

University of Montana

ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, &
Professional Papers

Graduate School

1979

Eggshell conductance and respiration during development in a burrowing and non-burrowing bird

Geoffrey French Birchard
The University of Montana

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

Let us know how access to this document benefits you.

Recommended Citation

Birchard, Geoffrey French, "Eggshell conductance and respiration during development in a burrowing and non-burrowing bird" (1979). *Graduate Student Theses, Dissertations, & Professional Papers*. 6959.
<https://scholarworks.umt.edu/etd/6959>

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.

EGGSHELL CONDUCTANCE AND RESPIRATION
DURING DEVELOPMENT IN A
BURROWING AND NON-BURROWING BIRD

By

Geoffrey F. Birchard

B.A., The Colorado College, 1975

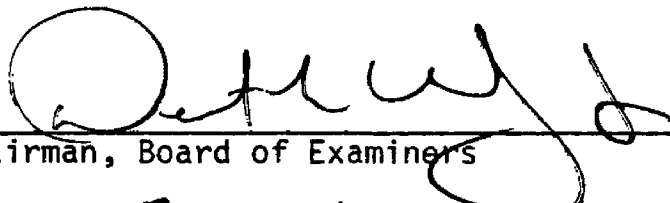
Presented in partial fulfillment of
the requirements for the degree of

Master of Arts

UNIVERSITY OF MONTANA

1979

Approved by:



Chairman, Board of Examiners



Dean, Graduate School

5/29/79

Date

UMI Number: EP37760

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI EP37760

Published by ProQuest LLC (2013). Copyright in the Dissertation held by the Author.

Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against unauthorized copying under Title 17, United States Code



ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

6-6-79

Birchard, Geoffrey, F., 1979 Zoology

Eggshell conductance and respiration during development in a burrowing and non-burrowing bird.

Director: Delbert L. Kilgore, Jr. *DLS*

Burrows provide protection for their occupants from predators and adverse weather. However, for avian embryos a fossorial existence may also present serious problems. Water vapor and carbon dioxide tensions may be higher and oxygen tensions lower than normal atmospheric levels interfering with normal diffusive exchange of these gases between the egg and atmosphere. Most importantly, the high humidity would prevent the water loss necessary for air cell formation and hatching.

Eggs were collected from the burrows (mean depth 0.56 m) of Bank Swallows (*Riparia riparia*) and the nests of Barn Swallows (*Hirundo rustica*). Physical dimensions, water vapor conductance ($G_{H_2O}, \mu l \cdot day^{-1} \cdot torr^{-1}$), and oxygen consumption during development were determined. From these data a steady-state model was developed to describe gas relations between the nest and the egg.

Development of a chorioallantois (CA) was found to increase the magnitude of G_{H_2O} in both species ($p < 0.01$). This increase is also associated with increases in P_m and A_p . Undeveloped Bank Swallow eggs have a higher G_{H_2O} (395 vs 378; $p < 0.02$) than Barn Swallows while with CA development there is only a trend toward a higher G_{H_2O} (633 vs 545; $p < 0.2$). This increase in G_{H_2O} is associated with a strong trend toward an increase in A_p ($p < 0.1$) and a significant increase in P_m ($p < 0.05$).

There was a logarithmic increase in oxygen consumption with development in both species. Mean pre-pipping oxygen consumptions were 1.49 and 1.75 $ml O_2 \cdot h^{-1}$ for Bank and Barn Swallows, respectively.

The greater G_{H_2O} of Bank Swallow eggs would facilitate water loss in humid burrows and therefore, proper air cell formation. With the increase in G_{H_2O} , O_2 and CO_2 conductance also increases, and the calculated air cell tensions of these gases in Bank Swallow eggs are higher and lower, respectively, than those in Barn Swallows. This greater ability to exchange oxygen and carbon dioxide gas would be advantageous for Bank Swallow eggs in light of burrow gas concentrations.

TABLE OF CONTENTS

	PAGE
ABSTRACT -----	ii
LIST OF ILLUSTRATIONS -----	v
LIST OF TABLES -----	vi
ACKNOWLEDGMENTS -----	vii
CHAPTER	
PART I	
THE EFFECT OF THE BURROW ENVIRONMENT ON EGG CONDUCTANCE	
I INTRODUCTION -----	1
II MATERIALS AND METHODS -----	5
Physical dimensions -----	6
Conductance, Permeability, and Effective	6
Pore Area -----	6
Statistical Analysis -----	7
III RESULTS -----	8
Physical dimensions -----	8
Conductance, Permeability, and Effective	
Pore Area -----	8
Model of Nest and Air Cell Gas Tensions -----	11
IV DISCUSSION -----	14
Effect of Chorioallantoic Development -----	14
Interspecific Comparison -----	16
Model of Nest and Air Cell Gas Tensions -----	16
Advantage of Increased Conductance for Egg O ₂	
and CO ₂ Exchange Within Burrows -----	19
V SUMMARY -----	20

PART II

EGG OXYGEN CONSUMPTION IN TWO SPECIES OF SWALLOWS:

ONTOGENY AND RELATION TO PREDICTIONS

I	INTRODUCTION -----	23
II	MATERIALS AND METHODS -----	25
III	RESULTS AND DISCUSSION -----	26
IV	SUMMARY -----	31
	LITERATURE CITED -----	32
	APPENDIX I -----	AI-I

LIST OF ILLUSTRATIONS

FIGURE	PAGE
1. Relationship between oxygen consumption and embryonic age in Bank Swallow eggs-----	26a
2. Relationship between oxygen consumption and embryonic age in Barn Swallow eggs-----	26b

LIST OF TABLES

TABLE	PAGE
1. Bird and mammal burrow gas concentrations-----	3
2. Physical dimensions of swallow eggs-----	9
3. Effect of chorioallantoic development on conductance permeability, and effective pore area of the eggshells of Bank and Barn Swallows-----	10
4. Model of nest and air cell gas tensions (torr)-----	17
5. Comparison of experimentally determined and predicted oxygen consumptions for Bank and Barn Swallows----	30

ACKNOWLEDGMENTS

I wish to thank James Gore and Craig Althen for their help in excavating and measuring Bank Swallow burrows during the early phases of this work. Dona Boggs, Dr. G. Patent and Dr. D. Bilderback supplied helpful criticism of various drafts of the manuscript for which I am most appreciative. Special thanks is given to Dr. Delbert Kilgore who not only assisted with various parts of this project but whose help and encouragement as a major professor during my 2½ years at Montana made the time spent productive, meaningful professionally and enjoyable.

PART I
THE EFFECT OF THE BURROW ENVIRONMENT
ON EGG CONDUCTANCE

CHAPTER I

INTRODUCTION

The calcareous shell of bird eggs is not a solid structure but is breached by numerous microscopic pores (Tyler, 1969; Tullet, 1975). The diffusive exchange of oxygen necessary for metabolism and the elimination of carbon dioxide occurs through these pores (Bartels, 1972; Paganelli et al., 1975; Erasmus and Rahn, 1976). Water vapor is also lost from the egg through these pores (Kendeigh, 1940; Romanoff and Romanoff, 1943; Tyler, 1969; Drent, 1970, Rahn and Ar, 1974). However, the total loss of water has been found to be well regulated in all species studied, amounting to 14-18 percent of the initial weight of the egg and is independent of incubation time (Drent, 1970; Rahn and Ar, 1974, Rahn et al., 1975; Ar and Rahn, 1979). This water loss forms the air cell in avian eggs which is necessary for hatching as it is this structure which provides the room for the embryo to take its first breath and fill its lung-air-sac system (Romanoff, 1968; Rahn et al., 1976) before pipping the shell.

