THERMAL ENVIRONMENT AND TOLERANCE OF EMBRYONIC WESTERN GULLS[1]

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The thermal environment and tolerance of eggs and embryos of western gulls (*Larus occidentalis wymani*) on San Nicolas Island, California, were determined. Incubated egg temperature measured by telemetry ranged between 30 and 36 C and averaged 33.4 and 34.2 C for two different nests; the former underwent pronounced cycles of heating during the day and cooling at night. Exposed eggs underwent a daily thermal excursion between 6 and 50 C. Embryos could maintain heartbeat between 11 and 46 C. Eggs which are exposed to solar radiation heat slowly (about 5 C/h). Diurnal exposure during parental absence does not, therefore, result in embryonic mortality unless exposure persists for several hours. Embryos recover completely after overnight exposure to relatively cool temperatures. Short-term exposure does not, therefore, constitute an immediate threat to embryonic survival. Adult gulls in this colony do not closely defend their nests and will leave them exposed in the presence of an intruder. The behavior of the parent gull and physiological tolerance of the embryos in reference to the thermal environment form an adaptive suite of characters contrasting with those of other gulls nesting under hot and arid conditions.

INTRODUCTION

Parental incubation of eggs provides a relatively stable environment within which embryonic development of birds proceeds (White and Kinney 1974; Drent 1975). High and constant egg temperature is the most familiar result of this incubation; however, conditions affecting the water balance of the egg are also known to be important (Rahn, Ackerman, and Paganelli 1977). The nest environment is subject to considerable disruption when the parent bird leaves during feeding trips or in response to disturbance associated with predation or intraspecific intrusion in the nest area. Disruption will be particularly important for ground-nesting birds with exposed nests, such as many colonially nesting seabirds. Although considerations of the incubation process normally emphasize keeping the eggs warm, shading is an equally important parental task in environments dominated by solar radiation. Exposure of eggs in ground-nesting situations may produce rapid overheating and embryonic death because of high radiant heat loads on the eggs. Our previous studies (Bartholomew and Dawson 1979; Bennett and Dawson 1979) on a colony of Heermann's gulls (*Larus heermanni*) in a warm and arid environment indicated a potential for substantial thermal problems if incubation were disrupted. We now examine the

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thermal environment of the eggs of western gulls (*Larus occidentalis wymani*) in a cooler, more temperate situation and the thermal effects of temporary disruption of incubation. Embryos of approximately 1 wk development were studied since young avian embryos appear more susceptible to heat damage than do older ones (Romanoff 1960). A companion study examines thermoregulation in young hatchling birds in the same colony (Dawson and Bennett 1981).

MATERIAL AND METHODS

COLONY DESCRIPTION

The thermal environment of the eggs and embryos of western gulls was measured in early May, 1979, on San Nicolas Island, Ventura County, California (33°14′N, 119° 27′W). The nesting colony studied consisted of approximately 1,000 nesting pairs of birds and was restricted to a northwest-projecting peninsula on the western end of the island (fig. 1). The peninsula is an area of low-lying and gently sloping sand dunes, extensively covered with iceplant, *Gasoul* (*Mesembryanthemum*) *crystallinum*, sand verbena (*Abronia maritima*), silver beachwood (*Ambrosia chamissonis*), and locoweed (*Astragalus traskiae*). The gulls construct stick nests in and among clumps of this vegetation. In this locality the colony is directly exposed to the prevailing winds from the northwest. Moreover, morning fog is common. Consequently, this site (10–30 m in altitude) remains considerably cooler than the interior of the island, which rises to 300 m. Ground-level air temperatures in the shade during our study were recorded on Wahl Temperature Recorders (Models 732-27 and 731-16). Soil (sand) temperature in the colony was measured with a thermocouple coated with epoxy and sand and located 1–2 mm below the sand surface. This temperature was recorded at half-hour intervals throughout the study. Soil surface temperature was found to be the best indicator of heat stress in a similar study on a breeding colony of Heermann's gulls (Bartholomew and Dawson 1979). Air temperatures from other sections of the island were obtained from the Department of the Navy. Eggs were collected under California Scientific Collector's permit 514 to A. F. B. and U.S. Fish and Wildlife permit PRT 2-285-5C to George L. Hunt.

