

ONTOGENY OF OXYGEN CONSUMPTION BY EMBRYOS OF TWO SPECIES OF SWALLOWS (HIRUNDINIDAE)

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ABSTRACT.—Both Bank and Barn swallow embryos show an exponential increase in oxygen consumption (\dot{M}_{O_2}) during development with a substantial rise in \dot{M}_{O_2} occurring upon hatching. The pattern observed in these species is similar to that observed in other altricial birds. Measured pre-pipping \dot{M}_{O_2} values (1.45 and 1.75 $\text{cm}^3\text{O}_2 \cdot \text{h}^{-1}$, respectively) agree well with those predicted on the basis of egg weight, but diverge markedly from predictions based on incubation time and water vapor conductance. The findings here support the recent proposal of Hoyt et al. (1978b) that air cell oxygen tensions are positively related to initial egg weight and that the relationships predicting pre-pipping \dot{M}_{O_2} on the basis of incubation time and water vapor conductance need to be re-examined.

The developmental pattern of oxygen consumption (\dot{M}_{O_2}) and the magnitude of the pre-pipping \dot{M}_{O_2} has been of great interest to physiologists studying avian eggs (Romanoff 1967, Rahn et al. 1974, Hoyt et al. 1978a, b). It now appears that there are two basic patterns in the ontogeny of oxygen consumption, each associated with the type of young hatched: altricial or precocial. Altricial birds show an exponential increase in oxygen consumption throughout development with a substantial rise in \dot{M}_{O_2} upon hatching (Vleck et al. 1979). Precocial species also show an exponential increase in metabolism during development, but before hatching there is a "plateau" in \dot{M}_{O_2} (Romanoff 1967, Drent 1970, Rahn et al. 1974, Hoyt et al. 1978b). This stabilization of \dot{M}_{O_2} in precocial bird embryos results from a similar stabilization of growth rate during late incubation (Vleck et al. 1979). The pre-pipping \dot{M}_{O_2} is also of considerable importance in birds as it is the maximum rate attained while the chick remains within the shell and determines, at least in part, the air cell gas tensions which have been proposed as the stimuli for hatching (Vischedijk 1968, Rahn et al. 1974).

Air cell oxygen tension in avian eggs is a function of both \dot{M}_{O_2} of the embryo and egg O_2 conductance and is supposedly similar (about 104 torr) for all eggs at the time just prior to pipping (Rahn et al. 1974). Constancy of air cell oxygen tensions assumes that if embryonic \dot{M}_{O_2} changes then there will be compensatory changes in egg-shell conductance. This suggestion has recently been challenged by Hoyt et al. (1978b). They

have postulated that since embryonic metabolic rate is proportional to the 0.73 power and shell conductance to the 0.81 power of fresh egg mass (the gradient in partial pressure of oxygen is therefore proportional to the -0.08 power of fresh egg mass), air cell oxygen tensions should increase with increased egg mass. Eggs of large birds do have higher calculated air cell oxygen tensions (Hoyt et al. 1978b) so conversely we should expect eggs of small birds to have low air cell oxygen tensions.

Air cell oxygen tensions in the eggs of small birds can be estimated from measurements of shell conductance and "plateau" or pre-pipping \dot{M}_{O_2} . We report here on the ontogeny and pre-pipping values of \dot{M}_{O_2} in eggs of two species of altricial birds, Bank (*Riparia riparia*) and Barn (*Hirundo rustica*) swallows, which also lay small eggs (<2 g). Pre-pipping \dot{M}_{O_2} values are then compared with those predicted from the allometric relationships reported by Rahn et al. (1974), Hoyt et al. (1978a) and Ar and Rahn (1978). Also from these data and those reported on water conductance of eggs from these species (Birchard and Kilgore 1980) air cell oxygen tensions are estimated for a test of Hoyt's hypothesis.

MATERIALS AND METHODS

Eggs of Bank Swallows and Barn Swallows were collected in June 1978, in southwestern Montana and returned to the laboratory in Missoula. Eggs were then weighed, placed in a numbered cotton nest, and incubated at $37 \pm 1.5^\circ\text{C}$.

