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AVIAN INCUBATION: EGG TEMPERATURE, NEST HUMIDITY, AND BEHAVIORAL THERMOREGULATION IN A HOT ENVIRONMENT

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INTRODUCTION

Several species of Charadriiformes and also Lesser Nighthawks (*Chordeiles acutipennis*) nest in the area of the Salton Sea in southeastern California. The nesting environment at the Salton Sea, a man-made saline lake about 70 m below sea level and surrounded by the Sonoran Desert, is one of the harshest in the world. The summer nesting season is characterized by an almost total lack of cloud cover and by intense solar radiation due to the small amount of moisture in the atmosphere (it has rained once there in June since 1914, Ermak et al. 1976). Ground temperatures in the sun exceed 50°C almost daily; the maximum daily air temperature in the shade reaches or exceeds 37.8°C on an average of 110 days per year (Kercher and Buchanan 1976). In addition, the low ambient humidity can be stressful to incubating birds, depending on proximity of water, and wind direction, although little wind for convective cooling occurs within a few centimeters of the ground.

Despite these harsh conditions, birds nesting at the Salton Sea lay their eggs on the ground, sometimes without any nest lining, and generally avoid nesting near any vegetation or other sources of shade. To determine how birds cope with these stressful conditions while protecting their eggs and young from them, I studied the Black-necked Stilt (*Himantopus mexicanus*), American Avocet (*Recurvirostra americana*), Snowy Plover (*Charadrius alexandrinus*), Killdeer (*C. vociferus*), Gull-billed Tern (*Gelochelidon nilotica*), Forster's Tern (*Sterna forsteri*), Black Skimmer (*Rynchops niger*), and Lesser Nighthawk. My purpose was to determine if the eggs, young and/or adults experience thermal stress, how the stress is influenced by environmental factors, and the nature and derivation of mechanisms used by different species to mitigate the effects of these high temperatures.

Specifically, I compared the timing of breeding at the Salton Sea with the timing of breeding at coastal study sites and with that reported in the literature to determine if the birds nesting at the sea were avoiding the thermal stress of mid-summer breeding. In addition, I studied the humidity and thermal microenvironment of the egg-nest complex in detail at both the Salton Sea and coastal study sites. I also observed all species of Charadriiformes nesting at the Salton Sea to see if they used similar behavioral thermoregulatory mechanisms to cope with the thermal stress and to determine which, if any, of these mechanisms were used by incubating Lesser Nighthawks. All seven species of Charadriiformes nesting at the Salton Sea belly-soaked, i.e., transported water via the ventral plumage to their eggs and chicks (Maclean 1975). I studied this behavior to determine its effects on egg temperature and nest humidity, and attempted to determine its proximate causes and possible origins. As a consequence of frequent belly-soaking by incubating adults in saline and silt-laden water, some eggs become covered with a layer of salt and mud. I investigated the effects of such coverings on egg water loss, embryonic metabolism, crypsis, and near-infrared reflectivity.

STUDY AREA

The primary study sites were the Whitewater River delta region at the north end of the Salton Sea (NESS), Riverside County and on or near the Imperial Wildlife Area-Wister Unit near the south end of the Salton Sea (SESS), Imperial

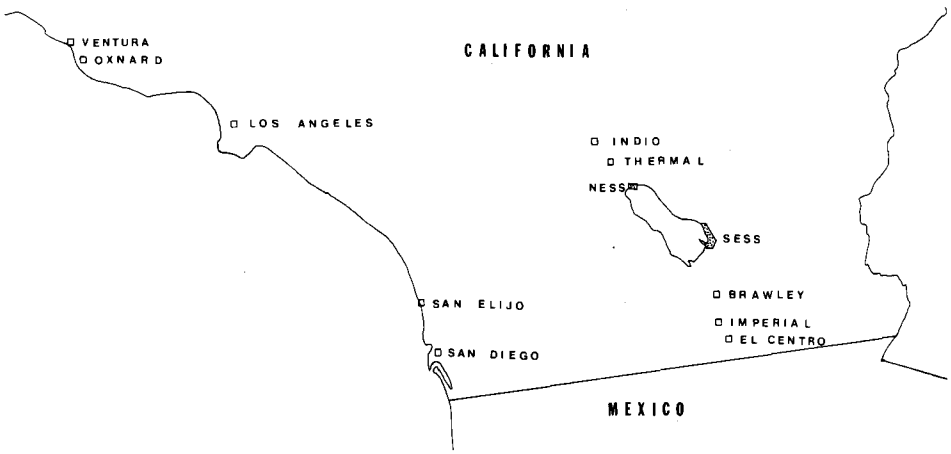

FIG. 1. Map of southern California showing locations of study areas and weather stations. Stippling denotes study areas at the north end of the Salton Sea (NESS) and the south end of the Salton Sea (SESS).

County (Fig. 1). For comparative purposes, limited studies also were conducted at several California coastal sites including the sewage treatment plant adjacent to the mouth of the Santa Clara River, Ventura, Ventura County, San Elijo Lagoon, San Diego County, and the salt works of San Diego Bay, San Diego County. Data presented are from the Salton Sea unless coastal sites are specified.

AMBIENT WEATHER DATA

The Salton Sea environment is one of the hottest of any in the world used for nesting by water birds. Because meteorological data for the Salton Sea are not available, I examined data from the nearest recording stations. The stations (Fig. 1) and their distances from the Salton Sea are Indio (28 km N), Thermal (17 km N), Brawley (21 km S), Imperial (33 km S), and El Centro (36 km S). Air temperatures above 48.9°C in the shade have been recorded in May, June, July, August, and September at Indio (California Department Water Resources 1970). Monthly temperature and precipitation data from Brawley and relative humidity data from Thermal are presented in Figure 2 (NOAA 1974). Temperature data at El Centro (Bennett 1975) and at Imperial (California Department Water Resources 1970) are similar to those reported for Brawley and Indio. Average annual precipitation (NOAA 1974) is 8.6 cm at Indio, 7.1 cm at Thermal, and 4.6 cm at El Centro. Almost no rain and minimal cloud cover occur during the summer. Cloudy skies at Indio average one day per month during June and three days per month for April, May, July, and August. Measurable rain in the Imperial Valley has fallen only once during June since 1914 (Ermak et al. 1976). Sustained high temperatures occur daily during the summer nesting season, and air temperatures in the shade of 37.8°C or higher are reached an average of 110 days each year (Kercher and Buchanan 1976). Maximum air temperatures recorded near the Salton Sea are 51.7°C at Indio and 51.1°C at Imperial.

Mean relative humidities at Thermal (27%) and Imperial (16%) are lowest in June and do not exceed 35% during the nesting season. However, Thermal and

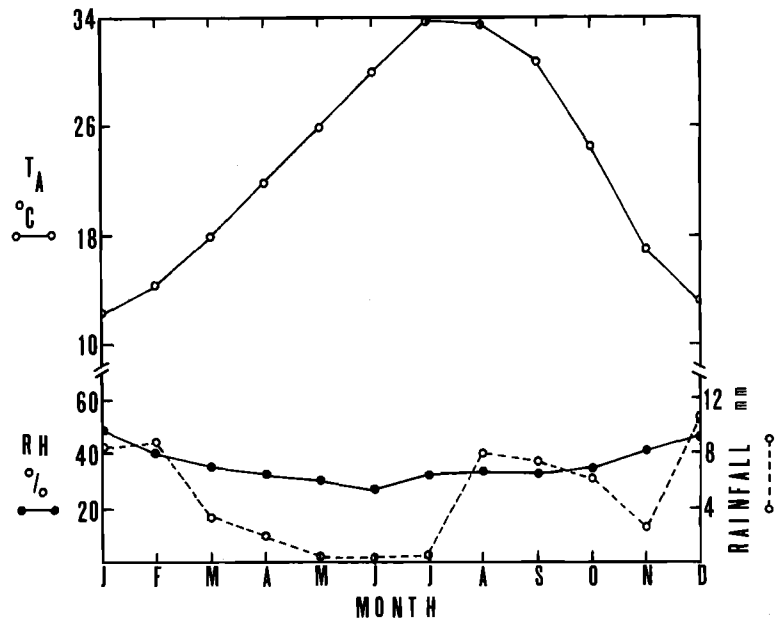

FIG. 2. Monthly mean ambient temperatures, relative humidities, and rainfall near the Salton Sea. Temperature and rainfall data are from Brawley, and relative humidity data are from Thermal.

Imperial are several kilometers from the sea, and higher humidities occur near surface water. Even so, the effect of the large evaporating surface of the sea on local humidity generally is not felt at distances greater than 0.4 km from the shoreline (MacDougal 1914). The effects of wind and irrigation water on ambient humidities near nests will be discussed later. Mean wind velocity (1.3 m above ground) at El Centro during March and April is 4.6 $m \cdot sec^{-1}$ and during June, July, and August is 4.1 $m \cdot sec^{-1}$ (Ermak et al. 1976). Daily ambient temperatures and humidity were recorded within 50 m of nests at the Salton Sea (Fig. 3). Temperatures peaked bewteen 14:00 and 17:00, and humidities were highest during the night. Ambient humidities of 20–30% were recorded on several days during the heat of the day. The mean humidities are higher than those recorded at Thermal (Fig. 2) because of the proximity of surface water.

The ameliorated climate of the coastal sites contrasts sharply with that of the harsh desert site. Mean monthly temperatures are lower and humidities higher (Fig. 4; NOAA 1974). The average daily summer temperature ranges are 15–20°C (Ruffner and Blair 1974), and daily humidity during June ranges from 56 to 85%. Precipitation averages 26.4 cm at San Diego, 32.0 cm at Los Angeles, and 37.6 cm at Oxnard and occurs primarily from November to April at all three sites (NOAA 1974). Cloud cover also is more extensive at the coastal sites, occurring on an average of 9 days (San Diego) and 10 days (Los Angeles) during the month of June.

