The Condor 86:339–341
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THERMOREGULATION IN NEWLY HATCHED BLACK-LEGGED KITTIWAKES

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The development of gull chicks is typically considered semi-precocial, because the birds remain in or near the nest for some days after hatching and depend on parental care, but hatch with downy coverings and possess some thermoregulatory ability (Drent 1967; Palokangas and Hissa 1971; Dawson et al. 1972, 1976; Dunn 1976; Dawson and Bennett 1980, 1981). Newly hatched chicks of several gull species in the genus *Larus* have been studied with respect to thermoregulatory function. These studies suggest that the heat transfer coefficient (conductance) is not correlated with climatic conditions in the breeding area, whereas the thermogenic ratio (maximum increase in metabolism during cold-exposure) seems to show some correlation with breeding distribution (Dawson and Bennett 1981). Thus, chicks of the Common Black-headed Gull (*L. ridibundus*) and the Ring-billed Gull (*L. delawarensis*) can double their metabolic rate above the basal rate (BMR) when exposed to cold (Palokangas and Hissa 1971, Dawson et al. 1976), whereas those of the Laughing Gull (*L. atricilla*), which breed in warmer climates, are able to increase their metabolic rate by only 50% (Dawson et al. 1972).

The Black-legged Kittiwake (*Rissa tridactyla*) has a circumpolar holarctic distribution, breeding in tundra, boreal, and temperate climatic zones (Voous 1960). Since the kittiwake thus breeds farther north than most other gulls, one could hypothesize that the chicks have special thermoregulatory capabilities. To test this, we studied body temperature regulation in newly hatched chicks of kittiwakes breeding at 79°N latitude.

MATERIAL AND METHODS

We conducted our study at Ny Aalesund, Svalbard (79°N, 12°W) during June and July 1982. Ambient temperature during the study period ranged from 0°C to 5°C. Eggs were collected from a nearby colony and placed in a temperature-controlled incubator. The incubator was kept at 37°C and 60% relative humidity. After hatching, the chicks were allowed to dry before being used in experiments. The mean body weight of the chicks was 33.3 g (SD = 2.0 g, n = 11).

Oxygen consumption ($\dot{V}_{O_2}$) was measured by a manometric respirometer, which was connected to a compensatory chamber by a water-filled V-shaped tube. A 25% NaOH solution acted as CO_2-absorber in the respirometer chamber. Constant pressure was assured by injecting pure oxygen from a graduated syringe into the respirometer chamber. The amount of oxygen injected equalled the oxygen consumed. All values of $\dot{V}_{O_2}$ are given in STPD conditions. Immediately after an experiment, body temperature (T_B) was measured using a thermocouple placed in the rectum. Measurements of oxygen consumption and body temperature were obtained after two hours exposure to the experimental (ambient) temperature (T_A). The ambient temperature was varied betwen 15.5°C and 40°C by adjusting the temperature of the thermostat-controlled water-bath in which the manometric chambers were submerged. During periods of stabilization, the respirometer chamber was flushed with atmospheric air at a rate of 100 ml min^{-1}.

In order to measure respiratory frequency during heat stress, chicks were heated by applying a heat lamp (60 W) at an appropriate distance (15–25 cm). Body temperature was measured with a thermocouple placed in the rectum. The placement of the heat lamp was adjusted to give a heating rate of 0.2–0.3°C min^{-1}. The breathing rate was counted visually and the frequency calculated by counting the frequency during defined time periods using a stopwatch.

RESULTS AND DISCUSSION

The thermoneutral zone for the hatchling kittiwakes was very narrow and extended from 33°C to 35°C (Fig. 1). The basal metabolic rate at thermoneutrality was 1.34 ml O_2 g^{-1} h^{-1} (7.48 mW g^{-1}) and the mean T_B was 37.9°C. The measured metabolic rate was only 67% of the predicted rate for an adult non-passerine bird of similar size in the activity phase (α-phase), which is 11.09 mW g^{-1} (Aschoff and Pohl 1970). In other species of gulls, BMRs of chicks range between 82% and 121% of the expected adult level (Dawson and Bennett 1981).