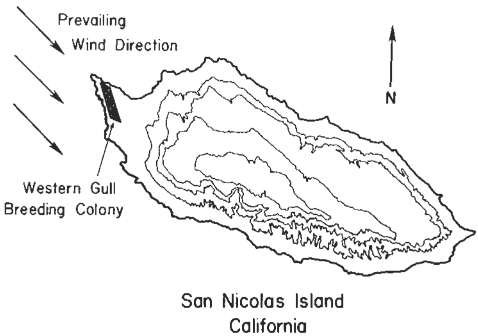

FIG. 1.—The location of the breeding colony of western gulls on San Nicolas Island, California. Elevation contours are 60 m.

THERMAL ENVIRONMENT OF GULL EGGS

Our study period coincided with a period of unusually high daytime temperatures and clear skies that fostered very hot conditions in the gull colony. The temperature of incubated eggs was estimated by use of egg models that were monitored continuously for a 3-day period during the middle of the nesting season. Construction of these models involved placing temperature transmitters in two eggs obtained from the colony. The transmitters (Model TT-1U, J. Stuart Enterprises, Grass Valley, California) were embedded in fluid-tight encapsulants, and each measured approximately 3 cm × 1 cm × 1 cm. The eggshells were opened with a razor blade and the contents removed. A transmitter was inserted and the model was filled with gelatin and sealed with quick-setting adhesive. These models were substituted for one egg in each of two three-egg nests which were under constant incubation and were easily observed from our observation post. At the time of this substitution, incubation was in the fifth or sixth day, as subsequently determined by examination of the embryos (see below). The parent gulls immediately accepted the models and incubated them with the rest of their clutch for the duration of our study. The transmitters had a range of approximately 0.5 km. They broadcast on 148.5500 and 148.6000 MHz frequencies, which were monitored every half-hour with a Realistic Model PRO-2001 Scanner Receiver. The transmitters were calibrated with a Schultheiss quick-registering thermometer before implantation in and after removal from the eggs; the calibration did not shift during this interval.

Other models were created to determine the equilibrium temperatures of exposed eggs at various times of the day. The contents of two additional eggs were removed, a thermocouple (Cu-constantan, 24 gauge) was inserted into the middle of each egg, and the contents were replaced with a solution of gelatin. The thermocouple was glued in place, sealing the egg. One egg was placed in vegetation and the other on open sand, 1 and 2 m from an incubated nest, respectively. This site was surrounded by other nests in which incubation was proceeding. The egg temperatures were read on a Wescor thermocouple thermometer (Model TH-50 or TH-60) at half-hour intervals for 3 days. The gelatin-filled models faithfully tracked the temperature of intact eggs; model eggs and eggs into which thermocouples had been inserted directly both heated in the sun and cooled in the shade with temperatures that varied less than 0.2 C from each other.

The effects of restricting wind convection were measured by monitoring temperatures of three eggs placed in the sun from 1200–1500 Pacific daylight time (PDT) (all subsequent time specifications are also in PDT). The eggs, which had been fitted with thermocouples, were positioned in immediately adjacent areas, one on open sand, another on open sand with a V-shaped, 10-cm baffle of foam rubber oriented to block wind convection, and the third on the vegetation.

THERMAL TOLERANCE OF EMBRYOS

Tolerance of the embryos to acute thermal exposure was determined by monitoring heart rate in week-old embryos (mean age 7–8 days, range 5–6 days to 8–9 days) over a range of temperatures. Embryos were aged according to developmental stage of domestic fowl (Hamburger and Hamilton 1951), adjusted for the longer incubation period of the gull (approximately 28 days). Details of the experimental procedure are reported in Bennett and Dawson (1979). Intact embryos were excised from their eggs and placed in a solution of 0.9% NaCl. Embryonic temperature was changed approximately 1 C/min by placing the containers on a hot plate or on crushed ice. The frequency of cardiac beating was monitored visually until cessation for 1 min at cold temperatures or fibrillation or seizure at high temperatures. At these points, embryos were immediately returned to more moderate temperatures and cardiac contractions resumed their former frequency.

The thermal tolerance of embryos in intact exposed eggs was measured by opening a clutch of three eggs after each of the following periods of exposure: 1300–1400 (midday), 0900–2000 (daytime), and 2000–1100 (night). The two latter clutches, which were placed in an abandoned nest, were assembled by removing one egg from each of three three-egg nests. A gelatin-filled model egg with a thermocouple was also included in the clutch. At the end of the exposure, the eggs were opened and the embryos were examined for motor activity and persistence of heartbeat.