SALINITY

The salinity of the Salton Sea is currently about 39 parts per thousand (ppt) total dissolved solids (TDS) compared to 36 ppt TDS for the oceans. Since the

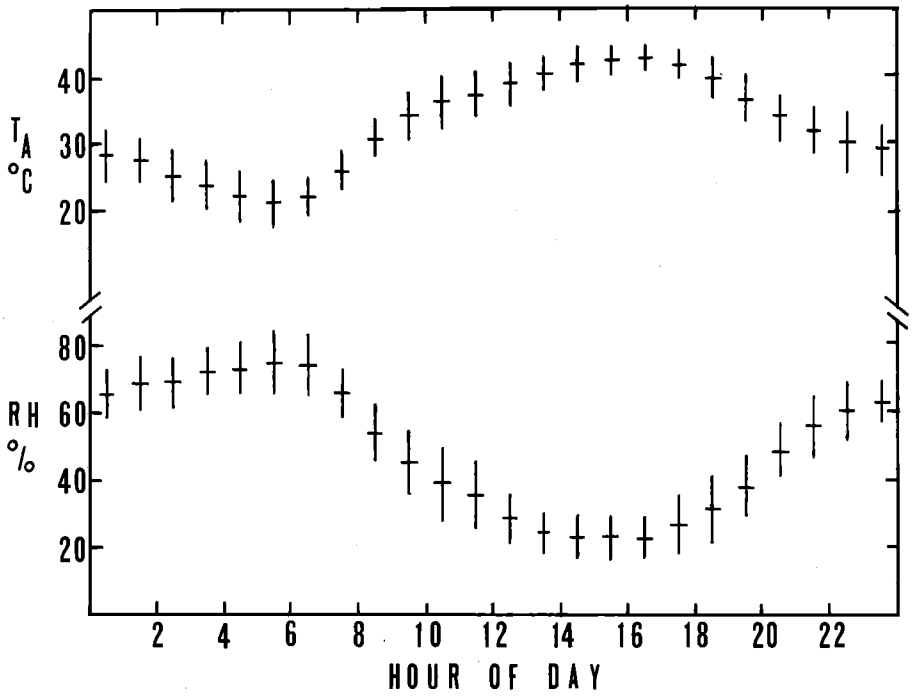

FIG. 3. Shaded ambient temperatures and relative humidities at ground level near nests at the Salton Sea at different times of day. Data plotted are the mean (horizontal line) ± one standard deviation (vertical line) for seven days in June and early July, 1977 and 1978.

early 1920's, the TDS's in the Salton Sea have ranged from about 32 to 43 ppt (California Department Water Resources 1970). Shorebirds nesting on or near the Imperial Wildlife Area-Wister Unit drink and belly-soak in waters that range from about 1 ppt TDS (irrigation water from the Colorado River) to 3 ppt TDS (irrigation drainage canals). Occasionally, stilts nest near evaporating pools which, by the end of the incubation period, may reach 405 ppt TDS (Coachella Valley County Water District water analysis).

MATERIALS AND METHODS

EGG AND NEST DATA

Eggs were individually numbered with India ink, and nests were marked with numbered wooden tongue depressors. Inside nest diameter and depth were measured to the nearest mm. Distance from the nest to water and distance to the nest of the nearest neighbor (conspecifics or other species) were also recorded on the first visit to the nest. Distance to water varied at some nests during the course of incubation with flooding or drainage of the nearby impoundments. Eggs were weighed at each visit with a Pesola scale graduated to 0.1 g or with a torsion balance accurate to 1 mg to determine daily mass loss = daily water loss ($\dot{M}_{H_2O}$, in $mg \cdot day^{-1}$). Fresh egg masses are those of eggs weighed within 24 hours of laying. Eggs were weighed without attempting to remove adherent mud. Presence

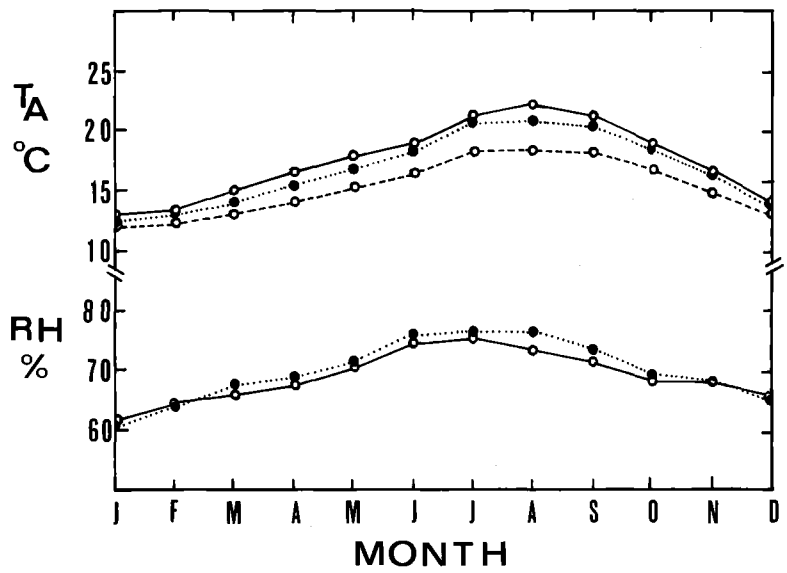

FIG. 4. Ambient temperatures and relative humidities near the coastal study sites. Legend: O- - -O Oxnard; O———O San Diego; ●·····● Los Angeles.

or absence of mud was noted at the time of weighing, and data for "clean" eggs and muddy eggs were analyzed separately.

Water-vapor conductance (G_{H_2O}, in $mg \cdot day^{-1} \cdot torr^{-1}$; 1 torr = 1 mm Hg = 133 Pascal) was determined in the laboratory. Eggs were placed over silica gel at a constant temperature, and mass loss was determined daily with an analytical balance accurate to 0.1 mg for a minimum of four days. Mean daily mass loss divided by the saturation vapor pressure within the egg (vapor pressure outside the egg is zero due to the silica gel) gave G_{H_2O} (Ar et al. 1974):

$$G_{H_2O} = \frac{\dot{M}_{H_2O}}{\Delta P_{H_2O}} \quad (1)$$

where $\dot{M}_{H_2O}$ is the daily mass loss of the egg and ΔP_{H_2O} is the vapor pressure gradient across the eggshell. Conductance was determined at 37°C because this approximates egg temperature in nature. Corrections to 25°C and sea level barometric pressure were made to facilitate comparison with values reported in the literature, since conductance varies with temperature (Paganelli et al. 1978) and barometric pressure (Paganelli et al. 1971). In some instances, fresh eggs of known conductance were placed in other nests. Daily mass losses of the calibrated eggs of known conductance were used to determine vapor pressure gradients in nests (equation 1). Division of daily mass loss of the remaining eggs by the vapor pressure gradient, thus determined, provided conductance values for these eggs in the nests. This assumes that temperatures of all eggs in a particular nest are the same and that nest air temperature and nest humidity are uniform for all eggs within the clutch. These assumptions are probably reasonable for 2–4 egg clutches.

The effect of a layer of mud on water-vapor conductance was determined for shorebird and chicken (*Gallus gallus*) eggs. After conductance of "clean" eggs was measured for four days, a thin (0.5–1.0 mm) layer of mud (obtained from the Salton Sea nesting environment) was applied to the surface of the egg and dried for 24 hours over silica gel. Conductance of mud-covered eggs was then determined over the next four days using the same procedure as used for clean eggs. The effect of salt on water-vapor conductance was determined in a similar manner. Clean eggs were weighed for four days, dipped in salty water from the Salton Sea three times (allowed to dry between each dip), dried over silica gel for 24 hours, and weighed for the next four days.

Shell thickness (with membranes intact) of eggs collected at the Salton Sea was measured with a micrometer measuring device (Federal "35", Federal Products Corp., Providence, R.I.) at the Western Foundation of Vertebrate Zoology. A minimum of five measures at different points were obtained and averaged for each egg. Egg shells were weighed on an analytical balance accurate to 0.1 mg. Masses of egg shells with drain holes greater than 5 mm in diameter were not used.

Surface area (A) and volume (V) were obtained using equation 4 ($A = 4.835W^{0.662}$) of Paganelli et al. (1974) and equation 12 ($A = 4.940\ V^{0.667}$) of Hoyt (1976), where W = fresh egg mass. In addition, volumes of three stilt eggs were determined by water displacement (see Hoyt 1976). Initial density was obtained by dividing fresh egg mass by volume. The total effective pore area (A_P) can be calculated once shell thickness (= pore length = L) and water-vapor conductance are known (Ar et al. 1974), using the equation $A_P = 0.447\ G_{H_2O} \cdot L$ (Rahn et al. 1976).

Temperature Data

Ambient temperature data were obtained from U.S. Weather Service records for stations near the Salton Sea or coastal study sites, from a calibrated recording hygrothermograph in a meteorological box placed within 50 m of some nests, and from thermistor probes placed on the ground and 5 cm above it inside a bottomless meteorological box to give shaded ambient temperature at the level occupied by nesting birds. The white meteorological box measured 20 cm × 20 cm × 70 cm. All four sides were louvered and thus open to air flow. Ground and air (5 cm above the ground) temperatures in the shade, thus recorded, seldom differed by more than 1.0°C (Grant 1979). Therefore, all shaded ambient temperatures reported here are those actually measured at ground level. Ground temperature in the shade is the temperature of the ground surface shaded from all sources of radiation throughout the day and night. This approximates the temperature to which eggs would be exposed if also shaded throughout the day and night.

Ground temperatures in the sun were obtained by placing a thermistor probe or a thermometer on ground that had been exposed to full insolation. The probe tip was shaded from the sun during the actual measurement. Black-bulb temperatures were measured by inserting a thermistor probe or thermometer into a small sphere painted flat black and exposed to full insolation and wind at either 5 cm or 1.3 m above ground, though black-bulb temperatures are of limited value in approximating the total heat load on an animal (see Bakken and Gates 1975 for discussion). Water temperature was measured with a thermistor probe 2.5 cm

below the surface near sites where belly-soaking occurred. All environmental temperatures were monitored essentially simultaneously at 5–15 minute intervals during the day and approximately hourly at night (black-bulb not recorded at night) with the aid of up to 350 m of extension cables, various probes, and a multichannel, battery powered, Yellow Springs Instrument telethermometer.

Nest air temperatures were obtained by positioning a thermistor probe in the floor of the nest between the eggs. Egg temperatures were obtained by inserting a thermistor probe into the egg so that the probe tip lay at the top center of the yolk (near the embryo). The hole made for the probe was sealed with wax, and a portion of the probe lead was taped to the side of the egg. I was able to monitor egg, nest air, and environmental temperatures simultaneously from a blind up to 100 m away. Egg and nest air temperatures were recorded about every 10 minutes during daylight and approximately hourly at night. Diel temperatures were calculated on the basis of 10 hours × nocturnal mean plus 14 hours × diurnal mean divided by 24 hours. Nocturnal temperatures were obtained between 20:00 and 06:00, and diurnal temperatures were recorded between 06:00 and 20:00. Nests generally were monitored continuously for a minimum of 24 hours. All egg and nest air temperatures used in the calculations are those obtained after the bird had covered the eggs for a minimum of 30 minutes. Some egg and nest air temperature data had to be discarded because of technical problems with the instruments or because activities of a bird changed the position of a probe. In general, however, the birds were tolerant of probes in eggs and on the nest floor. Mud on some of the eggs concealed the presence of the thermistor probe.

To evaluate the effect of high egg temperature on incubation behavior, I constructed four egg-heating units (wire wound around an O-ring) and inserted them into four stilt eggs (specimens without collection data, obtained from the Western Foundation of Vertebrate Zoology). The heater units were wired in parallel and connected to a resistor on a circuit board. An extension cable connected the resistor and egg heaters to a cigarette lighter adaptor in an automobile. A thermistor probe was sealed within one egg to monitor egg temperature, and all eggs were filled with water prior to use in the field. Wires, the resistor, and the circuit board were buried near the nest. I controlled the rate and extent of temperature increase of eggs under the incubating bird by manipulating the circuit closure at the automobile up to 100 m away.

Body temperatures of one male stilt were recorded during incubation to evaluate the role of body temperature in initiating belly-soaking behavior. The bird was captured at the nest with a trap made of slip-nooses of monofilament line. A calibrated X-M temperature transmitter (Mini-Mitter Company, Inc., Indianapolis, Indiana) was inserted into the abdominal cavity. The bird tolerated the surgical procedure well. He shared incubation duties at the nest with his mate for the next 60 hours while I recorded data from a blind 100 m away.