At T_As exceeding the thermoneutral zone both $\dot{V}_{O_2}$ and T_B increased (Fig. 1). In addition, the respiratory frequency also increased as T_B exceeded the thermoneutral level (Fig.

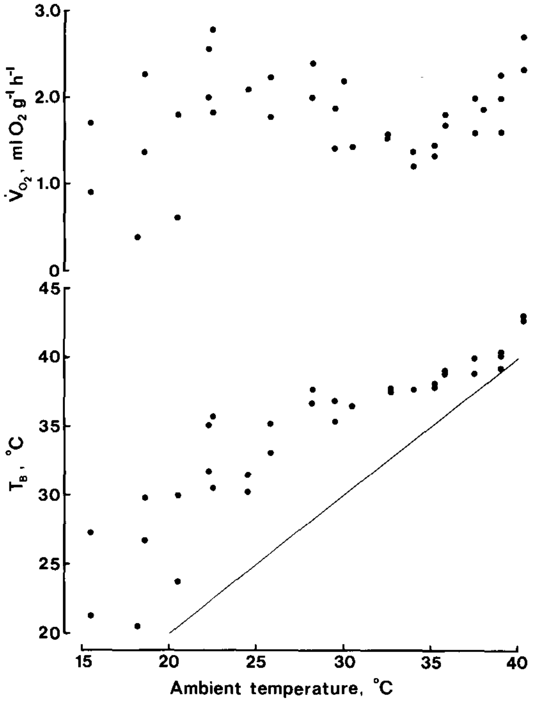

FIGURE 1. Relation of oxygen consumption ($\dot{V}_{O_2}$) and body temperature (T_B) after two hours exposure to different ambient temperatures in hatchling Black-legged Kittiwakes. Each point represents one experiment. Data are from 11 chicks. Each chick was tested at two to four different ambient temperatures (chosen randomly), and two to three hours elapsed between successive measurements on a given chick. The diagonal line marks equivalence between ambient and body temperature.

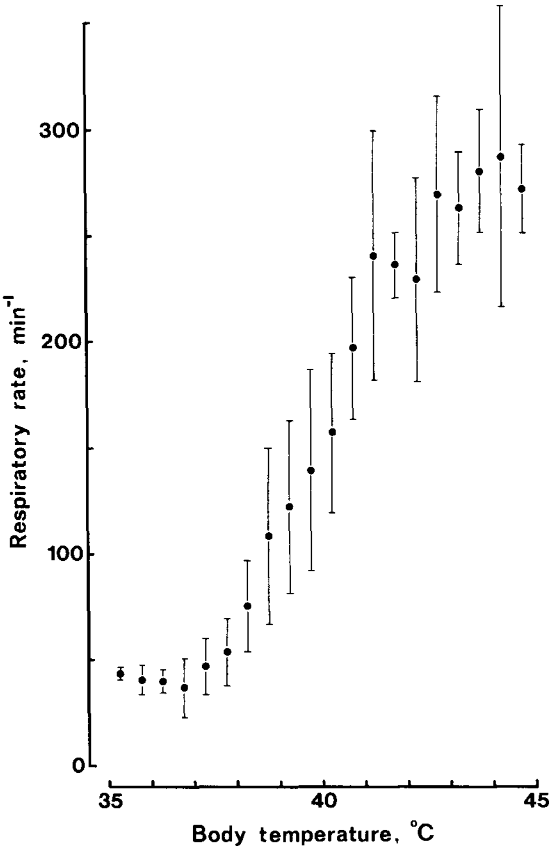

FIGURE 2. Respiratory rate in relation to body temperature in hatchling Black-legged Kittiwakes, based on 303 measurements from eight chicks. For each half-degree interval, the mean value ± 1 SD is given. Each value is thus based on from 3 to 27 measurements (mean 15).