RESULTS

THERMAL ENVIRONMENT OF THE COLONY

The environmental temperature and that of the exposed egg models for May 11–12 are presented in figure 2. Air temperatures in the interior of San Nicolas Island reached 29–31 C on the days of our study. However, temperatures at the colony site remained relatively cool (18–20 C daily maxima). Despite these relatively cool air temperatures, intense solar radiation heated the soil in the colony to 49–50 C, and the exposed egg models also incurred high heat loads. The temperature of the egg in the vegetation more closely approximated open-soil temperatures, heating to 49 and 44 C on May 11 and 12, respectively. The egg exposed on the open sand heated to only 39–40 C. Egg and soil temperatures declined to minimal values of 6–11 C during the night.

The difference in equilibrium temperatures between the eggs on open sand and on vegetation appear to be caused by lower wind convection about the latter egg. The temperatures of exposed eggs heating on open sand, on sand with blocked convection, and on vegetation are presented in figure 3. The egg on open sand heated more slowly and remained at a lower temperature than either of the others, the temperatures of which were indistinguishable.

Eggs which were exposed when the parent gull left the nest heated slowly even during the hottest part of the day. For example, a 1-h exposure of a clutch of three eggs produced a rise in temperature less than 5 C (fig. 4). All embryos survived this exposure (see below).

INCUBATION TEMPERATURE

The temperature of two egg models incubated by gulls fluctuated considerably: 30.2–36.0 C in nest A and 31.9–35.9 C in nest B (fig. 5). Mean temperatures for the 3 days of observation were 33.4 C ± 0.11 SE (no. = 127) and 34.2 C ± 0.07 SE (no. = 124), respectively. These mean incubation temperatures are significantly different ($P < .001$, *t*-test). Pronounced daily thermal cycles were evident in nest A: egg temperature declined at night and rose during the day. No persistent thermal rhythm occurred in the egg in nest B.

THERMAL TOLERANCE OF THE EMBRYOS

The acute effects of embryonic temperature on heart rate are shown in figure 6. Heart function persists over a very broad thermal range between 11 and 46 C (upper blocking temperature = 46.1 C ± 0.45 SE, no. = 7; lower blocking temperature = 11.2 C ± 0.30 SE, no. = 7). Exposure to blocking temperatures and return to intermediate temperatures resulted in the resumption of former beating frequencies. Between these limits, heart rate varies directly with temperature. Between 30 and 35 C, which approximates incubation temperature, heart rate increases from 100 to 140 beats/min (Q_{10} = 1.9). Further warming up to 40 C increases heart rate up to 190 beats/min (Q_{10} = 1.9). Response varies

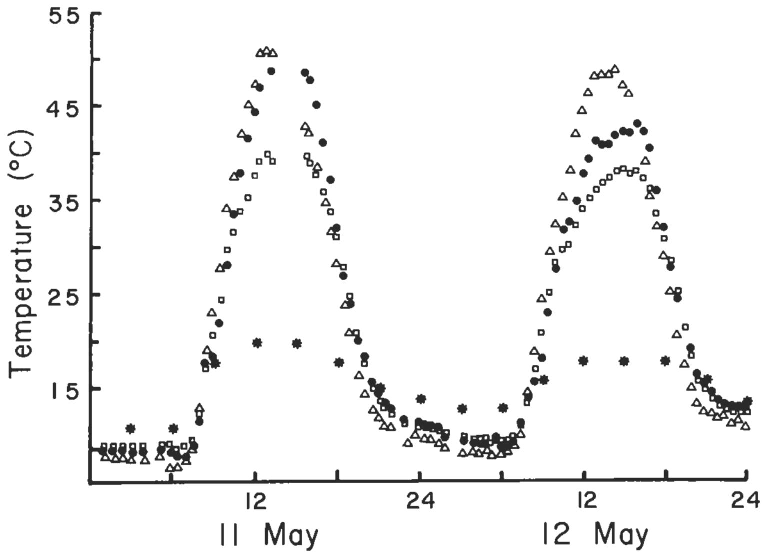

FIG. 2.—Temperatures in the gull colony on May 11–12, 1979. Air temperatures in the shade = stars, soil (sand) temperature = triangles, model egg adjacent to vegetation = circles, model egg on open sand = squares.

above 40 C, the frequency of contraction stabilizing or decreasing up to blocking temperatures. Below 30 C, heart rate declines rapidly with decreasing temperature (Q_{10} = 3.0 at 25–30 C, 5.4 at 20–25 C, and 6.9 at 15–20 C).