Humidity Data

Ambient humidity data for the study areas were obtained from U.S. Weather Service data (recorded 1.3 m above ground), from a recording hygrothermograph placed on the ground within 50 m of some nests, and from calibrated silica gel-filled chicken eggs placed under shade platforms at ground level 1 m from many nests. Chicken eggs were used for ambient hygrometers because of their large

size and shell strength which reduced breakage from repeated use. Eggshell hygrometers were constructed as described in Rahn et al. (1977). To calibrate them, eggs filled with silica gel were maintained over water (100% relative humidity) at 37°C, and mass gain was recorded over the next 24 hours. Mass gain divided by the vapor pressure gradient gives conductance (equation 1) for a particular egg. Eggs were then emptied and refilled with fresh silica gel, and the process was repeated. Conductance values for each individual egg were averaged. Chicken eggs were used to measure ambient vapor pressure (P_I) near nests. Stilt and avocet egg hygrometers were used to measure nest vapor pressure (P_N) under the incubating bird. Due to abrasion in the nest and in handling, conductance values may change in eggs used repeatedly. Chicken egg hygrometers changed very little over the course of two summers, but some stilt and avocet egg hygrometers changed significantly (one egg doubled its conductance, probably due to an undetected hairline crack). For this reason eggs were recalibrated after two or three one-day intervals in the nests. Egg hygrometers were left in the nest for only 24 hours, as small eggs develop significant back pressure after two days (Rahn et al. 1977; pers. obs.). This technique with small eggs requires a field balance capable of measuring mass gain to 1 mg. Eggs can, however, be filled with silica gel in the laboratory, weighed, sealed in two plastic bags with minimal amounts of air inside, and transported to the field for use. The mean mass of eggs double-bagged after 24 hours in the nest and transported to the laboratory for accurate weighing differed from that of control eggs treated similarly by only 2%.

Solar Radiation

Solar radiation in millivolts was measured with an MK I-G Sol-A-Meter Silicon Cell pyranometer within 50 m of nests under study. I converted mv to $cal \cdot cm^{-2} \cdot min^{-1}$ according to $mv \cdot 0.224 + 0.087$. Multiplication of $cal \cdot cm^{-2} \cdot min^{-1}$ by a conversion factor of 697.8 gives insolation in $watts \cdot m^{-2}$. Solar radiation was recorded every 15 minutes.

Wind

Wind velocity was measured every 15 minutes during daylight hours at many nests with a Dwyer wind meter 5 cm above ground within 50 m of nests. Topography near nests was generally flat (little to no vegetation or hills near nests to disrupt air flow).

Water Uptake of Feathers

To estimate the quantity of water transported to the nest by belly-soaking Charadriiformes, water uptake measurements were made on belly feathers obtained from specimens (all collected during the summer) in the Dickey Collection, University of California, Los Angeles. Dry feathers were weighed to 0.1 mg, thoroughly wetted with water, drained to eliminate excess water, and weighed immediately (see Cade and Maclean 1967). Water uptake for each feather in mg H_2O per mg dry feather mass was calculated according to (wet mass-dry mass)/dry mass.

Oxygen Consumption of Eggs

Oxygen consumption of nine stilt eggs of known age was measured daily in the laboratory during the entire course of incubation. Ambient temperature was main-

tained at 37.0 ± 0.5°C. Ambient humidity ranged between 28 and 40.5%; at these humidities daily mass loss approximated that measured in the field. Four eggs were coated with mud and three with salt; two served as "clean" controls. The chick in one mud-covered egg died during pipping. Data for that egg were used up to day 18, as oxygen consumption gradually declined after that point. Oxygen consumption was measured with a Beckman E-2 paramagnetic oxygen analyzer. Eggs were suspended in a short plexiglass tube to prevent breakage. A plexiglass syringe served as the metabolic chamber. The methodology is described by C. Vleck (1978). The equation used to calculate oxygen consumption is that of D. Vleck (1978):

$$\dot{V}_{O_2} = \frac{V(F_I - F_E)}{(1 - F_E)t} \tag{2}$$

where $\dot{V}_{O_2}$ = rate of oxygen consumption in $cm^3 \cdot hr^{-1}$; V = volume in cm^3 of dry air in the metabolic chamber at the start; F_I = initial fractional concentration of O_2 in dry, CO_2-free air; F_E = end fractional concentration of O_2 in dry, CO_2-free air, and t = elapsed time in hours. All gas volumes were corrected to standard temperature and pressure (STPD: 0°C, 760 mm Hg), and volume (V) corrections of the beginning sample were adjusted for the volume of the egg, the plexiglass holder, rubber bands, and the volume of water vapor within the syringe.

Egg Reflectance

Reflectivity of mud (dry and wet) was measured spectrophotometrically by G. S. Bakken at Indiana State University, Terre Haute. Mud used was that obtained near stilt nests at the Wister Unit, Salton Sea. Data for reflectance of dry clean museum eggs of stilts, avocets, Killdeers, and Forster's Terns appear in Bakken et al. (1978).

Temperature of Copper Stilt Chick

A copper cast of a one-day old stilt body was made, fitted with a thermocouple, and covered with the original skin. This taxidermy mount (without legs) served as a thermometer to assess the heat load (radiation and convection) on stilt chicks. The stilt model was positioned 5 cm above dry ground near an empty stilt nest, and its environmental equilibrium temperature was monitored continuously for 24 hours.

In the field I usually placed the thermistor probes in nests and eggs at dawn or dusk and monitored temperatures and behaviors for the next 12–72 hours without disturbance. On some occasions at dawn and dusk I briefly disturbed incubating birds to weigh eggs and to check probe positions in the nest.

TIMING OF BREEDING

Timing of nesting at the Salton Sea was investigated to determine if the Charadriiformes were avoiding the period of extreme summer heat, though only the Killdeer and stilt were studied in detail throughout the nesting period. The earliest date on which Killdeer eggs were laid at the Salton Sea was 17 March (Fig. 5), and first young were found on 15 April. The latest clutch was found on 1 July, and young were present until the end of August. Peak initiation of egg-laying was about 1 May, and peak hatching was about 1 June. Bunni (1959) reported Killdeer eggs as early as 6 April and as late as 26 June in Michigan. Bent (1929) gave egg

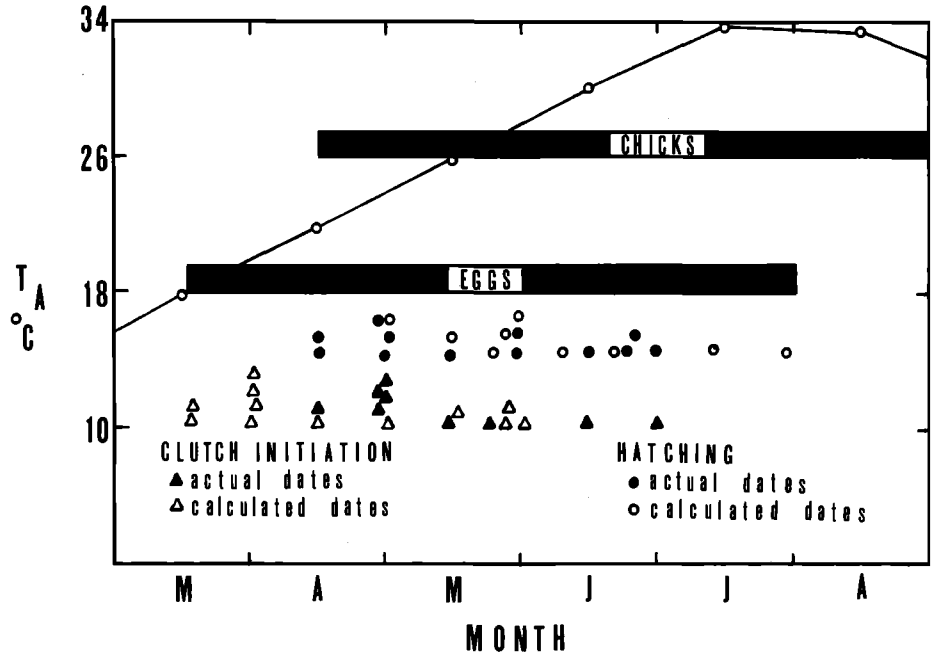

FIG. 5. Nesting chronology of the Killdeer at the Salton Sea, 1975–1978. Calculated dates are based on an incubation period of 25 days and an egg-laying period of 4 days. Mean ambient temperatures during the nesting season are plotted (line) by month.

dates from early March to mid-July for various portions of the United States. Thus, nesting chronology of the Killdeer at the Salton Sea seems to agree with those reported for other localities.

The earliest date for egg laying for the stilt at the Salton Sea was 2 April, and the latest sets (2) of attended eggs were found on 16 August. Active stilt nests at coastal sites were found between 21 April and 23 July (latest visits to any coastal area). Median egg-laying was about 15 May, and median hatching date was about 14 June for the stilt at the Salton Sea (Fig. 6). Most eggs were laid before July and, thus, before the hottest time of the year. However, the nesting period of stilts at the Salton Sea does not differ from that of birds studied at coastal sites (Ventura and San Diego), nor does it differ from that reported by Bent (1927) for birds in other parts of the United States.

Data on avocet nesting chronology are less precise because fewer nests were studied over long periods of time and because this species rarely breeds at the Salton Sea. First avocet eggs were laid on 22 May (calculated by assuming 25 days for incubation and 4 days for egg-laying), and the latest hatching occurred on 4 July at the Salton Sea. The earliest egg date at Ventura was 5 May. Studies of Forster's Tern nests were undertaken between 31 May and 13 July at the Salton Sea. Calculating backward (25 days for incubation and 3 days for egg-laying interval) gave a clutch-initiation date of 16 May for a newly hatched chick found on 13 June. Eleven active Forster's Tern nests were found on 13 July at the Salton Sea, and, if successful, young probably did not fledge until late August.

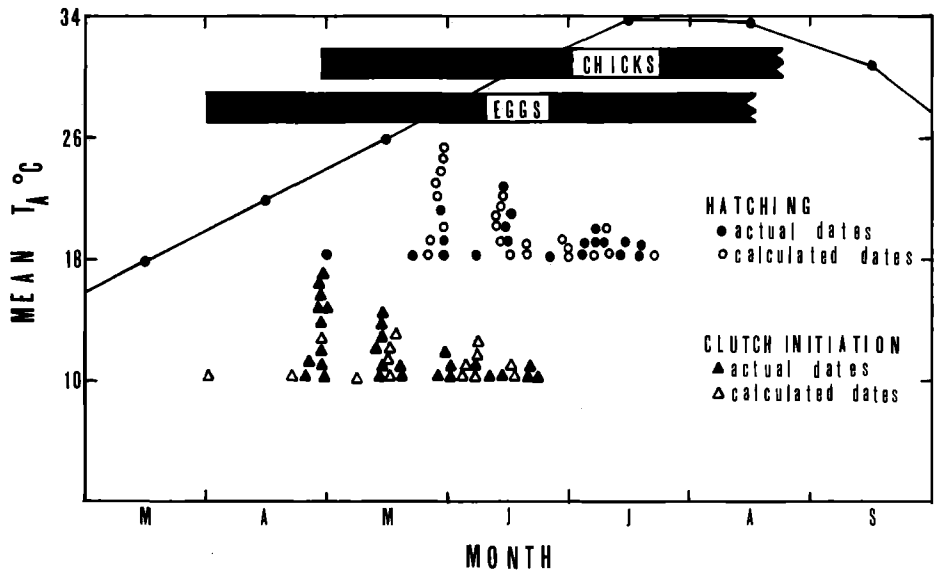

FIG. 6. Nesting chronology of the Black-necked Stilt at the Salton Sea, 1975–1978. Calculated dates are based on an incubation period of 25 days and an egg-laying period of 4 days. Mean ambient temperatures during the nesting season are plotted (line) by month.

