

AN ALTITUDINAL CLINE IN CONDUCTANCE OF CLIFF SWALLOW (*PETROCHELIDON PYRRHONOTA*) EGGS TO WATER VAPOR

PAUL R. SOTHERLAND,¹ GARY C. PACKARD,¹ THEODORE L. TAIGEN,¹
AND THOMAS J. BOARDMAN²

¹*Department of Zoology and Entomology and* ²*Department of Statistics,*
Colorado State University, Fort Collins Colorado 80523, USA

ABSTRACT.—The rate of diffusion of water molecules through air is inversely related to atmospheric pressure; diffusivity of water vapor, therefore, is greater at high altitudes than at low elevations. Assuming that conservation of water in avian eggs is essential for normal development and hatching of embryos, we predicted that eggs laid by birds nesting at high altitudes would have lower conductances to water vapor under standard conditions than eggs laid by conspecifics nesting at low elevations, thereby compensating for the increased potential for transpirational water loss from eggs at high altitudes. To test this hypothesis, we collected eggs of Cliff Swallows, (*Petrochelidon pyrrhonota*) along an altitudinal gradient of 1,627 m in north-central Colorado and adjacent Wyoming and determined conductances of the eggs to water vapor under controlled laboratory conditions. Water-vapor conductance of eggs decreases with increasing altitude of nesting sites, as predicted by our hypothesis. Additionally, eggs containing embryos with a well developed chorioallantoic membrane have higher conductances to water vapor than eggs lacking a well developed chorioallantois, indicating that conductance to water vapor increases during the course of development. *Received 29 January 1979, accepted 6 September 1979.*

EGGS of birds decrease in mass throughout incubation owing to the outward diffusion of water vapor through pores in the calcareous shell (Ar et al. 1974, Rahn et al. 1976). Whereas the loss of some water is essential to the formation of an air cell from which an embryo takes its first breath in the hours immediately before hatching (Romijn and Roos 1938), the loss of large quantities of water is detrimental to the embryo (Barrott 1937). Thus, there is an optimum for loss of water from incubating eggs, and departure from this optimum (in either direction) may cause increased mortality.

Paganelli et al. (1975) demonstrated that the rate at which gas molecules diffuse through air is inversely related to barometric pressure. Because barometric pressure declines with increasing altitude, gas molecules must diffuse at greater rates at high altitudes than at low altitudes. Thus, if the rate of decline in mass of an avian egg is measured at sea level and that same egg then is transported to 3,000 m above sea level and its rate of decline in mass measured again, the rate of decline in mass at 3,000 m should be greater than at sea level, simply because water vapor diffuses outward more rapidly at the lower barometric pressure (see Aggazzotti 1913). Consequently, bird eggs laid at high altitudes potentially can lose greater amounts of water vapor than eggs laid at lower elevations.

Quinn et al. (1945) investigated the effect of selective breeding on the rate of decline in mass during incubation of eggs of domestic fowl. Using White Leghorn chickens "having a common origin" (we assume the authors meant the same flock), Quinn et al. (1945) developed one line of chickens producing eggs that decreased in mass at a high rate when incubated under controlled conditions and a second line producing eggs that decreased in mass at a low rate when incubated under the same conditions. These results indicate that the rate of decline in mass experienced by eggs during incubation is, at least in part, a heritable character of the hens producing

those eggs, and that given a sufficient selective pressure, the average rate of decline in mass of eggs in a population can be changed over several generations. Thus, if excessive loss of water vapor at low barometric pressure is a selective force sufficient to cause a disproportionately high hatching success of eggs having relatively low rates of decline in mass during incubation, then one might expect to find eggs laid by birds at high altitudes to exhibit lower rates of decline in mass under standard conditions than eggs laid by conspecifics at low elevations.

Cliff Swallows (*Petrochelidon pyrrhonota*) nest from sea level (Sykes 1976) to approximately 3,000 m in elevation (see below). Assuming that conservation of water is essential for normal development and hatching of avian embryos, we predicted that eggs laid by swallows nesting at high altitudes would have lower rates of decline in mass under controlled conditions than eggs laid by birds nesting at low elevations. In this paper we report results of an investigation of the rates of decline in mass of Cliff Swallow eggs collected from colonies found along an altitudinal gradient in north-central Colorado and south-central Wyoming. We also discuss how the differences in the rates of decline in mass may affect water loss from these eggs during incubation.

