

- conductance, shell thickness, and functional pore area. *Condor* 76:153-158.
- BLANKESPOOR, G. W., J. OOLMAN, AND C. UTHE. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. *Auk* 99:363-365.
- CAREY, C. 1979. Increase in conductance to water vapor during incubation in eggs of two avian species. *J. Exp. Zool.* 209:181-186.
- CAREY, C. 1983. Structure and function of avian eggs, p. 69-104. In R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- CAREY, C. 1986. Tolerance of variation in eggshell conductance, water loss and water content by Red-winged Blackbird embryos. *Physiol. Zool.* 59:109-122.
- CAREY, C., S. D. GARBER, E. L. THOMPSON, AND F. C. JAMES. 1983. Avian reproduction over an altitudinal gradient. II. Physical characteristics and water loss of eggs. *Physiol. Zool.* 56:340-352.
- DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. *Behaviour Suppl.* 17:1-132.
- FRIEDMANN, H. 1929. *The cowbirds: a study in the biology of social parasitism*. Charles C Thomas Publ., Springfield, IL.
- PAYNE, R. B. 1977. The ecology of brood parasitism in birds. *Ann. Rev. Ecol. Syst.* 8:1-28.

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## CHANGES IN WATER-VAPOR CONDUCTANCE OF COMMON CANARY EGGS DURING THE INCUBATION PERIOD<sup>1</sup>

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*Key words:* Common Canary; *Serinus canarius*; chorioallantois; water-vapor conductance; incubation period.

Drent (1970) and Rahn and Ar (1974) postulated some time ago that the conductance of the avian eggshell to water ( $G_{H_2O}$ ) was constant throughout incubation and indeed that seems to be the case for large precocial eggs. However, the  $G_{H_2O}$  increases nearly 50% during the first few days of incubation in several altricial species of songbirds including Red-winged Blackbirds *Agelaius phoeniceus* and American Robins *Turdus migratorius* (Carey 1979), Cliff Swallows *Hirundo pyrrhonata* (Sotherland et al. 1980), and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* (Hanka et al. 1979). The reasons for the increase are still unclear, although they may be related to the development of the chorioallantoic membrane (Sotherland et al. 1979, 1980; Birchard and Kilgore 1980), abrasion of the shell during incubation (Carey 1983), or the small size of the eggs of altricial birds (Birchard and Kilgore 1980).

In this paper, I describe changes in the  $G_{H_2O}$  of Common Canary (*Serinus canarius*) eggs during the 13-day incubation period. Because I used fertile and sterile eggs in this study and because some were incubated by canaries and others were incubated artificially, I was able to determine if embryonic development and/or abrasive changes in the shell were responsible for changes in the  $G_{H_2O}$  of the eggs.

### MATERIALS AND METHODS

I collected freshly laid eggs from the nests of canaries in my colony each morning during the nesting season, within 1 to 5 hr of laying. The eggs were marked with a felt-tipped pen for identification and were weighed on a Sartorius balance accurate to 0.1 mg. Their  $G_{H_2O}$  was determined by the method of Ar et al. (1974). They were kept in small sealed containers over silica gel at an average constant

temperature of 23.85°C (range: 23.3 to 24.4°C) for five days during which they were weighed at roughly 24-hr intervals. Conductance values were corrected to 25°C and 760 torr. I have assumed, as others apparently have (Carey 1979, Hanka et al. 1979, Sotherland et al. 1980), that the egg's  $G_{H_2O}$  remains constant during the period of calibration. This assumption is supported by the fact that daily changes in each egg's mass during these five-day periods of calibration were nearly constant.

Once calibrated, the eggs were placed either in the nest of an incubating hen with three other noncalibrated eggs (clutch size was maintained at four eggs) or on a bed of fine sand in sealed containers kept in a water bath at 34°C (typical egg temperature during incubation by birds in my study). The calibrated eggs were incubated under the hen or in the water bath for 3, 6, 9, or 12 days. At that time, I removed and reweighed them and then recalibrated them for an additional five days as above. Finally, I candled them and then blew them to ascertain if they were fertile, i.e., I checked for the presence of embryos and extraembryonic membranes. I examined changes in the conductance of 79 sterile eggs and 16 fertile ones.