Lesser Nighthawk eggs were found between 18 April and 14 July at the Salton Sea. This coincides with the range of egg dates (16 April–11 July) reported by Bent (1940) for the United States. Black Skimmers breed opportunistically at the Salton Sea when suitable nest sites become exposed (Grant and Hogg 1976). Eggs were found there between 15 May and 27 September (last visit to colony).

In summary, none of the species studied avoids the heat by nesting either extremely early or late in the season in this portion of its breeding range. Eggs of all species have been found in June and July.

THERMAL BIOLOGY OF THE EGG

One way in which incubating adults may minimize heat stress is by allowing eggs to reach high but sublethal temperatures (i.e., allowing some heat storage). In species with eggs that exhibit heat storage, however, adults must be sensitive to egg temperatures and capable of preventing overheating. To shed some light on behavioral means of egg temperature regulation, I performed a number of experimental manipulations. As a basis for these manipulations, I first documented nest parameters and egg temperatures during undisturbed incubation.

NEST AND EGG PARAMETERS

Nest measurements, clutch size, distance to water, and nearest neighbor nest distances were recorded for all species and localities (Table 1). All Charadriiformes studied make a shallow scrape in the substrate which may be lined with small clumps of soil, sticks, feathers, or shells. Nighthawks build no nest; eggs are simply laid on the ground. Some stilts built nests that were 20 cm or more above the substrate when water levels gradually rose in the immediate vicinity

TABLE 1

NEST MEASUREMENTS, CLUTCH SIZE, AND NEST PLACEMENT OF SPECIES STUDIED[1]

Species	Nest diameter (mm)	Nest depth (mm)	Clutch size	Distance to water (m)	Distance to nearest neighbor (m)[2]
H. mexicanus	132.0 ± 12.4 (111) [100.0–160.0]	25.6 ± 11.0 (111) [0–51.0]	3.9 ± 0.4 (152) [2–5]	15.9 ± 21.6 (128) [0–91.4]	46.2 ± 52.9 (60) [1.4–274.3]
H. mexicanus[3]	132.1 ± 11.1 (7) [110.0–145.0]	15.7 ± 15.1 (7) [0–40.0]	3.8 ± 0.4 (9) [3–4]	18.1 ± 22.5 (5) [1.2–45.7]	33.6 ± 4.3 (2) [30.5–36.6]
R. americana	146.6 ± 8.5 (5) [140.0–160.0]	36.6 ± 7.8 (5) [30.0–50.0]	3.7 ± 0.5 (6) [3–4]	22.2 ± 25.9 (9) [0.4–61.0]	19.6 ± 18.5 (8) [4.6–61.0]
C. alexandrinus	80.0 (1)	20.0 (1)	2.7 ± 0.6 (3) [2–3]	16.0 ± 9.8 (2) [9.1–22.9]	24.4 (1)
C. vociferus	119.8 ± 13.9 (23) [100.0–150.0]	28.6 ± 7.5 (23) [15.0–40.0]	3.8 ± 0.4 (30) [3–4]	37.6 ± 45.0 (31) [0.9–182.9]	109.4 ± 115.2 (5) [6.1–274.3]
S. forsteri	—	—	2.5 ± 0.5 (12) [2–3]	0 (3) [0]	—
R. niger[4]	296.2 ± 44.1 (13) [260.0–400.0]	64.2 ± 17.1 (13) [40.0–90.0]	2.9 ± 0.8 (13) [1–4]	1–10 (13)	2.5 ± 1.2 (11) [1.4–5.0]
C. acutipennis	0 (9)	0 (9)	2.0 ± 0 (8) [2]	45.6 ± 53.8 (9) [0.9–150.0]	18.8 ± 5.8 (3) [12.2–22.9]

[1] Data presented: mean ± one standard deviation; sample size in parentheses; range in brackets.
[2] Any nesting species (not necessarily conspecific).
[3] Data from coastal sites; all other data from the Salton Sea.
[4] From Grant and Hogg (1976).

of these nests (for a review of nest building in response to rising water levels see Hamilton 1975). Black Skimmer nests were scrapes dug into bars or islands composed almost entirely of Acorn Barnacle (*Balanus amphitrite*) shells.

Clutch sizes are within the ranges of those reported elsewhere (Bent 1927, 1929, 1940). The small average clutch size that I recorded for skimmers (Table 1) may have been due both to late nesting (16 August–27 September, 1975) and second nesting attempts. Nests of all charadriiform species at the Salton Sea generally were placed near water. However, some Killdeer and stilt nests were found as many as 183 m and 91 m away, respectively.

It was not possible to observe most nests frequently enough to determine hatching success accurately. Conservatively, 22 stilt nests (37.9%) and nine Killdeer nests (40.9%) at the Salton Sea hatched at least one young (Grant 1979).

The exact time of egg-laying was determined in three instances. An avocet laid its fourth egg at 09:18 on 8 May 1976. At one stilt nest egg number 3 was laid at 14:34 on 31 May 1977, and egg number 4 was laid at 16:16 on 1 June 1977. Thus, egg-laying may occur in both the cool early morning hours and during the heat of the day at the Salton Sea.

Nest Air and Egg Temperatures

Mean diel nest air temperatures for the different species ranged from 32.8 to 35.2°C (Table 2). Drent (1975) reported a mean nest air temperature of 34°C for birds in general. Mean diel egg temperature for the different species ranged from 34.9 to 38.1°C (Table 2). This encompasses most of the range reported for non-passerines (Drent 1975). Daytime egg and nest air temperatures exceeded nocturnal temperatures at the Salton Sea in all cases from which data are available.

For the stilt, the diurnal temperature of eggs from incomplete clutches (34.8°C) was lower than that of eggs from completed clutches (37.9°C) but is within the range at which embryonic development should proceed (Drent 1975). Eggs are usually laid on consecutive days, but all hatch within a 24-hr period. Egg temperatures of the incomplete 2 and 3-egg clutches (during egg-laying period) are higher than expected if one assumes incubation commenced with the last egg. Some auditory stimulation and retardation probably occur among the eggs within a clutch and insure nearly synchronous hatching (Freeman and Vince 1974), but this was not tested (see section on oxygen consumption of stilt eggs for further discussion). Indications of synchronization of hatching are present in *Limosa limosa* (Lind 1961) and *Vanellus malabaricus* (Jayakar and Spurway 1965) in which last eggs laid required less time for emergence than earlier eggs. Egg temperature data for the latter two species during the egg-laying interval were not given. Simultaneous hatching can be achieved by delaying the onset of incubation until the last egg is laid, but the thermal environment at the Salton Sea is such that eggs must be incubated or shaded for at least 10 hrs each day to prevent overheating. The first egg laid is maintained near incubation temperatures for a minimum of 30 hrs before the last egg (4-egg clutch) is laid.

The temperatures of incubated eggs generally increased with increasing ambient temperatures. This was true for the Killdeer (Fig. 7) and Lesser Nighthawk (Fig. 8) at the Salton Sea and for the avocet (Fig. 9) at both the Salton Sea and at Ventura. In the Forster's Tern (Fig. 10) incubated egg temperatures increased at

TABLE 2

DIURNAL, NOCTURNAL, AND DIEL NEST-AIR AND EGG TEMPERATURES OF BIRDS AT THE SALTON SEA AND VENTURA[1]

Species	Location	Day		Night		Diel[2]	
		Nest Air	Egg	Nest Air	Egg	Nest Air	Egg
H. mexicanus	Salton Sea	37.1 ± 3.1 (361)	37.9 ± 2.1 (586)	32.5 ± 1.9 (11)	35.2 ± 2.6 (44)	35.2	36.8
H. mexicanus[3]	Salton Sea	36.9 ± 3.0 (47)	34.8 ± 4.7 (96)	—	—	—	—
H. mexicanus	Ventura	—	37.2 ± 1.3 (58)	—	—	—	—
R. americana	Salton Sea	36.1 ± 1.9 (45)	36.8 ± 1.7 (94)	31.2 ± 1.3 (7)	35.7 ± 1.8 (23)	34.0	36.3
R. americana	Ventura	—	34.5 ± 3.0 (132)	—	35.4 ± 0.9 (28)	—	34.9
C. vociferus	Salton Sea	37.2 ± 4.5 (76)	37.1 ± 2.3 (142)	26.7	32.4 ± 2.1 (3)	32.8	35.1
S. forsteri	SESS	38.0 ± 3.2 (96)	38.2 ± 2.1 (172)	—	—	—	—
S. forsteri	NESS	31.5 ± 1.4 (160)	34.8 ± 1.5 (320)	—	—	—	—
C. acutipennis	Salton Sea	—	39.5 ± 1.8 (47)	31.9 ± 3.3 (8)	36.1 ± 0.4 (5)	—	38.1

[1] Data presented: temperature °C ± one standard deviation; sample size in parentheses.
[2] Diel temperatures calculated using diurnal temperatures for 14 hrs and nocturnal temperatures for 10 hrs.
[3] All complete clutches except for this row.

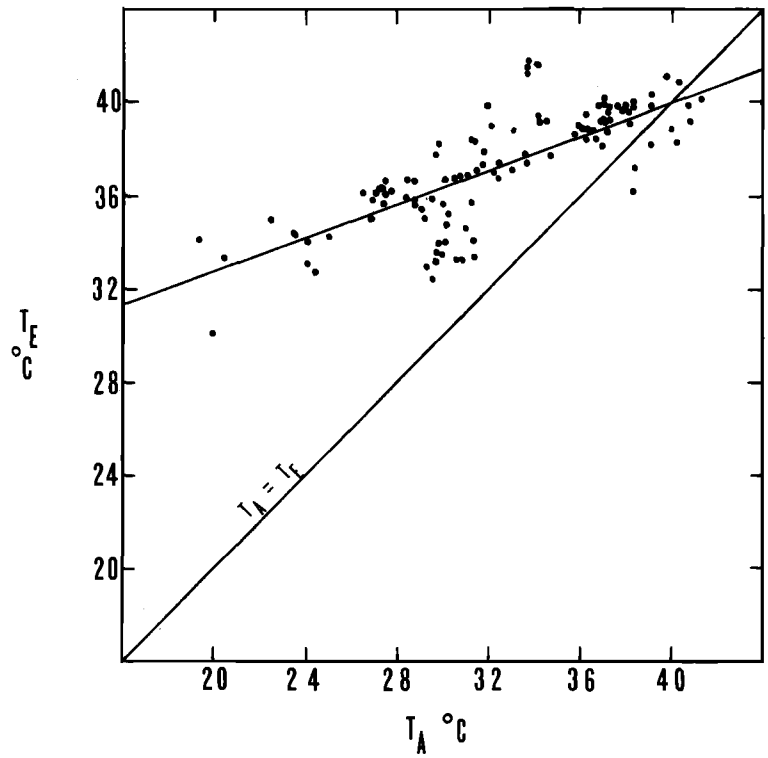

FIG. 7. The relationship between ambient temperature (T_A) and incubated egg temperature (T_E) of the Killdeer. Regression equation based on 142 data points from 2 nests: $T_E = 25.57 + 0.36T_A$, $r = 0.740$, $P < 0.01$.

