

# FIELD AND LABORATORY STUDIES OF THE THERMAL RELATIONS OF HATCHLING WESTERN GULLS<sup>1</sup>

WILLIAM R. DAWSON AND ALBERT F. BENNETT

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109; and  
School of Biological Sciences, University of California, Irvine, California 92717

(Accepted 8/6/80)

Field and laboratory studies were undertaken on thermoregulatory capabilities during the first 24 h after hatching in chicks of the western gull (*Larus occidentalis wymani*). Body temperatures ( $T_b$ ) of 12 such hatchlings brooded in their nests on San Nicolas Island, California, averaged  $38.0 \pm 0.60$  SE C between 0900 and 2000 h. Hatchlings unprotected by a parent heated rapidly (up to 1 C/min) in the midday sun and commenced panting at  $T_b > 40$  C. Panting did not stabilize  $T_b$ , and coordination and equilibrium were lost at 44–45 C. One chick recovered from a  $T_b$  of 46.2 C. Still higher  $T_b$  could develop with prolonged exposure to direct sunlight. Unlike new hatchlings, unprotected older chicks ( $\geq 15$  h) moved to the shelter provided by vegetation when risk developed of overheating in the sun. Unbrooded hatchlings ( $> 24$  h) became hypothermic at night with air and soil temperatures of 16–17 C. Laboratory observations indicated that chicks in this age class can tolerate  $T_b$  as low as 14–18 C. Body temperatures at which various motor patterns reappear during passive rewarming from such  $T_b$  were determined. During the first day after hatching, western gulls have insulative capacities below those anticipated for adult birds of similar size, despite the seemingly luxuriant character of the chicks' down. The basal metabolic rate (BMR) for the western gull hatchlings (mean body mass, 58.0 g) is  $8.26 \text{ mW} \cdot \text{g}^{-1}$ , which approximates values predicted for an adult nonpasserine bird of similar size. These less than 1-day-old chicks can increase metabolic rate to  $1.9 \times$  BMR at cooler ambient temperatures ( $T_a$ ). They increase evaporative cooling at 42.9–44.0 C sufficiently to dissipate the heat produced in metabolism. Parental attentiveness normally prevents large fluctuations of  $T_b$  of hatchling gulls under cool  $T_a$  at night or direct insolation during the day. Such protection is especially important during the latter period, owing to the relatively narrow interval between normal and upper lethal  $T_b$  for these young chicks.

## INTRODUCTION

The developmental state of birds at hatching varies from precocial to altricial depending on the group considered. Gulls (*Larus*) represent an intermediate condition in which new hatched chicks possess a

<sup>1</sup>We thank the Department of the Navy for permission to work on San Nicolas Island and to use its facilities. W. D. Flora and T. Wieberg, security personnel on the island, were especially helpful to our study. Chief Biologist R. Dow was very accommodating in arranging our visit. Support for this investigation was provided in part by NSF grants DEB 77-25487 and PCM 77-24208, and NIH grant 1 K04 AM00351-01.

*Physiol. Zool.* 54(1):155–164. 1981.

© 1981 by The University of Chicago. 0031-935X/  
81/5401-8033\$02.00

luxuriant coat of down but initially show only limited locomotor and thermoregulatory capacities. We have investigated these capacities in hatchlings of three species breeding under different climatic conditions (Dawson, Hudson, and Hill 1972; Dawson, Bennett, and Hudson 1976; Dawson and Bennett 1980) in an effort to determine whether thermoregulatory abilities in the day following hatching vary inter-specifically in a manner correlated with environmental conditions within the breeding ranges of the taxa involved. We have also sought to assess the extent to which short-term disruption of parental attentive patterns can place eggs and nascent young in jeopardy under particular sets of condi-

tions. This report summarizes our continued studies of the western gull (*Larus occidentalis*). We have already reported briefly on the subspecies of this bird breeding in the Gulf of California, Mexico (*L. o. livens*) (Dawson and Bennett 1980). We now summarize a more extensive study of *Larus occidentalis wymani*. The breeding distribution of this subspecies encompasses islands along the Pacific Coast of North America from central California to Baja California.

#### MATERIAL AND METHODS

During June 1979, thermal responses in the first 24 h after hatching were studied in western gull chicks (*Larus occidentalis wymani*) from the breeding colony on San Nicolas Island, Ventura County, California. Chicks in this age class will be referred to as "hatchlings" hereafter. Details of location and structure of the San Nicolas Island colony are given by Bennett, Dawson, and Putnam (1980). Hatchling gulls were collected under California Scientific Collector's Permit no. 514 to Bennett and Federal Fish and Wildlife Permit no. PRT-2-285-5C to George L. Hunt.

#### FIELD OBSERVATIONS

Body temperature and thermally relevant behavior of young gulls in their nests were studied both at night and during the day. Ground-level air temperature in the shade was measured with Wahl thermal recorders (models 732-27 and 731-16). Temperature of the sand was measured with a copper-constantan thermocouple coated with epoxy and sand and located 1-2 mm below the sand surface. The leads for this thermocouple were connected to a Wescor Model TH-50 thermocouple thermometer.