Because of the important interrelationship between shell structure and water loss from the egg, it would be reasonable to assume that as incubation time and/or nest conditions vary, an adjustment would be made in the rate of water loss from the egg, that is the egg's conductance, to maintain the same total fractional weight loss. Coles (1936)

first proposed this thesis in order to explain differences in porosity of chicken eggs from geographic districts with different humidities. More recently other examples of adaptive decreases and increases in water vapor conductance have been reported. A decreased egg conductance is associated with the increased diffusivity of gases at high altitude (Wangensteen et al., 1974; Rahn et al., 1977; Packard, Sotherland, and Packard, 1977) and to increased incubation times (Ar et al., 1974). In wet nesting birds (Lomholt, 1976a) and in birds whose eggs are exposed to abnormal nest O_2 and CO_2 concentrations (Seymour and Rahn, 1978), an increased egg conductance is found. It is likely that egg conductance will also be adjusted to other microenvironments of high humidity and lower O_2 and higher CO_2 concentrations than normal atmospheric levels, for example those within subterranean burrows.

Birds which carry out their nesting activities in burrows are inaccessible to predators and insulated from adverse weather changes, particularly temperature (Hoogland and Sherman, 1976; White, Bartholomew, and Kinney, 1978). However, burrow microenvironments are disadvantageous for the avian egg as they are microclimates of high humidity. Also oxygen and carbon dioxide concentrations in bird burrows may be considerably lower and higher, respectively, than in the normal atmosphere. In the air within bird and mammal burrows (Table 1), the relative humidity is at or near 100 percent in almost all cases, and levels of oxygen as low as 15 percent and carbon dioxide as high as 6.5 percent have been recorded.

High humidity low oxygen and high carbon dioxide concentrations have been found to significantly decrease hatchability in the eggs of chickens (for review see Lundy, 1969), pigeons and ring doves (Riddle,

Table I: Bird and mammal burrow gas concentrations

Species	Relative Humidity	Oxygen		Carbon Dioxide		Reference
	%	Volume %		Volume %		
	Average	Average	Minimum	Average	Maximum	
<u>Birds</u>						
<i>Merops apiaster</i>	100	18.3	15	3.3	6.5	White <i>et al.</i> , 1978
<i>Riparia riparia</i>		18.1	15.1	2.6	5.3	Appendix I
<u>Mammals</u>						
<i>Geomys bursarius</i>	88	16.8	6	0.8	2.3	Kennerly, 1964
<i>Geomys pinetis</i>	99.4	19.5	16.7	1.4	2.6	McNab, 1966
<i>Thomomys bottae</i>		15.5 - 20.5		0.6 - 3.8		Darden, 1970
<i>Spermophilus tridecemlineatus</i>		18.9	13.7	1.8	6.2	Studier and Procter, 1971
<i>Spermophilus beecheyi</i>		17.6	15.4	2.9	4.0	Baudinette, 1974
<i>Citellus parryi albusus</i>			20	0.3	1.0	Williams and Rausch, 1973
<i>Dipodomys spectabilis</i>	100			0.5 - 1.3		Kay, 1974
<i>Dipodomys merriami</i>			19.7		1.3	Soholt, 1974
<i>Spalax ehrenbergi</i>		16.5	14.0	3.0	4.8	Arieli <i>et al.</i> , 1977
<i>Marmota broweri</i>			4.0	1.7	9.5	Williams and Rausch, 1973
<i>Oryctolagus cuniculus</i>		13 - 14		7 - 8		Hayward, 1966
<i>Tachyglossus aculeatus</i>			13.9		6.9	Bentley <i>et al.</i> , 1967

1924). These decreases in hatchability are probably due to the following: 1) a high humidity would expectably decrease water loss from the egg, thereby hindering proper air cell formation; 2) lower oxygen concentrations would decrease the partial pressure of oxygen in the blood going to the developing tissues and result in reduced tissue oxygenation; and 3) high carbon dioxide concentrations would hinder the diffusion of CO_2 out of the egg, probably disrupting the blood and tissue acid-base balance, and lead to a respiratory acidosis.

It is my hypothesis that the eggs of burrowing birds have undergone selection for an increased conductance in order to compensate for a high microclimatic humidity. This increase would allow adequate water loss for proper air cell formation and secondarily might also aid the exchange of oxygen and carbon dioxide. To test this hypothesis, the water vapor conductance of eggs of a burrowing species and an open-nesting species were compared and a simple steady-state model of nest and pre-pipping air cell gas tensions was developed from these data to demonstrate the advantages of such an adaptive increase.

CHAPTER II

MATERIALS AND METHODS

Eggs were collected from a number of burrows of Bank Swallows (Riparia riparia) and the nests of Barn Swallows (Hirundo rustica). These two species were chosen because of their taxonomic and ecological similarities (Bent, 1963; Mayr and Bond, 1943). Collections were made in June, 1978, in southwestern Montana at an average elevation of 970 m.

The Barn Swallow occupies an open mud nest which is usually adhered to cliffs or man-made structures such as bridges (Bent, 1963). Bank Swallows construct and occupy burrows in sandy banks set well above ground level (Petersen, 1955; Bent, 1963). The burrows at the Bank Swallow colony where collections were made consisted of oval tunnels with dimensions of about 4 x 7.5 cm and had a mean depth of 56 cm (range 33-82 cm). The nest chamber is located at the back of the tunnel and is a moderate enlargement of the tunnel with a very simple nest of straw lining its floor.

The average clutch size was 5 eggs for both species. A single egg from each clutch was used for the measurements described below, as eggs from the same clutch are likely to have similar porosities (Dunn, 1923; Tullet, 1975).

A. Physical Dimensions

Egg volume was obtained by water displacement using a device similar to that of Hanson (1954). The imprecision of measurements using this device was less than 0.005 ml. Imprecision is used here as defined by Eisienhart (1968).

Initial egg weights were determined by multiplying measured egg volumes by 1.038, the predicted density of a one gram egg (Paganelli, Olzawaka, and Ar, 1974).

Egg length and breadth were determined using a vernier caliper readable to 0.001 cm and rounded to the nearest 0.01 cm. These values were used to calculate the elongation index (length/breadth) as an indicator of egg shape (Hoyt, 1976).

Surface area of the shell was calculated for each egg using the equation of Hoyt (1976). The accuracy of this equation varies with egg shape. At the elongation indices observed in Bank and Barn Swallow eggs this equation has a predicted error of less than one percent.

Shell thickness was measured using a caliper readable to 0.0001 inches. A ball attachment was used to compensate for shell curvature. Three measurements were taken on a shell fragment which included the egg equator, averaged, and converted to microns.

B. Conductance, Permeability, and Effective Pore Area

The weight loss method described by Ar et al., (1974) was used to determine egg conductance. Weight loss was assumed to be entirely due to loss of water vapor (Drent, 1970; Rahn and Ar, 1974; Rahn et al., 1976). Eggs were checked for the presence of chorioallantoic development by candling, placed in desiccators maintained at 25 C, and weighed for 5 days at approximately 24 hour intervals or until a steady weight

loss was achieved. Weights were recorded to the nearest 0.1 mg. The rate of water loss ($\text{mg}\cdot\text{day}^{-1}$) was then determined using a least squares linear regression procedure. The rate of water loss was converted to $\dot{V}_{\text{H}_2\text{O}}$, divided by 23.7 torr, the water vapor pressure difference across the eggshell (assuming the air within the egg is saturated with water vapor at 25 C and the water vapor tension within the desiccator is essentially 0) to get water vapor conductance ($G_{\text{H}_2\text{O}}$) in units of $\mu\text{l STP}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$. These values were then corrected to sea level (Ar et al., 1974). Permeability (P_m) in turn was calculated for each egg by dividing its $G_{\text{H}_2\text{O}}$ by its calculated surface area.

Effective pore area (A_p) in mm^2 was calculated as described by Ar et al. (1974). A revised constant as given by Rahn et al. (1976) was used in this calculation. Because of the inverse relationship between the diffusion coefficients for gases and barometric pressure (Paganelli et al., 1975), this constant was multiplied by 760/676 to correct for the average barometric pressure in our laboratory at the time egg conductances were determined.

C. Statistical Analysis

The Student's t-test was used to determine the statistical significance of differences between means. A critical t value with a $p < 0.05$ was used to determine significance.

