1978

Metabolism of Avian Embryos: Ontogeny and Temperature Effects in the Ostrich

Donald F. Hoyt, *Harvard University*
David Vleck, *University of Washington - Seattle Campus*
Carol M. Vleck, *University of Washington - Seattle Campus*

Condor, 80:265–271

METABOLISM OF AVIAN EMBRYOS: ONTOGENY AND TEMPERATURE EFFECTS IN THE OSTRICH

DONALD F. HOYT
DAVID VLECK
AND
CAROL M. VLECK

In the first comparative consideration of the metabolism of avian embryos, Rahn et al. (1974) made several important assumptions and offered a number of interesting predictions. One of their assumptions was that the relation between metabolic rate and incubation age (days incubated) is the same in all avian species as it is in the chicken (*Gallus gallus*). A second important assumption was that the partial pressures of oxygen and carbon dioxide in the air cell during the plateau phase are essentially the same in all species, regardless of egg mass and incubation period. This assumption led Rahn et al. to predict that, for eggs of different species but of the same mass (W), "plateau" metabolic rate ($\dot{m}_{O_2}$)* is inversely related to the length of the incubation period (I) and can be predicted most accurately from the equation:

$$\dot{m}_{O_2} = 267 \cdot W/I \qquad (1)$$

Embryonic metabolism increases with egg mass (Rahn et al. 1974). Therefore, the eggs of the Ostrich (*Struthio camelus*), which are the largest laid by any living species of bird, offer an important opportunity to test the validity of these assumptions and the accuracy of the prediction. In the present study we measured the rate of oxygen consumption of Ostrich eggs during incubation at 35°C and determined the water vapor conductance of the shell. This permitted us to calculate the air cell gas tensions. Additionally, we determined the values of a number of important physical parameters and the effect of moderate temperature changes on metabolic rate.

METHODS

EGGS, SHELL CONDUCTANCE (G_{H_2O}) AND EGG VOLUME

Eggs were donated by the San Diego Wild Animal Park (San Diego Zoological Society), Escondido, California. Two different groups of eggs were collected shortly after laying in May and June 1976, held at room temperature (about 22°C), and put into an incubator at 35°C within a week of collection. Shell conductances of eight eggs were measured prior to incubation by the method of Ar et al. (1974). Egg volumes were determined prior to incubation from the difference between the weight of the egg in air and the weight when suspended in water. (Eggs were dried and reweighed after immersion in water, and there was no significant absorption of water.) This difference, which equals the weight of water displaced by the egg, was corrected to egg volume by dividing by the density of water. The same data permitted the calculation of egg density.

TERMS AND SYMBOLS

For the sake of uniformity, we use the terms and symbols of Rahn et al. (1974). These include "W" for fresh egg mass and "$\dot{m}_{O_2}$" for the rate of oxygen consumption which, in our report, has units of cm^3 (STPD)/h.

INCUBATION AND OXYGEN CONSUMPTION

The data are from two groups of five eggs which were collected and put into the incubator about two weeks apart. In each group, two eggs were incubated for the entire incubation period at 35°C, and three eggs were used for the experiments on the effect of temperature on metabolic rate ("Q_{10}" experiments). Every morning we determined the rate of oxygen consumption of each egg at 35°C. The three eggs used in the Q_{10} experiments were then transferred to an incubator at either 32.5°C or 37.5°C and allowed to come to thermal equilibrium. Egg surface temperatures were monitored with a thermocouple covered with a small piece of foam rubber and held against the shell with a rubber band. The egg was assumed to be in thermal equilibrium when the surface temperature stabilized. This normally required several hours. The rate of oxygen consumption at the experimental temperature was then determined, and the eggs were returned to the incubator at 35°C. The rate of oxygen consumption of the eggs maintained at 35°C was determined a second time concurrently with that of the experimental eggs.