Newly hatched animals were located by marking pipped eggs within the colony and surveying the nests several times a day for emerging chicks. Adult gulls would leave their nests readily when approached, exposing the eggs or young to ambient conditions. Rectal temperatures ( $T_b$ ) of brooded hatchlings were measured with a quick-registering Schultheiss thermometer (in-

sertion  $> 1$  cm) within 1 min after the departure of the parent. The influence of direct insolation on body temperature and behavior of a few animals within their own nests was observed. However, most hatchlings were transferred to an abandoned nest at the edge of the colony, adjacent to our observation post. This minimized our disruption of brooding in the colony. Three hatchlings and three 1-2-day-old chicks were exposed individually to midday (1200-1400 h Pacific Daylight Time [PDT]) conditions for periods of 10-25 min. Three other hatchlings were exposed individually for periods of 90-120 min in the abandoned nest at night (2000-2300 h PDT). Air ( $T_{air}$ ) and sand surface ( $T_{soil}$ ) were measured frequently and behavior noted continuously. If the chicks began to heat or cool excessively, they were immediately sheltered at more moderate temperatures. Following recovery, all chicks were marked and returned to their original nests; all were surviving at the conclusion of our observations several days later.

#### LABORATORY STUDIES

Pipped eggs and eggs in late developmental stages, as determined by buoyancy in fresh water, were marked as to nest of origin and transported to the University of California, Irvine, for thermoregulatory studies on chicks within the first 24 h following emergence. At the conclusion of the experiments, these birds were returned to their respective nests on the island. Parental birds began brooding them immediately upon their return.

The thermoregulatory capacity of the hatchling gulls was assessed through their metabolic and thermal responses in 2-h tests at constant ambient temperatures ( $T_a$ ) between 16 and 45 C. Unless otherwise noted, all measurements were made during the daytime (1000-1600 h PDT). Animals were fed canned cat food between experiments. Details of the methodology for the 2-h tests are described by Dawson et al. (1976). Oxygen content of air flowing from metabolic chambers was monitored with an Applied Electrochemistry Model

S-3A oxygen analyzer during the final 10 min of exposure. Oxygen consumption was calculated for upstream flow monitoring and  $O_2$  analysis of dry,  $CO_2$ -free air according to the method of Depocas and Hart (1957); all volumes reported are standard temperature and pressure, dry (STPD). Flow rates of air through the chamber averaged 600 ml/min at moderate  $T_a$  and nearly 3.0 liters/min at high temperatures (44–45 C). The higher rate of flow was utilized to maintain chamber humidity at a low level. At approximately 31 and 44 C, water loss and oxygen consumption were measured simultaneously. The former was accomplished by absorption of water vapor in the excurrent air stream, using tubes containing anhydrous calcium sulfate (Drierite). In these determinations, the birds rested on a wire platform above mineral oil, which prevented evaporation from voided urine and feces. Body temperature and mass were measured immediately before and after a 2-h test.

When chicks were exposed to low  $T_a$ ,  $T_b$  fell and the hatchlings became comatose. The recovery of behavioral capacity was examined as the animals passively warmed to higher temperatures (see Dawson et al.

1976). The  $T_b$  at which specific actions, such as vocalization or righting response, were resumed was measured with a quick-registering thermometer. The four animals in these experiments recovered completely from the cold exposure.

## RESULTS

### FIELD OBSERVATIONS

The location of the San Nicolas Island gull colony on an exposed, low-lying sand peninsula results in more moderate temperatures than elsewhere on the island. Shaded  $T_{air}$  in the colony during our study averaged 17 C at night and 25 C during the day; comparable temperatures for the interior of the island were 16 and 35 C. The radiant heat load in the colony during the day was considerable, with  $T_{soil}$  reaching 49 C and remaining above 45 C for at least 2 h each day. Sand and air temperatures were similar at night.

Body temperatures of 12 hatchling gulls brooded in their nests and measured between 0900 and 2000 h PDT averaged 38.0 C ( $\pm 0.60$  SE). Young chicks exposed in the nest during midday began to heat rapidly; body temperature rose as fast as 1 C/min (fig. 1). The fate of any chick un-

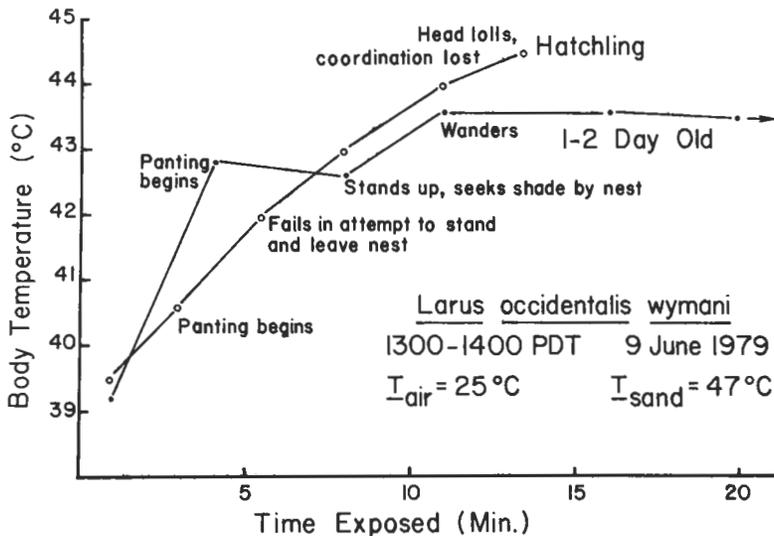


FIG. 1.—Rise in body temperatures upon diurnal exposure of a hatchling (open circles) and a 1-2-day-old western gull chick (closed circles).