CHAPTER III

RESULTS

A. Physical Dimensions

A comparison of the physical dimensions of Bank and Barn Swallow eggs is shown in Table 2. Bank Swallows have a smaller egg than Barn Swallows as indicated by their volumes and weights. This size difference is reflected in a proportionate reduction of length and breadth in Bank Swallow eggs when compared to Barn. Egg shape, as indicated by the elongation index, is not statistically different, but shell thickness of the Bank Swallow eggs is significantly less than that of Barn ($p < 0.001$).

B. Conductance, Permeability and Effective Pore Area

Development of the chorioallantois (CA) was found to have a statistically significant effect on G_{H_2O} in both species (Table 3), the conductance without development of a CA being about 2/3 to 1/2 of that with CA development in Bank and Barn Swallows, respectively. This difference in conductance accounts for the observed differences in P_m and A_p between the groups with and without a CA present.

Because of the effect of CA development on G_{H_2O} , the comparison of Bank and Barn Swallow G_{H_2O} was made using similar developmental stages (Table 3). In the comparison of conductance in the absence of a CA,

Table 2: Physical Dimensions of Swallow Eggs

	N	Wt. g	Volume cm ³	Surface Area cm ²	Length cm	Breadth cm	<u>Length</u> <u>Breadth</u>	Shell Thickness μ
Bank Swallow	29	1.5	1.43 (0.10)	6.3	1.77 (0.06)	1.26 (0.04)	1.41 (0.06)	52.8 (3.6)
Barn Swallow	38	1.8	1.73 (0.18)	7.1	1.89 (0.10)	1.33 (0.04)	1.42 (0.07)	58.0 (5.0)
			p<0.001		p<0.001	p<0.001	N.S.	p<0.001

Note S.D. in parentheses.

Table 3: Effect of Chorioallantoic Development on Conductance, Permeability, and Effective Pore Area of the Eggshells of Bank and Barn Swallows.

	N	Conductance $\mu\text{l}\cdot\text{d}^{-1}\cdot\text{torr}^{-1}$	N	Permeability $\mu\text{l}\cdot\text{d}^{-1}\cdot\text{torr}^{-1}\cdot\text{cm}^{-2}$	Functional Pore Area mm^2
BANK SWALLOW					
Without	11	395 (133)	11	62 (21)	0.0065 (0.002)
With	16	633 (250)	15	107 (44)	0.011 (0.005)
		$p < 0.01$		$p < 0.01$	$p < 0.01$
BARN SWALLOW					
Without	15	278 (74)	15	40 (10)	0.005 (0.001)
With	24	545 (99)	24	75 (15)	0.010 (0.002)
		$p < 0.001$		$p < 0.001$	$p < 0.001$

there is a significant difference between species with Bank Swallows having a higher conductance (Bank = 395, Barn = 278; $p < 0.02$). With development of the CA, there is also a trend towards higher conductance in Bank Swallows (Bank = 633, Barn = 545; $p < 0.2$).

Permeability is also significantly higher in Bank Swallow eggs when compared to Barn both without (Bank = 62, Barn = 40; $p < 0.01$) and with (Bank = 107, Barn = 75; $p < 0.05$) the CA present. Effective pore area shows a very strong trend towards an increased value in the comparison without a CA (Bank = 0.0065, Barn = 0.005; $p < 0.1$), but when the comparison is made with a CA present, the difference is not statistically significant.

C. Model of Nest and Air Cell Gas Tensions

The rate of diffusive transport of any gas across the eggshell (\dot{V}_X) can be calculated using the following generalized equation (Metcalfe, 1967; Wangenstein and Rahn, 1970-1971):

$$\dot{V}_X = G_X \cdot \Delta P_X \quad (1)$$

Where G_X is the eggshell conductance to the gas and ΔP_X is the effective partial pressure difference of the gas across the eggshell. This equation can be rearranged to calculate ΔP_X .

$$\Delta P_X = \frac{\dot{V}_X}{G_X} \quad (2)$$

Values obtained with equation (2) can be used to estimate average tensions of water vapor in the air surrounding the egg and the oxygen tensions in the air cell.

The P_{H_2O} between the egg and nest necessary to achieve a normal water loss was calculated using equation (2) and measured values of G_{H_2O} . Assuming that the eggs of both species lose 14 percent of their initial weight during incubation and that this total water loss occurs at a constant rate during incubation, \dot{V}_{H_2O} was calculated using the equation of Rahn and Ar (1974):

$$\dot{V}_{H_2O} = (F \cdot \frac{W}{I}) \cdot 1.24 \quad (3)$$

Where F is the fractional weight loss during incubation (%), W is the initial egg weight (μg), I is the incubation time (days), and 1.24 is a conversion factor ($\mu\text{l}/\mu\text{g}$). Observed incubation times of 15 days were used for both Bank and Barn Swallows (Petersen, 1955; Samuel, 1971). The ΔP_{H_2O} for Bank Swallow eggs is 27 torr and that for those of Barn Swallows 38 torr.

The average nest water vapor tension was obtained by substrating the ΔP_{H_2O} from 47 torr, the P_{H_2O} within the air cell at 37 C. For Bank Swallows the average nest P_{H_2O} is 20 torr while in Barn Swallow nests it is 9 torr. Assuming an air temperature of 37 C around the egg, these values would correspond to relative humidities of 43 percent for Bank and 19 percent for Barn Swallows.

The ΔP_{O_2} across the eggshell was also calculated using equation (2). Water vapor conductance was converted to G_{O_2} by multiplying it by 0.85 (Paganelli *et al.*, 1978). Oxygen consumption during the course of incubation was determined for both species (Part II). The mean pre-pipping oxygen consumption of Bank and Barn Swallow embryos was 1.49 and 1.75 $\text{ml O}_2 \text{ STP} \cdot \text{h}^{-1}$, respectively. These \dot{V}_{O_2} values were used in equation (2) since they represent the metabolic maximum for the developing embryo within the shell. The ΔP_{O_2} for Bank Swallow eggs is 66

torr and that for Barn Swallow eggs, 91 torr. If these values are subtracted from the "effective" oxygen tension of 149 torr (air saturated with water vapor at 37 C), air cell oxygen tensions can be estimated (Wangensteen and Rahn, 1970-1971). For Bank and Barn Swallows the values obtained are 83 and 58 torr, respectively. That is, the air cell oxygen tension in Bank Swallow eggs just prior to pipping of the shell is considerably higher than that in Barn Swallow eggs.

Air cell P_{CO_2} was assumed to be inversely related to P_{O_2} . This assumption is reasonable given that the respiratory exchange ratio for bird eggs near hatching is about 0.71 (Romanoff, 1968; Visschedijk, 1968a) and that the ratio of the diffusion coefficients and egg shell conductances of these gases also approximates this value (Paganelli et al., 1978). This inverse relationship also fits well with the observed gaseous concentrations within egg air cells where they have been directly determined (Wangensteen and Rahn, 1970-1971; Wangenstein et al., 1974).

CHAPTER IV

DISCUSSION

Bank Swallows and Barn Swallows are very similar morphologically and ecologically with the exception of their nesting habits (Mayr and Bond, 1943; Bent, 1963). This difference in nesting, burrowing vs an open nest, creates a different nest microenvironment which is reflected in a comparison of egg water vapor conductance.

Effect of Chorioallantoic Development

The developmentally related increase in water vapor conductance observed in Barn and Bank Swallow eggs (Table 3) has also been found in the eggs of House Wrens (Kendeigh, 1940) and more recently in Cliff Swallows (Packard, pers. comm.). However, in the Herring Gull (Drent, 1970), in chickens (Wangensteen et al., 1970-1971), and in two species of gulls (Morgan, Paganelli, and Rahn, 1978), there is a constant rate of egg water loss during incubation. The differences in egg weight of the birds where this developmentally related increase in conductance has been seen and species where it has not, suggests that this phenomenon may be size related and, perhaps, is somehow interrelated with the recent suggestion of Snyder (1978) that the allometric relationship between egg conductance and initial egg weight is different for eggs smaller than 4.5 g. Increases have also been found in the oxygen

filtration coefficient (Romanoff, 1943; Romijn, 1950), oxygen flux across the shell (Kutchai and Steen, 1971; Lomholt, 1976b; Tullet and Board, 1976), and carbon monoxide diffusing capacity of eggs with development (Temple and Metcalfe, 1970). Whether the increase in water vapor conductance during development is related to changes in the shell membranes or to some other alteration is unknown at this time. Because of the increase in G_{H_2O} with the onset of development, interspecific comparisons of the type being made here should be made with either fertile undeveloped or accurately aged eggs.