At the end of incubation the oxygen consumption of the embryos was measured in an open system. Prior to that, a closed system was used. For the closed system measurements the respirometry chamber was a 1-gallon (ca. 4.0 l) metal paint can fitted with a 3-way valve. Before taking the initial air sample, the respirometry chamber with the egg inside was placed in a constant temperature cabinet, allowed to come to thermal equilibrium, and sealed. Before removing the initial air sample, 120 cm^3 of warm air was injected into the can with a syringe and stirred by pumping air from the can in and out of the syringe. Then 100 cm^3 of air was removed with a syringe for the determination of initial oxygen concentration (F_I). Immediately after this sample had been removed, the valve was opened so that the extra 20 cm^3 of air could escape and allow the air pressure in the can to equalize with the atmospheric pressure. The time interval between the initial and final air sampling

* Due to typographic limitations, a lower case "m" with a dot, rather than a capital "M" with a dot, is used throughout this article.

was adjusted to produce a decrease in oxygen concentration of approximately 1%. This required more than 12 h at the beginning of incubation and less than 15 min at the end. The final oxygen concentration (F_E) was also determined on 100 cm^3 of air. This sample, however, was obtained without injecting any air into the can prior to its removal. This procedure resulted in a decrease in the air pressure in the can of about 3%. Fractional concentration of O_2 in the air samples was measured with a Beckman E2 paramagnetic oxygen analyzer. The equation used to calculate rate of oxygen consumption ($\dot{m}_{O_2}$) was:

$$\dot{m}_{O_2} = V \cdot (F_I - F_E)/t \cdot (1 - F_E) \quad (2)$$

where the symbols have the following definitions:

V = gas volume in respirometer chamber (at standard temperature and pressure, dry). (cm^3)

F_I = initial fractional oxygen concentration in a dry, CO_2 free gas sample from the respirometer. (unitless)

F_E = end fractional oxygen concentration in a dry, CO_2 free gas sample from the respirometer. (unitless)

t = elapsed time between initial and end sampling. (hours)

Water vapor and CO_2 were removed from the air samples prior to analysis by injecting the sample into the oxygen analyzer through a tube containing successively, silica gel, sodium asbestos anhydride (Ascarite), and silica gel.

We did not measure initial concentrations of water vapor or CO_2 in the respirometer. V was calculated from the difference between chamber volume and egg volume, assuming that the gas in the chamber was 50% saturated with water vapor and contained negligible CO_2 at the start of each experiment. This assumption reduces the maximum magnitude of errors in $\dot{m}_{O_2}$ due to the initial concentration of water vapor to less than ±3.5% (Vleck 1978).

The oxygen consumption of Ostrich embryos immediately before and during hatching was measured in an open circuit system. The respirometry chamber was a 20-liter glass jar fitted with a 1-cm thick plexiglass top. The air temperature in the respirometer chamber was monitored with a thermocouple in the excurrent air stream. An air flow of 2.0 l (STPD)/min through the chamber was maintained by a Brooks mass flow meter. Water and CO_2 were removed by passing the air through a tube containing Ascarite and silica gel before measuring excurrent oxygen content (F_E) by a Beckman G2 paramagnetic oxygen analyzer. Oxygen consumption was calculated by equation (2) of Hill (1972).

Diffusion across the shell contributes to a time lag between actual and observed changes in metabolic rate. This means that the rate of oxygen consumption we measured reflected the rate of consumption by the embryo at an earlier time. When the eggs were in the open circuit system, we frequently observed that a sudden noise, change in light level in the respirometry chamber or movement of the egg would be followed by a measurable change in the rate of oxygen consumption. These changes occurred three to five minutes after the disturbance. We assume that the embryo's responses to these disturbances included a change in metabolic rate, and that three to five minutes represents the time lag inherent in the open circuit system combined with the lag caused by the shell. Such a time lag would introduce no important errors in our measurements.

