

In conclusion, it seems impossible that a nightjar could sing for eight minutes without replenishing its oxygen. It seems equally unlikely that sufficient oxygen could be acquired during the 25–40 ms gap between sound pulses. The temporal and amplitude pattern of their song suggests that nightjars may sustain long vocalizations by singing one part of their song, the short trill, during inhalation.

Why sing for so long? I have preliminary data that suggest there is individual variation in the maximum length of song; this implies that song length may have evolved under sexual selection or as an assessment cue of fighting ability.

John Brackenbury, Abbot Gaunt, John Krebs, Fernando Nottebohm, Ray Owen, Jr., and James Rooney kindly commented on the manuscript. The research was made possible by grants from the Association of American Rhodes Scholars and the Rhodes Trust. Maxine Horne typed the manuscript, and Vikki Kogut prepared the figure.

#### LITERATURE CITED

- BRACKENBURY, J. H. 1978a. A comparison of the origin and temporal arrangement of pulsed sounds in the songs of the Grasshopper and Sedge warblers, *Locustella naevia* and *Acrocephalus schoenobaenus*. *J. Zool. (Lond.)* 184:187–206.
- BRACKENBURY, J. H. 1978b. A possible relationship between respiratory movements, syringeal movements, and the production of song by Skylarks *Alauda arvensis*. *Ibis* 120:526–528.
- CALDER, W. A. 1970. Respiration during song in the Canary (*Serinus canaria*). *Comp. Biochem. Physiol.* 32:251–258.
- CHAMBERLAIN, D. R., W. B. GROSS, G. W. CORNWELL, AND H. S. MOSBY. 1968. Syringeal anatomy in the Common Crow. *Auk* 85:244–252.
- GAUNT, A. S., R. C. STEIN, AND S. L. L. GAUNT. 1973. Pressure and air flow during distress calls of the Starling, *Sturnus vulgaris* (Aves: Passeriformes). *J. Exp. Zool.* 183:241–262.
- GAUNT, A. S., AND S. L. L. GAUNT. 1977. Mechanics of the syrinx in *Gallus gallus*. II. Electromyographic studies of *ad libitum* vocalizations. *J. Morphol.* 152:1–20.
- GREENEWALT, C. H. 1968. Bird song: acoustics and physiology. Smithsonian Institution, Washington, D.C.
- KNEUTGEN, J. 1969. "Musikalische" Formen im Gesang der Schamadrossel (*Kittacincla macroura* Gm.) und ihre Funktionen. *J. Ornithol.* 110:246–285.
- MISKIMEN, M. 1951. Sound production in passerine birds. *Auk* 68:493–504.
- PEIPONEN, V. A. 1965. On hypothermia and torpidity in the nightjar (*Caprimulgus europaeus* L.). *Ann. Acad. Sci. Fennicae (AIV)* 87:1–15.
- PEIPONEN, V. A. 1966. The diurnal heterothermy of the nightjar (*Caprimulgus europaeus* L.). *Ann. Acad. Sci. Fenn. (A IV)* 101:1–35.

*Edward Grey Institute of Field Ornithology, Department of Zoology, Oxford, U.K. Present address: School of Forest Resources, University of Maine, Orono, Maine 04469. Accepted for publication 28 May 1979.*

*Condor*, 82:103–105

© The Cooper Ornithological Society 1980

## METABOLISM AND THERMOREGULATION IN HATCHLING WESTERN GULLS

WILLIAM R. DAWSON

AND

ALBERT F. BENNETT

Parental attentiveness provides hatchlings of many precocial and semiprecocial birds with a large measure of protection from the vagaries of the thermal environment. Nonetheless some of these species differ in thermoregulatory capacity of newly hatched chicks, in correlation with climatic conditions during the breeding season. For example, hatchling ducks of species breeding exclusively in the arctic and subarctic tend to have better control of body temperature in cool environments than do those of species with wider and more southerly distributions (Koskimies and Lahti 1964). A similar pattern seems to exist for hatchling gulls. Black-headed Gulls (*Larus ridibundus*) and Ring-billed Gulls (*L. delawarensis*) can approximately double their rates of heat production over basal levels when subjected to cold stress on the day of hatching (Kespaik and Davydov 1966, Dawson et al. 1976). In contrast, Laughing Gulls (*L. atricilla*), which appear to breed under somewhat warmer conditions, can increase

theirs by only 50% (Dawson et al. 1972). The range of metabolic capacity among hatchling gulls may be even greater than these values indicate, for the genus *Larus* includes more than 30 species whose respective breeding ranges embrace a latitudinal span from the arctic to the subantarctic. As opportunities arise, we are attempting to assess the extent of differences in thermoregulatory capacities among hatchlings of these species. We report here observations on chicks representing the subspecies of Western Gull (*Larus occidentalis livens*) breeding in the Gulf of California, Mexico.