METHODS

Eggs of Cliff Swallows were collected from seven colonies located along an altitudinal gradient extending from Pawnee Creek (elevation 1,268 m) in northeastern Colorado to South Park (elevation 2,895 m) in the mountains of central Colorado (Table 1). Only one egg was taken from each nest, because eggs laid by a single female are likely to exhibit similar rates of decline in mass under controlled conditions (Sotherland et al. 1979), and because more reliable estimates of population parameters are obtained by collecting one egg from each of several nests than by collecting several eggs from each of a few nests (Sotherland et al. 1979).

Following transport to our laboratory at Colorado State University, the eggs were placed randomly in vented desiccators above anhydrous calcium sulfate to maintain a dry atmosphere. The desiccators were held in a constant temperature cabinet at 25°C. The mass of each egg was determined six times on an analytical balance at intervals of 24 h, and the rate of decline in mass, which reflects the loss of water vapor (Rahn et al. 1976), was computed using a linear regression procedure. Subsequently, the volume of each egg was determined by displacement of water (see Lynn and von Brand 1945), the length and breadth measured with a vernier caliper, and surface area calculated using equations 13 and 15 of Hoyt (1976).

Each egg was then opened, the mass of the embryo determined, and the stage of embryonic development noted. Eggshells were rinsed with distilled water and allowed to dry in air at room temperature. Shell thickness was measured at the blunt pole, equator, and pointed pole of each egg using a dissecting microscope equipped with a calibrated ocular scale. Thickness was measured from the outer surface of each shell to the outer surface of the outer shell membrane, a distance assumed to approximate the length of pores traversing the eggshell (Tullett et al. 1975). The values for each egg were averaged to yield a representative value for thickness of the shell.

Because vapor density inside the eggs approximated the vapor density above pure water at 25°C (i.e. $23 \mu\text{g}\cdot\text{cm}^{-3}$; see Lomholt 1976, Taigen et al. 1978), and because vapor density in the desiccators was approximately $0 \mu\text{g}\cdot\text{cm}^{-3}$, the conductance of eggs to water vapor was calculated using the equation:

$$G_v = \dot{M}_v / \Delta\rho_v, \quad (1)$$

where G_v is conductance of an egg to water vapor ($\text{cm}^3\cdot\text{d}^{-1}$), \dot{M}_v is the rate of decline in mass of the egg in a desiccator ($\text{mg}\cdot\text{d}^{-1}$), and $\Delta\rho_v$ is the difference in vapor density across the eggshell ($\text{mg}\cdot\text{cm}^{-3}$). (To convert water-vapor conductance of an egg at 25°C from units of $\mu\text{g}\cdot\text{d}^{-1}\cdot\text{torr}^{-1}$ to units used here, multiply the former by $1.0302 \text{ cm}^3\cdot\text{torr}\cdot\mu\text{g}^{-1}$.) The boundary layer of still air surrounding an egg adds little to the total resistance to water loss (Tracy and Sotherland 1979), so conductance of an egg to water vapor is a function of the size and/or number of pores through the shell and not of the boundary-layer conductance. Conductances were adjusted to barometric pressure at sea level by multiplying each value by the ratio of mean barometric pressure during the experiment to the mean barometric pressure at sea level (101.325 kPa).

TABLE 1. Summary of information on Cliff Swallow colonies.