Eggs may be uncovered for substantial periods during the day without apparent harm to the embryos. The embryos in a clutch exposed for 1 h in the heat of the afternoon (fig. 4) maintained cardiac activity and general limb movements after the exposure. However, exposure of a clutch for the entire day (0900–2000, May 11) killed the embryos. Temperature of a model egg in this clutch rose to 49 C and stayed above

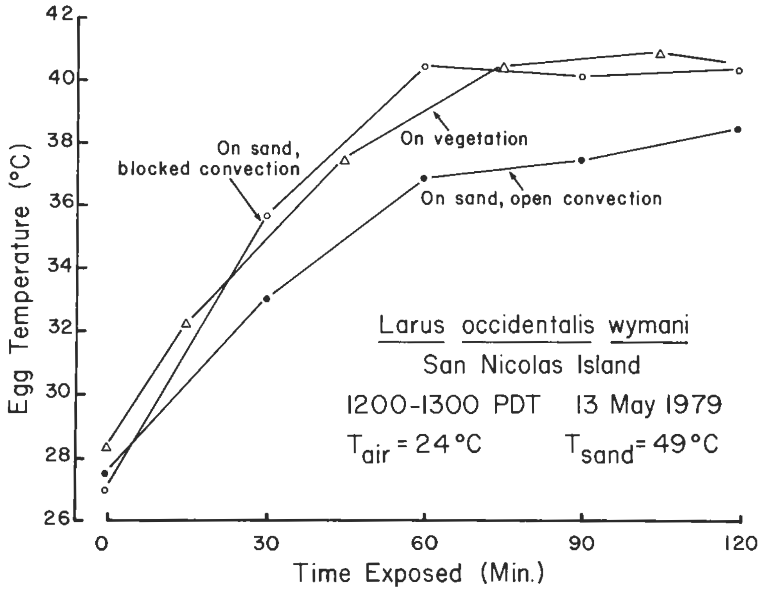

FIG. 3.—The effects of wind convection on temperature of exposed eggs

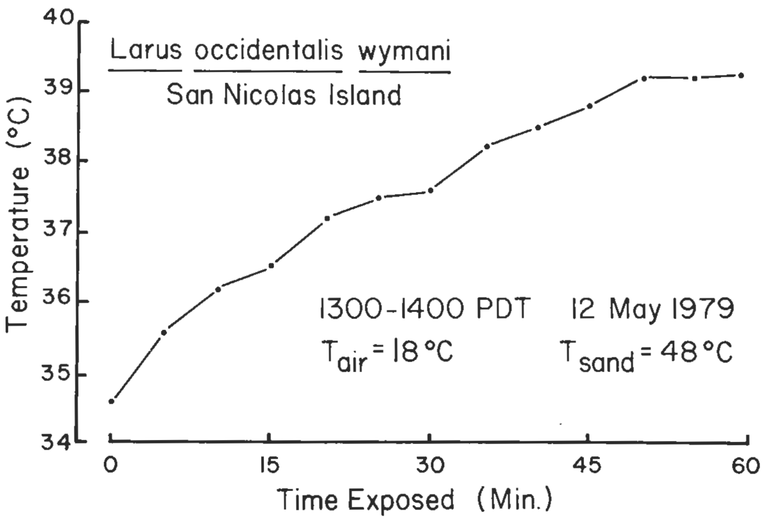

FIG. 4.—Temperature rise in a clutch of three eggs from which an incubating gull was chased at midday. Core egg temperature was measured with an inserted thermocouple.

