June, 1979

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Source: *Physiological Zoology*, Vol. 52, No. 3 (Jul., 1979), pp. 363-377
Published by: The University of Chicago Press. Sponsored by the Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology
Stable URL: http://www.jstor.org/stable/30155757
Accessed: 24-05-2016 18:16 UTC

METABOLISM OF AVIAN EMBRYOS: PATTERNS IN ALTRICIAL AND PRECOCIAL BIRDS[1]

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(Accepted 1/19/79)

We measured rate of oxygen consumption ($\dot{V}_{O_2}$) of individual eggs in five species of birds. The pattern of oxygen consumption during development differs markedly between altricial and precocial species. The $\dot{V}_{O_2}$ increased throughout incubation in eggs of the altricial species (*Poephila guttata*, *Ploceus cucullatus*, and *Columba livia*). In eggs of the precocial species (*Coturnix coturnix* and *Anser anser*) $\dot{V}_{O_2}$ increased during the first 75% of incubation but then remained relatively constant until shortly before hatching. Growth patterns of embryos of *Poephila* and *Coturnix* differ in the same way as their patterns of oxygen consumption differ. We suggest that a decline in growth rate late in incubation results in the stabilization of $\dot{V}_{O_2}$ in the precocial species. In growing embryos, $\dot{V}_{O_2}$ increases with (body mass)$^{0.92}$. The exponent is higher than that characterizing metabolism-mass relations of adult birds because of the energy demands of rapid embryonic growth. In both altricial and precocial species, eggshell conductance to gases is adapted primarily to regulate water loss and does not obviously limit $\dot{V}_{O_2}$ of the embryo. The $\dot{V}_{O_2}$ prior to pipping is more closely correlated with egg mass (and thus embryo mass) than with eggshell conductance. As a result, oxygen tensions in the air cells of *Poephila* and *Ploceus* eggs just prior to pipping are surprisingly low, only 72 and 85 torr, respectively.

As avian embryos develop, their rates of oxygen consumption increase. Hoyt, Vleck, and Vleck (1978) showed that the pattern of this increase can vary greatly in eggs of different sizes. Different avian species have very different modes of embryonic development, ranging from the highly precocial Anseriformes which can walk, swim, and dive shortly after hatching to highly altricial Passeriformes which are naked, have closed eyes, and are incapable of locomotion and thermoregulation at hatching (Nice 1962). We wondered whether differences in mode of development might also result in differences in the pattern of increase in oxygen consumption. Embryonic oxygen consumption has been measured in only a few species: the House Wren, *Troglodytes aedon*, (Kendeigh 1940); domestic chicken, *Gallus gallus* (Barott 1937; Romijn and Roos 1938; Romijn and Lokhorst 1951; Wangensteen and Rahn 1970/71); domestic duck, *Anas* sp (Khaskin 1961); and four ratite species (Calder 1978; Hoyt et al. 1978, Vleck, Vleck, and Hoyt, in press). Patterns of growth in altricial and precocial chicks have been studied (Ricklefs 1968, 1973), but there is virtually no comparative information on embryonic development in altricial and precocial species.

During incubation the avian egg exchanges water vapor as well as oxygen

[1] We thank N. E. Collias and C. Jacobs for lending Village Weaverbird eggs and W. Stevens for lending domestic goose eggs. G. A. Bartholomew and T. R. Howell critically read and improved the manuscript. This research was supported by N.S.F. grant DEB 75-14045 administered by G. A. Bartholomew. The computer work was supported by intramural funds granted by the UCLA Campus Computing Network.

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with its environment. The movement of both these gases occurs by diffusion through the air-filled pores of the shell (Wangensteen and Rahn 1970/71; Wangensteen, Wilson, and Rahn 1970/71). Therefore conductance of the eggshell must be adapted so that the fluxes of both oxygen and water are compatible with embryonic development and hatching. Conductance to water vapor is constant throughout incubation (Drent 1970; Rahn and Ar 1974), and the flux of water vapor varies with the water-vapor pressure gradient across the shell. Flux of oxygen into the egg is equal to the rate of oxygen consumption of the embryo. Conductance of the egg to oxygen is constant after about the first third of incubation (Kutchai and Steen 1971; Lomholt 1976*a;* Tullett and Board 1976), but flux of oxygen increases as the embryo grows and the rate of oxygen consumption rises.

We report (1) the rate of oxygen consumption throughout incubation and (2) conductance properties to gases in eggs of five species, including three altricial species—Zebra Finch, *Poephila guttata*, Village Weaverbird, *Ploceus cucullatus*, and domestic pigeon, *Columba livia*—and two precocial species—Coturnix or Japanese Quail, *Coturnix coturnix*, and domestic goose, *Anser anser*. The first of these measurements allows us to discuss the relationship between ontogeny of metabolism and growth in species with different developmental strategies. The two measurements together allow us to address the question of how eggshell conductance to gases is adapted to embryonic requirements.

MATERIAL AND METHODS

EGGS

Goose, pigeon, weaverbird, Zebra Finch, and some of the Coturnix eggs were obtained from captive breeding colonies at or near the University of California, Los Angeles. Some Coturnix eggs were obtained commercially from a local supplier. Eggs were weighed immediately after receiving them and then put in an incubator. All pigeon, Coturnix, and Zebra Finch eggs had been freshly laid. Some of the weaverbird and goose eggs had been incubated for unknown periods in the nest. Age of these eggs was estimated by comparing the oxygen consumption and time of hatching with that of eggs of known age.