Our experimental subjects were obtained from Isla Partida, Baja California Norte, Mexico (28°54'N, 113°3'W) on 29 April–1 May 1976. During this period, nights were cool, days were warm, and solar radiation was intense. Conditions were similar to those on nearby Isla Rasa (10 km SE), where we had made micrometeorological measurements from 18–28 April 1976, in connection with studies of Heermann's Gulls (*L. heermanni*). Daily minimal and maximal temperatures at nest height on Isla Rasa averaged 12.9°C (range, 8.4–16.7°C) and 32.2°C (range, 28.7–34.7°C), respectively. Intensity of solar radiation reached 1036 W/m<sup>2</sup> at midday on 19 April 1976, and was near this level on several subsequent days.

Following collection, newly hatched Western Gulls were transferred for study to the nearby R/V *Dolphin*, and then exposed to constant ambient temperatures ( $T_a$ ) between 16° and 35.3°C for two-hour periods. These concluded with measurement of oxygen con-

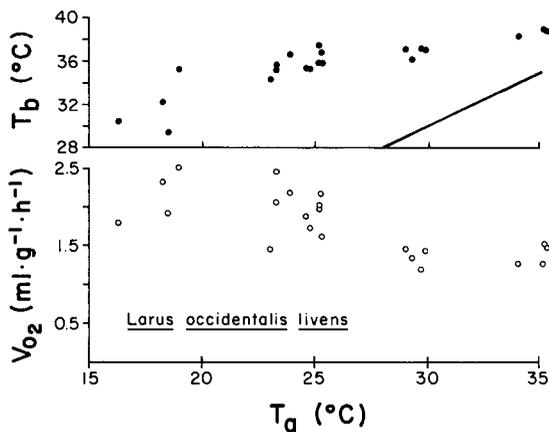


FIGURE 1. Relation of body temperature ( $T_b$ ) and oxygen consumption ( $\dot{V}_{O_2}$ , corrected to STPD) to ambient temperature ( $T_a$ ). The diagonal line marks equivalence between  $T_b$  and  $T_a$ . All measurements were made at the conclusion of two-hour exposures to single  $T_a$ 's. The figure omits three values of BMR [1.08, 1.30, and 1.35 ml (g·h)<sup>-1</sup>] for which exact values of  $T_a$  are unavailable.

sumption ( $\dot{V}_{O_2}$ ) and body temperature ( $T_b$ ), using procedures and instrumentation described by Dawson et al. (1972, 1976). None of the 15 hatchlings studied was used in more than two tests and these were separated by at least two hours, during which the birds were kept at an  $T_a$  of 25°C and fed canned cat food. All of the gulls were returned to their respective nests at the conclusion of measurements.

Daytime  $\dot{V}_{O_2}$ 's of hatchling Western Gulls at 29°–35.3°C were taken as basal metabolic rates (BMR). These averaged  $1.35 \pm 0.041$  (S.E.) ml (g·h)<sup>-1</sup> for the 11 birds tested (mean body mass 65.4  $\pm$  1.27 g). This mean BMR represents 94, 82, and 103% of the respective values predicted for a 65.4-g adult non-passerine by the Lasiewski-Dawson (1967) equation, the Aschoff-Pohl equation for the active ( $\alpha$ ) portion of the daily cycle, and the A-P equation for the inactive ( $\rho$ ) portion of the daily cycle (Aschoff and Pohl 1970). These percentages resemble those obtained in similar comparisons involving daytime measurements of BMR in hatchling Herring Gulls (*L. argentatus*; Drent 1967), and Ring-billed Gulls (see Table 2 in Dawson et al. 1976). The BMR of gull chicks thus approaches the metabolic rate characterizing adult non-passerine birds of similar size, even though the  $T_b$  of these chicks is below that of mature birds (cf. Fig. 1 and values for adult gulls given by Neumann et al. 1968).