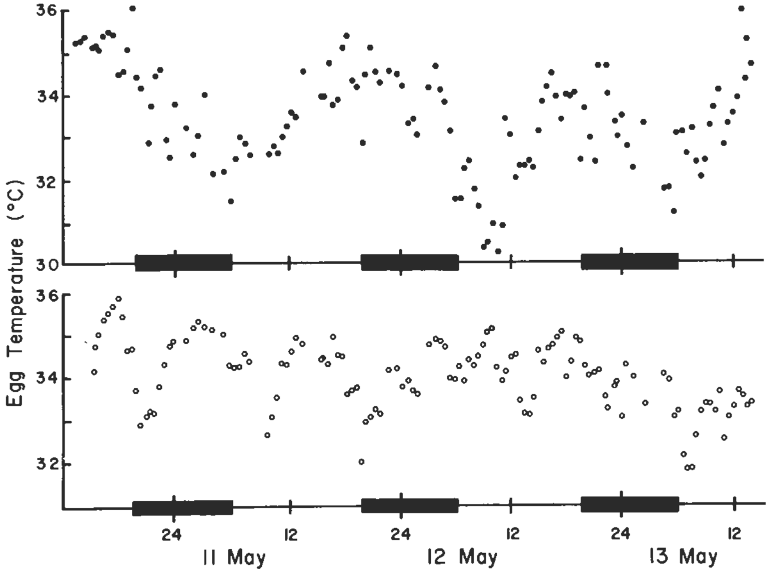

FIG. 5.—Telemetered temperature of incubated model eggs in two adjacent nests. Nest A = solid circles; nest B = open circles. Time is PDT; shaded bars indicate nighttime.

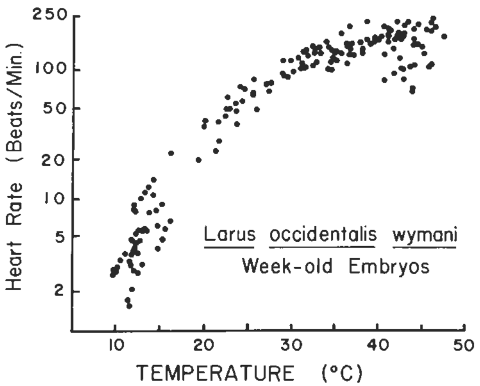

FIG. 6.—The thermal dependence of heart rate in week-old embryos of western gulls.

47 C for over 3 h during the period. The only sign suggestive of heat damage was the coagulation of the blood in the vessels surrounding the air space of the egg, immediately beneath a portion of the shell that was fully exposed to solar radiation. Presumably, these vessels would have heated to substantially greater levels than those attained by the egg generally. Some eggs do survive prolonged diurnal exposure: one that had been abandoned in a nest for at least 2 days (May 10–12) contained a viable embryo. It appears significant that the nest containing this egg was located away from vegetation and received substantial wind convection. The maximal temperature in this nest reached only 41 C on May 13. The extent of opportunities for wind convection appears critical in determining whether exposed eggs will overheat.

The extent of the chilling imposed by nocturnal exposure apparently does not harm embryos at this stage of development. The abandoned egg mentioned previously survived 2 nights' exposure. A clutch uncovered for 1 night (2000–1100, May 11–12) cooled to 9 C and remained below 11 C for 6 h. Upon rewarming in the sun, all embryos observed showed vigorous heartbeats and body movements.

PARENTAL BEHAVIOR DURING INCUBATION

The parental gulls of the San Nicolas colony seemed generally unaggressive. Little squabbling occurred between birds at adjacent nests. No damaged or opened eggs were found in the colony, and the incidence of chick mortality appeared far less than in other gull colonies in which we have worked. No attempt was made by adult gulls to eat eggs opened during the thermal tolerance experiments. Little aggression is shown toward intruders. These gulls normally cover their eggs continuously; our egg models were incubated constantly as verified by binocular sightings during measurements. The longest exposure of these eggs was about 3 min. However, the gulls rapidly rise from their nests when we approached to within approximately 50 m, even during the hottest part of the day. They did not return while an intruder remained, even during periods lasting more than 1 h.

Adult gulls in the colony did not appear to undergo heat stress during the day. Only intermittent gaping (see Bartholomew and Dawson 1979) was observed in most sitting gulls during the heat of the day. Gaping rarely culminated in panting. Only once were birds with slightly elevated scapular feathers (see Bartholomew and Dawson 1979) seen in the colony.

DISCUSSION

Western gull eggs on San Nicolas tolerated acute exposure to ambient conditions, and several hours of parental inattention produced no apparently irreversible thermal damage to the embryos. Nocturnal exposure and chilling, even to levels which suppress heartbeat, apparently do not harm the embryo. Such tolerance is common among many species of birds during the early stages of development (Matthews 1954; Romanoff 1960; Lundy 1969; Wheelwright and Boersma 1979). Although heat stress is potentially a greater threat to survival, exposed eggs heated rather slowly in reference to lethal temperatures, which are over 10 C greater than thermal levels during incubation. The slow rise in exposed egg temperature results from a number of factors, including the large mass of the eggs (approximately 100 g), the high reflectance of gull eggshells in the near-infrared (Bakken et al. 1978), and convective heat loss from the eggs to the cooler air. Prolonged diurnal exposure can be lethal in unfavorable nest locations, either by direct exposure of the heart to damaging temperatures or by blockage of blood flow in the circulatory system. However, given the normal attentive pattern of the adults and the slow rise in temperature of exposed eggs, heat damage would rarely be normally encountered by eggs in this colony. This situation contrasts strongly with that we found to be later encountered by chicks in this colony. Severe heat stress developed with only 15 min of diurnal exposure (Dawson and Bennett 1981).