attended by a parent depends largely upon its age. Hatching animals that recently emerged from their eggs are uncoordinated and unable to escape from the nest. They begin panting when  $T_b$  exceeds 40 C and make attempts to stand up and leave the nest. These are usually unsuccessful and coordination and equilibrium are lost at 44–45 C. They are then unable to effect any further directed attempts at escape, and death would occur with prolonged exposure. Loss of coordination occurred with 13 (fig. 1) and 25 min of midday exposure of two recently hatched chicks. It should be noted, however, that these  $T_b$  are not in themselves fatal or injurious, at least over the short term. We discovered one unconscious hatchling with a  $T_b$  of 46.2 C, which had been pinned beneath a sibling. It recovered in the shade and was returned to its nest.

Older chicks are able to escape from the nest upon heat exposure. One 15-h-old hatchling and three chicks approximately 1–2 days old were exposed to direct solar radiation. Body temperature rose rapidly, thereby reducing the tendency of the chicks to gain heat from the environment. Panting did not begin until  $T_b$  exceeded 42 C. The chicks then stood up and left the nest. The 15-h chick at a  $T_b$  of 44.5 C ran for shade under the vegetation. The older chicks continued wandering in the nest area, and their  $T_b$ 's stabilized at 43–44 C for periods in excess of 10 min.

At night when  $T_{air}$  and  $T_{soil}$  were 16–17 C, exposed hatchlings became hypothermic (fig. 2), body temperatures of three individuals dropping 5.4, 7.5, and 8.5 C during the first hour of exposure. Motor control and vocalization were progressively lost as  $T_b$  dropped below approximately 30 C. The sequence of loss of these behaviors corresponded inversely to their recovery upon rewarming (see below). Chicks were rewarmed under a lamp before being returned to their nests.

#### LABORATORY OBSERVATIONS

**Body temperature.**—Body temperatures at the conclusion of 2-h tests at single  $T_a$

between approximately 10–45 C are illustrated in figure 3. Body temperature is relatively stable between  $T_a$  of 20 and 35 C and is described by the equation:  $T_b = 33.75 + 0.147 T_a$ , where  $T_b$  and  $T_a$  are in degrees Celsius (no. = 26;  $F = 17.51$ ;  $P < .01$ ). Below 20 C animals tended to become hypothermic, cooling to between 33 and 18 C over the course of the 2-h experiments at 16–18 C. The three birds tested at 44 C ( $T_a$ ) became hyperthermic.

**Oxygen consumption.**—The relation of oxygen consumption ( $\dot{V}_{O_2}$ ) to  $T_a$  at the completion of the 2-h tests is also illustrated in figure 3. The  $\dot{V}_{O_2}$  for individuals remaining

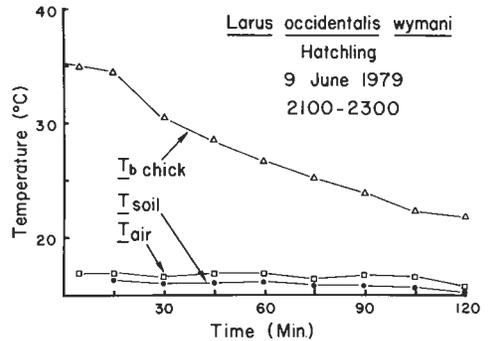


FIG. 2.—Decline in  $T_b$  upon nocturnal exposure of a hatchling western gull.

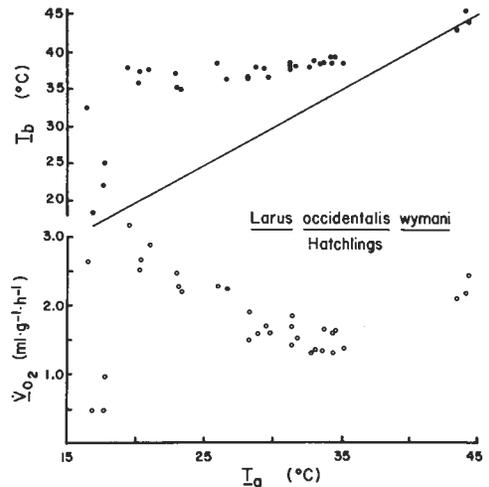


FIG. 3.— $T_b$  and oxygen consumption  $\dot{V}_{O_2}$  of hatchling western gulls after 2 h at various  $T_a$ .