The Western Gulls we studied possessed some ability to thermoregulate below thermal neutrality (Fig. 1), as do newly hatched gulls of other species. Thus only a minor dependence of  $T_b$  on  $T_a$  is apparent between 22.5° and 35°C. The equation relating these variables in this interval is:

$$T_b = 29.2 + 0.27 T_a$$

with  $T_b$  and  $T_a$  in degrees C (S.E. of estimate, 0.695;  $r^2$ , 0.77; F ratio, 68.48). Performance was more variable below 22.5°C and some of the chicks had cooled several degrees by the end of the two-hour tests. An inverse relation exists between  $\dot{V}_{O_2}$  for euthermic chicks ( $T_b > 35.0^\circ\text{C}$ ) and  $T_a$  between 19° and 30°C. This can be described by the following equation:

$$\dot{V}_{O_2} = 4.92 - 0.12 T_a$$

where  $\dot{V}_{O_2}$  and  $T_a$  are in ml (g·h)<sup>-1</sup> and degrees C, respectively (S.E. of estimate, 0.200;  $r^2$ , 0.77; F ratio, 43.18). Metabolic data were converted to a thermal basis and heat transfer coefficients (thermal conductances),  $h$ , were calculated [ $h = 4.8 \dot{V}_{O_2} / (T_b - T_a)$ ] (where  $h$ ,  $\dot{V}_{O_2}$ , and temperatures are in cal [g·h·°C)<sup>-1</sup>, ml [g·h)<sup>-1</sup>, and degrees C, respectively). For hatchlings maintaining  $T_b$  at or above 30°C,  $h$  ranges from 1.44 to 2.12 cal (g·h·°C)<sup>-1</sup> [ $1.67$  to  $2.46 \times 10^{-3}$  W(g·°C)<sup>-1</sup>] at  $T_a$  near 35°C to 0.61 to 0.81 cal (g·h·°C)<sup>-1</sup> [ $7.09$  to  $9.41 \times 10^{-4}$  W(g·°C)<sup>-1</sup>], indicating a capacity for controlling heat loss. The mean of  $h$  for the 16–19°C interval is 0.72 cal (g·h·°C)<sup>-1</sup> [ $8.38 \times 10^{-4}$  W(g·°C)<sup>-1</sup>], which is 50% higher than the value of 0.48 cal (g·h·°C)<sup>-1</sup> [ $5.57 \times 10^{-4}$  W(g·°C)<sup>-1</sup>] predicted for a 65.4-g adult bird with Lasiewski et al.'s (1967) equation. Insulation is the reciprocal of  $h$  and hatchling Western Gulls thus appear markedly inferior to adult birds of comparable size in ability to conserve heat. Among these chicks, the down thickness averages 10.3, 10.5, and 4.3 mm in the centers of the back, abdomen, and crown, respectively. When  $h$  is expressed in cal (g<sup>0.49</sup>·h·°C)<sup>-1</sup> to minimize the complication of differences in body size on comparisons of hatchlings (see Dawson et al. 1976, for discussion), values for the three Western Gulls remaining warmer than 30°C at  $T_a$  of 16–19°C range from 4.78 to 7.11 cal (g<sup>0.49</sup>·h·°C)<sup>-1</sup>. This compares with 5.25 and 4.72–5.75 cal (g<sup>0.49</sup>·h·°C)<sup>-1</sup> for hatchling Laughing and Ring-billed gulls, respectively (Dawson et al. 1972, 1976). Thus, when differences in body size are minimized, newly hatched Western Gulls do not appear to differ substantially from the young of these other species in their inherent insulation capacity.

Hatchling gulls studied thus far have only modest capacities for augmenting heat production in the cold. The three highest metabolic rates observed in the present study average 1.8 times BMR, placing newly hatched Western Gulls from the Gulf of California in an intermediate position between the Ring-billed and Black-headed gulls (Dawson et al. 1976, Kespak and Davydov 1966) on the one hand, and the Laughing Gull (Dawson et al. 1972) on the other (see introductory paragraph). Superficially, at least, this rank appears to correlate with the general thermal conditions encountered by the four species during the breeding season.

This study was supported in part by grants from the National Science Foundation (DEB 76-7817 and DEB 77-25487 to WRD and PCM 75-10100 to AFB). We especially wish to thank Dr. Bernardo Villa Ramirez, Instituto de Biología, Universidad Autónoma de México, for his valuable assistance. The crew of R/V *Dolphin* (Scripps Institution of Oceanography, University of California, San Diego) was most helpful to our study. We thank the Government of Mexico and the Office of the Secretary of External Relations for permission to operate in Mexican territorial waters and collect the gulls used in our study (Permit No. 502113, March 20 1976).

#### LITERATURE CITED

- ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541–1552.
- DAWSON, W. R., A. F. BENNETT, AND J. W. HUDSON. 1976. Metabolism and thermoregulation in hatchling Ring-billed Gulls. Condor 78:49–60.
- DAWSON, W. R., J. W. HUDSON, AND R. W. HILL. 1972. Temperature regulation in newly hatched Laughing Gulls (*Larus atricilla*). Condor 74:177–184.
- DRENT, R. H. 1967. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). E. J. Brill, Leiden.