TEMPERATURE EFFECTS

The change in the rate of a physiological process resulting from a change in temperature is most conveniently discussed in terms of the Q_{10} of the process. The Q_{10} indicates the change in rate resulting from a 10°C change in temperature. A Q_{10} of 2 is common in many physiological systems and indicates that the rate doubles with a 10°C increase in temperature. If there is no change in the rate, the Q_{10} is 1.0. Q_{10} was calculated from the equation:

$$\log Q_{10} = (\log R_2 - \log R_1) \cdot 10/(T_2 - T_1) \quad (3)$$

where T_1 and T_2 are the temperature (K) at which the corresponding rates of oxygen consumption (R_1 and R_2) were determined. Because the embryos were growing, the rates of oxygen consumption changed between the morning and afternoon measurements. Therefore, Q_{10} was calculated from the difference between: (1) the rate of oxygen consumption at an experimental temperature (determined in the afternoon) and (2) a rate calculated for the same time by linear interpolation between the rates measured at 35°C on the same and succeeding mornings.

RESULTS

OXYGEN CONSUMPTION

Oxygen consumption at 35°C (Fig. 1) reached a peak on about the 41st day of incubation and then declined until just before pipping, on day 45, when it again increased to nearly the same rate as on day 41 (Table 1). The total amount of oxygen consumed between day 8 (when the first measurements of oxygen consumption were made) and the prepipping increase, averaged 75.3 ± 2.3 l. (As can be seen from Fig. 1, the amount consumed during the first nine days is insignificant.) In all individuals studied, the rates of oxygen consumption increased exponentially during the first 33 days of incubation. The equations describing the relation between the rate of oxygen consumption and incubation age (D_{inc}) prior to day 34 are similar for the individual eggs, and the equation for the pooled data is:

$$\log \dot{m}_{O_2} = -0.752 + 0.088 \cdot D_{inc} \quad (4)$$

($r^2 = 0.961$; a total of 210 observations on eight different eggs)

SHELL CONDUCTANCE AND AIR CELL OXYGEN TENSION

The mean water vapor conductance (G_{H_2O}) of our Ostrich eggs was 187.2 mg/day·torr ($N = 8$; SD = 29.25; mean fresh mass = 1589 g). The following equations (Rahn et al. 1974, Paganelli et al. 1978) are used in calculating air cell oxygen tension ($P_{A_{O_2}}$ in torr) from the rate of oxygen consumption ($\dot{m}_{O_2}$ in cm^3/h) and the water vapor conductance of the shell (G_{H_2O} in mg/day·torr):

TABLE 1. Observed rates of oxygen consumption at 35°C and calculated partial pressures of oxygen in the air cell at different stages in incubation.

Stage of incubation	$\dot{m}_{O_2}$ (cm³(STPD)/h)	SD	N	Fresh weight (g)	ΔP_{O_2}* (torr)	SD	$P_{A_{O_2}}$** (torr)
Peak (Day 41)	229	23.4	7	1446	27.2	5.1	120
"Pre-internal pipping" (Day 45)	181.8	10.1	4	1449	21.6	6.1	125
Immediately before pipping (Day 45)	210.1	17.5	4	1409	24.9	8.2	122

* $\Delta P_{O_2} = 24 \cdot \dot{m}_{O_2}/G_{O_2}$; $G_{O_2} = 1.08 \cdot G_{H_2O} = 202$ cm³ O_2/day · torr.
** $P_{A_{O_2}} = 147 - \Delta P_{O_2}$.

$$G_{O_2} = 1.08 \cdot G_{H_2O} \quad (5)$$

$$\Delta P_{O_2} = 24 \cdot \dot{m}_{O_2}/G_{O_2} \quad (6)$$

$$P_{A_{O_2}} = P_{I_{O_2}} - \Delta P_{O_2} \quad (7)$$

where: G_{O_2} = O_2 conductance of shell (cm³/day·torr)

ΔP_{O_2} = O_2 partial pressure gradient across the shell (torr)

$P_{I_{O_2}}$ = "effective" (Wangensteen and Rahn 1970) ambient O_2 tension (average value during our experiment was 147 torr).