In both Bank and Barn Swallows the increased conductance to water vapor in eggs in which the chorioallantois has developed is associated with significant increases in both the permeability and effective pore area (Table 3). These increases in P_m and A_p are due solely to an increased conductance and are not due to any changes in physical parameters of the eggs such as surface area or shell thickness.

There is little data on water vapor conductance with which to compare the present results; none exists for Bank Swallow eggs and there has been only one study of Barn Swallow eggs (Packard *et al.*, 1977). It is difficult to compare the Barn Swallow G_{H_2O} and P_m values obtained here with those reported in the earlier study as the developmental state of the eggs was not considered. However, the means of all the conductance and permeability values from developed and undeveloped Barn Swallow eggs ($G_{H_2O} = 446 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$, $P_m = 62 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}\cdot\text{cm}^{-2}$) agree reasonably well with values obtained from the regression equations of Packard *et al.* (1977) extrapolated to an elevation of 970 m ($G_{H_2O} = 531 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$, $P_m = 72 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}\cdot\text{cm}^{-2}$).

Interspecific Comparison

Bank Swallows have an increased G_{H_2O} relative to Barn Swallows. This increase in G_{H_2O} appears to be due to an increase in the effective pore area. Whether this increase in A_p is due to an increase in pore number or pore size is not known. Pore distribution was found to be non-random in both species, preventing quantification of pore number. Permeability is also greater in Bank Swallow eggs, the result of the higher G_{H_2O} and smaller egg size of this species. The smaller size of Bank Swallow eggs is to be expected on the basis of different adult female weights (Rahn, Paganelli, and Ar, 1975). Adult female Barn Swallows weigh 22% more than adult female Bank Swallows. From the allometric relationships between G_{H_2O} and initial egg weight (Ar and Rahn, 1978), one would expect Barn Swallow eggs to have a higher conductance than Bank Swallows (i.e., $768 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$ vs $662 \mu\text{l}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$), just the reverse of what was actually observed in this study.

Model of Nest and Air Cell Gas Tensions

In Table 4, the difference in partial pressures of water vapor and oxygen and the nest and air cell tensions of these and other gases have been summarized. The average ΔP_{H_2O} values calculated for both Bank Swallows (27 torr) and Barn Swallows (38 torr) are in good agreement with previously published values on other species (Rahn and Ar, 1974; Rahn *et al.*, 1976; Rahn, Ackerman, and Paganelli, 1977; Yom-Tov, Ar, and Mendelsohn, 1978), and the nest water vapor tensions calculated from these ΔP_{H_2O} values are in line with what would be expected given the two different nest environments: burrow vs open nest. A P_{H_2O} of 20 torr in the air surrounding an egg in a Bank Swallow nest (Table 4) would be at or near the saturation vapor pressure at normal burrow temperatures

Table 4: Model of Nest and Air Cell
Gas Tensions (torr)

	Air Cell		Effective		Nest
BANK SWALLOW (I = 15)					
H ₂ O	47		47	$\Delta P_{H_2O} = 27$	20
O ₂	83	$\Delta P_{O_2} = 66$	149		155
CO ₂	66		0		0
N ₂	564		564		585
Total	760		760		760

BARN SWALLOW (I = 15)					
H ₂ O	47		47	$\Delta P_{H_2O} = 38$	9
O ₂	58	$\Delta P_{O_2} = 91$	149		157
CO ₂	91		0		0
N ₂	564		564		594
Total	760		760		760

(20-25 C). This prediction fits well with field observations over the two month period encompassing egg laying and fledging which suggests that burrow air is saturated with water vapor. The soil surrounding the burrow was always quite damp except very near the entrance. The calculated ΔP_{H_2O} values and field observations indicate that the Bank Swallow egg when compared to the Barn has undergone selection for an increased conductance in response to a higher average nest microclimate humidity to allow for adequate water loss for proper air cell formation.

The pre-pipping air cell oxygen tensions calculated for Bank and Barn Swallow eggs (Table 4) are significantly lower than the constant value of 104 torr suggested by Rahn *et al.* (1974). This difference may be due to the fact that pre-pipping \dot{V}_{O_2} in swallow embryos does not appear to be adjusted to the longer incubation times and lower G_{H_2O} than expected (Rahn and Ar, 1974; Ar and Rahn, 1978) and that swallow eggs are rather small. Hoyt, Vleck, and Vleck (1978b) have recently suggested that pre-pipping air cell O_2 tensions like conductance (Ar and Rahn, 1978) and \dot{V}_{O_2} (Hoyt, Vleck, and Vleck, 1978a) show an inverse relationship to initial egg weight. If the allometric relationships for \dot{V}_{O_2} and G_{H_2O} cited above are combined, G_{H_2O} converted to G_{O_2} , and substituted into equation (2) then ΔP_{O_2} should increase with decreasing egg weight as follows:

$$\Delta P_{O_2} = \frac{\dot{V}_{O_2}}{G_{O_2}} = \frac{26.4 \cdot W^{.726}}{1.08 \cdot (0.384 \cdot W^{.814})} = 63.7 \cdot W^{-.088} \quad (4)$$

Using this equation a one gram egg would have ΔP_{O_2} across the shell of 63.7 torr and an air cell P_{O_2} of 85 torr. The air cell P_{O_2} in small eggs, those less than 4.6 g, may be even more severe if as Snyder (1978) has suggested, they have a lower conductance than predicted by the

Ar and Rahn (1978) equation.

Advantage of Increased Conductance for
Egg O_2 and CO_2 Exchange Within Burrows

If one assumes that Bank Swallows can tolerate the same air cell oxygen tensions as Barn Swallows, it is possible to estimate the advantage an increased egg conductance in relation to burrow gas concentrations. The difference between the air cell P_{O_2} values of Bank and Barn Swallows (25 torr) can be subtracted from the effective P_{O_2} to obtain the effective O_2 tension (124 torr), where the air cell P_{O_2} will equal that in a Barn Swallow egg. Assuming burrow P_{CO_2} shows an inverse relationship to P_{O_2} (White et al., 1978; Appendix I), this 25 torr drop in effective P_{O_2} would be equivalent in partial pressures to a gaseous environment composed of 17.4% O_2 and 3.14% CO_2 . Based on personal observations and those in the literature, these values are well in line with what may be seen by the eggs of Bank Swallows. Thus, an increased egg conductance is not only advantageous for water vapor loss but also for the diffusive exchange of O_2 and CO_2 , where the concentrations of these gases may be significantly altered from normal atmospheric concentrations such as within a subterranean burrow.

CHAPTER V

SUMMARY

The eggs of a burrowing bird, the Bank Swallow, and an open-nesting bird, the Barn Swallow, were compared in an attempt to elucidate possible adaptations to a fossorial nesting habit. Egg physical dimensions, water vapor conductance, permeability, and effective pore area were determined for a single egg from each clutch. From these data a steady-state model was developed to describe the gas relations between the egg and nest of both species.

A comparison of the physical dimensions showed that Barn Swallow eggs were larger but of the same shape as Bank Swallow eggs. This size difference is mostly the result of differences in adult female weights. The smaller egg of Bank Swallows also has a significantly thinner shell than that of Barn Swallow eggs.

A significant increase in water vapor conductance (G_{H_2O}), permeability (P_m), and effective pore area (A_p) were found to be associated with the development of the chorioallantois (CA) in both species. Because of the effect of CA development on G_{H_2O} , the comparison between the Bank and Barn Swallow eggs was made with similar developmental stages. Without CA development, Bank Swallow eggs have a higher G_{H_2O} than Barn Swallow eggs, while with CA development, there is only a trend toward a higher G_{H_2O} . This increase in G_{H_2O} in undeveloped Bank

Swallow eggs appears to be due to an increase in A_p . Permeability is also greater in Bank Swallow eggs with and without a CA relative to Barn Swallows. The increases in G_{H_2O} in Bank Swallow eggs relative to Barn Swallows was just the reverse of what would be expected from the developed allometric relationship between G_{H_2O} and egg weight.