Relative humidity in the incubators was adjusted so that eggs lost about 16%–18% of their initial mass during incubation, as is typical for naturally incubated eggs (Drent 1970). Some eggs were incubated in Aminco constant-temperature cabinets where temperature was regulated within ± 0.2 C and were turned by hand several times a day. All weaverbird eggs and those of finch, quail, and pigeon used to study growth were incubated in a commercial forced-draft incubator with temperature regulated within ± 0.5 C and were automatically turned once every 2 h. Incubator temperatures used are given in table 1. Mean nighttime egg temperature under incubating Village Weaverbirds is 36.5 C (White and Kinney 1974), so eggs of this species were incubated at a lower temperature than the others. Egg temperatures measured under incubating Zebra Finches and pigeons were 36.0–37.0 C at the center of the egg and 38.5–38.8 C at the top of the egg (unpublished data). We had little or no success hatching these eggs at 35 or 39 C, so only data on eggs incubated at 37.5 C are reported.

Volume of each egg was determined from the difference in apparent weight of the egg suspended in air and in water or by the direct measure of water displacement as described by Hoyt (1976).

TABLE 1

INCUBATION PARAMETERS OF THE FIVE SPECIES OF BIRDS MEASURED IN THE PRESENT STUDY

Species	Length of Incubation (Days)	Initial Egg Mass (g ± SD)	Incubator Temperature (°C)	No. of Eggs	
				Total	Hatched
Poephila guttata (Zebra Finch)	14	.93± .08	37.5	15	8
Ploceus cucullatus (Village Weaverbird)	12	2.82± .36	36.5	12	6
Columba livia (domestic pigeon)	17	18.49± 1.50	37.5	8	5
Coturnix coturnix (Coturnix Quail)	17	10.01± .97	37.5	3	3
Anser anser (domestic goose)	28	125.9 ±11.4	37.5	11	10

Water-vapor conductance was measured by the method of Ar et al. (1974) in which water loss of eggs kept in a desiccator at constant temperature and pressure is monitored by measuring change in mass.

OXYGEN CONSUMPTION

Oxygen consumption of individual eggs was measured throughout incubation until the chick hatched or the embryo died. Data from eggs in which the embryo died during incubation were used only from that portion of incubation in which the oxygen consumption was similar to that of eggs that hatched. The most common cause of embryonic death was breakage of the eggs through handling. We measured oxygen consumption in each egg at least once a day until hatching. In the latter part of incubation two or more measurements were made each day.

We measured the rate of oxygen consumption using two techniques. For the Zebra Finch, weaverbird, and most of the Coturnix and pigeon-egg measurements we used a closed system. To prevent breakage each egg was kept in a short, open-ended Plexiglas tube. The metabolic chamber consisted of either a glass 100 cm^3- or Plexiglas 250 cm^3-syringe. The Plexiglas syringes were sufficiently impermeable to oxygen that four gas samples with a fractional O_2 concentration of about 20% (1% below ambient) had not significantly changed in composition after 12 h (mean change in percent O_2 was +0.013%).

Volumes of egg and egg holder were subtracted from the total volume of the syringe to calculate the volume of air in the syringe. The plunger was removed and the egg was placed in the syringe and allowed to come to thermal equilibrium within the incubator. The plunger was then replaced and the syringe was flushed with fresh warm incubator air and the open end sealed with a three-way stopcock. A sample of air from the incubator was used to determine the initial oxygen concentration. The sealed syringe was left in the incubator until the fractional concentration of oxygen inside was reduced about 1%, requiring from 10 min to several hours depending on the type and age of the egg. After the period of measurement, nearly all the air in the syringe could be expelled with the plunger for determination of final oxygen concentration.

Oxygen concentration of initial and end air samples was measured with a Beckman E-2 paramagnetic oxygen analyzer. Prior to analysis, water vapor and CO_2 were removed by injecting the air sample through a tube containing silica gel and sodium hydroxide-coated asbestos (Ascarite). Rate of oxygen consumption was calculated by using the

following formula for a closed, constant-volume system (Vleck 1978):

$$\dot{V}_{O_2} = \frac{V(F_I - F_E)}{(1 - F_E)t} \quad (1)$$

where

$\dot{V}_{O_2}$ = rate of oxygen consumption in $cm^3 \cdot h^{-1}$,
V = volume of dry air in the metabolic chamber at the start,
F_I = initial fractional concentration of O_2 in dry, CO_2-free air,
F_E = fractional concentration of O_2 in dry, CO_2-free air in the end sample,
t = elapsed time in h.

The term $(1 - F_E)$ corrects for the effect of removing CO_2 and water vapor on fractional O_2 concentration of the sample. All gas volumes are corrected to STP (0 C, 760 torr).

The only major error in this method of oxygen determination is due to the water vapor content of V. We assumed this water-vapor content was 50% of saturation at the incubator temperature because under this assumption the maximum error in $\dot{V}_{O_2}$ is less than $\pm 3\%$ (Vleck 1978).

The closed-system respirometer chamber for the goose eggs was a 2-liter metal paint can with an airtight lid fitted with a three-way stopcock. An egg was placed in the can and allowed to come to thermal equilibrium. The can was sealed and about 120 cm^3 of incubator air injected into it with a syringe through the three-way stopcock. After mixing the air in the can by pumping the plunger of the syringe in and out several times, a 100 cm^3-sample was withdrawn to determine F_I. Pressure in the chamber was equilibrated with atmospheric by allowing the added 20 cm^3 of air to escape before closing the three-way stopcock. After the appropriate time interval the air in the chamber was mixed by connecting an empty syringe to the can via the three-way stopcock and pumping the syringe plunger; then a 100 cm^3-air sample was withdrawn to determine F_E. Fractional oxygen concentrations of initial and end samples were analyzed and $\dot{V}_{O_2}$ calculated as described above.