homeothermic throughout these tests reached a minimum of  $1.48 \pm 0.05$  SE ml  $(g \cdot h)^{-1}$  ( $8.26$  mW  $\cdot g^{-1}$ ) at  $T_a$ 's of 32.8–35.2 C. For comparative purposes, we have taken this as representing the basal metabolic rate (BMR) for the hatchlings (mean body mass,  $58.0 \pm 1.47$  SE g). Below ca. 33 C,  $\dot{V}_{O_2}$  rises with decreasing  $T_a$  down to approximately 19.5 C (fig. 3). This relation appears linear and is described by the equation  $\dot{V}_{O_2} = 5.36 - 0.13 T_a$ , where  $\dot{V}_{O_2}$  and  $T_a$  are in ml  $O_2$   $(g \cdot h)^{-1}$  and  $^{\circ}C$ , respectively. Below 19.5 C the chicks did not sustain elevated metabolic rates over 2-h tests. The capacities of three chicks for heat defense were assessed at 44–45 C. Their  $\dot{V}_{O_2}$  at the end of 2 h were between 2.0 and 2.5 ml  $O_2$   $(g \cdot h)^{-1}$  ( $11.2$ – $14.0$  mW  $\cdot g^{-1}$ ). This elevation above basal level probably reflects the efforts being expended in evaporative cooling (see below), but may also be related to the hyperthermia that developed (fig. 3).

**Evaporative cooling.**—Rates of evaporative water loss ( $\dot{m}_{we}$ ) were determined for four hatchlings at 31.4–31.8 C and for three at 42.9–44 C, as well. The rates averaged 2.07 and 19.53 mg  $(g \cdot h)^{-1}$ , representing dissipation of 1.40 and 13.17 mW  $\cdot g^{-1}$ , respectively. The higher rates were accompanied by vigorous panting movements. They allowed the three birds to dissipate an average of 105% of their heat production at 43–44 C. Such a figure imparts little capacity for maintaining  $T_b$  below  $T_a$ , as indicated by data included in figure 3.

**Down thickness.**—Hatchling western gulls appear well insulated once their down becomes fluffy following emergence. The thickness of the dorsal down coat ranges from 10 to 13 mm (mean, 11.2 mm). Individual filoplumes which reach 15 mm in length are scattered through the down. The thickness of the ventral coat measured on the midline 2 cm anterior to the remnant of the yolk sac ranges from 9 to 10 mm and averages 9.8 mm.

**Heat transfer coefficients.**—Simultaneous measurements of  $\dot{V}_{O_2}$ ,  $T_b$ ,  $T_a$ , and, in certain instances,  $\dot{m}_{we}$  for hatchling gulls permit estimation of heat transfer (thermal conductance) coefficients with the following

equations:  $h = \dot{H}_m(T_b - T_a)^{-1}$  and  $h_d = (\dot{H}_m - H_e)(T_b - T_a)^{-1}$ . The symbols  $h$  and  $h_d$  represent an overall heat transfer coefficient and such a coefficient corrected for evaporative cooling, respectively;  $\dot{H}_m$  is rate of heat production in calories  $(g \cdot h)^{-1}$  (taken as the product of  $4.8 \times \dot{V}_{O_2}$ );  $H_e$  is the rate of evaporative cooling in calories  $(g \cdot h)^{-1}$  (taken as the product of  $0.58 \times \dot{m}_{we}$ ); and  $T_b$  and  $T_a$  are in degrees Celsius. Values for  $h$  and the few available for  $h_d$  are plotted in figure 4. In the former case, results of observations at  $T_a > 35$  C have been excluded as the augmentation of  $\dot{m}_{we}$  in this range probably produces serious distortion of the values. Below  $T_a = 34$  C, where  $\dot{m}_{we}$  is not strongly temperature dependent,  $h$  gradually declines with decreasing  $T_a$ , suggesting some capacity on the part of chicks for adjusting nonevaporative heat loss. Minimal values of  $h$  in our tests lie between 16 and 25 C in animals maintaining  $T_b$  in excess of 30 C. The eight obtained range from 0.74 to 0.90 cal  $(g \cdot h \cdot C)^{-1}$  ( $0.86$ – $1.05$  mW  $\cdot g^{-1} \cdot C^{-1}$ ) and average  $0.81 \pm 0.017$  SE cal  $(g \cdot h \cdot C)^{-1}$  ( $0.94 \pm 0.20$  SE mW  $\cdot g^{-1} \cdot C^{-1}$ ).

With Meeh's formula for surface area ( $cm^2 = 10 g^{0.67}$ ), these heat transfer coefficients can be converted to surface-specific terms (keeping in mind that this

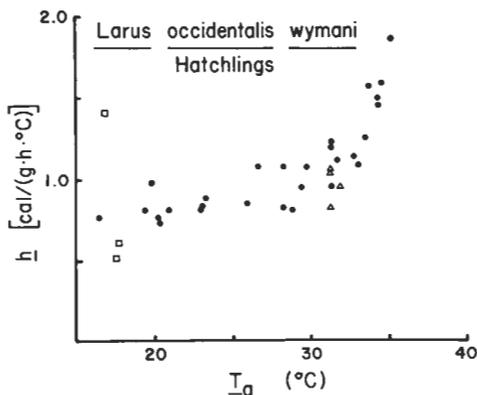


FIG. 4.—Heat transfer coefficients (thermal conductance) of hatchling western gulls over a range of  $T_a$ . Closed circles = total values ( $h$ ) for normothermic chicks ( $T_b > 30$  C); squares = total values ( $h$ ) for hypothermic chicks ( $T_b \leq 25$  C); triangles = values ( $h_d$ ) corrected for evaporative water loss.