The data within each group (eggs incubated artificially; eggs incubated by a canary) were analyzed by paired *t*-tests and Student-Newman-Keuls tests. Student's *t*-tests and analysis of variance (ANOVA) were used to compare data between groups. Percentages were converted to their arcsin equivalents for analysis (Zar 1974).

### RESULTS

#### STERILE EGGS

The  $G_{H_2O}$  of sterile eggs increased 65 to 66% in the first three days of incubation, irrespective of whether they were incubated by canaries or in a water bath. This change was very highly significant ( $P < 0.001$ , paired *t*-test). Thereafter the  $G_{H_2O}$  was relatively constant through Day 9 of incubation (percent changes in  $G_{H_2O}$  for Days 3, 6, and 9 were not significantly different; Table 1). The conductance then declined appreciably (but the decrease was significant only in the group of eggs incubated by canaries) so that on Day 12 it approached the  $G_{H_2O}$  of freshly laid eggs (Day 0 in Table 1).

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TABLE 1. Changes in the  $G_{H_2O}$  (in  $mg\ d^{-1}\ torr^{-1}$ ) of infertile Common Canary eggs when incubated by canaries or in a water bath.

Conditions of incubation	Number of eggs	$G_{H_2O}$ on day of incubation <sup>1</sup>					Change in $G_{H_2O}$ (%) <sup>2</sup>
		Day 0	Day 3	Day 6	Day 9	Day 12	
Incubated in nests by canaries	10	0.4557 (0.0692) ***	0.7531 (0.1841) **	0.6791 (0.1679)	0.7243 (0.3427)	0.4665 (0.3125)	65.3a
	8	0.4283 (0.0754)					58.6a
	6	0.4155 (0.0720)					74.3a
	4	0.4587 (0.2052)					1.7b
Incubated in a water bath at 34°C	10	0.4630 (0.0991) ***	0.7682 (0.1389) ***	0.7737 (0.1225) ***	0.8130 (0.1419)	0.5902 (0.1072)	65.9a
	13	0.4747 (0.0523)					63.0a
	13	0.4952 (0.1194)					64.2a
	15	0.4792 (0.0564)					23.2a

<sup>1</sup> Values (means [ $\pm$ 95% confidence limits]) in each row are significantly different (paired *t*-test, two-tailed) if asterisks are present: (\*\* =  $P < 0.005$ , (\*\*\*) =  $P < 0.001$ ).

<sup>2</sup> For each group in this column (eggs incubated by canaries, or eggs incubated in a water bath), values that are not followed by the same letter are significantly different at the 0.05 level (Student-Newman-Keuls test, using arcsin equivalents of percentages); values followed by the same letter are not significantly different from one another.

TABLE 2. Changes in the  $G_{H_2O}$  (in  $mg\ d^{-1}\ torr^{-1}$ ) of fertile Common Canary eggs when incubated by canaries or in a water bath.

Conditions of incubation	Number of eggs	$G_{H_2O}$ on day of incubation <sup>1</sup>					Change in $G_{H_2O}$ (%)
		Day 0	Day 3	Day 6	Day 9	Day 12	
Incubated in nests by canaries	2	0.6168	1.1940	1.3357 **	0.7053 (0.1804)	0.6497 (0.5266)	93.6
	2	0.4903					172.4
	5	0.4630 (0.1385)					52.3
	4	0.3975 (0.0796)					63.4
Incubated in a water bath at 34°C	3	0.3666		0.5462			49.0

<sup>1</sup> Values (means [ $\pm$ 95% confidence limits]) in each row are significantly different (paired *t*-tests, two-tailed) if asterisks are present: (\*\* =  $P < 0.005$ ).

The average  $G_{H_2O}$  values of eggs incubated by canaries vs. those incubated in a water bath were not significantly different on Days 3 to 12 of incubation. When initially calibrated, eggs had conductance values that averaged 56 to 69% (depending on the group) of the  $G_{H_2O}$  predicted by the allometric equation  $G_{H_2O} = 0.384W^{0.814}$  (Ar and Rahn 1978), in which units of  $G_{H_2O}$  are  $\text{mg d}^{-1} \text{ torr}^{-1}$  and  $W$  (in g) is the egg's mass. Conductance values on Days 3, 6, and 9 averaged 88 to 109% of the conductance predicted by the same equation. On Day 12, the eggs'  $G_{H_2O}$  had diminished to 65 to 84% of predicted values.