When the water vapor conductance data determined here were used in developed steady-state models describing the relationship between egg gas tensions and those in the nest, it appeared that the increase in G_{H_2O} of Bank Swallow eggs was advantageous in two ways: 1) it would allow the necessary water loss for proper air cell formation in the more humid environment within a burrow and 2) it would facilitate diffusive O_2 and CO_2 exchange under abnormal microclimatic gas concentrations. Bank Swallow eggs seemingly have undergone selection for an increase in G_{H_2O} to compensate for the higher P_{H_2O} and P_{CO_2} values and lower P_{O_2} values encountered within burrows.

PART II
EGG OXYGEN CONSUMPTION IN TWO SPECIES OF SWALLOWS:
ONTOGENY AND RELATION TO PREDICTIONS

CHAPTER I

INTRODUCTION

The developmental pattern of oxygen consumption (\dot{V}_{O_2}) and the magnitude of its pre-pipping value has been of great interest to physiologists studying avian eggs (Romanoff, 1968; Rahn, Paganelli, and Ar, 1974; Hoyt et al., 1978a, 1978b).

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{V}_{O_2} upon hatching (Hoyt et al., 1978a). While precocial species show a similar exponential increase, but for a prolonged period before hatching there is a "plateau" period followed by a rise in \dot{V}_{O_2} just before and after hatching (Romanoff, 1968; Drent, 1970; Rahn et al., 1974; Hoyt et al., 1978b). Pre-pipping \dot{V}_{O_2} is of considerable importance as it is the maximum attained while the chick remains within the shell and is intimately related to the air cell gas tensions which have been proposed as the stimuli for hatching (Vissidiijk, 1968b; Rahn et al., 1974).

Air cell gas tensions are a function of both \dot{V}_{O_2} and egg O_2 conductance and are also supposedly constant for all eggs at the time just prior to pipping (Rahn et al., 1974). Several relations based on these

assumptions have been proposed to predict \dot{V}_{O_2} from initial egg weight, water vapor conductance, and incubation time. In this study the ontogeny of \dot{V}_{O_2} in two species of swallows was considered and the experimentally determined pre-pipping \dot{V}_{O_2} values compared with those obtained from the predictive equations.

CHAPTER II
MATERIALS AND METHODS

Bank Swallow (Riparia riparia) and Barn Swallow (Hirundo rustica) eggs 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 ± 1.5 C.

Oxygen consumption of each egg was measured daily at 37 C using microrespirometers constructed using the design of Davis (1966). Temperature was maintained by submerging the respirometer chambers in water baths. "Ascarite" was used as a CO₂ absorbant. After transfer of the egg to the respirometer, 1 h was allowed for temperature re-equilibration before the vessel was sealed and readings recorded. Oxygen consumption determinations lasted 40-120 min, and micrometer readings were recorded every 10-15 min depending on the magnitude of the \dot{V}_{O_2} . A least squares linear regression analysis was performed of the micrometer readings over time to determine the rate of change in $\mu\text{m}\cdot\text{h}^{-1}$ which was then converted to $\text{ml O}_2 \text{ STP}\cdot\text{h}^{-1}$.

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

CHAPTER III
RESULTS AND DISCUSSION

The relationships between \dot{V}_{O_2} and D_{inc} are shown in Figures 1 and 2 for Bank and Barn Swallows, respectively. Both species show an exponential increase in \dot{V}_{O_2} with the greatest increase occurring upon hatching (C). The regression equations and standard error of the estimate for the pooled data for each species are:

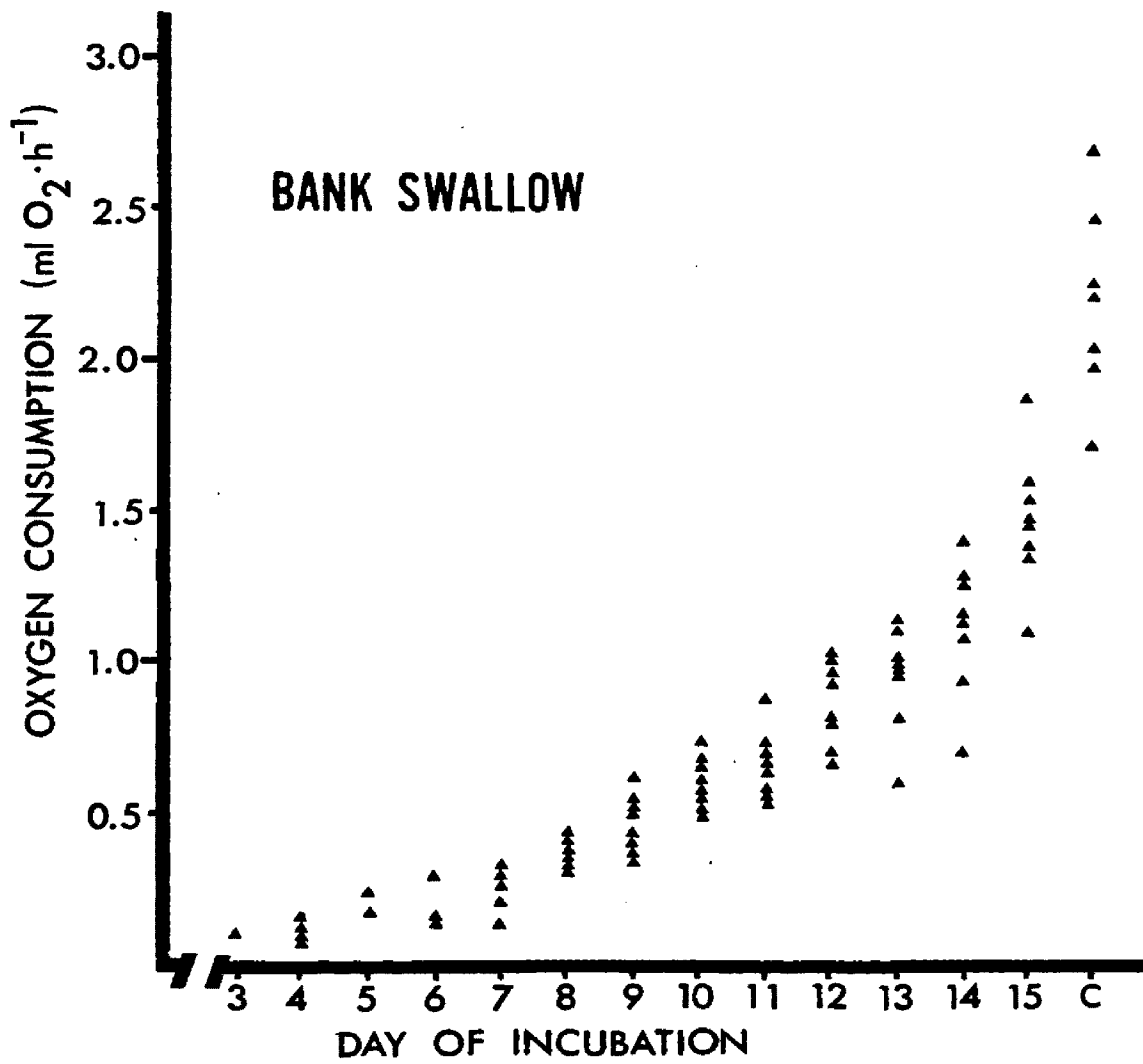
$$\text{Bank} \quad \log \dot{V}_{O_2} = 0.09585 D_{inc} - 1.2405 \quad s_{y \cdot x} = 0.001$$