When $\dot{V}_{O_2}$ exceeded 7 $cm^3 \cdot h^{-1}$ in the Coturnix, pigeon, and goose eggs, the oxygen consumption of individual eggs could be monitored continuously in an open-flow system. Individual eggs were placed in a glass chamber which was supplied with warm air at rates from 50 to 200 $cm^3 \cdot min^{-1}$ maintained with a Brooks Thermal Mass Flowmeter or calibrated Brooks Rotameter. Air leaving the chamber was dried and CO_2 removed by passing it through silica gel and Ascarite. Oxygen concentration was measured with a Beckman G-2 paramagnetic oxygen analyzer and $\dot{V}_{O_2}$ calculated from equation 2 of Hill (1972).

GROWTH OF EMBRYOS

Patterns of embryonic growth in the Zebra Finch and Coturnix were determined from embryos of known age. Rate of oxygen consumption of each egg was measured, then the embryo was removed, freed of membranes and yolk sac, blotted dry, and immediately weighed to the nearest milligram. We used 25 finch eggs varying in age from 4 to 14 days and 25 quail eggs varying from 10 to 17 days. In addition we measured oxygen consumption and embryo mass in six pigeon eggs between 13 and 17 days old.

RESULTS

OXYGEN CONSUMPTION

In eggs of the precocial species, Coturnix and geese, oxygen consumption increased nearly exponentially during the first 75% of incubation (figs. 1 and 2). Thereafter oxygen consumption remained nearly constant until shortly before pipping. At this point oxygen

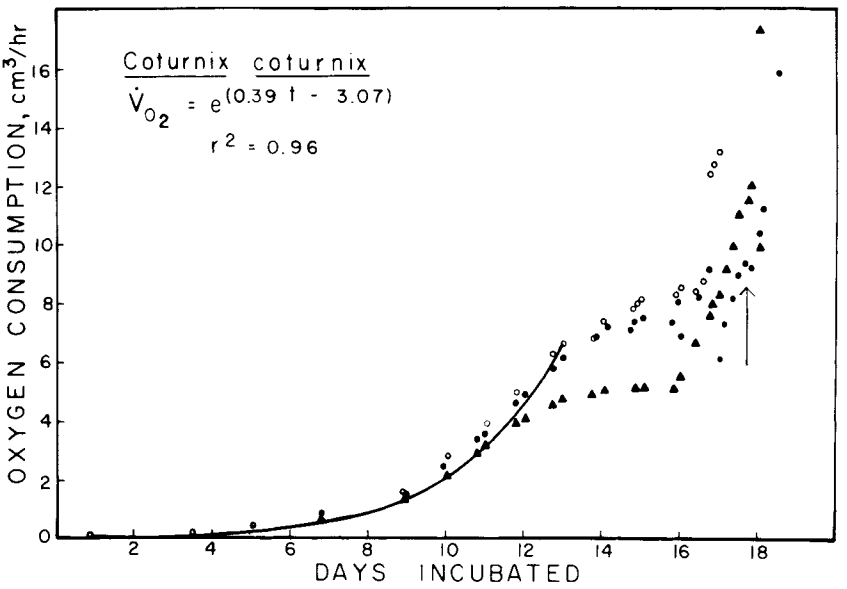

FIG. 1.—The relationship between embryonic oxygen consumption and days of incubation in the Coturnix Quail, *Coturnix coturnix;* 87 measurements on three eggs. Each egg is indicated with a different symbol. For clarity of graphing, in this and figs. 2–5, nearly identical values are not plotted separately but appear as a single point. The arrow on day 17 indicates hatching. The data through day 13 are fitted by an exponential curve; the equation for the exponential is shown. Coefficient of determination (r^2) is given as an indication of goodness of fit of the semilog-transformed data used to calculate the exponential equation.

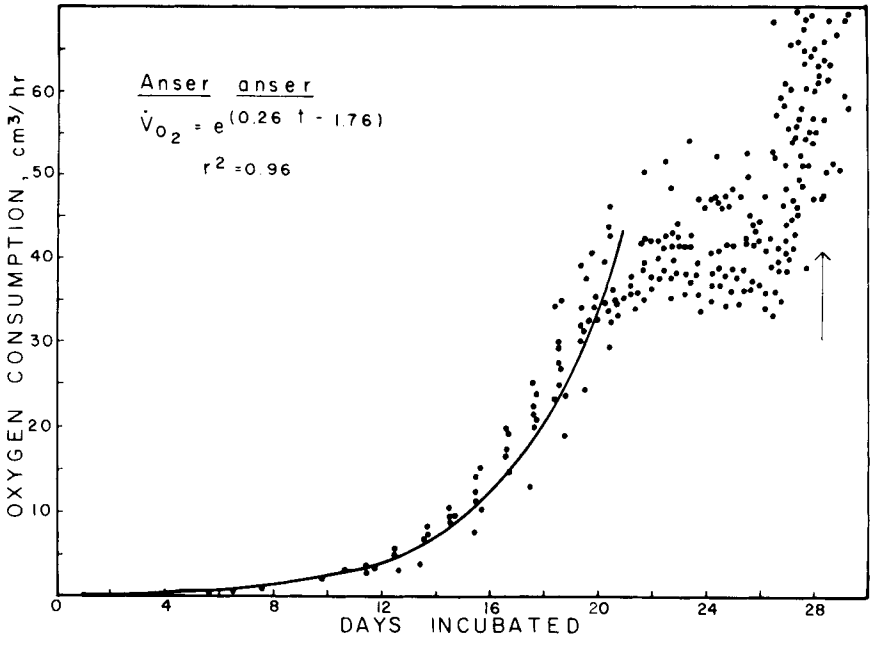

FIG. 2.—The relationship between embryonic oxygen consumption and days of incubation in the domestic goose, *Anser anser;* 425 measurements on 11 eggs. The data through day 20 are fitted by an exponential curve. Statistics as in fig. 1.

consumption again increased as the embryo broke into the air cell (internal pipping) and initiated pulmonary respiration (Visschedijk 1968). The quail eggs pipped on day 16 and hatched on day 17. The goose eggs pipped on day 27 and hatched on day 28. The pattern is different in artricial species. Oxygen consumption of Zebra Finch eggs increased exponentially throughout incubation (fig. 3). In the eggs of Village Weaverbird and pigeon, oxygen consumption increased continuously and showed no plateau (figs. 4 and 5).