Site	Location	Elevation (m)	Predicted barometric pressure (kPa)
1	T8N, R54W, S31, Logan County, Colorado	1,268	86.79
2	T7N, R70W, S1, Larimer County, Colorado	1,609	83.19
3	T9N, R69W, S11, Larimer County, Colorado	1,638	82.79
4	T10N, R70W, S22, Larimer County, Colorado	1,812	81.06
5	T14N, R70W, S8, Albany, County, Wyoming	2,210	77.06
6	T12S, R76W, S12, Park County, Colorado	2,719	72.26
7	T10S, R77W, S24, Park County, Colorado	2,895	70.79

RESULTS

Conductance of eggs to water vapor was used as the dependent variable in a stepwise multiple regression analysis. The potential independent variables in the analysis were (1) volume of eggs, (2) surface area of eggs, (3) thickness of eggshells, (4) number of eggs in nests from which eggs were collected (not to imply clutch size), (5) presence or absence of a chorioallantoic membrane in contact with the inner surface of eggshells (entered as a dummy variable, where 0 indicated presence of a chorioallantoic membrane and 1 indicated absence of a chorioallantoic membrane), and (6) mean barometric pressure predicted for the altitude of each colony (see List 1971, Tracy et al. 1978).

Results of this analysis indicated that there was a significant effect of chorioallantoic development on the conductance of eggs to water vapor ($F_{1,110} = 38.6$, $P < 0.001$), with eggs possessing a chorioallantois having higher conductances than eggs lacking this organ. Additionally, conductances of eggs collected from colonies characterized by high barometric pressures (low altitude) were higher than conductances of eggs collected from colonies characterized by low barometric pressures (high altitude) ($F_{1,109} = 14.1$, $P < 0.001$).

Because all eggs having a developed chorioallantois were collected (by chance) from low altitude colonies (colonies 1-4), it is possible that the statistical relation between conductance and chorioallantoic development is spurious, stemming from a bias introduced by our sampling procedure. To understand better the relation between conductance of these eggs to water vapor and development of embryos contained in the eggs, we performed a two-way analysis of variance (Bancroft 1968) on data for eggs from colonies that had eggs containing a chorioallantois (colonies 1-4), where presence or absence of a chorioallantois and nesting colony were the two factors by which we classified conductance. We found that conductances of eggs having a chorioallantois were significantly different from those of eggs lacking this organ (Table 2). Because the mean conductance of eggs having a chorioallantois ($687.4 \text{ cm}^3 \cdot \text{d}^{-1}$) was greater than that of eggs not having a chorioallantois (486.7

TABLE 2. Summary of two-way analysis of variance (method of weighted squares of means) performed to assess the influence of embryonic development on conductance of swallow eggs to water vapor.

Source	Degrees of freedom	Sum of squares	Mean squares	F-ratio	P
Chorioallantois	1	343 045	343 045	19.6	<0.001
Colonies	3	50 546	16 849	1.0	0.42
Interaction	3	77 468	25 823	1.5	0.23
Error	47	820 648	17 460		

TABLE 3. Mean values (SE in parentheses) for variables used in multiple regression analysis. Data are for eggs lacking a well developed chorioallantois. See Table 1 for elevations and predicted barometric pressures.

Site	<i>n</i>	Conductance (cm ³ ·d ⁻¹)	Volume (cm ³)	Surface area (cm ²)	Average shell thickness (mm)	Number of eggs in nests
1	17	459.2 (30.4)	2.12 (0.04)	8.19 (0.10)	0.069 (0.001)	2.6 (0.2)
2	7	595.5 (45.0)	2.10 (0.05)	8.14 (0.14)	0.072 (0.003)	3.4 (0.2)
3	8	514.0 (58.6)	2.12 (0.06)	8.18 (0.16)	0.073 (0.002)	3.5 (0.2)
4	8	465.7 (72.3)	2.08 (0.04)	8.09 (0.10)	0.071 (0.001)	3.0 (0.3)
5	22	321.4 (24.6)	2.28 (0.05)	8.59 (0.12)	0.071 (0.001)	2.0 (0.2)
6	12	261.8 (18.2)	2.18 (0.06)	8.37 (0.16)	0.070 (0.001)	1.8 (0.2)
7	21	381.8 (35.8)	2.22 (0.03)	8.43 (0.07)	0.070 (0.001)	3.2 (0.2)

cm³·d⁻¹), we conclude that conductances of Cliff Swallow eggs to water vapor increase as the contained embryos undergo development.