SESS but decreased at NESS with increasing ambient temperatures. The eggs at NESS were incubated in nests of floating cattail. The bottoms of these nest cups were frequently wet. Temperatures of incubated Black-necked Stilt eggs increased with increasing ambient temperatures regardless of location, clutch completion, or the time of day (Fig. 11). These temperatures ranged from 30.3 to 43.7°C. Purdue (1976) demonstrated a similar increase in egg temperatures with rising ambient temperatures in the Snowy Plover. Nest air temperatures also increased with ambient temperatures in all species for which data were obtained.

EGG HEATING EXPERIMENTS

Eggs were removed from several stilt nests and temporarily replaced with four heater-equipped eggs to determine if hot eggs provided the immediate or proximate stimulus for initiating belly-soaking. Belly-soaking normally occurred between 08:30 and 18:30, and in order to isolate the effect of high egg temperatures on belly-soaking from the effects of other thermal stresses, the egg had to be heated under the bird during the relatively cool part of the day (dusk and/or dawn). I was unable to perform this experiment at night as night vision equipment was not available. Much feeding activity and little egg-coverage occurred during

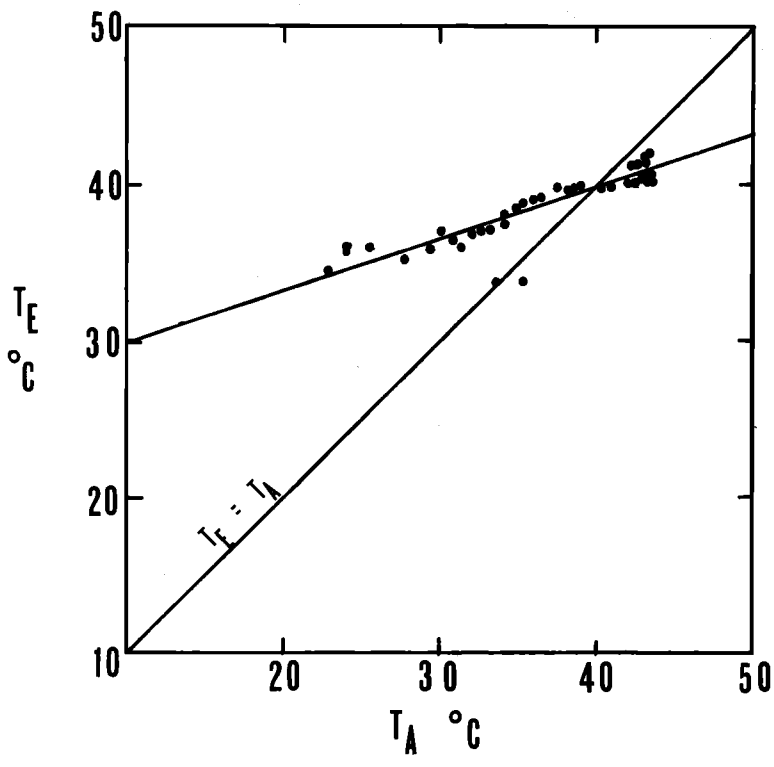

FIG. 8. The relationship between ambient temperature (T_A) and incubated egg temperature (T_E) of the Lesser Nighthawk. Regression equation based on 51 data points (duplicate points are not plotted) from 2 nests: $T_E = 26.34 + 0.334T_A$, $r = 0.890$, $P < 0.01$.

the few "cool" hours at dusk and dawn. However, the data obtained when stilts returned to the nest and sat on the hot eggs are informative.

At nest #34, the male settled onto eggs at 06:31 (T_E = 40.0°C). At 06:33 (T_E = 48.0°C) he jumped off the nest, went to the water's edge, and vigorously preened his upper breast but did not belly-soak. At nest #36 heating was initiated at 05:16 (T_E = 37.8°C) with the male incubating. By 05:27 egg temperature had climbed to 42.0°C with no overt response by the bird. At 05:32 egg temperature was 44.0°C, and still no response was noted. At 05:41 (T_E = 45.2°C) the male stood up, looked at the eggs, and walked in upright threat posture toward a Snowy Egret (*Egretta thula*) feeding 1.4 m away. The eggs were uncovered until this male settled back onto the eggs at 06:18 (T_E = 38.6°C initially). The eggs were heated again. By 06:47 T_E had climbed to 44.1°C, and the male had not responded overtly. Between 06:50 and 07:20, I maintained egg temperature between 45.0 and 46.8°C. I noted no response during this time. At 07:23 the male left the nest, walked to the water, and dipped in its bill. The bird returned to the nest, began to pant, and sat down on the eggs at 07:25 after peering into the nest cup. I unplugged the heater at this time. Belly-soaking at this nest was first seen at 09:45 on this date and last seen at 16:54. At 18:06 (T_E = 38.9°C) I plugged in the

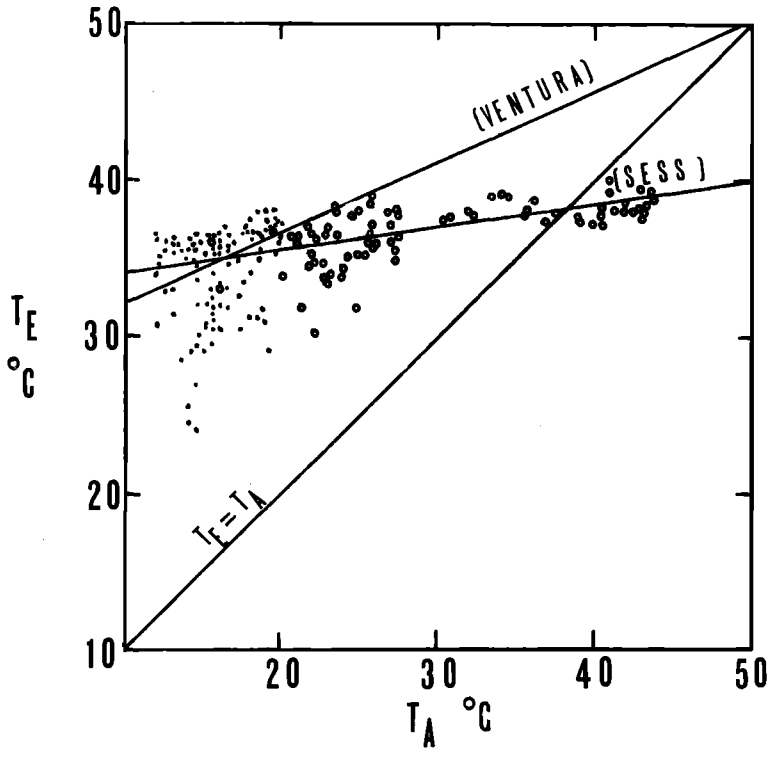

FIG. 9. The relationships between ambient temperature (T_A) and incubated egg temperature (T_E) of the American Avocet at two sites. Regression equation for Ventura based on 160 data points from 4 nests: $T_E = 27.16 + 0.467T_A$, $r = 0.375$, $P < 0.01$. Regression equation for SESS based on 117 points from 3 nests: $T_E = 32.60 + 0.140T_A$, $r = 0.649$, $P < 0.01$.

heater; egg temperature (with the female on the nest) reached 41.0°C at 18:10 when the female left the nest to feed and preen her breast.

At nest #9 I began heating the uncovered eggs at 18:00 (T_A = 24.6°C); the male sat on the eggs at 18:17. Shortly after, strong cool winds (up to 8 $m \cdot sec^{-1}$) began to blow and did so continuously throughout the night. With this wind and the bird on the nest, the maximum egg temperature reached prior to darkness (19:00) was 39.1°C. The incubating bird did not pant.

It seems clear from the data obtained at stilt nest #36 that 30 min on the eggs at temperatures of 45°C or greater did not, by itself, induce belly-soaking. The fact that belly-soaking occurred in other stilts at high shaded ambient temperatures when eggs were at the mean incubation temperature further suggests that egg temperature is not the proximate stimulus for belly-soaking.

LETHAL EGG TEMPERATURES

Stilt eggs have hatched in the field after being exposed to egg temperatures above 42°C for short intervals. In nest #38 egg temperatures ranged between 42.0 and 42.9°C for three hours, and hatching occurred. Egg temperatures as high as 43°C occurred at some nests (duration usually 15 min or less), and these eggs

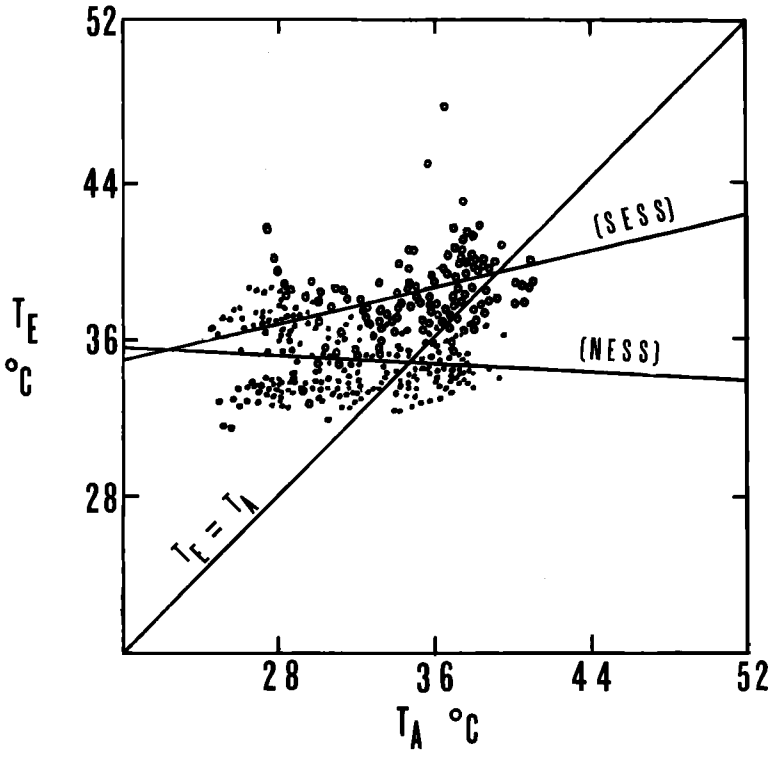

FIG. 10. The relationships between ambient temperature (T_A) and incubated egg temperature (T_E) of the Forster's Tern nesting in two habitats. Regression equation for SESS based on 162 data points from 4 nests: $T_E = 30.41 + 0.219T_A$, $r = 0.369$, $P < 0.01$. Regression equation for NESS based on 316 data points from 4 nests: $T_E = 36.56 - 0.056T_A$, $r = -0.129$, $P < 0.05$.

probably hatched (nest empty on next visit with no signs of predation). An egg close to pipping that had been rolled from a nest late on the afternoon of 22 June 1976 contained a live young (vocalizations heard). I returned it to the nest. By the next morning it was obvious that this nest had been abandoned, so I inserted a thermistor probe in the egg, positioning it to lie between membranes and the thoracic vertebrate of the chick. This egg was then moved alternately between shade and sun to determine temperature tolerance. For most of this day (5 hrs) the egg was maintained at 42°C with brief periods of about 46°C (Fig. 12), yet the chick survived. Calling and shell breaking (pipping) generally increased during intervals of increasing temperatures. However, a brief and rapid climb of egg temperature to 47.7°C was lethal. Lundy (1969) reported lethal egg temperatures for the chicken embryo of between 42.4 and 48.3°C, depending on its age. Many House Wren (*Troglodytes aedon*) embryos exposed to 41.1–43.9°C for 1 hr (Baldwin and Kendeigh 1932) and Heermann's Gull (*Larus heermanni*) embryos exposed to 43°C for 1 hr (Bennett and Dawson 1979) died.