The results of the calculations are presented in Table 1.

THE EFFECT OF TEMPERATURE ON METABOLISM

Q_{10} is significantly correlated with temperature (T) and incubation age (D_{inc}):

$$Q_{10} = 17.235 - 0.017 \cdot D_{inc} - 0.049 \cdot T \quad (8)$$
$$(-3.45) \qquad (-3.51)$$

($r_2 = 0.152$; a total of 135 observations on seven different eggs)

(The values in parentheses are the student's *t* values for the slopes for the independent variables.) This indicates that changes in temperature have less effect on the rate of oxygen consumption at higher temperatures and in older embryos. A decrease in Q_{10} as temperature increases is commonly observed in biological systems (Schmidt-Nielsen 1975: 266). The decreased Q_{10} in older embryos might indicate the development of thermoregulatory abilities, but the low correlation coefficient (0.152) suggests that caution should be used in attributing biological significance to these results.

INCUBATION PERIOD

The incubation temperature (35°C) used in this study was the maximum temperature measured in the center of a water-filled Ostrich egg being incubated by an adult Ostrich (unpubl. data); this value is close to those of 34–36°C reported by Siegfried and Frost (1974). The average incubation period we noted was 47 days, which is slightly longer than the values of 40–44 days reported from field studies (Sauer and Sauer 1966, and Leuthold 1970). In view of the wide scatter reported from field studies and the artificial incubation conditions in our study, it is difficult to interpret the meaning of this difference. Consequently, in subsequent calculations we will use the incubation period observed under natural conditions (42 days).

The sequence of events varied considerably in the four spontaneous hatchings which were

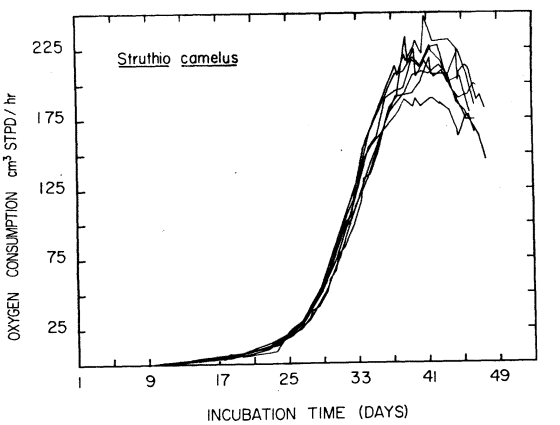

FIGURE 1. The rate of oxygen consumption versus days of incubation for the Ostrich. The lines connect rates measured in the same egg at 35°C (the data from the Q_{10} experiments are not included). For clarity, no data on the increase in oxygen consumption associated with hatching have been included in the figure.

TABLE 2. Summary of chronology of hatching in four spontaneous hatchings.

Egg #	First increase in oxygen consumption		Pipped		Elapsed time: first increase $\dot{m}_{O_2}$ to pip	Hatched		Elapsed time: pip to hatch
	Day	Time	Day	Time		Day	Time	
41	45	15:30	45	17:00	1.5 h	47	14:00	45
28	*	*	45	19:00	*	46	10:40	15.7
34	*	*	46	00:00	*	46	18:00	18
43	45	17:00	47	07:00	38 h	47	15:00	8

* Indicates no observation because eggs were not in open-flow system

observed (Table 2). In the two which were monitored continuously in the open flow system (#41 and #43) the rate of oxygen consumption began to rise during the afternoon of the 45th day of incubation and rose steadily in about 1½ hours to approximately the same rate as the peak value reached on day 41. In one case, it remained constant at this level for about 20 min, and the egg was pipped. In the other case, pipping was delayed 38 h, during which time the rate of oxygen consumption increased slowly to a rate about 20 cm^3/h higher than the level reached on day 41.