Because there was a significant difference between conductances of eggs with a chorioallantois and those of eggs without a chorioallantois, and because eggs with a chorioallantois were not found in all of the colonies from which we collected eggs, we excluded data for eggs having a well developed chorioallantois from further consideration. We subsequently performed a stepwise multiple regression analysis, as described previously, using the data for eggs containing undeveloped embryos (Table 3). Two of the independent variables, barometric pressure and number of eggs, contributed significantly to the variation in conductance of these eggs to water vapor (Table 4). Predicted barometric pressure for the altitudes of the colonies entered the regression first, accounting for 15.6% of the total variation in conductance. The number of eggs in each nest from which an egg was collected entered the regression next, and we can explain an additional 13% of the total variation in conductance by including this variable in the regression equation. No other potential independent variable contributed significantly to the variation in conductance. Thus, the final regression model allows us to explain 28.6% of the total variation in conductance of these eggs to water vapor.

DISCUSSION

Ontogenetic change in conductance.—The characters of an eggshell governing the conductance of that egg to water vapor are (1) the length of the pores traversing the

TABLE 4. Summary of stepwise multiple regression analysis of water-vapor conductance of eggs lacking a well developed chorioallantois.

Step	Variable entered	Degrees of freedom	<i>F</i> -ratio to enter	<i>P</i>	<i>R</i> ²
1	Barometric pressure	1,93	17.2	<0.001	0.156
2	Number of eggs	1,92	16.8	<0.001	0.286

shell and (2) the functional pore area (Paganelli et al. 1975), where conductance is inversely proportional to the former and directly proportional to the latter. Therefore, an increase in the diameter and/or number of pores or a decrease in thickness of the eggshell results in an increase in conductance of the egg to water vapor. Because the average conductance to water vapor of Cliff Swallow eggs having a chorioallantois is 41% greater than the average conductance of Cliff Swallow eggs lacking a chorioallantois, there must have been a change during incubation in pore geometry and/or in number of pores in the shell of eggs with a chorioallantois.

Assuming that our measure of shell thickness is a reliable estimate of the actual length of the diffusion pathway for water vapor through eggshells, we performed a two-way analysis of variance on data for shell thickness, where presence of a chorioallantois and nesting site were the two factors by which we classified eggshell thickness. We used only the data for eggs collected from colonies from which we sampled eggs having a chorioallantois (i.e. localities 1–4). There is a significant difference ($F_{1,46} = 6.1$, $P < 0.001$) between the average thickness of shells of eggs with a chorioallantois and the average thickness of shells of eggs lacking a chorioallantois, the average value being 5.6% less for eggs with a chorioallantois (0.067 mm) than for eggs without a chorioallantois (0.071 mm).

Because the percent change in conductance of an egg is equal to the percent change in functional pore area minus the percent change in thickness, and because we observed a 41% increase in conductance and only a 5.6% decline in shell thickness, there remains a considerable portion of the change in conductance that we cannot explain. Perhaps the distance we measured as the thickness of each eggshell is not an accurate representation of the actual length of the barrier to diffusion of water vapor through a shell. If this is the case, it is possible that the change in the actual length of the diffusion barrier, resulting from the removal of calcium from the inner surface of eggshells (see Crooks and Simkiss 1975), may have been greater than estimated here. Alternatively, if the distance we measured as the thickness of an eggshell actually is a good representation of the barrier to diffusion of water vapor, it is possible that pores that did not pass completely through a shell at the time an egg was laid were opened as a result of the removal of calcium from the inner surface of the eggshell.

In any case, we show a significant increase in conductance of these eggs to water vapor, and we show a significant decrease in the average thickness of the shells of these eggs—both changes accompanying development of the chorioallantois. Thus, conductance is not constant throughout incubation, as has been assumed by other workers (Rahn and Ar 1974, Packard et al. 1977), and ontogenetic changes in water-vapor conductance should be considered in future investigations of the physiology and/or morphology of avian eggs.