CLUTCH SIZE AND EGG TEMPERATURE

Supernormal clutches (probably laid by two or more females) containing as many as 8 eggs have been found in some stilt (Lamb and Howell 1913; Bent 1927;

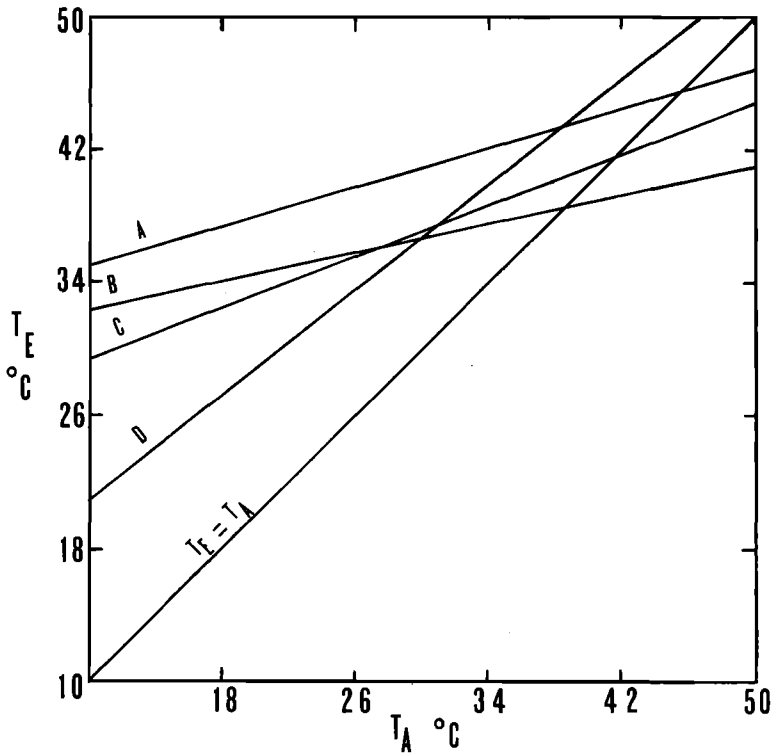

FIG. 11. Relationship between ambient temperature (T_A) and incubated egg temperature (T_E) of the Black-necked Stilt. Regression equations are: Ventura (A), daytime with completed clutches from two nests, $T_E = 32.26 + 0.288T_A$, N = 58, r = 0.520; Salton Sea (B), daytime with completed clutches from 12 nests, $T_E = 30.11 + 0.217T_A$, N = 586, r = 0.598; Salton Sea (C), night with completed clutches from seven nests, $T_E = 25.58 + 0.384T_A$, N = 44, r = 0.645; Salton Sea (D), daytime with incomplete clutches from three nests, $T_E = 13.31 + 0.779T_A$, N = 96, r = 0.739. All values significant, $P < 0.01$.

Gibson 1971; Holgerson 1971) and avocet (Lamb and Howell 1913; Mitchell 1917; Vermeer 1971) nests. The largest stilt clutches found during this study were of 5 eggs (N = 2) at the Salton Sea and 4 eggs (N = 7) at the coastal sites (Table 1). The largest avocet clutches found contained 4 eggs (N = 4). To test whether stilts would accept and cover adequately (i.e., prevent lethal egg temperatures) supernormal clutches at the Salton Sea, I artificially enlarged two clutches with eggs that had been used previously for temperature recordings at other nests. Peak ground temperatures in the shade were similar at the two nests, 40.8°C at #34, 42.3°C at #14, as were the nesting substrate and distance to surface water. Nest #34 was modified by adding three eggs to increase clutch size to seven eggs. Three eggs were fitted with thermistor probes. The temperature of the three eggs being monitored at this nest did not exceed 41.6°C (similar egg temperatures were reached in normal clutches).

At nest #14, where the clutch was enlarged from 3 to 6 eggs, egg position was virtually unchanged throughout the study. Egg temperatures for all three eggs monitored simultaneously generally spanned 2°C or less. Egg temperature did not

TABLE 3

PHYSICAL PARAMETERS OF SHELLED EGGS[a]

Species	Fresh egg mass (g)	Volume (cm^3)	Density ($g \cdot cm^3$)	Surface area (cm^2)	Length (cm)	Width (cm)
H. mexicanus	21.0 ± 1.4 (29)	19.9 ± 1.3 (29)	1.055 ± 0.001 (29)	36.2 ± 1.6 (29)	4.38 ± 0.17 (222)	3.05 ± 0.10 (222)
R. americana	32.4 ± 1.2 (6)	30.6 ± 1.1 (6)	1.058 ± 0.008 (6)	48.3 ± 1.2 (6)	5.03 ± 0.18 (21)	3.36 ± 0.09 (21)
C. alexandrinus	7.49 (1)	7.15 (1)	1.048 (1)	18.3 (1)	3.15 ± 0.65 (4)	2.21 ± 0.03 (4)
C. vociferus	14.1 ± 0.9 (13)	13.4 ± 0.9 (13)	1.051 ± 0.001 (13)	27.9 ± 1.2 (13)	3.83 ± 0.16 (49)	2.71 ± 0.05 (49)
C. acutipennis	5.75 ± 0.39 (13)[b]	—	—	—	2.71 ± 0.10 (9)	1.98 ± 0.05 (9)

[a] Data presented: mean ± one standard deviation; sample size in parentheses.
[b] Egg mass at first visit to the nest; may not equal fresh egg mass.

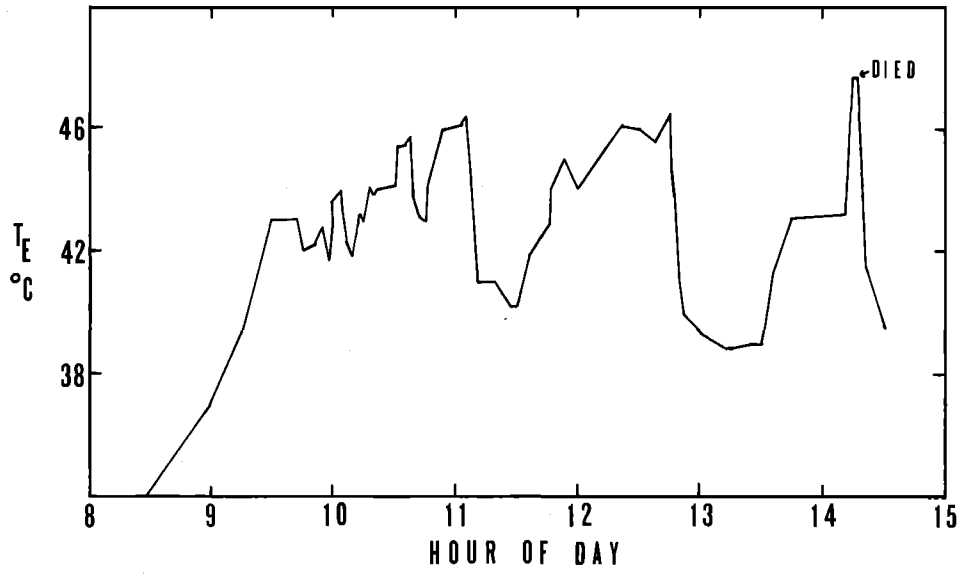

FIG. 12. Temperatures of a pipped egg of the Black-necked Stilt on 23 June 1976. Death occurred at 47.7°C. Shaded ambient temperature ranged from 32–40°C during this experiment.

exceed 41.3°C, while shaded ambient temperature reached 42.3°C. Attentiveness coupled with frequent belly-soaking at this nest prevented lethal high temperatures in the three eggs monitored. The number of belly-soaks at both experimental nests was less than that recorded on equally hot days at other nests with normal clutches.

EGG WATER LOSS AND NEST HUMIDITY

To determine how water loss from the egg-nest complex was affected by the hot, dry atmosphere, I measured all factors governing egg water loss.

PHYSICAL DIMENSIONS OF EGGS AND SHELLS

Physical dimensions of eggs and shells of all species studied appear in Tables 3 and 4. Fresh egg masses are similar to values reported by Schönwetter (1967)

TABLE 4

PHYSICAL PARAMETERS OF EGG SHELLS†

Species	Mass (g)	Thickness (mm)	A_P (mm²)§
H. mexicanus	1.40 ± 0.23 (3)	0.224 ± 0.017 (22)	0.555 ± 0.100 (8)
R. americana	2.08 (1)	0.236 ± 0.005 (7)	0.562 ± 0.250 (4)
C. alexandrinus	0.51 ± 0.04 (6)	0.157 ± 0.008 (6)	0.093 ± 0.003 (4)
C. vociferus	0.83 ± 0.03 (8)	0.167 ± 0.005 (8)	0.161 ± 0.031 (8)
S. forsteri	—	0.206 ± 0.014 (7)	0.376 ± 0.080 (3)
C. acutipennis	0.413 ± 0.029 (4)	0.142 ± 0.007 (4)	0.064 ± 0.008 (3)

† Data presented: mean ± one standard deviation; sample size in parentheses.
§ Functional pore area; for calculation, see text and Rahn et al. (1976).

TABLE 5

INCUBATION PERIODS AND PHYSICAL PROPERTIES OF EGGS†

Species	I††	Measured $\dot{M}_{H_2O}$	Predicted $\dot{M}_{H_2O}$‡	Measured G_{H_2O}§	Predicted G_{H_2O}#	F	GI/W
H. mexicanus	25	153.3 ± 40.8 (289)	142.6	5.03 ± 0.8 (12)	4.6	18	6.12
*H. mexicanus**	25	149.5 ± 45.0 (21)	—	5.73 ± 1.05 (2)	—	—	—
R. americana	24.2	163.4 ± 41.4 (27)	196.6	4.84 ± 2.09 (4)	6.5	12	3.69
C. alexandrinus	26.3	37.9 ± 6.1 (8)	66.6	1.23 ± 0.05 (4)	2.0	13	4.39
C. vociferus	25.1	77.1 ± 27.2 (51)	106.3	1.86 ± 0.32 (11)	3.3	14	3.40
*S. forsteri***	24.2	79.9 ± 33.9 (20)	143.7	3.23 ± 1.42 (4)	4.6	09	3.76
C. acutipennis	19	39.6 ± 11.8 (7)	54.8	0.92 ± 0.1 (3)	1.6	13	3.11

† I = incubation period in days; $\dot{M}_{H_2O}$ = daily water loss in mg; G_{H_2O} = water-vapor conductance in $mg \cdot day^{-1} \cdot torr^{-1}$; F = fractional water loss expressed as a percent; and GI/W = conductance × incubation period/fresh egg mass. Data presented = mean ± one standard deviation, sample size in parentheses.