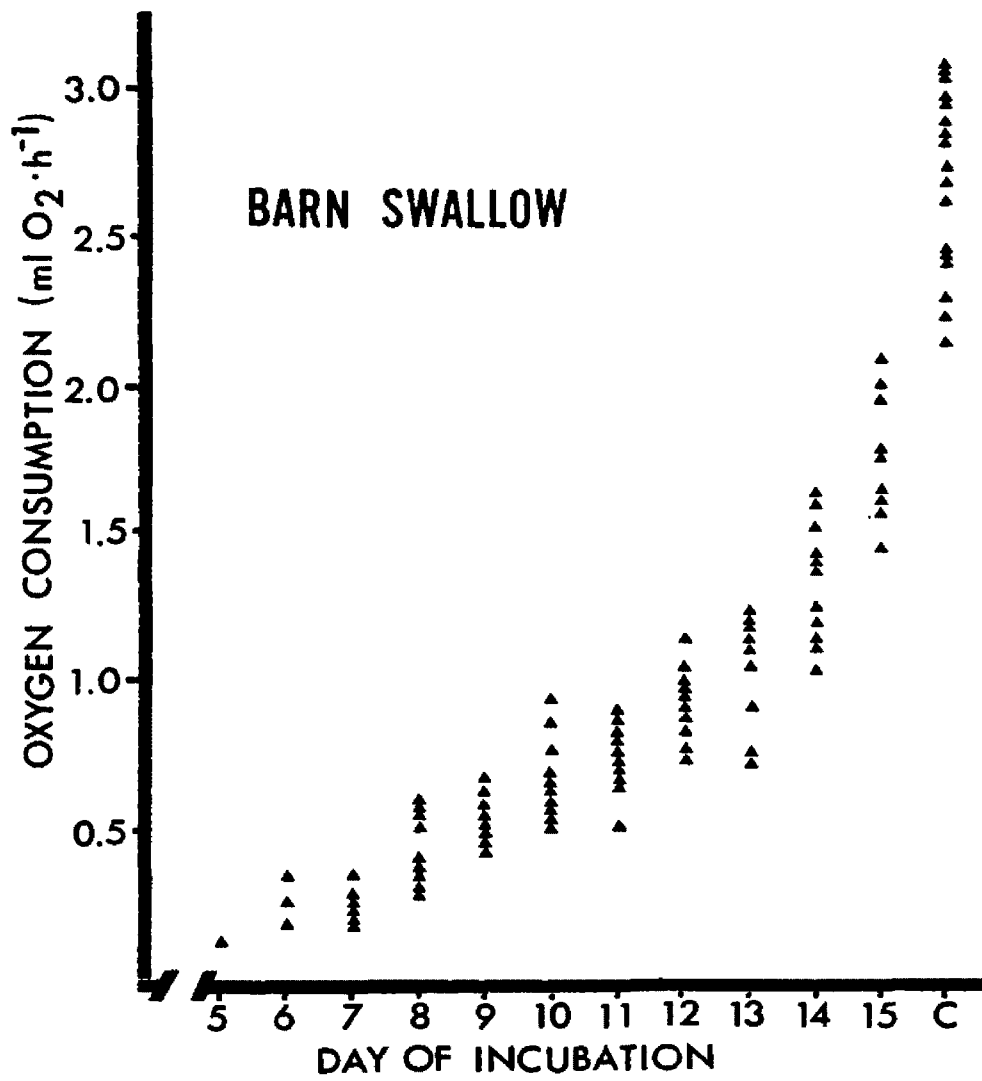
$$\text{Barn} \quad \log \dot{V}_{O_2} = 0.09635 D_{inc} - 1.198 \quad s_{y \cdot x} = 0.001$$

Statistical analysis shows that embryonic age accounts for 90.4% and 88.3% of the variation seen in \dot{V}_{O_2} in Bank and Barn Swallows, respectively. This ontogenetic pattern in \dot{V}_{O_2} is typical of other altricial avian species (Hoyt et al., 1978a). Pre-pipping \dot{V}_{O_2} was 1.49 ml $O_2 \cdot h^{-1}$ in Bank Swallows and 1.75 ml $O_2 \cdot h^{-1}$ in Barn Swallows. These values agree well with values (1.48 ml $O_2 \cdot h^{-1}$ and 1.69 ml $O_2 \cdot h^{-1}$) predicted from the allometric relationship proposed by Hoyt et al. (1978a) for 34 species based on initial egg weight in grams (W):

$$\dot{V}_{O_2} = 26.4 W^{.726} \quad (1)$$

Where W equals 1.5 g and 1.8 g for Bank and Barn Swallows, respectively.





In 1974, Rahn et al. proposed that pre-pipping air cell gas tensions are very similar for all birds ($P_{O_2} \approx 104$, $P_{CO_2} \approx 37$ torr) and that these concentrations act as the stimulus for hatching. This supposition combined with previous work by the same authors showing that fractional water loss over the incubation period is also nearly constant (14-18% of W) (Rahn and Ar, 1974; Rahn et al., 1976; Morgan et al., 1978) led them to suggest that \dot{V}_{O_2} is also adjusted to water vapor conductance (G_{H_2O}) and incubation time (I), pre-pipping \dot{V}_{O_2} being positively correlated with G_{H_2O} and negatively correlated with I. These relationships between \dot{V}_{O_2} and G_{H_2O} and I are presented below.

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

$$I = 12.03 W^{.217} \quad (2)$$

and rearranged, pre-pipping \dot{V}_{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). With equation (3)

$$\dot{V}_{O_2} = \frac{317.6 W}{I} \quad (3)$$

the predicted \dot{V}_{O_2} for Bank Swallow eggs was $1.32 \text{ ml } O_2 \cdot h^{-1}$ and was $1.59 \text{ ml } O_2 \cdot h^{-1}$ for Barn Swallows. When the predictions from this equation are compared with the experimentally obtained values it is obvious that \dot{V}_{O_2} has not undergone any reduction to compensate for the longer than predicted I (predicted incubation times from equation (2) is: Bank = 13 days, Barn = 13.7 days) in fact the percentage difference in \dot{V}_{O_2} between observed and predicted is almost equivalent to the percentage difference in observed and predicted I.

Ar and Rahn (1978) have recently proposed a constant relating W , I , and G_{H_2O} for all eggs:

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

If equation (4) is solved for I and substituted into equation (3), \dot{V}_{O_2} of swallows may be predicted from G_{H_2O} (equation 5) where G_{H_2O} is $0.510 \text{ mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$ for Bank and $0.440 \text{ mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$ for Barn Swallows. With equation (5), the predicted \dot{V}_{O_2} for Bank Swallow eggs was

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

$1.32 \text{ ml } O_2 \cdot h^{-1}$ and was $1.13 \text{ ml } O_2 \cdot h^{-1}$ for Barn Swallows. The results of this equation show that \dot{V}_{O_2} is not adjusted to G_{H_2O} in these species particularly in Barn Swallows where the predicted value is 36% less than what has been measured here.

Bank Swallows show better, although not good agreement, with the value 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. This increase in conductance would also aid in the exchange of O_2 and CO_2 within the burrow which may be significantly different (O_2 lower, CO_2 higher) from normal atmospheric (Appendix I).

The oxygen consumption values determined experimentally and predicted from equations 1, 3, and 5 for Bank and Barn Swallows have been summarized in Table 5. The implications of the predicted values obtained with equations 3 and 5 are that air cell P_{O_2} should be much lower and P_{CO_2} much higher in these species than the constant values proposed by Rahn et al. (1974). This confirms previous calculations (Part I) and

supports the recent suggestions by Hoyt et al. (1978b) that air cell P_{O_2} may not be constant in all species but show a positive relationship with egg weight, and that the relationships between \dot{V}_{O_2} and I and \dot{V}_{O_2} and G_{H_2O} should be reexamined.

Table 5: Comparison of experimentally determined and predicted oxygen consumptions for Bank and Barn Swallows.

	Oxygen Consumption ($\text{ml O}_2 \cdot \text{h}^{-1}$)	
	Bank Swallow	Barn Swallow
This study	1.49	1.75
$26.4 W^{.726}$ (1)	1.48	1.69
$317.6 \frac{W}{I}$ (3)	1.32	1.59
$61.9 G_{\text{H}_2\text{O}}$ (5)	1.32	1.13

CHAPTER IV

SUMMARY

Oxygen consumption (\dot{V}_{O_2}) during development was determined in two species of swallows. The experimentally determined pre-pipping \dot{V}_{O_2} values for both species were then compared with those calculated from existing predictive equations based on initial egg weight, incubation time (I), and water vapor conductance (G_{H_2O}).