Oxygen consumption of each egg was measured daily at 37°C using closed-system microrespirometers constructed using the design of Davies (1966). Tem-

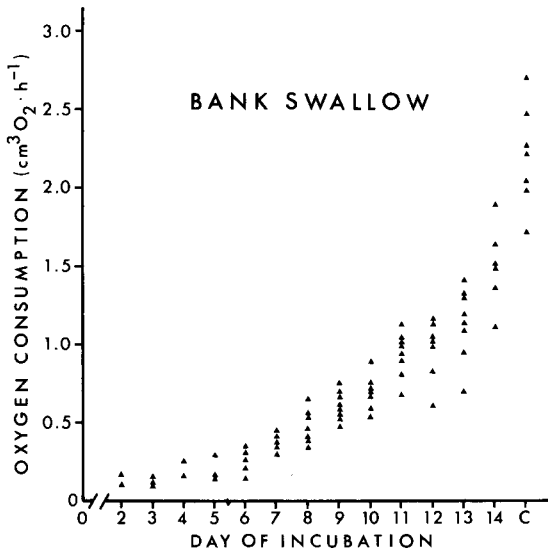


FIGURE 1. Relationship between oxygen consumption and developmental age in Bank Swallow embryos. C denotes the oxygen consumption of hatchlings.

perature was maintained by submerging the respirometer chambers in water baths. "Ascarite" was used as a CO_2 absorbent. After transfer of the egg to the respirometer, one hour was allowed for temperature equilibration before the vessel was sealed and readings recorded. Determinations of oxygen consumption lasted 40 to 120 min. Micrometer readings were manually recorded every 10 to 15 min depending on the magnitude of the \dot{M}_{O_2} . A least-squares linear regression analysis was performed on the micrometer readings over time to determine the rate of change in $\mu\text{m} \cdot \text{h}^{-1}$ which was then converted to $\text{cm}^3 \text{O}_2 \text{STP} \cdot \text{h}^{-1}$.

Embryonic age (D_{inc}) was determined in two ways: 1) if hatching occurred, previous data were traced back sequentially from that point and 2) if the embryo died after 12–13 days of incubation (stopped consuming O_2), time to hatching was estimated by autopsy and then traced back sequentially from that point. The reported incubation times of 15 days were used for each species (Petersen 1955, Samuel 1971).

RESULTS AND DISCUSSION

The relationships between \dot{M}_{O_2} and embryonic age are shown in Figures 1 and 2 for Bank and Barn swallows, respectively. Both species show an exponential increase in \dot{M}_{O_2} with development (D_{inc}). The regression equations and standard error of the estimate ($s_{y \cdot x}$) for the pooled data for each species are:

$$\text{Bank Swallow } \log \dot{M}_{\text{O}_2} = 0.0959 D_{\text{inc}} - 1.1441, s_{y \cdot x} = 0.001 \quad n = 79$$

$$\text{Barn Swallow } \log \dot{M}_{\text{O}_2} = 0.0962 D_{\text{inc}} - 1.1017, s_{y \cdot x} = 0.001 \quad n = 102.$$

Statistical analysis shows that embryonic age accounts for 90.4% and 88.3% of the variation (computed as a percent of the total sums of squares explained by regression; Steel and Torrie 1960) observed in \dot{M}_{O_2} in