PHYSICAL PARAMETERS

The values of several physical parameters of Ostrich eggs are presented in Table 3. The densities (gm/cm^3) of four eggs determined within four days of laying were: 1.154, 1.153, 1.156, and 1.157. Since all of these eggs must have lost some water before the determination of density, a reasonable estimate of the density at laying is 1.16. The volume of an egg can be predicted (Stonehouse 1963) from the value $L \cdot B^2$ (where L = length and B = maximum breadth). The relationship between volume (in cm^3) and $L \cdot B^2$ (each in cm) for Ostrich eggs is:

$$\text{Volume} = 29 + 0.5105 \cdot L \cdot B^2 \qquad (9)$$

($r^2 = 0.985$; $N = 18$)

TABLE 3. Physical values for Ostrich eggs.

	Units	N	SD	$\bar{x}$
WHOLE EGG				
Mass	(g)	44	—	1517[a]
Volume	(cm^3)	44[f]	134	1308
Density	(g/cm^3)	4	—	1.16[b]
Elongation[g]	unitless	18	0.06	1.25
Surface area	(cm^2)	—	—	584[c]
Water content	(%)	5	0.5	63
EGG SHELL				
Mass	(g)	9	31.86	279
Volume	(cm^3)	10	14.6	119[d]
Density	(g/cm^3)	9	0.08	2.36
% Total mass	(%)	9	1.1	18
EGG CONTENTS				
Density	(g/cm^3)	9	0.0086	1.04[e]

[a] Calculated from volume · density.
[b] Average of four freshly collected eggs (see text).
[c] Predicted from elongation and volume with equations 14 and 15 of Hoyt 1976.
[d] Whole egg volume–internal volume.
[e] (Whole egg mass – shell mass)/internal volume.
[f] Twenty eggs used for the determination of volume were borrowed from Lion Country Safari, Orange Co., California.
[g] Elongation = length/breadth.

DISCUSSION

The relation between metabolic rate and incubation age (days incubated) has been studied in the eggs of the chicken (Romijn and Roos 1938, Romijn and Lokhorst 1951, 1960, Barott 1937, Wangensteen and Rahn 1970), domestic duck, (*Anas* sp.; Khaskin 1961), House Wren (*Troglodytes aedon*; Kendeigh 1940), and the Herring Gull (*Larus argentatus*; Drent 1970). In the eggs of the chicken and the duck, the rate of oxygen consumption increases nearly exponentially during the first 80% of the incubation period and remains relatively constant during the remaining "plateau phase" (Rahn et al. 1974). The plateau phase ends with an increase in rate which lasts for several hours, and, finally, the egg is pipped. In chicken eggs, the rise at the end of the plateau phase occurs when the embryo penetrates the air cell (Visschedijk 1968a). Visschedijk (pers. comm.) refers to this as "internal pipping."

The rate of oxygen consumption by the Ostrich egg also increases nearly exponentially during the first part of incubation (equation 4). However, this "exponential" phase is followed by a decline of about 25% during the following six days. Finally, the rate of oxygen consumption increases just before pipping. This rise may coincide with "internal pipping" and the beginning of the transition from chorio-allantoic to pulmonary respiration.

This pattern of oxygen consumption is more complex than that reported in the chicken and duck, and its discussion requires additional terminology. The term "plateau" is not strictly applicable because the rate of oxygen consumption is not constant. We refer to the maximum rate of oxygen consumption (observed on day 41 in our Ostrich eggs) as the "peak rate" and the rate observed immediately prior to the rise associated with pipping as the "pre-internal pipping rate" ("pre-IP rate"). It is interesting to note that the rate of oxygen consumption of the chicken embryo decreases slightly during the last 20% of the incubation period (Wangensteen and Rahn 1970, Barott 1937: Table 2 at 99°F, Romijn and Roos 1938, Romijn and Lokhorst 1951, Visschedijk 1968a) which has been commented upon only once (Visschedijk 1968a). The rate of CO_2 production by the Herring Gull embryo also declines slightly (Drent 1970). However, in these smaller species the peak is not much higher than the pre-IP rate, giving the appearance of a "plateau" near the end of incubation. Rahn et al. (1974) reported "plateau" metabolic rates, determined shortly before initiation of pulmonary respiration. This value is comparable to the pre-IP rates we reported, but the latter term is preferable because a true plateau is absent, in some eggs.