Both Bank and Barn Swallow embryos show a logarithmic increase in oxygen consumption throughout development with a substantial rise in \dot{V}_{O_2} occurring upon hatching. This pattern is similar to that observed in other altricial species. Experimentally determined pre-pipping \dot{V}_{O_2} values also agree well with those predicted on the basis of egg weight for both species, but showed a marked divergence with those predicted on the basis of I and G_{H_2O} . This lack of agreement between experimentally determined and predicted \dot{V}_{O_2} values based on I and G_{H_2O} suggest that pre-pipping air cell oxygen tensions in swallows should be much lower and carbon dioxide tensions much higher than the constant values proposed by previous investigators as the stimulus for hatching in other birds. The findings here support the proposals of Hoyt et al., (1978b) that air cell oxygen tension is inversely related to initial egg weight and that the relationships predicting pre-pipping \dot{V}_{O_2} on the basis of I and G_{H_2O} need to be reexamined.

LITERATURE CITED

- Ar, A. and H. Rahn. (1978) Interdependence of gas conductance, incubation length, and weight of the avian egg. pp. 227-236. In, Respiratory function in birds, adult and embryonic. J. Piiper, ed. Springer-Verlag, Berlin. 310 p.
- 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.
- Arieli, R., A. Ar., and A. Shkolnik. (1977) Metabolic responses of a fossorial rodent (Spalax ehrenbergi) to simulated burrow conditions. *Physiol. Zool.* 50:61-75.
- Bartels, H. (1970) Prenatal respiration. In, *Frontiers of Biology*. A. Neuberger and E.L. Tatum, Ed. North-Holland, Amsterdam. 199 p.
- Baudinette, R.V. (1974) Physiological correlates of burrow gas conditions in the California ground squirrel. *Comp. Biochem. Physiol.* 48A:733-743.
- Bent, A.C. (1963) Life histories of North American flycatchers, larks, swallows and their allies. Dover Publ., N.Y. 553 p.
- Bentley, P.J., C.F. Herreid II, and K. Schmidt-Nielsen. (1967) Respiration of a monotreme, the echidna, Tachyglossus aculeatus. *Am. J. Physiol.* 212:957-961.
- Coles, R. (1936) Egg quality: The influence of climate and soil. *Agriculture, Lond* : 43:317-332.
- Darden, T.R. (1970) Respiratory adaptations of a fossorial mammal, the pocket gopher (Thomomys bottae). Ph.D. thesis, University of California, Davis.
- Davis, P.S. (1966) A constant pressure respirometer for medium sized animals. *Oikos* 17:108-112.
- Drent, R.H. (1970) Functional aspects of incubation in the herring gull. *Behav. Suppl.* 17:1-132.
- Dunn, L.C. (1923) The variation of eggs in the rate at which they lose weight. *Poult. Sci.* 2:199-204.
- Eisenhart, C. (1968) Expression of the uncertainties of final results. *Science*, N.Y. 160:1201-1204.
- Erasmus, B. Dew., and H. Rahn. (1976) Effects of ambient pressures, He and SF₆ on O₂ and CO₂ transport in the avian egg. *Resp. Physiol.* 27:53-64.

- Hanson, H.C. (1954) Apparatus for the study of incubated bird eggs. *J. Wildl. Manage.* 18:191-198.
- Hayward, J.S. (1966) Abnormal concentrations of respiratory gases in rabbit burrows. *J. Mamm.* 47:723-724.
- Hoogland, J.L., and P.W. Sherman. (1976) Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. *Ecol. Monogr.* 46: 33-58.
- Hoyt, D.F. (1976) The effect of shape on the surface-volume relationships of bird eggs. *Condor* 78:343-349.
- Hoyt, D.F., C.E.M. Vleck, and D. Vleck. (1978a) Metabolism of avian embryos: Comparative ontogeny. pp. 237-238. In, Respiratory function in birds, adult and embryonic. J. Piiper, ed. Springer-Verlag, Berlin. 310 p.
- Hoyt, D.F., D. Vleck, and C.M. Vleck. (1978b) Metabolism of avian embryos: Ontogeny and temperature effects in the ostrich. *Condor* 80: 265-271.
- Kay, F.R. (1974) Influence of the burrow environment on body temperature, oxygen consumption and water loss of the banner-tailed kangaroo rat, Dipodomys spectabilis. Ph.D. thesis, New Mexico State University.
- Kendeigh, S.C. (1940) Factors affecting length of incubation. *Auk* 57: 449-513.
- Kennerly, T.E. (1964) Microenvironmental conditions of the pocket gopher burrow. *Texas J. Sci.* 16:395-441.
- Kutchai, H., and J.B. Steen. (1971) Permeability of the shell and shell membranes of hen's eggs during development. *Resp. Physiol.* 11:265-278.
- Lomholt, J.P. (1976a) Relationship of weight loss to ambient humidity of bird eggs during incubation. *J. Comp. Physiol. B* 105:189-196.
- Lomholt, J.P. (1976b) The development of the oxygen permeability of the avian egg shell and its membranes during incubation. *J. Exp. Zool.* 198:177-184.
- Lundy, H. (1969) A review of the effects of temperature, humidity, turning, and gaseous environment in the incubator on the hatchability of the hen's egg. pp. 143-176. In, The fertility and hatchability of the hen's egg. T.C. Carter and B.M. Freeman eds. Oliver and Boyd, Edinburgh.
- McNab, B. (1966) The metabolism of fossorial rodents: A study of convergence. *Ecology* 47:712-733.

- Mayr, E., and J. Bond. (1943) Notes on the generic classification of the swallows, Hirundinidae. *Ibis* 85:334-341.
- Metcalfe, J. (1967) The oxygen supply of the foetus. pp. 258-271. In, Ciba Foundation Symposium, Development of the Lung. A.V.S. de Reuck and R. Porter, eds. Little Brown & Co., Boston.
- Morgan, K.R., C.V. Paganelli, and H. Rahn. (1978) Egg weight loss and nest humidity during incubation in two Alaskan gulls. *Condor* 80: 272-275.
- Packard, G.C., P.R. Sotherland, and M.J. Packard. (1977) Adaptive reduction in permeability of avian eggshells to water vapour at high altitudes. *Nature* 266:255-256.
- Paganelli, C.V., A. Olszowaka, and A. Ar. (1974) The avian egg: Surface area, volume, and density. *Condor* 76:319-325.
- Paganelli, C.V., A. Ar, H. Rahn, and O.D. Wangensteen. (1975) Diffusion in the gas phase: The effects of ambient pressure and gas composition. *Resp. Physiol.* 25:247-258.
- Paganelli, C.V., R.A. Ackerman, and H. Rahn. (1978) The avian egg: In vivo conductances to oxygen, carbon dioxide, and water vapor in late development. pp. 212-218. In, Respiratory function in birds, adult and embryonic. J. Piiper, ed. Springer-Verlag, Berlin. 310 p.
- Petersen, A.J. (1955) The breeding cycle in the bank swallow. *Wilson Bull.* 67:235-286.
- 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. *Resp. Physiol.* 22: 297-309.
- Rahn, H., C.V. Paganelli, and A. Ar. (1975) Relations of avian egg weight to body weight. *Auk* 92:750-765.
- Rahn, H., C.V. Paganelli, I.C.T. Nisbet, and G.C. Whittow. (1976) Regulation of incubation water loss in eggs of seven species of terns. *Physiol. Zool.* 49:245-259.
- Rahn, H., R.A. Ackerman, C.V. Paganelli. (1977) Humidity in the avian nest and egg water loss during incubation. *Physiol. Zool.* 50: 269-283.
- Rahn, H., C. Carey, K. Balmas, B. Bhatia, and C. Paganelli. (1977) Reduction of pore area of the avian eggshell as an adaptation to altitude. *Proc. Natl. Acad. Sci. USA* 74:3095-3098.