†† Sources of data as follows: *H. mexicanus* (Hamilton 1975; this study); *R. americana* (Gibson 1971); *C. alexandrinus* (Rittinghaus 1956); *C. vociferus* (Bunni 1959; this study); *S. forsteri* (Bergman et al. 1970); *C. acutipennis* (Pickwell and Smith 1938).

‡ From Drent 1970.

§ Determined at 37.0°C and corrected to 760 mm Hg and 25°C.

From Ar and Rahn 1978.

* Ventura; all other data from Salton Sea.

** For predictive equations, fresh egg mass used = 21.2 g (Schönwetter 1967).

for all species except the avocet. Fresh avocet eggs that I weighed were 11.3% heavier than those he weighed, which suggests that some of his eggs may not have been fresh. Length, width, and shell masses are similar in the two samples. Predicted shell thicknesses (L), based on $L = 5.126 \times 10^{-3} W^{0.456}$ (Ar et al. 1974), where W = fresh egg mass, were similar to actual values obtained by Schönwetter and in this study (Table 4).

Volume (V) was determined for three stilt eggs by water displacement (Hoyt 1976) and averaged 19.92 ± 2.32 cm^3. This is similar to the value (19.87 cm^3) predicted from equation 4 ($A = 4.835 W^{0.662}$ where A = surface area) of Paganelli et al. (1974) and equation 12 ($A = 4.940 V^{0.667}$) of Hoyt (1976) based on fresh egg mass (W). Volume can also be predicted from the linear dimensions of the eggs (Hoyt 1979) by the formula $V = K_v \cdot L \cdot B^2$, where K_v is a common volume coefficient applicable to all eggs except those eggs that are very pointed (i.e., stilt, avocet, plover), L = length of egg in centimeters, and B = breadth or maximum width in centimeters. Hoyt (1979) calculated an average K_v of 0.509 ± 0.008 for all species, but the one stilt egg ($K_v = 0.467$) he measured deviated greatly. I determined volume and linear dimensions on 3 stilt eggs; their average K_v was 0.489 ± 0.051. Fresh egg mass (W) can be predicted from the equation $W = K_w \cdot L \cdot B^2$ (Hoyt 1979) where K_w = species specific weight coefficient. I empirically determined $K_w = 0.513 \pm 0.013$ for 13 fresh stilt eggs from the Salton Sea. K_w for the avocet was 0.532 ± 0.008 (N = 6) in this study, and K_w for the Killdeer was 0.523 (N = 1). The predictive values of these mass and volume equations are high and very useful in the field once the coefficients have been determined for the species studied.

INCUBATION PERIOD

Incubation period was measured as the time elapsed between the laying of the last egg and the hatching of the last egg. The Black-necked Stilt incubation period was 22 days at one nest and 27 days at another nest (clutch size was 4 in both).

TABLE 6

LOSS OF EGG MASS DURING DEVELOPMENT AND HATCHING, AND ADULT BODY MASS[a]

	H. mexicanus	*R. americana*	*C. vociferus*
Fresh egg mass (g)	21.0 (29)	32.4 (6)	14.1 (13)
Starred egg mass (g)	18.2 (42)	25.2 (3)	11.7 (15)
Pipped egg mass (g)	17.6 (10)	—	13.3 (1)
Chick mass (g)[b]	14.4 (23)	16.5 (1)[c]	9.4 (10)
Chick mass/egg mass	0.687	0.509	0.667
Adult body mass (g)			
Male	177.1 (6)[d]	304.0 (4)	80.5 (1)
Female	160.3 (12)[d]	293.3 (4)	
Fresh egg mass/adult female mass	0.131	0.110	0.175

[a] Data presented: means; sample sizes in parentheses.
[b] Chicks = dry hatchlings in the nest and less than one day old.
[c] Chick very weak; clutch mate dead 10 m from nest.
[d] From Hamilton (1975).

Monitoring of incubation temperatures in incomplete clutches suggested that for a large portion of this period eggs are maintained at temperatures high enough for development to proceed but not quite as high as mean incubation (full clutch) temperatures (see section on egg temperatures). On several occasions nests with incomplete clutches were left unattended at night; this rarely happened once the clutch was completed. Seven stilt eggs incubated in the laboratory hatched at 25–28 days (five hatched between days 25 and 26 and two between days 27 and 28), while maintained at 37°C and 28–40.5% relative humidity. Hamilton (1975) hatched two stilt eggs in the laboratory in 25 days but gave no data on temperature or humidity. Lint (1959) gave the incubation period for a hybrid stilt (*H. m. melanurus* × *H. m. mexicanus*) as 25 days. The incubation period for *H. novae-zelandiae* is 25–26 days (Sibson and McKenzie 1943) and for *Cladorhynchus leucocephalus* (McGilp and Morgan 1931), 28 days.

The incubation period for the Killdeer was 25 days in one nest at the Salton Sea. Bunni (1959) reported a mean incubation period of 25.1 days for five nests. The incubation period for the other species studied (Table 5) were taken from the literature. Predicted incubation periods based on $I = 11.64\ W^{0.221}$ (Ar and Rahn 1978) are similar to those in the literature (Table 5) except for the Snowy Plover (18.2 days predicted). The incubation period of 26.3 days reported by Rittinghaus (1956) was based on 43 nests. Boyd (1972) recorded a mean incubation period of 25.5 days in eight nests of this species in Kansas.

EGG MASS LOSS AND WATER-VAPOR CONDUCTANCE

Daily mass loss can be predicted by $\dot{M}_{H_2O} = 0.015\ W^{0.74}$ (Drent 1970). Actual daily mass loss in stilt eggs agrees well with that predicted (Table 5). In the other species actual daily mass losses were significantly lower than those predicted from fresh egg mass (Table 5).

Eggs lose water rapidly between starring (fine cracks and/or extrusive bumps on the shell surface) and pipping. This is clearly evident in stilts (Table 6) for which adequate data are available. Hatchlings averaged 50.9–68.7% of fresh egg

TABLE 7

WATER VAPOR PRESSURES IN THE NEST AND EGG, AND EGG TEMPERATURES†

	ΔP_{H_2O} (torr)			P_N (torr)			P_A (torr)			T_E	T_E
Column no.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
How obtained / Species	$\dot{M}_{H_2O}/G_{H_2O}$*	$\dot{M}_{H_2O}/G_{H_2O}$‡	P_A-P_N [7−6]	$P_A-\Delta P_{H_2O}$ [7−1]	$P_A-\Delta P_{H_2O}$ [7−2]	Actual§	From T_E [10]	$P_N+\Delta P_{H_2O}$ [6+1]	$P_N+\Delta P_{H_2O}$ [6+2]	Actual °C	Predicted from 9
H. mexicanus	29.9	28.4 ± 3.3 (5)	23.7	16.7	18.2	22.9 ± 7.4 (47)	46.6	52.8	51.3	36.8	38.6
H. mexicanus††	25.6	—	—	—	—	10.9 ± 3.9 (4)	—	36.5	—	—	—
R. americana	33.1	27.8 ± 5.5 (6)	21.3	12.2	17.5	24.2 ± 9.1 (6)	45.3	57.3	52.0	36.3	38.8
C. alexandrinus	30.3	29.9 ± 1.4 (3)	—	—	—	—	—	—	—	—	—
C. vociferus	40.4	32.1 ± 8.4 (8)	17.2	2.0	10.3	25.2 ± 3.6 (3)	42.4	65.6	57.3	35.1	40.6
S. forsteri	24.3	23.9 ± 6.1 (8)	21.3	17.4	17.8	20.4 ± 7.8 (6)	41.7	44.7	44.3	34.8**	35.9
C. acutipennis	42.1	29.4 ± 0.9 (3)	—	7.9	20.6	—	50.0	—	—	38.1	—

† ΔP_{H_2O} = water vapor pressure gradient; P_N = nest vapor pressure; P_A = vapor pressure within the egg; T_E = central egg temperature; $\dot{M}_{H_2O}$ = daily water loss from egg; G_{H_2O} = water-vapor conductance.

* Daily mass loss for all eggs of the species divided by conductance for all eggs of that species (Table 5).

‡ Daily mass loss of individual fresh eggs in nests for which actual conductance was known. Data presented = mean ± one standard deviation; sample size in parentheses.

§ Measured in nests with silica gel hygrometers. Data presented = mean ± one standard deviation; sample size in parentheses.

†† Data from coastal sites; all other data from the Salton Sea.

** Diurnal egg temperature at NESS assumed to equal diel egg temperature.

masses (Table 6). These values bracket the mean of 57% reported by D. Vleck et al. (1980) for 19 species. However, they are not yolk-free hatchling masses as were those of D. Vleck et al. (1980), and the 50.9% value for the one avocet chick seems abnormally low. It was weak, and its clutch mate was found dead near the nest.

Predicted water vapor conductances, based on $G_{H_2O} = 0.384\ W^{0.814}$ (Ar and Rahn 1978), for all species but the stilt, are significantly higher than those measured in the laboratory. This is anticipated, in view of the tight coupling between $\dot{M}_{H_2O}$ and G_{H_2O}, in nests where the vapor pressure gradient, ΔP_{H_2O}, averages about 27–35 torr (Rahn and Ar 1974; Rahn et al. 1977; Ar and Rahn 1978). Conductances for additional avocet and Killdeer eggs were determined in the field by placing fresh eggs of known conductance into nests of these species (see section on egg and nest data of Materials and Methods for procedures followed). Daily mass loss of the calibrated eggs and eggs in the nest provided conductance (equation 1) values for these eggs in the nest. This assumes that temperatures of all eggs in a particular nest are the same and that nest air temperature and nest humidity are uniform for all eggs within a clutch. These are probably safe assumptions with clutches of four eggs or less but would not be with larger clutches. Huggins (1941) reported differences in egg temperatures as great as 12.2°C ($\bar{X}$ = 5.6°C) in a large Mallard (*Anas platyrhynchus*) clutch (18 eggs). Conductance for nine field tested avocet eggs was 5.29 ± 1.28 and for seven field-tested Killdeer eggs, 1.92 ± 0.49. All calculations involving water-vapor conductance used values obtained in the laboratory.

Fractional Mass Loss

Egg mass loss during incubation has been shown recently to be due essentially to water loss (Grant et al. 1982). Thus, the fractional mass or water loss, F, can be obtained with the equation (Rahn and Ar 1974):

$$F = \frac{\dot{M}_{H_2O} \cdot I}{W} \tag{3}$$

where F = fraction of the initial mass which is lost during incubation, $\dot{M}_{H_2O}$ = daily water or mass loss of the egg ($mg \cdot day^{-1}$), I = incubation time (days), and W = initial or fresh egg mass (g). Fractional water loss ranged from 0.09 to 0.18 (Table 5) and averaged 0.13 ± 0.03 for the six species. This average figure agrees closely with the .14 or 14% for seven species of terns (Rahn et al. 1976), 15.6% for two species of gulls (Morgan et al. 1978), 15% for 90 species of birds (Ar and Rahn 1980), and 16% reported by Drent (1975) for birds in general.