2), which suggests that evaporative cooling mechanisms were elicited. Since the body temperature in adult kittiwakes (given as 39.8°C by Brent et al. [1983] and 40.3°C by Barrett [1978]) is about 2°C higher than the thermoneutral T_B in the chicks (37.9°C, Fig. 1), the present data support the idea that in newly hatched chicks the thermoregulatory set-point is below that of an adult (Myhre 1978, Myhre and Steen 1979). (The set-point is an assumed reference temperature of the body, deviations from which elicit thermoregulatory mechanisms.) Maunder and Threlfall (1972) and Barrett (1978) also reported sub-adult body temperatures in newly hatched kittiwakes, being 35.0°C and 38.9°C, respectively.

Below T_A of 33°C, $\dot{V}_{O_2}$ increased and at 22°C a maximum oxygen consumption was reached. Exposure to ambient temperatures below 22°C resulted in a reduced oxygen uptake (Fig. 1). Based on the mean $\dot{V}_{O_2}$ measured at 22°C (2.3 ml O_2 g^{-1} h^{-1}) and at thermoneutrality (1.34 ml O_2 g^{-1} h^{-1}) the thermogenic ratio becomes 1.72.

Maximum values of thermal conductance (h) occurred at ambient temperatures between 25.5°C and 30°C. The mean value of h was 0.247 ml O_2 g^{-1} h^{-1} $°C^{-1}$ (1.38 mW g^{-} $°C^{-1}$). The conductance was calculated as $\dot{V}_{O_2}/(T_B - T_A)$ and was thus equal to the "wet" thermal conductance according to Aschoff (1981). As the expected value of thermal conductance for an adult non-passerine bird in the α-phase is 0.97 mW g^{-1} $°C^{-1}$ (Aschoff 1981), the value for the kittiwake chicks was 42% higher than that for a non-passerine of the same size, i.e., the insulatory value is only 70% of the expected adult insulation. For an interspecific comparison, Dawson and Bennett (1981) expressed thermal conductance as mW $g^{-0.46}$ $°C^{-1}$, because h has been found to be mass-specific and to scale with the −0.54 power of body weight (Calder and King 1974). Expressed in this way, the thermal conductance of the kittiwake chicks becomes 9.16 mW $g^{-0.46}$ $°C^{-1}$. All other gull chicks for which this value has been calculated have thermal conductances in the range between 6.71 and 8.42 mW $g^{-0.46}$ $°C^{-1}$ (Dawson and Bennett 1981). Thus, the kittiwake chicks have the highest thermal conductance in relation to their weight found in newly hatched gulls.

Even though kittiwakes breed at high latitudes, the chicks hatch with a relatively poor thermoregulatory ability compared to other gull chicks. Their thermal conductance is higher and their basal metabolic rate is relatively low. In addition, the thermogenic ratio is within the range found in other species of gulls. Thus, kittiwake chicks must depend on parental care until endothermy is achieved at an age of six to eight days (Barrett 1978). The evolution of effective thermoregulatory ability in the newly hatched chicks has not been necessary for arctic-breeding gulls.

The study was supported by grants from the Danish Natural Science Research Council, G.E.C. Gads fond, and Tipsmidlerne. We thank Norsk Polarinstitutt for allowing us to use the facilities at Ny Aalesund.

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The Condor 86:341–342

PELAGIC RED CRABS AS FOOD FOR GULLS: A POSSIBLE BENEFIT OF EL NIÑO

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Swarms of live pelagic red crabs (*Pleuroncodes planipes*) began appearing in the surf and on beaches at San Nicolas Island (SNI; 33°15'N, 119°30'W), off southern California, in late December 1982. Although these crustaceans have occurred as far north as Monterey (Schmitt 1921, Glynn 1961), their distribution is centered off the western coast of Baja California and they occur only rarely in the Southern California Bight (SCB; Boyd 1967, Mais 1974). The most recent occurrence of this species north into the SCB was in 1972/1973 when a weak El Niño developed (G. Antonelis, pers. comm.). El Niño is defined as the appearance and persistence, for 6 to 18 months, of anomalously warm water in the Eastern Tropical Pacific (ETP) and is usually accompanied by large reductions in plankton, fish, and seabirds in many areas of the ETP (Barber and Chavez 1983, Cane 1983, Rasmussen and Wallace 1983). The most intense and unusual El Niño event in modern history began in May 1982 and was well developed by late autumn (Rasmussen and Hall 1983). This climatic change, which warmed coastal surface waters, and perhaps altered current flow in the SCB, appears to explain the northward extension of *Pleuroncodes* in 1982/1983.