The mean value of oxygen consumption at the end of the plateau for the goose and quail eggs and prior to the initiation of pulmonary respiration for the finch, weaverbird, and pigeon eggs is shown in table 2. Hereafter this value (plateau in precocial species, about 90% through incubation in altricial species) will be referred to as the "preinternal pipping" (pre-IP) rate of oxygen consumption.

EMBRYONIC GROWTH

Mass of Zebra Finch embryos increased continuously during incubation, whereas mass of Coturnix embryos reached a plateau before hatching (fig. 6). Because egg size was variable and only one growth measurement could be made on each embryo, we normalized embryo mass by dividing it by initial egg mass and multiplying the result by the mean initial egg mass for the species. The scatter in the data is partly due to differences in water content of the embryos. Water content in embryos of domestic fowl decreases from about 95% to 80% during incubation (Romanoff 1967). Zebra Finch growth rates we measured are presumably similar to those in nature because incubation period and hatchling mass of eggs artificially incubated at 37.5 C did not differ from naturally incubated eggs. (Domesticated Coturnix adults seldom incubate their eggs.)

The logarithm of oxygen consumption

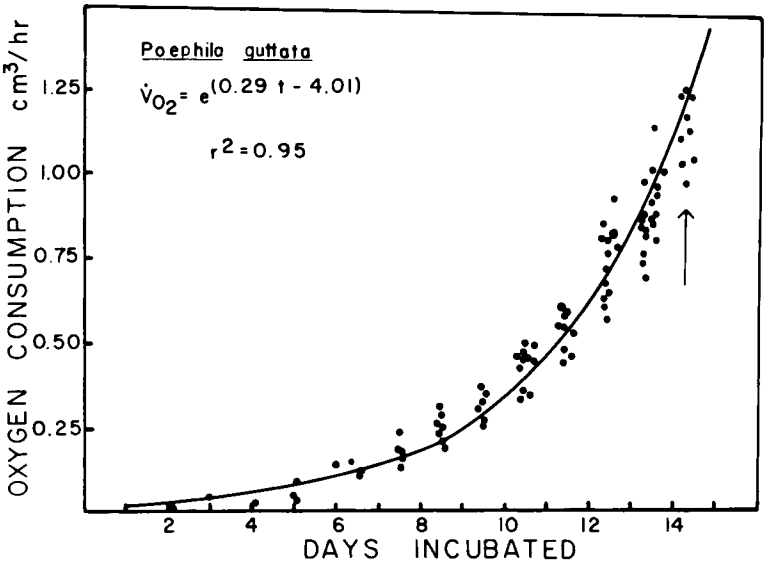

FIG. 3.—The relationship between embryonic oxygen consumption and days of incubation in the Zebra Finch, *Poephila guttata;* 141 measurements on 15 eggs. An exponential curve has been fitted to the data. Statistics as in fig. 1.

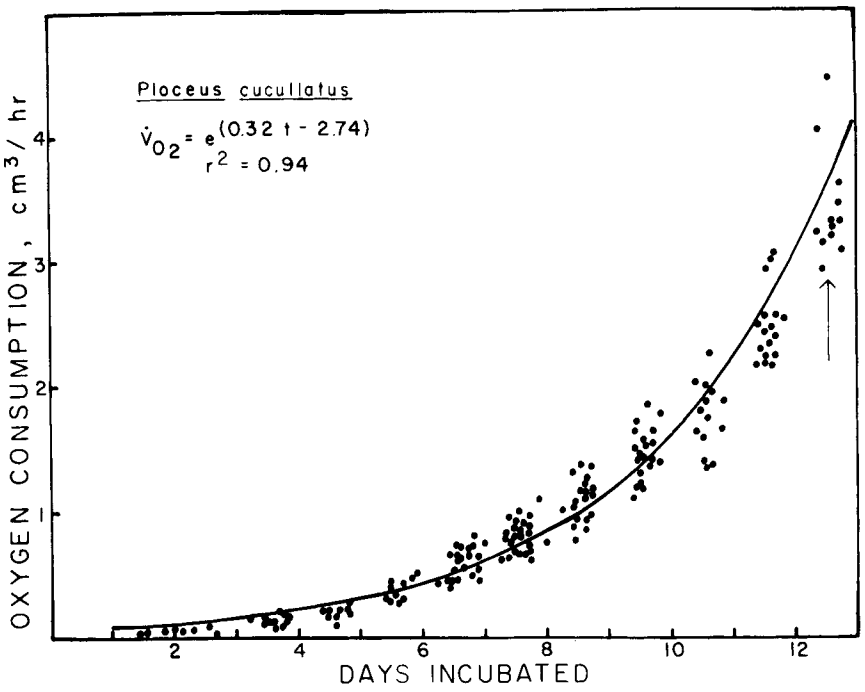

FIG. 4.—The relationship between embryonic oxygen consumption and days of incubation in the Village Weaverbird, *Ploceus cucullatus;* 262 measurements on 12 eggs. An exponential curve has been fitted to the data. Statistics as in fig. 1.