formula may not adequately estimate the outer surface area of the down, which is the important quantity for heat transfer). The coefficients in these terms (identified as  $h'$ ) range from 0.28 to 0.34 cal (cm<sup>2</sup>·h·C)<sup>-1</sup> (0.33–0.40 mW·cm<sup>-2</sup>·C<sup>-1</sup>) and average 0.31 ± 0.006 SE cal (cm<sup>2</sup>·h·C)<sup>-1</sup> (0.36 ± 0.007 SE mW·cm<sup>-2</sup>·C<sup>-1</sup>). In four metabolic tests at 31.4–31.8 C, simultaneous measurements of evaporative water loss allow determination of values of  $h_d$ , which average 0.96 ± 0.052 SE cal (g·h·C)<sup>-1</sup> (1.12 ± 0.060 mW·g<sup>-1</sup>C<sup>-1</sup>) versus 1.14 ± 0.061 SE cal (g·h·C)<sup>-1</sup> (1.33 ± 0.071 SE mW·g<sup>-1</sup>·C<sup>-1</sup>) for corresponding values of  $h$ . In surface specific terms, these values for  $h_d$  and  $h$  become 0.37 cal (cm<sup>2</sup>·h·C)<sup>-1</sup> (0.43 mW·cm<sup>-2</sup>·C<sup>-1</sup>) and 0.44 cal (cm<sup>2</sup>·h·C)<sup>-1</sup> (0.51 mW·cm<sup>-2</sup>·C<sup>-1</sup>), respectively. The latter coefficient thus exceeds  $h_d$  by approximately 18% at 31–32 C. This approximates the 20% noted in a comparison of  $h$  and  $h_d$  for the ring-billed gull at 25 C (Dawson et al. 1976).

#### RECOVERY FROM CHILLING

When exposed to  $T_a$ 's below 20 C, hatchling western gulls do not remain homeothermic and approach the  $T_a$  of their environment. They become comatose during hypothermia, losing all motor activity and responsiveness to external stimuli. As these chicks recover in a warm environment, motor functions and alertness reappear in a repeatable sequence over a narrow range of body temperatures. Table 1 summarizes the events, the sequence of their recovery, and the mean  $T_b$  in four hatchling western gulls heated at 0.30–0.33 C  $T_b$ /min. The chicks were chilled to  $T_b$ 's of 14–18 C and placed on their backs under an incandescent electric light. The first sign of recovery is a slight leg movement, which turns into leg shivering at 21 C. This becomes more vigorous with warming and is very pronounced at 25 C, accompanied by leg kicking. Wing movements, possibly indicative of pectoral shivering, begin at 20 C. More pronounced recovery begins at 28–30 C: the chicks begin to call weakly; their eyes open, although they are unresponsive to visual

TABLE 1

MEAN BODY TEMPERATURE OF RECOVERY OF FUNCTION UPON REWARMING AFTER COLD-INDUCED TORPOR IN HATCHLING GULLS

RESPONSE	$T_b$ (C)	
	Western Gull <sup>a</sup>	Ring-billed Gull <sup>b</sup>
First leg movement.....	19.5	17.5
Wing shivering begins.....	20.2	26
Leg shivering begins.....	21.2	20
First head movement.....	22.6	23
Vigorous leg shiver.....	24.8	...
First weak vocalization....	28.1	21
Eye opens.....	28.3	22
Rights self.....	29.5	26
First raucous call.....	29.5	26
Sits up.....	31.6	...
Response to visual stimulus	32.0	24
Wandering.....	35.5	28

<sup>a</sup> Mean body mass, 58 g; warming rate, 0.30–0.33 C/min; no. = 4.

<sup>b</sup> Mean body mass, 31 g; warming rate, 0.10–0.13 C/min; no. = 6 (data from Dawson et al. 1976).

stimuli; and they turn over to lie on their stomachs. At this point, their call becomes louder and more frequent. The chicks sit up and responsiveness to visual stimuli is regained at 32 C. They begin to wander at 35–36 C, where recovery appears complete. Following recovery, the animals ate vigorously and were subsequently returned to their respective nests.

#### DISCUSSION

In attempting to synthesize laboratory and field observations on the thermal responses of hatchling western gulls, it seems appropriate to develop some comparative perspective concerning various quantitative features of their thermoregulatory system. These features pertain primarily to insulation, metabolic level, thermogenic capacity, and evaporative capacity.