#### FERTILE EGGS

My data for fertile eggs are limited (Table 2). In cases where sample sizes were three or more eggs per group, trends were similar to those shown by sterile eggs (Table 1). Water vapor conductance was initially 51 to 66% of the value predicted on the basis of the mass of the egg according to the equation of Ar and Rahn (1978). It increased 49% by Day 6 of incubation (eggs incubated in a water bath) and 52% by Day 9 of incubation (eggs incubated by canaries); i.e., increased to 76 and 100%, respectively, of predicted values. The data also suggest that the conductance of the eggs increased during the first three days of incubation, but the number of eggs ( $n = 2$ ) is too small (Table 2) to provide a reliable estimate of how much conductance changed in that interval.

#### DISCUSSION

The eggs of Common Canaries, like those of other altricial songbirds studied thus far, exhibit increases in  $G_{H_2O}$  during early stages of incubation. The change (65 to 66%) is somewhat greater than that reported for Cliff Swallows (41%; Sotherland et al. 1980), or Red-winged Blackbirds and American Robins (47 and 48%, respectively; Carey 1979). What causes the increase is not clear, but it is apparently not due to the development of the embryo or its extraembryonic membranes (chorioallantois), as suggested by others (Birchard and Kilgore 1980, Sotherland et al. 1980), since it occurred in infertile as well as fertile eggs (Table 1). Furthermore, the  $G_{H_2O}$  values of infertile canary eggs that had been incubated for 9 or 12 days (Table 1) did not differ significantly ( $P > 0.05$ , ANOVA,  $F_{2,21} = 0.4717$  and  $F_{2,20} = 0.7480$  for 9 and 12 days, respectively) from the  $G_{H_2O}$  of fertile canary eggs incubated for the same amount of time (Table 2). If embryonic development by itself were responsible for some change in the shell's conductance, one would expect the values of fertile eggs to be significantly higher than those of infertile eggs on these days of incubation.

The  $G_{H_2O}$  of an egg depends directly on the total effective pore area of the shell ( $A_p$ ) and inversely on the length of the diffusion path for water ( $L$ ) across the shell, i.e., the length of the pores in the shell (Rahn et al. 1977). Increases in  $A_p$  were reported in eggs of Common Eiders (*Somateria mollissima*) during incubation, and several investigators have suggested that additional pores are opened in the eggshell during incubation (e.g., Birchard and Kilgore 1980; reviewed in Carey 1983). Hanka et al. (1979) described a decrease in pore length in the eggs of Yellow-headed Blackbirds during incubation. It is possible that the  $A_p$  of the shell increased, at least in the eggs that were incubated by canaries, due to abrasion of the surface during contact with other eggs, the nest, and the brood patch, or perhaps as a result of the egg-turning activity of the hen. However, my data do not support such a hypothesis since eggs that were incubated in a bed of sand (and were not moved during incubation) exhibited changes in  $G_{H_2O}$  as pronounced as those of eggs incubated by canaries (Table 1). In this respect, my data are consistent with those of Hanka et al. (1979) who reported that the  $G_{H_2O}$  of fertile blackbird eggs incubated in a force-draft incubator (and hence not subject

to abrasion) increased markedly during the first four days of incubation.

The increase in  $G_{H_2O}$  of Common Canary eggs during early incubation (Table 1) is probably not due to the removal of mineral from the shell, since the latter apparently does not occur in infertile eggs (Simkiss 1975). Sotherland et al. (1980) suggested that changes in the  $G_{H_2O}$  of Cliff Swallow eggs involved demineralization of the shell by the embryo developing within the egg. As Carey (1979, 1983) pointed out, however, calcium mobilization from the shell does not occur until after the shell's permeability to water vapor has already changed.

