2$ measurements should be made on some other altricial and precocial species in "big" and "small" eggs as most of the direct measurements reported in the literature have been carried out on medium-sized eggs and in precocial species.

TABLE 2. Oxygen and water vapor eggshell conductances, $G_{O_2}$, $G_{H_2O}$, ml[STPD]·(day·torr)$^{-1}$, respectively, of Ostrich eggs and their ratio (this study), as compared to the same conductance ratio of hen eggs (Paganelli et al. 1978) and to the ratio of the diffusion coefficients in nitrogen of oxygen and water vapor ($D_{O_2,N_2}/D_{H_2O,N_2}$). $n$ = number of observations.

| | $G_{O_2}$ | $G_{H_2O}$ | $G_{O_2}/G_{H_2O}$ | | $D_{O_2,N_2}/D_{H_2O,N_2}$ |
|---|---|---|---|---|---|
| | Ostrich | Ostrich | Ostrich | Chicken | Theoretical |
| Mean | 129 | 234 | 0.585* | 0.83 | 0.85 |
| ±SD | 57 | 46 | 0.152 | 0.02 | |
| $n$ | 14 | 14 | 14 | 5 | |

* Significantly different from $D_{O_2,N_2}/D_{H_2O,N_2}$ ratio ($P < 0.01$).

Our results for $G_{H_2O}$ were obtained during the final days of incubation. They were corrected for the temperature differences between the incubator and the egg (caused by the combined effect of evaporation and the metabolic activity of the embryo) and for the effect of $R_d$ on mass loss. The method of measuring $G_{H_2O}$ during incubation was similar to that of Meir and Ar (1987) and results were corrected to standard conditions (Ar et al. 1974). $G_{H_2O}$ of turkey eggs of the same strain has been measured previously both in desiccators (Meir et al. 1984a) and during incubation (Meir et al. 1984b) and both methods yielded the same values.

Hoyt et al. (1978b) measured $G_{H_2O}$ before incubation began and did not correct it for temperature differences between the egg and its environment. In spite of the differences in the methods our mean measured value of 174.8 mg·(day·torr)$^{-1}$ at 25°C is remarkably close to that measured by them, 187.2 mg·(day·torr)$^{-1}$. Swart et al. (1987) measured $G_{H_2O}$ during artificial incubation of Ostrich eggs and found a slightly lower value, 158.7 mg·(day·torr)$^{-1}$. When cor-

rected for the differences in egg mass, this value, 190.9 mg·(day·torr)$^{-1}$, is even higher than the one measured by us.

The $G_{O_2}$ calculated from measured $\dot{M}_{O_2}$ and $P_IO_2 - P_AO_2$ was 129 ml[STPD]·(day·torr)$^{-1}$ (Table 2). It is considerably lower than that predicted from allometric equations for egg mass and incubation duration, $G_{O_2}$ = 194 ml[STPD]·(day·torr)$^{-1}$ (Rahn and Ar 1974), lower than the value calculated from measured $G_{H_2O}$ in this work, $G_{O_2}$ = 185 ml[STPD]·(day·torr)$^{-1}$, in Hoyt et al. 1978b, 202 ml[STPD]·(day·torr)$^{-1}$, and in Swart et al. (1987), 206.8 ml[STPD]·(day·torr)$^{-1}$ (Ar et al. 1974). Recently it has been shown that eggshell conductance over the air cell may be higher than in other locations by a factor of up to 1.6 (Rokitka and Rahn 1987). If this is true for Ostrich eggs then our $G_{O_2}$ value calculated using $P_AO_2$ may be even overestimated.

The $G_{O_2}/G_{H_2O}$ ratio of the Ostrich egg in our study was 0.585. It is significantly lower ($P < 0.01$) than the theoretical ratio of 0.85 (from the respective diffusion coefficients) and from the ratio measured in chicken eggs by Paganelli et al. (1978) (Table 2). If our $G_{O_2}$ is overestimated as discussed above, then the $G_{O_2}/G_{H_2O}$ ratio would be further decreased. This discrepancy from the predicted indicates that the diffusion paths of these two gases in the Ostrich egg may differ in part. The temperature increase of 2.0°C which was measured between the surface area of the egg content where evaporation occurs and the incubator atmosphere presumably causes the saturated water vapor in the air cell to condense in part on the somewhat colder outer shell membrane and on the inner surface of the shell (Simkiss 1974), thus decreasing the available paths for $O_2$ (Ar et al. 1981), changing the site of evaporation and thereby affecting $G_{H_2O}$ (Seymour et al. 1987), and affecting the $G_{O_2}/G_{H_2O}$ ratio. This situation is similar to the conditions in a freshly incubated egg in which the eggshell membranes have not yet dried (Lomholt 1976, Tullett and Board 1976, Seymour and Piiper 1988). When the $P_AO_2$ values calculated by Hoyt et al. (1978b) are corrected according to the $G_{O_2}/G_{H_2O}$ ratio found in this study, they become close to the values directly measured by us (Fig. 2). Another possible explanation for the different $G_{O_2}/G_{H_2O}$ ratio is that $\dot{M}_{O_2}$ is not uniform over the whole egg surface thus causing different $P_AO_2$ values in different locations under the shell. A lower calculated $G_{O_2}/G_{H_2O}$ ratio is then possible if $\dot{M}_{O_2}$ and $P_AO_2$ under the air cell are relatively high. This possibility is most unlikely as it has been shown in other species that the conductance/perfusion ratio is usually higher in the blunt end than in the remainder of the egg (Sotherland et al. 1984, Rahn and Paganelli 1985, Rokitka and Rahn 1987).