The importance of wind convection in cooling the eggs is evident from our observations in the San Nicolas Island colony. Even the slight retardation of air movement caused by the presence of adjacent vegetation is sufficient to increase the rate of heating of diurnally exposed eggs and to increase their equilibrium temperatures. The exposed location of the San Nicolas colony (fig. 1) results in air temperatures which are nearly 10 C lower than those elsewhere on the island. The colony location is probably influenced by the thermal requirements of the adult gulls and the developing young. Extensive mortality of chicks during heat waves has been observed among western gulls nesting on the leeward side of nearby Santa Barbara Island (G. Hunt, personal communication). The principal breeding colonies of ground-nesting seabirds are all located on the windward sides of the Channel Islands (Hunt et al. 1979), the group of which San Nicolas and Santa Barbara are a part.

Incubation by western gulls served to confine egg temperature to 30–36 C, with mean temperatures for our test eggs of 33.4 and 34.2 C. These values lie somewhat below those reported for other species of gulls (Drent 1975; Rahn and Dawson 1979). Perhaps these discrepancies reflect real differences in incubation temperature among the gulls considered. However, they may well be due to differences in location of temperature sensors within the egg, in the time at which the measurements were made, in external conditions, or in the stage of incubation (see Drent 1975). Perhaps the most important finding to emerge from analysis of the thermal data obtained from our model eggs is that substantial differences in the level and pattern of incubation temperature can exist in the western gull even between adjacent nests with eggs at similar levels of development. One of these eggs cooled 2–5 C every night and rewarmed every day, even though incubation appeared continuous. In the case of the other model egg tested, fluctuations in egg temperature were smaller, the maximum in 24 h being 3 C. These differences suggest that specification of mean values for incubation temperature probably should be supplemented by description of the pattern and extent of thermal fluctuations.

The San Nicolas colony of western gulls faces a very different thermal environment from that of a colony of Heermann's gulls which we have previously studied (Bartholomew and Dawson 1979; Bennett and Dawson 1979; Rahn and Dawson 1979). The latter colony is located on Isla Rasa, Baja California Norte, Mexico, in the Gulf of California. It is subject to very high levels of solar radiation and high air and soil temperatures during the incubation period of the colony. The danger of embryonic overheating during the day in this colony is extreme: eggs heat to injurious levels in only 15 min of exposure. Unattended eggs attained temperatures sufficient to insure mortality on seven out of eight observation days. Paradoxically, the upper thermal limits of the Heermann's gull embryos are considerably lower than those of the western gulls from San Nicolas Island (41.1 vs. 46.1 C), where the danger of overheating upon exposure is much less. We determined these limits using identical methodology for the two species. Differences in parental behavior resolve this apparently nonadaptive situation. Adult Heermann's gulls sit very closely on their nests, even when approached by a human intruder. They can be approached to within approximately 5 m before leaving the nest. They will continue close incubation during the day even though undergoing prolonged and pronounced heat stress (Bartholomew and Dawson 1979). In contrast, adult western gulls readily leave their nests upon intrusion and remain away for its duration. Among this colony of western gulls, this exposure of the eggs entails little danger of aggressive attacks by other gulls. Predation on other gull eggs apparently does not occur among these birds. On the other hand, Heermann's gulls aggressively attack and eat eggs of each other and of other birds. Each colony has its own suite of adaptive behaviors and physiological limits associated with its thermal environment.

These interspecific differences prompt us to emphasize the intimate relations between physiological capacities of embryos and chicks and the attentive characteristics of the parents. This interaction may well transcend in interest the interspecific variation in thermal tolerance of the embryonic gulls or in the incubation behavior of the parents. This complex of behavior and physiology of different individual animals is an example at an intrageneric level of a situation summarized by Bartholomew and Dawson (1954) for herons, brown pelicans, and western gulls nesting in the same environment. In these animals, parental attentive behavior nicely compensates for the differences in physiological capacities at hatching of nestlings of the three species.

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