The increased conductance, whether due to variations in  $A_p$  or  $L$ , may be associated with the long-term exposure of eggs (sterile or fertile) to the high temperatures typical of incubation (34°C or higher). For example, unpublished data for Common Canary eggs ( $n = 5$ ) that I have used as hygrometers indicate that  $G_{H_2O}$  increased much more slowly at room temperature than at incubation temperature. The  $G_{H_2O}$ s of these eggs did not change significantly ( $P > 0.05$ , paired  $t$ -test, two-tailed) when they were exposed to room temperatures of 21 to 30°C for 6 to 20 days (initial  $G_{H_2O} = 0.7016 \pm 0.1586 \text{ mg d}^{-1} \text{ torr}^{-1}$  [mean  $\pm$  95% confidence limits];  $G_{H_2O}$  after 6 to 20 days at room temperature =  $0.6813 \pm 0.1338 \text{ mg d}^{-1} \text{ torr}^{-1}$ ; final  $G_{H_2O} = 87$  to 105% initial  $G_{H_2O}$ ). Nonetheless, the  $G_{H_2O}$  of canary eggs does increase when they are stored for long periods, even at cold temperatures. For example, I calibrated seven freshly laid eggs and then sealed them individually in Glad Wrap® and stored them in groups of two or three in small sealed plastic bags in a refrigerator. Their  $G_{H_2O}$  had increased significantly (by an average of 79%;  $P < 0.002$ , paired  $t$ -test, two-tailed) when I recalibrated them 38 days later (initial  $G_{H_2O} = 0.2827 \pm 0.0886 \text{ mg d}^{-1} \text{ torr}^{-1}$  [mean  $\pm$  95% confidence limits];  $G_{H_2O}$  after 38 days at cold temperatures =  $0.5060 \pm 0.1595 \text{ mg d}^{-1} \text{ torr}^{-1}$ ). Hence, the high temperatures during incubation may accelerate changes in conductance, but are not required for such changes to occur.

The  $G_{H_2O}$ s of Common Canary eggs also declined after Day 9 of incubation and were not significantly different from preincubation values on Day 12 of incubation (Tables 1 and 2). Hanka et al. (1979) also observed decreases in the  $G_{H_2O}$  of Yellow-headed Blackbird eggs after seven days of incubation. They offer no explanation for the decrease, and I have none to offer for canaries. However, my samples of fertile eggs (Table 2) and sterile eggs incubated by hens (Table 1) are small and hence the data should be viewed as tentative. My sample of sterile eggs that were incubated in a water bath (Table 1) is much larger and here the change in  $G_{H_2O}$  at Day 12 of incubation was not significantly different from that seen on Days 3, 6, and 9. In my experience, the  $G_{H_2O}$  of an occasional canary egg may decrease suddenly and unexpectedly at any time, but such changes are much more pronounced than those shown by eggs in this study. I do not therefore believe that the declining  $G_{H_2O}$  values in Tables 1 and 2 are of this nature.

In summary, my data not only indicate that Common Canaries are another altricial species whose eggs exhibit changes in  $G_{H_2O}$  during early stages of incubation, but they also show that such changes occur in sterile, as well as fertile, eggs and are therefore due to something other than the development of the embryo or its extraembryonic membranes. They also do not appear to be due to abrasion of the shell. These changes in  $G_{H_2O}$  may be accelerated by the high temperatures to which the eggs are normally exposed during incubation, but such temperatures are not required for such changes to occur.