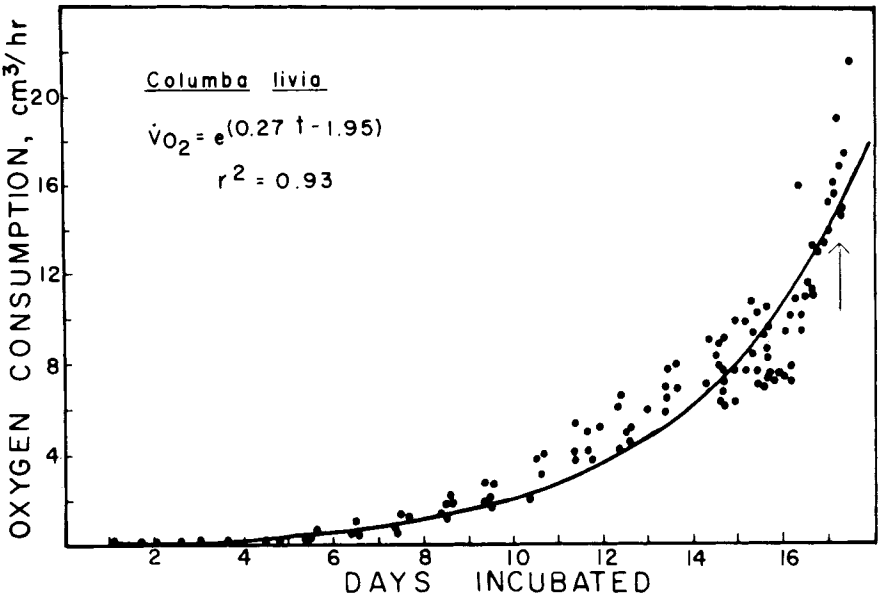

FIG. 5.—The relationship between embryonic oxygen consumption and days of incubation in the domestic pigeon, *Columba livia;* 142 measurements on 8 eggs. An exponential curve has been fitted to the data. Statistics as in fig. 1.

of Zebra Finch, Coturnix, and pigeon embryos increased linearly with the logarithm of embryo mass. The data from all three species are fit by a line with a slope of 0.92 (fig. 7). The equations for data analyzed for each species separately are

$$\text{Zebra Finch } \dot{V}_{O_2} = 1.18M^{0.79} \quad (\text{no.} = 25, r^2 = 0.95) \quad (2a)$$

$$\text{Coturnix } \dot{V}_{O_2} = 1.98M^{0.81} \quad (\text{no.} = 25, r^2 = 0.90) \quad (2b)$$

$$\text{Pigeon } \dot{V}_{O_2} = 0.84M^{1.23} \quad (\text{no.} = 7, r^2 = 0.87) \quad (2c)$$

where $\dot{V}_{O_2}$ is in $cm^3 \cdot h^{-1}$ and M is embryo mass in grams.

CONDUCTANCE

Conductance of the eggs to water vapor (G_{H_2O}) for each species is shown in table 3. Because diffusion coefficients vary with atmospheric pressure and temperature (Paganelli et al. 1976;

TABLE 2

PREINTERNAL PIPPING RATE OF OXYGEN CONSUMPTION ($\dot{V}_{O_2}$) IN EGGS OF FIVE SPECIES OF BIRDS

SPECIES	PREPIPPING $\dot{V}_{O_2}$ ($cm^3 \cdot Day^{-1}$)			
		Predicted		
	Measured	25.2 $M^{0.73}$	51.3 G_{H_2O}	267 $M \cdot I^{-1}$
Poephila guttata	20.3±2.47 (24)	24.6	12.8	18.5
Ploceus cucullatus	56.4±6.48 (22)	53.7	43.1	62.8
Columba livia	229.1±58.58 (23)	212.0	269.3	290.4
Coturnix coturnix	184.2±37.80 (14)	154.9[a]	199.9[b]	188.9[a]
Anser anser	968 ±190.4 (36)	859.8	1399.0	1200.6

NOTE.—Measured values are reported with ±SD; sample size in parentheses. Predicted values are based on eqq. (4)–(6) in the text.

[a] Average mass for the three eggs in which $\dot{V}_{O_2}$ was measured was 12.03 g.

[b] G_{H_2O} was measured in smaller *Coturnix* eggs (9.6 g) than those used for $\dot{V}_{O_2}$ experiment so the G_{H_2O} used here was the value in table 3 corrected by a factor of (12.03/9.6).

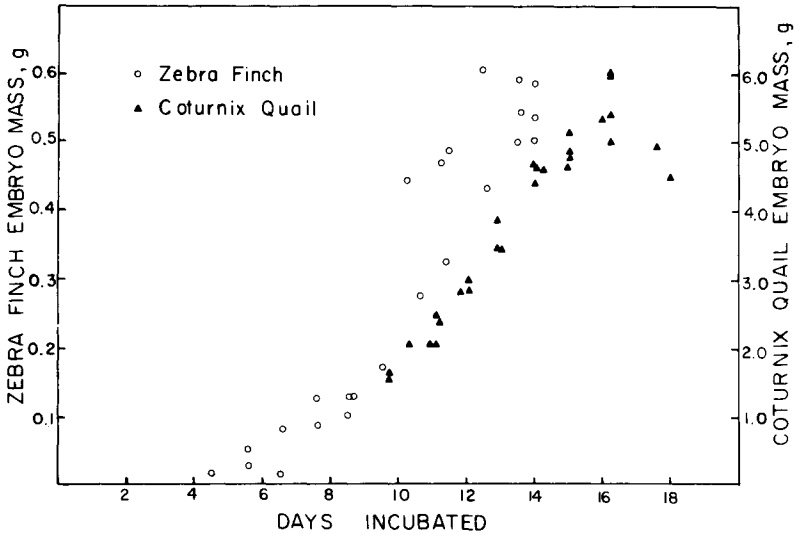

FIG. 6.—Yolk-free embyo mass as a function of days of incubation in the Zebra Finch (○) and Coturnix Quail (▲). The yolk-free mass of the embryo is expressed as percentage of its initial egg mass times the mean initial egg mass for that species. Zebra Finch chicks hatch on day 14, Coturnix Quail chicks hatch on day 17.