The crabs continued to wash up on the beaches at SNI through July 1983 although they appeared to be most abundant from January through March and in early May. We also saw large numbers of crabs in the waters near San Miguel, San Clemente, Santa Catalina, Santa Barbara, and Los Coronados islands and in San Diego Bay.

From late December 1982 to early January 1983, the number of roosting Herring Gulls (*Larus argentatus*) also increased at several areas at SNI. This species is generally uncommon at and around the Southern California Channel Islands in winter although adults have been reported to be fairly common further offshore at that season (Yocom 1947, Sanger 1973, Harrington 1975, Garrett and Dunn 1981). Townsend (1968) reported "small numbers" of Herring Gulls at SNI from September through March, and Rett (1947) also noted these gulls in spring at SNI. Hunt et al. (1980) found 40 Herring Gulls at SNI in March 1976. We have also observed small numbers of these gulls at SNI in past years (Table 1). However, in late January 1983, 10,000 to 12,000 Herring Gulls roosted on SNI. These gulls were abundant through March and remained, in lesser numbers, through late April. Groups of several thousand birds roosted at four sites on SNI on rocky and sandy beaches and on rock ledges near the surf. These birds fed on live red crabs in the surf, or occasionally on those recently washed ashore. Small numbers of Ring-billed (*Larus delawarensis*), Heermann's (*L. heermanni*) and California (*L. californicus*) gulls were also present in winter 1983 but were not more abundant than in previous years (Table 1).

Western Gulls (*L. occidentalis*) breed at the western end of SNI in summer and roost there during other seasons (Schreiber 1970). In winter and spring, they usually roost on rookery areas at night, leave just after sunrise, and return just before or shortly after sunset. Roosts are usually abandoned by all birds during the day except during stormy or very foggy weather, when most birds remain at roosts continuously. In winter, roosting adult Western Gulls are territorial at rookery areas and presumably occupy those territories that are later used for breeding. Small groups of adult and immature gulls also roost along the coastline near the west end of SNI in late afternoon and during stormy or foggy weather. In winter and early spring 1983, when red crabs were abundant, most gulls roosted on territories at rookery areas continuously, regardless of weather. Individuals apparently left occasionally, however, to feed on red crabs in the surf and on those washed up on nearby beaches; feces and regurgitated pellets were composed almost entirely of crab exoskeletons in winter and early spring, 1983.

We also observed large numbers of Herring Gulls (8,000 to 10,000) and Western Gulls (1,000 to 2,000) roosting on several beaches on the northwest coast of San Miguel Island (SMI; 34°02'N, 120°22'W) and feeding on red crabs in the surf in late February 1983. Although we have no data on absolute abundance of Herring Gulls at SMI in past years, these gulls were relatively uncommon in winter from 1979 to 1982 (Stewart, pers. observ.). Hunt et al.

TABLE 1. Counts of roosting gulls at SNI in winter.

	L. argentatus		*L. occidentalis*		*L. delawarensis*		*L. heermanni*		
Date	Adults	Immatures	Adults	Immatures	Adults	Immatures	Adults	Immatures	*L. californicus*
1 Feb. 1980	104	8	375	29	84	11	15	11	16 (Total)
21 Feb. 1981	91	12	297	31	52 (Total)		19	10	22 (Total)
25 Jan. 1982	123	13	310	20	60 (Total)		25	10	10 (Total)
24 Jan. 1983	10,000–12,000	100–200	2,105[a]	279[a]	67 (Total)		13	12	13 (Total)

[a] Apparent increase due to change in roosting behavior during winter 1982/1983. See text for explanation.