In other characteristics the Ostrich egg appears to be close to the values predicted according to its mass. For example, the cooling rate of the Ostrich egg in steady state was calculated after Drent (1975) as follows: Cooling rate = $(\dot{H} - \dot{E}v)/(\Delta T \cdot C \cdot W)$. Where $\dot{H}$ is the heat production rate calculated from $\dot{M}_{O_2}$ (Brody 1945) and has the value of 1.12 W, $\dot{E}v$ is the evaporative heat loss rate in the incubator calculated from water loss rate = 0.14 W, $C$ is the assumed heat capacity of the egg content = 3.35 J·(degrees·g)$^{-1}$ (Drent 1975), $W$ is the actual egg mass during measurements (1,450 g) and $\Delta T$ = 2.0°C. The value found of $1.01 \cdot 10^{-4}$ °C·(°C·sec)$^{-1}$ is similar to that predicted based on values reported by Drent (1975). Its inverse, the time constant (9,895 sec), is similar to that given by Turner (1985).

From $\dot{H}$, $\dot{E}v$, and $\Delta T$ in steady state it is also possible to calculate the thermal conductance of the Ostrich egg: The difference $(\dot{H} - \dot{E}v)$ is the "dry" heat flux which amounts to 0.98 W. Dividing by $\Delta T$ of 2°C yields a conductance of 0.49 W·°C$^{-1}$ or a heat resistance of 2.04°C·W$^{-1}$, which corresponds to the value calculated from the equation given by Turner (1985) of 1.90°C·W$^{-1}$. This conductance value is higher than that predicted from mass in still air (0.33 W·°C$^{-1}$, Sotherland et al. 1987). Our measurements were made under steady state incubator conditions. Air convection around the eggs may be responsible for the higher value of thermal conductance that we have calculated. Also, in contrast to Sotherland et al. (1987) who used dummy eggs with no internal heat convection, our measurements were made with eggs containing living embryos, and circulation may increase heat conductance (Tazawa et al. 1988).

Incubation duration and the ratio between the hatchling mass and egg mass (64.2%) are also similar to that predicted for other avian species (Rahn and Ar 1974, Ar and Rahn 1985).

Since we find that PreIp $P_AO_2$ and $P_ACO_2$ in the Ostrich egg are similar to "normal" air cell gas pressures (Paganelli and Rahn 1984), but that the ratio of $G_{O_2}/G_{H_2O}$ is different from that usually predicted (Paganelli et al. 1978), we suggest that, whatever the mechanism for this dissocia-

tion, the difference in the mass power of allometric equations between $G_{H_2O}$ and $\dot{M}_{O_2}$ (and presumably $G_{O_2}$) is essential for controlling egg temperature during the final stages of incubation. In this stage, egg content temperature is 1–2.5°C higher than the incubator (or nest) temperature due to metabolic heat production (Martin and Insko 1935, this study). Heat production of the egg increases with approximately 0.74 power of egg mass (Rahn et al. 1974; Hoyt et al. 1978a, 1978b; Hoyt and Rahn 1980) while heat resistance decreases as −0.60 power of egg mass (Turner 1985). As a result, for a given incubation temperature, egg temperature may increase with egg mass at equivalent incubation stages and reach temperatures possibly causing damage to the embryo. However, increased evaporation facilitated by increased $G_{H_2O}$ (and low nest humidity; Swart et al. 1987) may help in keeping the temperature of large eggs like Ostrich eggs within the physiologically tolerable range. Thus, it seems that there is an advantage in an increased $G_{H_2O}$ in large eggs above the value dictated by $\dot{M}_{O_2}$ and in a departure from the constant proportion between $G_{O_2}$ and $G_{H_2O}$.

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