Paganelli, Ackerman, and Rahn 1978), these results are expressed at 760 torr and a temperature of 25 C (=298 K) for comparison with other values in the literature (Ar and Rahn 1978). The G_{H_2O} at the incubation temperature can be calculated by multiplying by the factor $(T_{inc}/298\ K)^{0.5}$ where incubation temperature is expressed in Kelvin (Paganelli et al. 1978).

DISCUSSION

METABOLISM AND GROWTH PATTERNS

Ontogeny of oxygen consumption.—Altricial and precocial species differ markedly in the ontogeny of oxygen consumption. Rate of oxygen consumption increases throughout incubation in eggs of altricial Zebra Finches, Village Weaverbirds, and pigeons, but it reaches a plateau during late incubation in eggs of the precocial Coturnix and domestic goose. Similar plateaus in embryonic metabolism occur in the precocial do-

TABLE 3

WATER-VAPOR CONDUCTANCE (G_{H_2O}) AND THE RELATIONSHIP BETWEEN G_{H_2O}, INCUBATION PERIOD (I), AND EGG MASS (M) IN FIVE SPECIES OF BIRD EGGS

Species	G_{H_2O} [mg(Day·Torr)$^{-1}$]	$G_{H_2O} \cdot I/M$ [mg(g·Torr)$^{-1}$]
Poephila guttata	.25± .06 (10)	3.61
Ploceus cucullatus	.84± .15 (18)	3.57
Columba livia	5.25± .90 (10)	4.83
Coturnix coturnix	3.11± .29 (10)	5.51[a]
Anser anser	27.27±3.68 (10)	6.06

NOTE.—G_{H_2O} values are corrected to 760 torr and 25 C and reported with ± SD; sample size in parentheses.

[a] Average mass of *Coturnix* eggs in which G_{H_2O} was measured was 9.6 g.

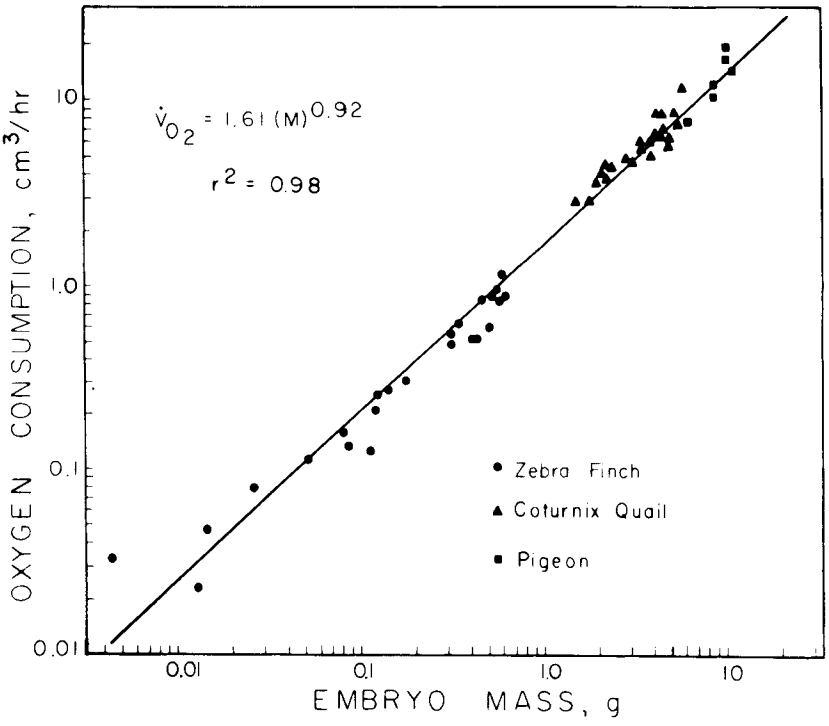

FIG. 7.—Embryonic oxygen consumption versus yolk-free embryo mass. $\dot{V}_{O_2}$ was measured immediately before weighing embryos. The data are from 25 Zebra Finch embryos (mass 0.004–0.619 g), 25 Coturnix Quail embryos (mass 1.51–6.05 g), and 7 domestic pigeon embryos (mass 3.90–10.79 g). The regression line is fitted by the least-squares method and the formula is shown; r^2 is the coefficient of determination for the log-transformed data.

mestic fowl (Barott 1937; Romijn and Roos 1938; Romijn and Lokhorst 1951; Wangensteen and Rahn 1970/71) and domestic duck (Khaskin 1961), whereas no plateau occurs in the altricial House Wren (Kendeigh 1940). A semiprecocial species, the Herring Gull, *Larus argentatus*, follows an intermediate pattern. Metabolism reaches a plateau for only 2–3 days before hatching (Drent 1970). The gull's incubation period is the same as that of the domestic goose, but the precocial goose has a 5–6-day plateau period in oxygen consumption.

Growth patterns.—Different patterns in the ontogeny of metabolism reflect different patterns in embryonic development. Embryo mass increases continuously throughout incubation in the altricial Zebra Finch, whereas it reaches a plateau in the precocial Coturnix (fig. 6). The absolute growth rate, defined as grams of tissue added per day, therefore remains high in Zebra Finch embryos but drops dramatically in Coturnix near the end of incubation. Growth rate also declines near the end of incubation in the precocial domestic fowl, duck, and goose (Romanoff 1967). Growth rate does not decline late in incubation in embryos of small altricial birds like the House Wren (calculated from data in Kendeigh 1940) or Starling, *Sturnus vulgaris* (Ricklefs, personal communication) but does decline in the larger pigeon (Romanoff 1967).

The similarities between growth patterns and ontogeny of oxygen consumption are not unexpected. Absolute growth rates increase until the end of incubation in small altricial species, and rate of oxygen consumption increases along with embryo mass. Declining growth rates of precocial birds near the end of incubation result in plateaus in embryo mass and in plateaus, or even declines (Hoyt et al. 1978; Vleck et al., in press) in rate of oxygen consumption. Unlike altricial hatchlings, precocial chicks possess functional sensory, neuromuscular, and thermoregulatory systems. Maturation of these systems may take some time after tissue growth is essentially complete but may require relatively little energy. This could account for the decline in growth rate and the pattern of metabolism before hatching in embryos of precocial species.