Minimal values for the heat transfer coefficient  $h$  average 0.94 ± 0.20 SE mW (g·C)<sup>-1</sup> (range, 0.86–1.05 mW·g<sup>-1</sup>·C<sup>-1</sup>) in hatchling western gulls from San Nicholas Island. Mean minimal values of  $h$  for hatchlings of other gulls are given in table 2. The reciprocal of this coefficient represents a rough index of insulation, and the tabulation presented thus suggests some

TABLE 2

METABOLIC AND THERMOREGULATORY CHARACTERISTICS OF HATCHLING (&lt;24 h) GULLS

SPECIES	BODY MASS (g)	HEAT TRANSFER COEFFICIENT ( <i>h</i> )		BMR AS % OF ADULT LEVEL <sup>a</sup>		THERMOGENIC RATIO <sup>b</sup>	EVAPO-RATIVE COOLING RATIO <sup>c</sup>	REFERENCE
		(mW·g <sup>-1</sup> ·°C <sup>-1</sup> )	(mW·g <sup>-0.46</sup> ·°C <sup>-1</sup> )	A-P <sub>α</sub>	A-P <sub>ρ</sub>			
<i>Larus argentatus</i> :								
Day	57.4	...	...	80	(101)	...	...	Drent 1967
Day <sup>d</sup>	...	.87	7.79	...	...	3.4	...	Dunn 1976
Night	59.1	...	...	(62)	78	...	...	Koskimies unpubl., cited in Drent 1967
<i>L. atricilla</i>	28.4	1.12	6.82	96	121	1.5	1.2	Dawson et al. 1972
<i>L. delawarensis</i>	34.06	.99	6.71	82	103	2.1	1.5-2.0	Dawson et al. 1976
<i>L. occidentalis</i> :								
<i>L. o. livens</i>	65.4	.84	8.03	82	103	1.8	...	Dawson and Bennett 1980
<i>L. o. wymani</i>	58.0	.94	8.42	86	109	1.9	1.1	This study
<i>L. ridibundus</i>	26.8	...	...	(108)	135	2.1	...	Kespaik and Davydov 1966, Palokangas and Hissa 1971

<sup>a</sup> The adult level is that predicted for a nonpasserine of similar body mass, using the Aschoff-Pohl (1970) equations for the BMR of animals during the active (A-P<sub>α</sub>) and resting (A-P<sub>ρ</sub>) phases of their daily cycle. The less pertinent percentage is enclosed within parentheses.

<sup>b</sup> Thermogenic ratio is the factor by which the maximal metabolic rate observed at cool T<sub>a</sub> is related to BMR of hatchlings.

<sup>c</sup> Evaporative cooling ratio represents rate of evaporative cooling/concurrent rate of heat production.

<sup>d</sup> Dunn (1976) does not indicate the body mass of the chicks she studied. The apparent BMR of these individuals appears substantially less than the mean value reported by Drent (1967) for hatchlings of *L. argentatus* during the day (<4.8 cal g<sup>-1</sup>·h<sup>-1</sup> vs. 6.62 cal g<sup>-1</sup>·h<sup>-1</sup>). Dunn presents only a few metabolic values, and the figures for *h* and thermogenic ratio should probably be regarded only as provisional estimates, pending acquisition of further data.

minor differences in heat-conserving abilities among hatchlings of the various species. The most conspicuous variable with which these differences might be linked is body size. The coefficient *h*, when expressed on a mass-specific basis, has been shown to scale with the -0.54 power of body mass (Calder and King 1974), so the effect of any differences in size should be eliminated by expression of *h/g*<sup>0.46</sup>. Values expressed in this manner are also presented in table 2. The variation evident among them seems uncorrelated with climatic conditions in the breeding ranges of the various taxa (cf. values for *Larus atricilla* and *L. delawarensis*, which breed in subtropical and tropical maritime situations and mid-latitude inland areas, respectively). Perhaps this reflects the efficacy of the brooding that hatchling gulls ordinarily receive from their parents or the fact that these young show considerable tolerance of acute hypothermia.

Calder and King (1974) provide an equation relating *h* for adult nonpasserines to

body mass:  $h = 4.72 m^{-0.54}$ , where *h* is in mW (g·C)<sup>-1</sup> and *m* is body mass in g. The value predicted with this equation for a 58 g adult is 0.52 mW (g·C)<sup>-1</sup>. This is only 55% of the mean minimal value for *h*, 0.94 mW (g·C)<sup>-1</sup>, determined for chicks of the western gull from San Nicolas Island. As was found for gull hatchlings of other species (Dawson et al. 1976; Dawson and Bennett 1980), the insulative capacities of the chicks in our study thus are initially well below those expected for adult birds of comparable size.

The value of 8.26 mW·g<sup>-1</sup> that we have taken as the basal metabolic rate (BMR) for the hatchling western gulls from San Nicolas Island can be conveniently compared with values predicted for a 58-g adult nonpasserine, using allometric equations based on those of Aschoff and Pohl (1970). These equations give BMRs of 9.55 and 7.59 mW·g<sup>-1</sup> for an adult nonpasserine this size in the active (α) and inactive (ρ) portions of its daily cycle, respectively. The

observed rate for the chicks thus represents 86% ( $\alpha$ ) and 109% ( $\rho$ ) of the predicted values. Since our determinations were made during the daytime, the former percentage appears more pertinent. The hatchling western gulls thus may be regarded as having a BMR that is slightly below the level in adult nonpasserines of similar size. In this, they resemble gull chicks of most other species (table 2). However, chicks of ducks and gallinaceous birds, which generally are considered to be more precocial than those of gulls, show BMRs that tend to be proportionately much lower than those of adult birds of similar size (Koskimies 1962; Koskimies and Lahti 1964; see also table 2 in Dawson et al. 1976).