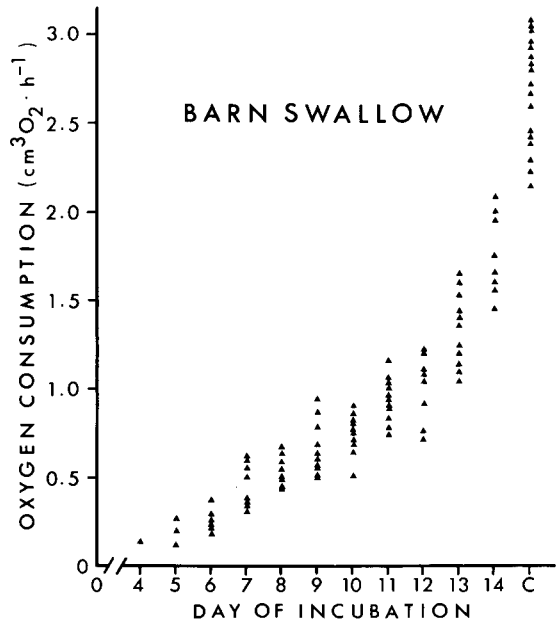


FIGURE 2. Relationship between oxygen consumption and developmental age in Barn Swallow embryos. C denotes the oxygen consumption of hatchlings.

Bank and Barn swallows, respectively. These ontogenetic patterns in \dot{M}_{O_2} are typical of other altricial birds (Vleck et al. 1979).

Pre-pipping (pre-internal pipping) \dot{M}_{O_2} was $1.49 \text{ cm}^3 \text{O}_2 \cdot \text{h}^{-1}$, in Bank Swallows and $1.75 \text{ cm}^3 \text{O}_2 \cdot \text{h}^{-1}$ in Barn Swallows. These values are mean metabolic rates of embryonic swallows on day 14, which is 93% of the incubation period of these altricial species (Vleck et al. 1979). They agree well with those values ($1.48 \text{ cm}^3 \text{O}_2 \cdot \text{h}^{-1}$ and $1.69 \text{ cm}^3 \text{O}_2 \cdot \text{h}^{-1}$, respectively) predicted from the allometric relationship proposed by Hoyt et al. (1978a) for 34 species of birds based on initial egg weight (W)

$$\dot{M}_{\text{O}_2} = 26.4W^{0.726} \quad (1).$$

For Bank and Barn swallows, W is 1.5 and 1.8 g, respectively.

Rahn et al. (1974) proposed that pre-pipping air cell gas tensions are very similar for all birds ($P_{\text{O}_2} \approx 104$ torr, $P_{\text{CO}_2} \approx 37$ torr) and that these tensions provide the stimulus for hatching. This supposition, combined with previous work by the same authors and others showing that fractional water loss over the incubation period is also similar (14–18% of W) (Rahn and Ar 1974, Rahn et al. 1976, Morgan et al. 1978), led them to suggest that \dot{M}_{O_2} is also adjusted to water vapor conductance ($G_{\text{H}_2\text{O}}$) and incubation time (I); pre-pipping \dot{M}_{O_2} being positively correlated

TABLE 1. Comparison of empirically determined and predicted pre-pipping oxygen consumption of Bank and Barn swallow embryos.

Determination	Oxygen consumption (cm ³ O ₂ · h ⁻¹)	
	Bank Swallow	Barn Swallow
Empirical results	1.49	1.75
Predictive equation (1) 26.4 W ^{0.726}	1.48	1.69
Predictive equation (3) 317.6 W/I	1.32	1.59
Predictive equation (5) 61.9 G _{H₂O}	1.32	1.13

with G_{H₂O} and negatively correlated with I. These relationships between \dot{M}_{O_2} and G_{H₂O} and \dot{M}_{O_2} and I are presented below.

If equation (1) is multiplied by the following allometric relationship predicting incubation time from W (Rahn et al. 1974):

$$I = 12.30W^{0.217} \quad (2)$$

and rearranged, pre-pipping \dot{M}_{O_2} of swallows can be predicted from equation (3) using the observed incubation times of 15 days for both swallow species (Petersen 1955, Samuel 1971).

$$\dot{M}_{O_2} = 317.6W/I \quad (3)$$

The predicted \dot{M}_{O_2} for Bank Swallow eggs is 1.32 cm³ O₂ · h⁻¹ and is 1.59 cm³ O₂ · h⁻¹ for Barn Swallows. When the predictions from this equation are compared with the experimentally obtained values it appears that \dot{M}_{O_2} has not undergone a reduction in proportion to the longer than predicted I (predicted incubation times from equation (2) for Bank and Barn swallows, respectively, are 13 and 14 days).