Growth and metabolism.—The avian embryo is a particularly favorable system for examining the impact of growth on metabolism, because when embryo growth is rapid the cost of growth is likely to be a substantial part of total metabolic expenditure. Furthermore, confounding effects of activity and thermoregulation are minimal. It is instructive to analyze metabolic rates of embryos in terms of costs of maintenance and growth.

Maintenance costs and daily energy expenditure increase with body mass raised to about the 0.72 power in adult birds (Lasiewski and Dawson 1967; King, 1974), and it is reasonable to assume that maintenance costs for embryos scale in a similar fashion. It is possible that intraspecific scaling factors differ from these interspecific comparisons, but metabolic rate also scales with about the three-fourths power of body mass within a species in adult mice, rabbits, and dogs (Kleiber 1961). Comparable data for adult birds are not available.

In growing avian embryos, metabolic rate increases faster than predicted from the relationship of maintenance metabolism to body mass. Metabolic rate increases with mass raised to the 0.92 power in Zebra Finch, pigeon, and Coturnix embryos (fig. 7), and when the data for each species are analyzed separately the powers range from 0.8 to

1.2 (eqq. [2a]–[2c]). We suggest this increase in the scaling factor is due to the high energy cost of biosynthesis during rapid growth. As Brody (1945) pointed out, the energy cost of growth will result in total metabolism increasing more rapidly with mass during periods of rapid growth than during periods of declining growth. As a first approximation, we can assume that growth cost, or the rate at which energy is expended for biosynthesis, is proportional to absolute growth rate. This means that when absolute growth rate increases more rapidly with mass than does maintenance metabolism, growth costs result in a scaling factor for total metabolism greater than 0.72, the value predicted for maintenance alone.

Through most of incubation Zebra Finch and Coturnix embryos grow approximately exponentially (fig. 6). The exponential increase in rate of oxygen consumption during most of incubation (figs. 1–5) suggests exponential growth is equally characteristic of other avian embryos during this part of incubation. During exponential growth, absolute growth rate and growth cost increase with (mass)^1. Therefore, total metabolism of these embryos should be approximately proportional to mass raised to a power greater than 0.72, just as we observed. Similar relationships are apparent in the data of Blem (1975), O'Connor (1975), and Mertens (1977) on metabolism of rapidly growing altricial chicks after hatching.

PHYSIOLOGICAL SIGNIFICANCE OF EGGSHELL CONDUCTANCE

The porosity of an eggshell determines its conductance to both water vapor and oxygen. Our data suggest that conductance is adapted primarily to regulate water loss and has less influence on maximum rates of oxygen flux into the egg. Gas fluxes are equal to the product of the partial-pressure gradient across the shell and shell conductance. The pressure gradient of water vapor remains essentially constant throughout incubation because the air inside the egg is saturated at the incubation temperature. The gradient in oxygen pressure must increase as oxygen consumption (flux) increases so the partial pressure of oxygen inside the egg can become quite low relative to ambient air. As long as the embryo has the physiological capacity to extract oxygen for metabolism from the atmosphere inside the shell oxygen consumption can increase despite the diffusion barrier of the shell.

Water-vapor conductance.—The permeability of eggshells is such that most bird eggs lose about 14%–16% of their initial mass as water vapor during the course of incubation (Drent 1970; Rahn et al. 1976). To have the same fractional loss in mass requires that small eggs and those with long incubation periods have lower water-vapor conductances than large eggs and those with short incubation periods. For 90 species of birds' eggs, incubation period (I in days), initial egg mass (M in grams), and water-vapor conductance are related by the equation

$$\frac{I \cdot G_{H_2O}}{M} = 5.13 \text{ mg}(\text{g} \cdot \text{torr})^{-1} \quad (\text{SD} = 0.86) \quad \text{(Ar and Rahn 1978)}. \quad (3)$$

The calculated ratios for these three variables (conductance coefficients) for the species we studied are shown in table 3. The conductance coefficients for Coturnix and pigeon eggs are close to the mean values reported by Ar and Rahn (1978), but those of the other three species are more than 1 SD from the mean; low in the Zebra Finch and Village Weaverbird and high in the goose.

Total water loss is influenced by the gradient in water-vapor pressure across the shell as well as egg size, incubation period, and G_{H_2O}. Therefore when mean water-vapor pressure in the nest of a given species varies from the typical value in most bird nests, the conductance coefficient can also be expected to vary from the mean conductance coefficient (5.13) in order to keep egg water loss nearly the same. Very little information is available concerning typical gradients in water-vapor pressure in nests of incubating birds. Values between 14.5 and 26.8 torr have been measured in nests of 22 species (Lomholt 1976*b*; Rahn et al. 1976; Rahn, Ackerman, and Paganelli 1977; Morgan, Paganelli, and Rahn 1978). Both the Australian Zebra Finch and African Village Weaverbird are native to dry savannas in parts of their range (Immelmann 1965; Collias and Collias 1969). The low conductance coefficients for eggs of these species may reflect adaptations to reduce excessive water loss because nest water-vapor pressures are low. The domestic goose is descended from a ground-nesting bird which nests near water. The high value for eggs of this species may be due to high G_{H_2O} to increase water loss in a humid environment.