As noted above, the insulation of hatchling gulls seems limited by adult standards. Their abilities to remain homeothermic when unbrooded by a parent in moderate and cool environments thus depend primarily upon capacities for chemical thermoregulation. Previous studies (table 2) have indicated that these capacities are substantially more modest than those generally noted for adult birds (Dawson and Hudson 1970), usually not involving much more than a doubling of heat production over BMR (see Dawson et al. [1976] and Dawson and Bennett [1980] for detailed comparisons). Hatchlings representing the taxa of the western gull that have been studied conform to this pattern. Thermogenesis as it exists in gulls appears to occur primarily through shivering. If nonshivering thermogenesis does exist, it does not appear to be mediated by either catecholamines or to involve brown fat (Palokangas and Hissa 1971). Shivering by very young chicks probably depends primarily on the leg musculature, owing to its relatively large mass. The role of the limbs in heat production is considered further in connection with discussion of the events leading to recovery of chicks from hypothermia.

Our three measurements of evaporative water loss by hatchling western gulls at 43–44 C indicate that these chicks barely dissipate the heat produced by their metabolism at these temperatures. This is similar to the

performance of the laughing gull (*L. atricilla*) but is surpassed by that of the ring-billed gull (*L. delawarensis*) (table 2). The apparent differences between chicks of these latter two species and those of the western gull seem to reflect differences in both evaporative capacity and heat production at high  $T_a$ . The rates of evaporation by young western gulls at 43–44 C reach only 71% of the maximum value predicted for an adult bird of similar size, using the equation  $\dot{m}_{we} = 258.6 m^{0.80}$ , where  $\dot{m}_{we}$  is in mg H<sub>2</sub>O evaporated per minute and  $m$  is body mass in kilograms (Calder and King 1974, p. 337). On the other hand, rates for hatchling ring-billed gulls in this temperature range (Dawson et al. 1976) essentially match the value predicted for a 34.6-g adult. With regard to heat production, neither the laughing gull nor the ring-billed gull show a significant trend of metabolic rate with temperature above 35 C (Dawson et al. 1972, 1976), whereas the metabolic rates of the three western gull chicks at 43–44 C are approximately 50% above BMR. It is difficult to envision large-scale differences in the partial efficiencies of panting among such closely related species, and this leads us to suspect that the higher metabolic rates at 43–44 C in our western gull chicks are linked with greater restlessness in the heat.

Recovery of functional capacities by hatchlings of the western gull during arousal from a hypothermic state approximates the sequence noted in chilled ring-billed gulls of similar age (Dawson et al. 1976). Chicks of both species enter deep hypothermia in cool environments and recover completely upon rewarming. However, the ring-billed gull chicks generally regain competence at lower  $T_b$ 's than do western gull hatchlings (table 1). Vocalization and reestablishment of the righting and visual responses all occur at substantially lower body temperatures in the former species. Under laboratory conditions, ring-billed chicks recover and begin wandering and seeking shelter at temperatures where western gull chicks are still comatose. This comparison suggests the intriguing possibility of differences in the in-

ternal temperature thresholds for components of muscular thermogenesis in these species. In ring-billed gulls, muscular activity beginning at an esophageal temperature of 17.5 C was restricted to the legs, visible pectoral shivering commencing only after righting (26 C). In western gulls, on the other hand, muscular contractions in these areas began at virtually the same rectal temperature (20 C). If temperatures within the neuromuscular system approximate the measures of  $T_b$  employed, quite different thermal thresholds for particular behaviors appear to separate chicks of these species, and these are among the most pronounced interspecific differences in thermal response found in our studies on hatchling *Larus*. It should be noted, however, that rate of heating in this study was greater than that on the ring-billed hatchlings and the influence of this variable is not known (see table 1).

The limitations of the thermoregulatory capacities of western gull hatchlings in moderate cold or under direct insolation remind us that the functional thermoregulatory unit for these chicks in nature includes an attentive parent. The limited abilities of these young birds to balance thermogenesis and thermolysis generally suffice when accompanied by the brooding or shading provided by an adult. However, disruption of attentive patterns through agonistic behavior on the part of adults, death of one of the parents, or entry of predators such as foxes into breeding colonies can threaten the thermostasis of the chicks. Should a disruption occur at night, these young animals are threatened with hypothermia in the cool evening air. While this can lead to loss of neuromotor coordination, animals that had been cooled to 14–18 C fully recovered when rewarmed. At these temperatures, no capacity for spontaneous rewarming was evident, owing in part to the loss of any substantial capacity for muscular thermogenesis. The limitations of cold defense apparent immediately after hatching in unbrooded chicks disappear in the next few days (Bartholomew and Dawson 1954) with the further growth and development

of these birds. These processes lead to improved thermoregulatory capacities and to enhanced locomotor abilities, which allow movement into more favorable microenvironments. The efficacy of using shelter at night has earlier been documented for chicks of the western gull on Santa Barbara Island, California (*L. o. wymani*), and on Isla Angel de la Guarda, Baja California Norte, Mexico (*L. o. livens*) (Bartholomew and Dawson 1952, 1954).