The cause of the decline in the rate of oxygen consumption in the Ostrich eggs is still unknown. The fact that chicken and Herring Gull embryos exhibit a slight decline suggests that the phenomenon may not be unique to Ostriches. We assume that avian embryos, like other vertebrates, require oxygen for muscular activity, growth, and basal metabolism. We also assume that the basal component would not decline unless the body mass of the embryo decreased, and that such a decrease is unlikely. We therefore suggest that the observed decline in the rate of oxygen consumption is due to a decrease in the rate of growth of the embryo. Such a decrease has been noted at the end of incubation in the eggs of the domestic goose (Romanoff 1967). The decrease in the rate of oxygen consumption might be due to a decrease in the amount of muscular activity but available data do not support this hypothesis (Hamburger and Oppenheim 1967).

ALLOMETRY OF METABOLIC RATE

The pre-IP value for the Ostrich, in combination with the data on the 16 species summarized by Rahn et al. (1974) and the value (104 cm^3/h; W = 611 g) for the Greater Rhea (*Rhea americana*; Vleck et al., unpubl. data) yields the following relation between the "pre-internal pipping" rate of oxygen consumption (cm^3/day) and fresh egg mass (W, in g):

$$\dot{m}_{O_2} = 25.2 \cdot W^{0.730} \qquad (10)$$

($r^2 = 0.968$; N = 18)

This is similar to the relationship reported by Rahn et al. (1974).

If the data on oxygen consumption are converted to heat production (assuming 4.74 Kcal/L O_2) and the masses are expressed in kilograms, the following relationship is obtained:

$$MR = 18.5 \cdot W^{0.730} \qquad (11)$$

Where MR equals heat production (Kcal/day). The coefficient (18.5) in this equation differs from that in the equation relating basal heat production to body mass for adult passerine birds:

$$MR = 129 \cdot W^{0.724} \qquad (12)$$

and adult non-passerine birds:

$$MR = 78.3 \cdot W^{0.723} \qquad (13)$$

(both equations from Lasiewski and Dawson 1967). This is partly because fresh egg mass considerably over-estimates the mass of the metabolically active tissue. If it is assumed that the yolk-free hatchling mass equals 57% of fresh egg mass (Vleck et al., unpubl. data), the regression of heat production on yolk-free hatchling mass has a coefficient of 27.9. This means that the line relating embryonic metabolism to body mass is parallel to, but considerably below, the lines relating basal metabolism to body mass of adult birds. The reasons for this are yet unknown.

AIR CELL OXYGEN TENSION

Visschedijk (1968b) 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. Rahn et al. (1974) suggested that the partial pressures providing this stimulus are the same in all species, with $P_{O_2} = 104$ torr (SD = 5.33) and $P_{CO_2} = 37$ torr. The partial pressure of the oxygen in the air cell of the Ostrich egg during this phase is about 125 torr (Table 1).

Air cell oxygen tension may be an allometric function of fresh egg mass. We suggest this because shell conductance is proportional to the 0.81 power of fresh egg mass (Ar and Rahn 1978) and metabolic rate is proportion-

TABLE 4. Observed and predicted values of incubation period, shell conductance and the rate of oxygen consumption for Ostrich eggs. The two values have been predicted from weight alone (W) and from weight and incubation period combined (W/I).