Oxygen conductance.—Maximum flux of oxygen across the shell into the chorioallantoic blood vessels occurs at the pre-IP rate of oxygen consumption in the species studied here. Because oxygen follows the same diffusion pathways as water vapor, Rahn, Paganelli, and Ar (1974) have suggested that pre-IP rate of oxygen consumption should be directly related to G_{H_2O} and therefore also related to I (since G_{H_2O} and I are inversely related [eq. 3]) by the following equations:

$$\dot{V}_{O_2} = 51.3 G_{H_2O} \quad (4)$$

$$\dot{V}_{O_2} = 267 M \cdot I^{-1} \quad (5)$$

where $\dot{V}_{O_2}$ is in $cm^3 \cdot day^{-1}$ and M is initial egg mass in grams. Hoyt et al. (1978) have shown a close correlation exists between pre-IP $\dot{V}_{O_2}$ and initial egg mass for eggs ranging over three orders of magnitude in size. This relationship is

$$\dot{V}_{O_2} = 25.2 M^{0.73}. \quad (6)$$

It is instructive to compare the measured values for pre-IP $\dot{V}_{O_2}$ with the values predicted from equations (4)–(6) (table 2). Pre-IP rates of $\dot{V}_{O_2}$ of the weaverbird, pigeon, and goose eggs are best predicted by equation (6) which is based on mass alone, whereas equation (5) best predicts the actual $\dot{V}_{O_2}$ in the Zebra Finch and equation (4) best predicts the actual rate found in Coturnix. Pre-IP rates of oxygen consumption in the Ostrich, *Struthio camelus* (Hoyt et al. 1978) and Common Rhea, *Rhea americana* (Vleck et al., in press) are also best predicted by equation (6) based only on initial egg mass. In many species the rate of oxygen consumption just prior to pipping is not necessarily strongly tied to incubation period or shell conductance but is determined primarily by embryo mass, which is directly proportional to initial egg mass (Vleck et al., in press). The similarity of the exponent in equation (6) and that relating oxygen consumption to body mass of adult birds (Lasiewski and Dawson 1967) suggests that similar factors influence the scaling of metabolism in embryos just prior to pipping and in adults. Just before pipping embryonic growth is presumably complete. The lack of a growth component to metabolism at this time accounts for the difference between the exponents of 0.73 here and that of 0.92 (fig. 7) for growing embryos.

Air-cell oxygen tension.—It is possible to have high rates of embryonic oxygen consumption concomitant with low egg-

shell conductance if the gradient driving oxygen diffusion through the shell is also high. A high gradient necessitates a low oxygen tension in the air cell. We have calculated the air-cell oxygen tensions at the pre-IP rate of oxygen consumption (table 4) as follows: the conductance to water vapor (table 3) is used to calculate the conductance to oxygen (G_{O_2}) because the ratio G_{H_2O}/G_{O_2} is equal to the ratio of their diffusion coefficients (Paganelli et al. 1978). The oxygen-pressure gradient across the eggshell (ΔP_{O_2}) can then be calculated from a Fick diffusion equation

$$\Delta P_{O_2} = \frac{\dot{V}_{O_2}}{G_{O_2}}, \qquad (7)$$

where G_{O_2} is oxygen conductance of the eggshell in $cm^3(day \cdot torr)^{-1}$ at the incubation temperature. Air-cell oxygen tension (P_{AO_2}) is then equal to the difference between effective ambient oxygen tension (Wangensteen and Rahn 1970/71) and ΔP_{O_2}.

As $\dot{V}_{O_2}$ increases during incubation, P_{AO_2} declines; P_{AO_2} for the species we investigated here declined to values ranging from 72 torr to 114 torr just prior to pipping. Rahn et al. (1974) measured P_{AO_2} prior to pipping in 10 species and found a mean value of 104 torr (range, 98–114 torr). They suggested 104 torr may be typical P_{AO_2} for all bird eggs at this point in development. However, our calculated values, as well as those in large ratite eggs (112–126 torr [Hoyt et al. 1978; Vleck et al., in press]), indicate P_{AO_2} is more variable than previously thought. We suggest elsewhere that P_{AO_2} values may vary systematically with egg size (Vleck et al., in press).

TABLE 4

OXYGEN CONDUCTANCE (G_{O_2}), PARTIAL-PRESSURE GRADIENT OF O_2 ACROSS THE SHELL (ΔP_{O_2}), AND AIR-CELL OXYGEN TENSION (P_{AO_2}) AT THE PRE-IP RATE OF OXYGEN CONSUMPTION AND 37.5 C

Species	G_{O_2}[a] [$cm^3(Day \cdot Torr)^{-1}$]	ΔP_{O_2}[b] (Torr)	P_{AO_2}[c] (Torr)
Poephila guttata..	0.27	75	72
Ploceus cucullatus	0.91	62	85
Columba livia. . .	5.67	40	107
Coturnix coturnix.	3.36	55	92
Anser anser.	29.47	33	114

[a] $G_{O_2} = 1.081\ G_{H_2O}$ (Paganelli et al. 1978).
[b] $\Delta P_{O_2} = \dot{V}_{O_2}/G_{O_2}$ ($\dot{V}_{O_2}$ is from table 2).
[c] $P_{AO_2} = 147 - \Delta P_{O_2}$ (147 = mean effective ambient O_2 tension during $\dot{V}_{O_2}$ measurement; Wangensteen and Rahn 1970/71).

The Zebra Finch and Village Weaverbird eggs have low G_{O_2} values for their size, yet $\dot{V}_{O_2}$ is not proportionally reduced. As a result, P_{AO_2} values just before pipping are very low (72 and 85 torr, respectively). An additional decrease in oxygen tension must occur between the air cell and the blood. This gradient is about 50 torr in the domestic chicken (Freeman and Mission 1970; Tazawa, Mikami, and Yoshimoto 1971, Wangensteen 1972). The blood of the domestic chicken embryo shows an increasing oxygen affinity and oxygen-carrying capacity during incubation (Tazawa 1971; Tazawa, Ono, and Machizuki 1976). In the Zebra Finch and Village Weaverbird blood-oxygen tensions are probably very low and similar adaptions may be carried to an extreme, but this remains to be experimentally demonstrated.

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