Altitudinal cline in conductance.—The equation resulting from the regression analysis of data for eggs undergoing little (if any) incubation is

$$G = 10.14 (BP) + 55.76 (NE) - 541.54 \quad (2)$$

where G is conductance of eggs to water vapor at sea-level, BP is barometric pressure in kilopascals, and NE is the number of eggs in a nest at the time of collection. This equation can be used to predict conductance of eggs to water vapor when egg temperature is 25°C. The positive coefficient for the term describing “barometric pressure” indicates that an increase in barometric pressure (i.e. descent in

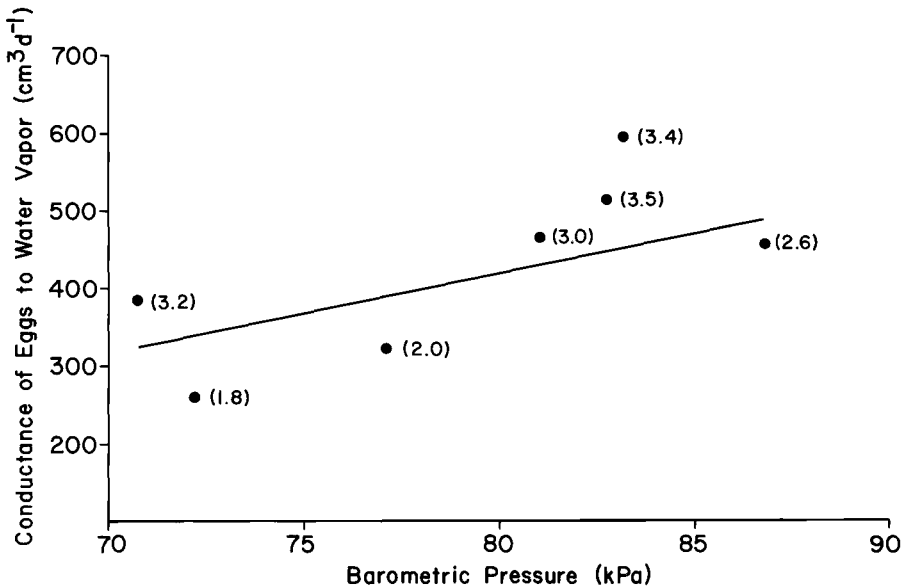


Fig. 1. Regression line plotted using Equation 2 and by setting NE equal to 2.7. Points represent mean conductances for each of the seven colonies; numbers associated with points are mean numbers of eggs in nests for each colony.

altitude) is accompanied by an increase in conductance of eggs to water vapor. Also, because the correlation coefficient for the relation between conductance and number of eggs is positive ($r = 0.39$), we interpret the positive coefficient for the term describing "number of eggs" to indicate that the first egg of a clutch has a lower water-vapor conductance than subsequent eggs laid by the same female. When an egg is collected from a nest containing only one egg, there is a greater chance for the egg to have a relatively low conductance than when an egg is collected from a nest containing several eggs. This intraclutch variation in conductance of eggs to water vapor may be the result of physiologic changes in female birds during the course of a laying cycle that affect the pattern of crystallization of eggshells and thereby influence the distribution and/or size of pores through the shells.

To demonstrate clearly the pattern we observed in our data, we plotted average conductances of eggs from the seven collecting sites against predicted barometric

TABLE 5. Summary of one-way analysis of variance of conductances of eggs to water vapor. Data are for eggs lacking a well developed chorioallantois.

Source	Degrees of freedom	Sum of squares	Mean squares	F-ratio	P
Total	94	2 520 863			
Among colonies	6	837 707	139 618	7.3	<0.001
Linear regression on barometric pressure	1	392 813	392 813	20.5	<0.001
Nonlinear ^a	5	444 894	88 978	4.7	<0.01
Within colonies	88	1 683 156	19 127		

^a Variation remaining after variation attributable to the linear regression of conductance on barometric pressure has been subtracted from the variation in conductance among colonies.