Parameter	Units	Observed	Predicted		Equations used to predict
			W	W/I	
I	days	42[a]	58	—	$I = 12.03 \cdot W^{0.217}$ [c]
G_{H_2O}	mg/day · torr	187.2[b]	126	197[f]	$G = 0.432 \cdot W^{0.78}$ [d]
$\dot{m}_{O_2}$	cm^3/h	181.8[b]	255	384[g]	$G = 5.2 \cdot W/I$ [e]
					$\dot{m} = 22.2 \cdot W^{0.772}$ [e]
					$\dot{m} = 267 \cdot W/I$ [e]

[a] From Sauer and Sauer 1966.
[b] From present study.
[c] From Rahn and Ar 1974.
[d] From Ar et al. 1974.
[e] From Rahn et al. 1974. The values predicted by these equations have been divided by 24 h.
[f] Predicted using W = 1589 (mean mass of eggs used for determination of G_{H_2O}).
[g] Predicted using W = 1450 (mean mass of eggs used for determination of $\dot{m}_{O_2}$).

al to the 0.73 power of fresh egg mass (equation 10). The gradient in partial pressure of oxygen (equation 6) should, therefore, be proportional to the –0.08 power of fresh egg mass. Unless oxygen tension in the nest (P_{IO_2}) is also a function of fresh egg mass, oxygen tension in the air cell (equation 7) should increase with fresh egg mass. The high oxygen tension in the air cell which we calculate for the Ostrich egg is consistent with this prediction.

THE RELATION BETWEEN INCUBATION PERIOD, SHELL CONDUCTANCE AND "PRE-IP" RATE OF OXYGEN CONSUMPTION

Rahn and Ar (1974) suggested that, in different species of birds with eggs of the same mass, the shell conductance is inversely related to the length of the incubation period. Eggs with different incubation periods would, therefore, experience the same fractional weight loss. The incubation period of Ostrich eggs is 28% shorter than predicted for an egg of its mass (Table 4). The shell conductance of the Ostrich egg is higher than predicted from mass alone but is close to the value predicted from mass and incubation period (Table 4). This supports the suggestion (Rahn and Ar 1974) that shell conductance is adapted to the length of the incubation period.

Rahn et al. (1974) suggested that the rate of oxygen consumption during the "plateau" (= pre-IP) phase is also inversely related to the length of the incubation period and can best be predicted from the equation:

$$\dot{m}_{O_2} = 267 \cdot W/I \qquad (14)$$

However, the pre-IP rate of oxygen consumption by Ostrich eggs is less than half the rate predicted by equation (14) and is much closer to the rate predicted from mass alone (Table 4). It is not clear whether this is due to some peculiarity of Ostrich eggs or to an erroneous assumption in the development of equation (14).

SUMMARY

The relation between metabolic rate and incubation age in the Ostrich is different from that reported previously for the chicken, duck, and Herring Gull. In the eggs of the Ostrich a peak rate occurs six days before pipping and is followed by a decline of about 25%. We suggest that this decline may be caused by a decrease in growth rate.

The allometric relationship between the metabolic rate shortly before pipping and fresh egg mass for several species of avian eggs is parallel to, but significantly below, the line relating basal metabolism to body mass in adult birds. Therefore, just before hatching, an avian embryo has a metabolic rate approximately one-third that of an adult bird of equal body mass.

The oxygen tension in the air cell shortly before pipping in the Ostrich egg is considerably higher than the mean value reported for other species. We suggest there may be an allometric relationship between air cell gas tensions and fresh egg mass.

The shell conductance of the Ostrich egg is adapted to its relatively short incubation period, but the rate of oxygen consumption before internal pipping is not.

ACKNOWLEDGMENTS

We thank G. A. Bartholomew and T. R. Howell for helpful advice and editorial suggestions, and J. Dolan, Wild Animal Park (San Diego Zoological Society),

Escondido, California, for providing the eggs. This research was conducted in the Department of Biology, University of California, Los Angeles, California and was supported by NSF grant DEB 75-14045 AO1 administered by G. A. Bartholomew. The computer work was supported by intramural funds granted by the UCLA Campus Computing Network.