The tolerance of hatchlings for hypothermia affords a relatively wide safety margin when parental attentiveness is interrupted under cool night conditions, but the same is not true during the day. Hatchlings can tolerate short-term elevations of  $T_b$  amounting to 6–8 C above levels maintained in the absence of thermal stress (fig. 3). This provides some margin of safety, but the rapidity with which the late May and early June sun can heat the hatchlings on San Nicolas Island suggests that they would be at substantial risk were there to be any prolonged disruption of parental attentiveness at midday.

The limited powers of heat defense apparent in western gull chicks make the location of breeding colonies for this species of critical importance. On San Nicolas Island, the colony is located on the exposed windward side of the island where the coolest air temperatures (see Results) and most favorable conditions for convective heat loss occur (see Bennett, Dawson, and Putnam 1980). The period of our study coincided with a heat wave in southern California and adjacent coastal waters, owing to a Santa Ana wind condition. No mortality due to this was observed during our study. However, the mortality rate of western gull chicks reached 90% on the leeward portion of Santa Barbara Island, 50 km to the northeast. Young in nests located on the windward portion of this island had a considerably lower incidence of mortality (G. Hunt, personal communication).

The observations on risks of overheating in western gulls appear to have relevance to a broad spectrum of environments in

which gulls breed. The problems of solar radiation for eggs and young in tropical and subtropical environments are well appreciated (see Howell, Araya, and Millie 1974; Bartholomew and Dawson 1979; Bennett and Dawson 1979). However, the problem is also apparent at mid- and high-temperate latitudes where exposure of young gull chicks to direct solar radiation with disruption of parental attentiveness can lead

to overheating and death (Barth 1951; Drent 1967; Dawson et al. 1976). As analysis of thermoregulatory capacities of young gulls proceeds, it will be important to consider not only the physiology of the young but the location of colony and nest sites as they affect heat exchange as well. Selection of colony site or nest site within a colony may well be crucial to successful rearing of young gulls.

## LITERATURE CITED

- ASCHOFF, J., and H. POHL. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* **29**: 1541-1552.
- BARTH, E. K. 1951. Kropptemperatur hos måkeunger. *Nytt Mag. Naturvidenskapene* **88**:213-245.
- BARTHOLOMEW, G. A., and W. R. DAWSON. 1952. Body temperature in nestling Western Gulls. *Condor* **54**:58-60.
- . 1954. Temperature regulation in young pelicans, herons, and gulls. *Ecology* **35**:466-472.
- . 1979. Thermoregulatory behavior during incubation in Heermann's gulls. *Physiol. Zool.* **52**:422-437.
- BENNETT, A. F., and W. R. DAWSON. 1979. Physiological responses of embryonic Heermann's gulls to temperature. *Physiol. Zool.* **52**:413-421.
- BENNETT, A. F., W. R. DAWSON, and R. W. PUTNAM. 1980. Thermal environment and tolerance of embryonic western gulls. *Physiol. Zool.* (**54**): 146-154.
- CALDER, W. A., and J. R. KING. 1974. Thermal and caloric relations of birds. Pages 259-413 in D. S. FARNER and J. R. KING, eds. *Avian biology*. Vol. 4. Academic Press, New York.
- DAWSON, W. R., and A. F. BENNETT. 1980. Metabolism and thermoregulation in hatchling western gulls (*Larus occidentalis livens*). *Condor* **82**:103-105.
- 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., and J. W. HUDSON. 1970. Birds. Pages 223-310 in G. C. WHITTOW, ed. *Comparative Physiology of Thermoregulation*. Vol. 1. Academic Press, New York.
- to overheating and death (Barth 1951; Drent 1967; Dawson et al. 1976). As analysis of thermoregulatory capacities of young gulls proceeds, it will be important to consider not only the physiology of the young but the location of colony and nest sites as they affect heat exchange as well. Selection of colony site or nest site within a colony may well be crucial to successful rearing of young gulls.
- DAWSON, W. R., J. W., HUDSON, and R. W. HILL. 1972. Temperature regulation in newly hatched laughing gulls (*Larus atricilla*). *Condor* **74**: 177-184.
- DEPOCAS, F., and J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* **10**:388-392.
- DRENT, R. H. 1967. Functional aspects of incubation in the herring gull (*Larus argentatus* Pont.). Brill, Leiden.
- DUNN, E. H. 1976. The development of endothermy and existence energy expenditure in herring gull chicks. *Condor* **78**:493-498.
- HOWELL, T. R., B. ARAYA, and W. R. MILLIE. 1974. Breeding biology of the gray gull, *Larus modestus*. *Univ. California Pub. Zool.* **104**:1-57.
- KESPAIK, J., and A. DAVYDOV. 1966. Factors determining the cold-hardiness of the *Larus ridibundus* L. on the first day after hatching [in Russian, English summary]. *Toimestised Eesti NSV Teaduste Akademia XV, Biol. Ser.* **4**, pp. 485-491.
- KOSKIMIES, J. 1962. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. *Ricerche Zool. Appl. Caccia* **4** (suppl.): 149-160.
- KOSKIMIES, J., and L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. *Auk* **81**:281-307.
- PALOKANGAS, R., and R. HISSA. 1971. Thermoregulation in young black-headed gull (*Larus ridibundus* L.). *Comp. Biochem. Physiol.* **38A**: 743-750.