- Riddle, O. (1924) On the necessary gaseous environment of the bird embryo. *Ecology* 5:348-362.
- Romanoff, A.L. (1943) Study of various factors affecting permeability of birds' eggshell. *Food Res.* 8:212-223.
- Romanoff, A.L. (1968) *Biochemistry of the avian embryo.* John Wiley & Sons, N.Y. 398 p.
- Romijn, C. (1950) Foetal respiration in the hen: Gas diffusion through the eggshell. *Poult. Sci.* 29:42-51.
- Samuel, D.E. (1971) The breeding biology of barn and cliff swallows in West Virginia. *Wilson Bull.* 83:284-301.
- Seymour, R.S., and H. Rahn. (1978) Gas conductance in the eggshell of the mound-building brush-turkey. pp. 243-246. *In*, *Respiratory function in birds, adult and embryonic.* J. Piiper, ed. Springer-Verlag, Berlin. 310 p.
- Snyder, G.K. (1978) Water vapor conductance in the avian eggshell: Adaptations related to egg weight and high altitude. *Physiologist* 21:113.
- Soholt, L.F. (1974) Environmental conditions in an artificial burrow occupied by merriami kangaroo rat, *Dipodomys merriami*. *J. Mamm.* 55:859-864.
- Studier, E.H., and J.W. Procter. (1971) Respiratory gases in burrows of *Spermophilus tridecemlineatus*. *J. Mamm.* 52:631-633.
- Tullet, S.G. (1975) Regulation of avian eggshell porosity. *J. Zool., Lond.* 177:339-348.
- Tullet, S.G., and R.G. Board. (1976) Oxygen flux across the integument of the avian egg during incubation. *Br. Poult. Sci.* 17:441-450.
- Tyler, C. (1969) Avian eggshells: Their structure and characteristics. *Int. Rev. Gen. Exp. Zool.* 4:81-130.
- 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.
- Wangensteen, O.D. (1972) Gas exchange by a bird's embryo. *Resp. Physiol.* 14:64-74.
- Wangensteen, O.D., and H. Rahn. (1970-1971) Respiratory gas exchange by the avian embryo. *Resp. Physiol.* 11:31-45.

- Wangensteen, O.D., D. Wilson, and H. Rahn. (1970-1971) Diffusion of gases across the shell of the hen's egg. *Resp. Physiol.* 11:16-30.
- Wangensteen, O.D., H. Rahn, R.R. Burton, and A.H. Smith. (1974) Respiratory gas exchange of high altitude adapted chick embryos. *Resp. Physiol.* 21:61-70.
- White, F.N., G.A. Bartholomew, and J.L. Kinney. (1978) Physiological and ecological correlates of tunnel nesting in the European bee-eater, Merops apiaster. *Physiol. Zool.* 51:140-154.
- Williams, D.P., and R.L. Rausch. (1973) Seasonal carbon dioxide and oxygen concentrations in the dens of hibernating mammals (Sciuridae). *Comp. Biochem. Physiol.* 44A:1227-1235.
- Yom-Tov, Y., A. Ar, and H. Mendelssohn. (1978) Incubation behavior of the Dead Sea sparrow. *Condor* 80:340-343.

APPENDIX I
 Microenvironmental Conditions
 Within Bank Swallow Burrows

The physical dimensions and number of chicks occupying burrows from which gas samples were taken over a 24 h period are summarized in Table A1. Oxygen concentrations (%) of these diel samples appear in Table 2, CO₂ concentrations in Table 3. Gas concentrations in other randomly collected samples are reported in Table 4. The mean and standard deviation for all %CO₂ and %O₂ determinations were 2.7±1.84% and 17.9±2.18%, respectively. Temperatures within two occupied burrows are summarized in Table 5 and Figure 1.

Relationship Between CO₂ and O₂
 Concentrations
 Within Bank Swallow Burrows

All burrow gas concentration data were combined. The relationship between percentage O₂ and percentage CO₂ was analyzed with a least-squares linear regression analysis. The regression equation and standard error of the estimate was:

$$\%O_2 = 21.07 - 1.17 (\%CO_2) \quad s_{y \cdot x} = 0.32$$

Table 1: Physical characteristics of burrows sampled for 24 h experiments.

	1	2	4A	5	6A	7	8A
Number of Occupants	none	*	2	6	*	3	4
Tunnel Depth (m)	0.84	0.73	0.73	---	0.47	0.51	0.66
Tunnel Height (m)	0.08	0.04	0.04	0.035	0.035	0.05	0.075
Tunnel Width (m)	0.04	0.07	0.08	0.065	0.075	0.08	0.045
Distance to Top of Bank (m)	1.26	0.36	0.87	0.70	0.87	0.75	0.66
Distance to Bottom of Bank (m)	1.50	1.25	1.5	2.0	1.5	4.0	0.9
Exposure	E	E	ESE	S	S	SW	ESE

*Birds left burrow at first light

Table 2: 24 h burrow O₂ concentrations (%).
Data for July 26-27, 1978.

	2	4A	5	6A	7	8A	1
Time							
1755	19.82						21.07
1855					19.19		
1955	19.95						20.33
2050		18.25		18.58	19.28		
2145			15.94		19.26	18.23	
2250	19.54	17.77		20.03			
005			17.24		18.87	15.11	
0120		19.49		17.19			20.46
0220			15.19		20.36	16.86	
0320	19.91	20.13		16.77			
0420			17.21		19.37	16.99	
0520	20.83			17.12			
0630			16.91		18.49		
0720	19.95	20.14		19.28			
0805			15.30		19.75	16.23	20.50
Mean	20.00	19.16	16.30	18.16	19.32	16.78	20.60

Table 3: 24 h burrow CO₂ concentrations (%).
Data for July 26-27, 1978.

	2	4A	5	6A	7	8A	1
Time							
1755	1.28						0.41
1855					2.32		
1955	1.23						0.49
2050		2.58		2.34	1.54		
2145			4.67		1.48	2.07	
2250	1.36	2.76		0.42			
0005			3.47		1.68	5.35	
0120		1.29		3.43			0.40
0220			5.18		0.36	3.88	
0320	0.96	0.63		3.88			
0420			3.21		1.40	3.78	
0520	0.65	0.68		3.47			
0630			3.63		2.26	4.15	
0720	0.771	0.51		2.30			
0805			4.96		1.02	4.26	0.41
Mean	1.04	1.40	4.19	2.64	1.51	3.92	1.43

Table 4: Determinations of burrow gas concentrations.
July 1978.

Date	Burrow Depth (cm)	Oxygen (%)	Carbon Dioxide (%)
7-15	45	18.22	2.17
	42	20.29	0.57
	36	17.91	2.69
7-16	47	15.06	4.51
	64	15.66	4.27
	52	14.14	5.41
7-17	53	13.99	6.01
	62	14.41	5.65
	72	16.55	3.85
7-18	71	13.21	6.68
	68	15.89	3.84
7-20	70	15.69	4.57
	70	14.18	5.94
	72	13.2	6.74
7-22	71	14.53	5.70
	64	16.05	4.11
	72	18.1	2.46
7-23	72	15.27	5.01
	64	16.72	3.66
	72	18.24	2.35

Table 5: Burrow temperature data

Burrow A		Burrow B	
Time	Temperature °C	Time	Temperature °C
July 26, 1978			
1943	28.8	2100	27.68
2105	28.64	2150	27.62
2145	29.16	2250	28.09
July 27, 1978			
0000	29.8	2355	28.08
0045	30.05	0050	28.28
0220	29.96	0215	28.59
0319	30.05	0322	28.82
0420	29.98	0417	28.68
0519	30.32	0525	28.63
0632	29.80	0628	28.66
0716	30.09	0720	28.62
0805	30.07	0803	28.72
0946	29.88	0944	28.42
1046	30.67	1040	28.25
July 28, 1978			
1224	30.76	1224	28.61
1322	30.19	1322	28.27
1424	30.60	1427	28.14
1519	29.67	1516	28.01
1617	29.58	1619	27.97
1719	29.53	1722	27.97
1840	29.38	1826	27.91