LITERATURE CITED

AR, A., C. V. PAGANELLI, R. B. REEVES, D. G. GREENE AND H. RAHN. 1974. The avian egg: Water vapor conductance, shell thickness, and functional pore area. Condor 76:153–158.

AR, A. AND H. RAHN. 1978. Interdependence of gas conductance, incubation length and weight of the avian egg. *In* J. Piiper [ed.], Respiratory function in birds, adult and embryonic. Springer-Verlag, Berlin.

BAROTT, H. G. 1937. Effect of temperature, humidity, and other factors on hatch of hen's eggs and on energy metabolism of chick embryos. U.S. Dep. Agric. Tech. Bull. 553:1–45.

DRENT, R. 1970. Functional aspects of incubation in the Herring Gull. Behaviour, Suppl. 17:1–132.

HAMBURGER, V. AND R. OPPENHEIM. 1967. Prehatching motility and hatching behaviour in the chick. J. Exp. Zool. 166:171–204.

HILL, RICHARD W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

HOYT, D. F. 1976. The effect of shape on the surface-volume relationships of birds' eggs. Condor 78:343–349.

KENDEIGH, S. C. 1940. Factors affecting length of incubation. Auk 57:499–513.

KHASKIN, V. V. 1961. Heat exchange in birds' eggs on incubation. Biophysics 6:97–107.

LASIEWSKI, R. C. AND W. R. DAWSON. 1967. A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69:13–23.

LEUTHOLD, W. 1970. Some breeding data on Somali Ostrich. E. Afr. Wildl. J. 8:206.

PAGANELLI, C. V., R. A. ACKERMAN, AND H. RAHN. 1978. The avian egg: *In vivo* conductance to O_2, CO_2 and water vapor in late development. *In* J. Piiper [ed.], Respiratory function in birds, adult and embryonic. Springer-Verlag, Berlin.

RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. Condor 76:147–152.

RAHN, H., C. V. PAGANELLI, AND A. AR. 1974. The avian egg: Air cell gas tension, metabolism and incubation time. Respir. Physiol. 22:297–309.

ROMANOFF, A. L. 1967. Biochemistry of the avian egg. John Wiley & Sons, New York.

ROMIJN, C., AND W. LOKHORST. 1951. Foetal respiration in the hen. Phys. Comp. Oecol. 2:187–197.

ROMIJN, C., AND W. LOKHORST. 1960. Foetal heat production in the fowl. J. Physiol. (Lond.) 150:239–249.

ROMIJN, C., AND J. ROOS. 1938. The air space of the hen's egg and its changes during the period of incubation. J. Physiol. (Lond.) 94:365–379.

SAUER, E. G. F., AND E. M. SAUER. 1966. The behavior and ecology of the South African Ostrich. Living Bird 5:45–75.

SCHMIDT-NIELSEN, K. 1975. Animal physiology. Cambridge University Press, London.

SIEGFRIED, W. R., AND P. G. H. FROST. 1974. Egg temperature and incubation behaviour of the Ostrich. Madoqua, Ser. 1 No. 3:63–66.

STONEHOUSE, B. 1963. Egg dimensions of some Ascension Island seabirds. Ibis 103:474–479.

VISSCHEDIJK, A. H. J. 1968a. The air space and embryonic respiration: 1. The pattern of gaseous exchange in the fertile egg during the closing stages of incubation. Br. Poult. Sci. 9:173–184.

VISSCHEDIJK, A. H. J. 1968b. The air space and embryonic respiration: 3. The balance between oxygen and carbon dioxide in the air space of the incubating chicken egg and its role in stimulating pipping. Br. Poult. Sci. 9:197–210.

VLECK, D. 1978. The energetics of activity and growth. Ph.D. diss. Univ. of California, Los Angeles.

WANGENSTEEN, O. D., AND H. RAHN. 1970. Respiratory gas exchange by the avian embryo. Respir. Physiol. 11:31–45.

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Address of second and third authors: Department of Zoology, University of Washington, Seattle, Washington 98195.
Accepted for publication 27 June 1977.