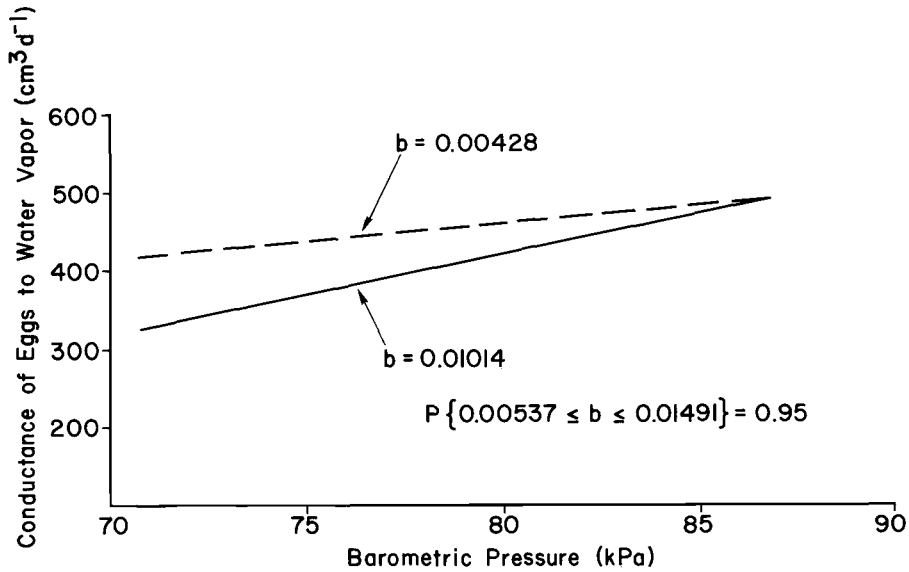


Fig. 2. Comparison of empirical regression of conductance on barometric pressure (solid line) to expected relation between conductance and barometric pressure where change in conductance just compensates for change in barometric pressure (dashed line).

pressure (Fig. 1). Plotted with these points is the regression line for conductance in relation to barometric pressure, generated by using equation (2) and by setting the number of eggs equal to the overall mean for number of eggs in nests at the time of collection ($NE = 2.7$). As indicated previously, this regression model accounts for 28.6% of the total variation in conductance to water vapor.

Total variation in water-vapor conductance of eggs lacking a chorioallantois is the sum of variation occurring within and among colonies (see Spence et al. 1968). Therefore, it may be somewhat misleading to indicate that 15.6% of the total variation in conductance of eggs in our sample is attributable to variation in barometric pressure, because differences in barometric pressure occur only among colonies and because intrapopulation variation in conductance may be appreciable.

To find out how much of the total variation in conductance is due to differences among colonies and how much to differences among eggs within colonies, we performed a one-way analysis of variance (see Sokal and Rohlf 1969) using data for eggs lacking a well developed chorioallantois. This analysis revealed that 47% of the variation in conductance among colonies is attributable to differences in predicted barometric pressure (Table 5), so the relation between conductance and predicted barometric pressure accounts for a more substantial portion of the interpopulation variation in conductance than might have been apparent on examination of Table 4. In addition, significant variation in conductance among colonies remains after removal of that variation due to the linear regression of conductance on barometric pressure (Table 5), but this additional variation in conductance probably is an artifact stemming from collecting eggs from nests at high altitudes, which contained fewer eggs on the average than nests at lower elevations, rather than actual variation among birds at various altitudes in their adaptation to the effects of barometric pressure (see Table 4, Fig. 1).

Initially, we predicted that eggs laid at high altitudes would have lower conductances to water vapor than eggs laid by conspecifics at lower elevations. A logical extension of this prediction is that differences in water-vapor conductance of eggs found over an altitudinal cline should just compensate for differences in barometric pressure found over the same altitudinal cline. Such an extension of the hypothesis, however, is not supported by data presented here (Fig. 2). The 95% confidence interval for the empirical slope of the regression of conductance on barometric pressure ($0.00537 \leq b \leq 0.01491$) does not include the slope of the regression expected if changes in conductance were just to compensate for changes in barometric pressure. Thus, overcompensation at high altitudes in reduction of conductance of eggs to water vapor is manifested by eggs of Cliff Swallows (Fig. 2) as well as by those of Barn Swallows (*Hirundo rustica*) (Packard et al. 1977). If conditions governing loss of mass are similar (other than differences in barometric pressure) at all altitudes, this overcompensation in conductance to water vapor would result in a smaller fractional decline in mass of eggs incubating at high altitudes. It may be that length of incubation, a variable to which fractional loss of mass is directly related (Rahn and Ar 1974), is greater at high altitudes because of the lower availability of oxygen (Smith et al. 1969), thereby necessitating a decrease in the conductance of eggs to water vapor greater than that required to compensate for an increase in the diffusivity of molecules of water vapor.

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