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## LITERATURE CITED

- AR, A., C. V. PAGANELLI, R. B. REEVES, D. B. GREEN, AND H. RAHN. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor* 76:153-158.
- AR, A., AND H. RAHN. 1978. Interdependence of gas conductance, incubation length, and weight of the avian egg, p. 227-236. In J. Piiper [ed.], *Respiratory function in birds, adult and embryonic*. Springer, New York.
- BIRCHARD, G. F., AND D. L. KILGORE, JR. 1980. Conductance of water vapor in eggs of burrowing and nonburrowing birds: implications for embryonic gas exchange. *Physiol. Zool.* 53:284-292.
- CAREY, C. 1979. Increase in conductance to water vapor during incubation in eggs of two avian species. *J. Exp. Zool.* 209:181-186.
- CAREY, C. 1983. Structure and function of avian eggs, p. 69-103. In R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. *Behaviour Suppl.* 17:1-132.
- HANKA, L. R., G. C. PACKARD, P. R. SOTHERLAND, T. L. TAIGEN, T. J. BOARDMAN, AND M. J. PACKARD. 1979. Ontogenetic changes in water-vapor conductance of eggs of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). *J. Exp. Zool.* 210:183-188.
- RAHN, H., R. A. ACKERMAN, AND C. V. PAGANELLI. 1977. Humidity in the avian nest and egg water loss during incubation. *Physiol. Zool.* 50:269-283.
- RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.
- SIMKISS, K. 1975. Calcium and avian reproduction. *Symp. Zool. Soc. Lond.* 35:307-337.
- SOTHERLAND, P. R., G. C. PACKARD, AND T. L. TAIGEN. 1979. Permeability of magpie and blackbird eggshells to water vapor: variation among and within nests of a single population. *Auk* 96:192-195.
- SOTHERLAND, P. R., G. C. PACKARD, T. L. TAIGEN, AND T. J. BOARDMAN. 1980. An altitudinal cline in conductance of Cliff Swallow (*Petrochelidon pyrrhonota*) eggs to water vapor. *Auk* 97:177-185.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.

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## REEVALUATION OF CHEEK PATTERNS OF JUVENAL-PLUMAGED BLUE-EYED AND KING SHAGS<sup>1</sup>

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*Key words:* Blue-eyed Shag; King Shag; juvenal plumages; *Phalacrocorax atriceps*; *Phalacrocorax albiventer*.

Blue-eyed (*Phalacrocorax atriceps*) and King shags (*P. albiventer*) occur allopatrically in certain subantarctic island groups and southern Argentina and Chile. The two species occur together in parts of extreme southern Argentina, Tierra del Fuego, and southern Chile. In adult *P. atriceps* (Fig. 1f) the cheek is white, the hindneck has only a narrow strip of black feathers, and there frequently is a white mid-dorsal patch. In adult *P. albiventer* (Fig. 1e) the cheek is glossy black, the hindneck is entirely black, and there is no white dorsal patch (Murphy 1936, Behn et al. 1955, Rand 1956, Humphrey et al. 1970, Devillers and Terschuren 1978). Unlike adult plumages, juvenal plumages of the two species are poorly known. During a study of the systematic relationships of *P. atriceps* and *P. albiventer*, I found that cheek patterns of juvenile *P. atriceps* resemble those of adult *P. albiventer* or apparent intermediates between the two species. This paper presents evidence concerning the identification of juvenile Blue-eyed and King shags and provides descriptions of juvenile head plumages of these species.

### METHODS

I examined 84 shag specimens in juvenal plumage or first prebasic molt for pattern and wear of cheek feathers and made a reference sketch of the cheek pattern of each specimen. Specimens examined were from Argentina ( $n = 38$ ), Chile ( $n = 14$ ), the Falkland Islands ( $n = 4$ ), Antarctica ( $n = 9$ ), the South Shetland Islands ( $n = 6$ ), South Georgia Island ( $n = 11$ ), and Macquarie Island ( $n = 2$ ). To determine the approximate amount of wear of juvenal cheek feathers, I measured lengths of four or five feathers on the black-white border at least 2 cm posterior to the throat pouch-feather edge of each of four juveniles in fresh plumage. I also measured four or five feathers in the same areas of each of four specimens determined by wear of juvenal remiges and rectrices to be approximately one year of age at collection. I measured only dark-tipped, obviously juvenal feathers in year-old birds, as molt had begun and some new feathers were present. To find whether the amount of wear thus approximated could account for visible lightening of the cheek area before the first prebasic molt, I measured the lengths of the dark tips on 15 randomly selected cheek feathers, located at least 2 cm posterior to the throat pouch-feather border of four juvenile specimens in fresh plumage.

### RESULTS

Specimens from localities of allopatry show that juvenile *P. atriceps* have dark-tipped cheek feathers and look superficially similar to adult *P. albiventer*. I found no white-checked juveniles in fresh plumage from areas in which

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