Ar and Rahn (1978) have recently proposed a constant relating W, I, and G_{H₂O} for all eggs:

$$G_{H_2O} \cdot I/W = 5.13 \pm 0.86 \quad (4)$$

If equation (4) is solved for I and substituted into equation (3), \dot{M}_{O_2} of swallows may be predicted from G_{H₂O} (equation 5), where G_{H₂O} is 0.509 mg · day⁻¹ · torr⁻¹ for Bank and 0.438 mg · day⁻¹ · torr⁻¹ for Barn swallows (G_{H₂O} values from Birchard and Kilgore 1980).

$$\dot{M}_{O_2} = 61.9G_{H_2O} \quad (5)$$

With equation (5) the predicted pre-pipping \dot{M}_{O_2} for Bank Swallow eggs is 1.32 cm³ O₂ · h⁻¹ and 1.13 cm³ O₂ · h⁻¹ for Barn Swallows. The results of the calculations show

that \dot{M}_{O_2} of smaller embryos is not adjusted to G_{H₂O} especially in Barn Swallows where the predicted \dot{M}_{O_2} value is 36% less than what has been measured.

Bank Swallows show better (although not good) agreement with the predicted values obtained using equation (5) but this agreement may be a spurious one. Bank Swallow eggs are laid in burrows and appear to have undergone an adaptive increase in conductance associated with a high microclimatic humidity (Birchard and Kilgore 1980). This increase in conductance would also aid in the exchange of O₂ and CO₂ within the burrow, which may be significantly different (O₂ lower and CO₂ higher) from normal atmospheric (Birchard 1979).

The oxygen consumption values determined experimentally and predicted from equations (1), (3), and (5) for Bank and Barn swallows have been summarized in Table 1. The implications of the predicted \dot{M}_{O_2} values obtained with equations (3) and (5) are that air cell P_{O₂} should be much lower and P_{CO₂} much higher in these species than the constant values proposed by Rahn et al. (1974). This confirms our (Birchard and Kilgore 1980) previous calculations of air cell gas tensions in these species (P_{O₂} = 81 and 56 and P_{CO₂} = 68 and 93, respectively, for Bank and Barn swallows). Our finding supports the recent suggestions by Hoyt et al. (1978b) that air cell P_{O₂} may not be constant in all species, but show a positive relationship with egg weight, and that the relationships between \dot{M}_{O_2} and I and \dot{M}_{O_2} and G_{H₂O} should be re-examined.

ACKNOWLEDGMENTS

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RECENT PUBLICATIONS

Migrant Birds in the Neotropics/Ecology, Behaviour, Distribution, and Conservation.—Edited by Allen Keast and Eugene S. Morton. 1980. Smithsonian Institution Press, Washington, DC. 576 p. \$15.00 paper; \$27.50 cloth. A symposium on the biology of migratory birds in the neotropics was sponsored in 1977 by the Smithsonian Institution's National Zoological Park and its papers are content of this large volume. Dealing with a wide range of species and places, the forty articles consider conservation, migration, distribution patterns, community structure, interactions between migrants and residents, foraging habits and competition, and the evolution of the nearctic-neotropical bird migration system. Some of the studies complement our knowledge of species whom North Americans see only during the breeding season. Others fill in our knowledge of neotropical ecology, long focussed solely on the resident species. Throughout, are ideas and data of value not only to ornithologists in various specialties but also to theoretical ecologists and those

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Biogéographie et Écologie/Synthèse sur la structure, la dynamique et l'évolution des peuplements de vertébrés terrestres.—Jacques Blondel. 1979. Masson, Paris. 173 p. Paper. Source: S. M. P. F. Corp., 14 East 60 Street, New York, NY 10022. This is a short, graduate-level French text on the ecological basis of animal distribution. It draws heavily on the work of MacArthur and others during the past fifteen years. The chapters cover patterns of distribution, community composition and structure, niche theory and the regulation of communities, ecological succession, and the dynamics of island populations. Diagrams, bibliography, index.