- KESPAIK, J., AND A. DAVYDOV. 1966. Factors determining the cold-hardiness of the *Larus ridibundus* L. on the first day after hatching. Toimetised Eesti NSV Teaduste Akademia XV, Biol. Seeria 4:485-491. In Russian with English summary.
- KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution of ten species of European ducks. Auk 81:281-307.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13-23.
- LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant

- Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797-813.
- NEUMANN, R. L., J. W. HUDSON, AND R. J. HOCK. 1968. Body temperatures. Part II. Birds, p. 334-343, Table 59. In P. L. Altman and D. S. Dittmer [eds.], Metabolism. Federation of American Societies of Experimental Biology, Bethesda, Maryland.

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109. Address of second author: School of Biological Sciences, University of California, Irvine, California 92717. Accepted for publication 12 September 1979.

Condor, 82:105-106  
© The Cooper Ornithological Society 1980

## CONDUCTANCE, PORE GEOMETRY, AND WATER LOSS OF EGGS OF CASSIN'S AUKLET

T. ROUDYBUSH  
L. HOFFMAN  
AND  
H. RAHN

The ratios of egg mass to body mass in the Alcidae are relatively large (Sealy 1975) when compared with those of most other groups of birds (Rahn et al. 1975). Cassin's Auklet (*Ptychoramphus aleuticus*) weighs about 165 g (Manuwal 1974b, Sealy 1975), and its single egg of about 29 g is twice that predicted from the egg mass-body mass relationship of birds in general (Rahn et al. 1975). The auklets nest in burrows and rock crevices, and during incubation the single egg is held between the lateral incubation patch and the wing (Manuwal 1974a, b). The incubation time of 38 days is considerably longer than the 25 days predicted for eggs of this size. It is of particular interest as it has been suggested that the functional egg characteristics such as conductance, water loss (Rahn and Ar 1974), and metabolism (Rahn et al. 1974) increase not only in proportion to their mass but are inversely related to incubation time. To see whether these generalizations apply also to Cassin's Auklet eggs, we measured the conductance and incubation water loss of these eggs

TABLE 2. Conductance and pore geometry.

	G	L	A <sub>p</sub>	N
	mg day <sup>-1</sup> torr	mm	mm <sup>2</sup>	
$\bar{x}$	4.08	0.23	0.419	3,295
S.E.	0.16	0.01	0.034	152
n	21	8	8	8

G = conductance, L = pore length, A<sub>p</sub> = total pore area, N = number of pores per egg, and r = radius of pore, where A<sub>p</sub> = .447 G · L (Rahn et al. 1974) and  $r = [A_p/N\pi]^{0.5} = 6.4 \mu\text{m}$ .

and described the physical dimensions of the egg and the shell as well as the pore geometry responsible for the egg conductance.

Eggs were collected in April 1977 and May 1978 on the Farallon Islands, west of San Francisco, California. The water vapor conductance was measured by the method of Ar et al. (1974). Egg volumes were measured by water displacement, and surface area and shell thickness by the method of Paganelli et al. (1974). Initial egg mass was obtained by weighing eggs after the air cell had been displaced with water, using a hypodermic syringe. In order to learn the number of pores the shells were boiled in 2.5% NaOH to remove protein fibers, then briefly etched in concentrated nitric acid. After drying, an aqueous solution of methylene blue was applied to the inner surface of the shell to render the pores more visible (Tyler 1953). Each egg was examined under a compound microscope and twenty fields (0.25 cm<sup>2</sup>) were counted and averaged.

TABLE 1. Physical dimensions of Cassin's Auklet eggs and shells.

	Egg						Shell			
	Mass g	Vol. cm <sup>3</sup>	Density g · cm <sup>-3</sup>	Area cm <sup>2</sup>	Length cm	Width cm	Mass g	Thick- ness mm	Vol. cm <sup>3</sup>	Density g · cm <sup>-3</sup>
$\bar{x}$	29.74	27.87	1.067	45.7	4.69	3.39	1.88	0.23	1.05	1.79
S.E.	0.6	0.6	.001	0.6	.03	.03	.08	0.01	—	—
n	14	14	14	14	14	14	8	8	8	8
Schönwetter (1963)	n = 80	28.0			4.67	3.37	1.88	0.22		
Manuwal (1974a)	n = 75	27.4			4.62	3.35				