Ar and Rahn (1978) have calculated the mean value for the constant of the $G \cdot I/W$ relationship to be 5.13 for 90 species of birds. The mean value of this constant was 4.08 ± 1.1 for six species in this study. My conductance constants are within two standard deviations of the mean calculated by Ar and Rahn (1978).

Egg, Nest, and Ambient Vapor Pressure

The water vapor pressure gradient between the inside of the egg and the outside of the shell (Table 7) was determined in three ways from the general equation (Ar et al. 1974):

$$\Delta P_{H_2O} = (P_A - P_N) = \frac{\dot{M}_{H_2O}}{G_{H_2O}} \quad (4)$$

where ΔP_{H_2O} = water vapor pressure difference between the inside and outside of the egg (torr), P_A = saturation vapor pressure within the egg (torr), P_N = water vapor pressure in the nest microclimate (torr), $\dot{M}_{H_2O}$ = daily water loss of the egg in the nest ($mg \cdot day^{-1}$), and G_{H_2O} = water-vapor conductance of the egg ($mg \cdot day^{-1} \cdot torr^{-1}$). As conductance varies with temperature (Paganelli et al. 1978), the G_{H_2O} values reported at 25°C (= 298 K) in Table 5 must be converted to 37°C (= 310 K). Multiplying G_{H_2O} by 1.02 [= $(310K/298K)^{\frac{1}{4}}$] corrects for the temperature effect (Paganelli et al. 1978). Sample sizes for $\dot{M}_{H_2O}$ are much larger than those for G_{H_2O}, and, consequently, some sample error cannot be avoided. To minimize sample error I also calculated ΔP_{H_2O} (Table 7: column 2) using daily mass losses of fresh eggs of known conductance placed in nests. The vapor pressure gradients thus determined range from 23.9 to 32.1 torr and closely approximate the 27–35 torr found in other species (Rahn and Ar 1974; Rahn et al. 1976; Ar and Rahn 1978; Morgan et al. 1978; Rahn and Dawson 1979). The vapor pressure gradients determined from mean egg temperature (P_A) and mean nest vapor pressure (P_N) are also presented for species (Table 7: column 3) where sufficient data were available. Agreement with predicted ranges is much less here, especially in the Killdeer, which simply may reflect sampling error. Nest vapor pressure was determined empirically (Table 7: column 6) with silica gel-filled stilt and avocet eggs placed in the nests and compared with nest vapor pressure (Table 7: columns 4, 5) derived from manipulation of equation 4. The most reliable values are those determined empirically. Nest relative humidity at the Salton Sea ranged from 36.8–67.6% which is similar to that (35–65%) found by Rahn et al. (1977) and Morgan et al. (1978) for a variety of species.

Vapor pressure within the egg (P_A) is a function of egg temperature. It was determined empirically (Table 7: column 7) and from manipulations of equation 4 (Table 7: columns 8, 9). Where sufficient data were available, egg temperature was predicted from nest vapor pressure determined with silica gel eggshell hygrometers and the vapor pressure gradient. (Table 7: column 2). Predicted egg temperatures (Table 7: column 11) closely approximated actual egg temperatures (Table 7: column 10). In most instances differences were less than 3°C.

Ambient vapor pressure (P_I) was measured with a recording hygrothermograph and with silica gel-filled chicken eggshell hygrometers placed on the ground within 1 m of nests under a shade platform. Mean hourly temperatures and relative humidities from the hygrothermograph were used to calculate mean hourly ambient vapor pressure (Table 8). For ventilation rate calculations I used P_I data from the eggshell hygrometers because the sample size was larger. For comparative purposes, P_I data (based on mean June relative humidity and temperature) from the closest U.S. Weather Service stations are also presented. In nearly all cases P_I was twice as great near the nests as at the weather stations where data are gathered 1.3 m above ground. In studies of this nature, it is essential that microclimatic data be gathered as near to the organisms studied as possible.

Nest Ventilation

The rate of removal from the microclimate of the nests (i.e., nest ventilation) of water lost from the egg can be calculated if the absolute humidities of the nest

TABLE 8

AMBIENT VAPOR PRESSURE (P_I) AND NEST VENTILATION RATES ($\dot{V}_N$)

Species	P_I (torr)			β‡	P_N§	$\dot{V}_N$
	Silica gel hygrometers†	Hygro-thermograph†	Weather station	(mg·l^{-1}·torr^{-1})	(torr)	(l·day^{-1})
H. mexicanus	16.0 ± 5.3 (56)	16.4 ± 2.4 (7)	8.6	.936	22.9	92.4
*H. mexicanus**	16.3 ± 5.1 (5)	—	11.6	.940	10.9	—
R. americana	16.9 ± 7.2 (10)	—	8.6	.940	24.2	88.1
C. vociferus	13.4 ± 2.2 (34)	14.8 ± 1.2 (4)	8.6	.943	25.2	26.3
S. forsteri	15.2 ± 1.7 (10)	20.8 ± 0.8 (2)	8.6	.947	20.4	40.5
C. acutipennis	14.0 ± 2.8 (46)	—	8.6	.940	20.6	12.8

† Data presented = mean ± one standard deviation; sample size in parentheses.
‡ β = transport coefficient, calculated from the mean nest air temperature in Table 2 or assumed to be 34°C (Drent 1975).
§ P_N = nest vapor pressure, from Table 7.
* Data from coastal sites; all other data from the Salton Sea.

and the ambient atmosphere are known, according to the equation (Rahn et al. 1976):

$$\dot{V}_N = \dot{M}_{H_2O}/[(P_N - P_I)\,\beta] \quad (5)$$

where $\dot{V}_N$ = nest ventilation (liters·day^{-1}), $\dot{M}_{H_2O}$ = water lost from the nest = water lost from the eggs (mg·day^{-1}), P_N = water vapor pressure in the nest (torr), P_I = water vapor pressure of the ambient environment (torr), β = transport or capacitance coefficient (mg·liters^{-1}·torr^{-1}; see Piiper et al. 1971), and where $(P_N - P_I)\,\beta$ = concentration difference of water vapor between the nest and the ambient atmosphere (mg·liters^{-1}). Substituting the appropriate values from Tables 5 and 8 into equation 5 yields the ventilation rates per clutch in Table 8. Calculated ventilation rates per egg range from 6 to 24 liters·day^{-1} ($\dot{V}_N/\bar{x}$ clutch size) and fall within the range reported for other species (Chattock 1925; Rahn et al. 1976; Rahn et al. 1977; Morgan et al. 1978; Rahn and Dawson 1979). The major shortcomings of the nest ventilation equation (5) are that it does not consider cutaneous water loss by the incubating bird (Rahn et al. 1976) or water uptake from the nest substrate, and that it does not allow for water input by belly-soakers. Water lost from the nest is assumed to be equal to that lost from the eggs.

Cutaneous water loss by birds historically has been thought to be minimal due to the lack of sweat glands and the dense covering of feathers. Recent studies (Bernstein 1971; Lasiewski et al. 1971) have shown, however, that 50% or more of the total evaporative water loss of birds maintained at 30–35°C occurs via cutaneous routes. Cutaneous evaporation accounted for the loss of 14–20% of metabolic heat production in the Roadrunner, *Geococcyx californicus*, and the Poorwill, *Phalaenoptilus nuttallii* (Lasiewski et al. 1971). It seems reasonable to predict that increased cutaneous water loss occurs through the brood or incubation patch(es) due to edema, high vascularity, and lack of feathers. Brood patches of incubating birds feel wet to the touch. This moisture may represent water lost from both the egg and the brood patch.

To quantify water transported to the nest by belly-soakers, I measured water uptake of belly feathers using the methods of Cade and Maclean (1967). For the highly modified feathers of male *Pterocles gutturalis* the mean uptake was 15.8

TABLE 9

WATER UPTAKE BY BELLY FEATHERS OF SALTON SEA CHARADRIIFORMES AND THE SANDGROUSE *Pterocles gutturalis*

Species	Water uptake[1,2]	Feather-mass[2] (mg)	No. wetted feathers[3]
P. gutturalis	15.8 ± 2.7 (8)	4.1 ± 0.9 (8)	—
R. americana	11.1 ± 2.3 (19)	3.0 ± 0.7 (19)	5
S. forsteri	10.7 ± 3.3 (17)	2.6 ± 0.6 (17)	3
C. vociferus	10.2 ± 7.2 (5)	1.1 ± 0.3 (5)	7
C. alexandrinus	9.3 ± 5.1 (15)	0.9 ± 0.4 (15)	5
H. mexicanus	9.3 ± 3.2 (38)	3.0 ± 0.9 (38)	6
G. nilotica	8.2 ± 1.8 (20)	3.9 ± 0.5 (20)	—
R. niger	6.2 ± 1.9 (10)	5.5 ± 1.5 (10)	—

[1] mg H_2O/mg dry feather mass.
[2] Data presented: mean ± one standard deviation; sample size in parentheses.
[3] Number of thoroughly-wetted feathers that take up more water than an egg loses in a day.

mg H_2O/mg dry feather mass (Table 9); Cade and Maclean (1967) obtained a value of 16.0 for belly feathers of the male of the same species. Thus, the results in the two studies are comparable.

Belly-soakers at the Salton Sea take up to 6.2 to 11.1 mg H_2O/mg dry feather mass (Table 9). Average uptake multiplied by mean dry mass per feather and divided into daily water loss ($\dot{M}_{H_2O}$) gives the number of thoroughly wet belly feathers required to put more water into the nest than an individual egg of that species loses in an entire day. Only 3–7 thoroughly wetted belly feathers are needed to add more water to the nest than an egg loses. On hot days some species may come to the nest with the entire belly wet 10–40 or more times. Up to 3 g of water may be brought to the nest by stilts at each nest relief. This was determined by holding a mounted stilt in the water (deep enough to wet the ventral feathers) for 5 sec while manipulating the belly feathers with my fingers. Stilts frequently dip 10–20 times (ca. one dip per sec) before relieving their mates; between dips they preen the belly feathers with water in the bill. If a stilt repeats this 29 times during a hot day (see section on belly-soaking), it will bring more grams of water to the nest than the weight of an entire clutch of four fresh eggs. Thus, the quantity of water added to the nest that must be removed exceeds that lost by the eggs by many orders of magnitude; this should be reflected in increased ventilation rates.

EMBRYONIC OXYGEN CONSUMPTION

I measured the oxygen consumption of nine known age stilt eggs during the entire course of incubation. Some eggs were covered with salt and mud. Since oxygen consumption rates of soiled and control eggs did not differ (see section on Effects of Salt and Mud on Eggs), embryonic metabolism data of all stilt eggs are combined here.

Oxygen consumption ($\dot{V}_{O_2}$) in the eggs of the precocial Black-necked Stilt increased nearly exponentially during the first 22 days (86%) of incubation (Fig. 13). A slight leveling occurred between days 22 and 23. In one instance (egg No. 16-1 salt-covered) the plateau in oxygen consumption lasted three days, but generally, it was only one day long (N = 5) or absent (N = 2). On day 24 oxygen

consumption increased again and continued to increase until hatching between days 25 and 26. Time of pipping varied from day 23 (N = 1) to day 24 (N = 5). Stilt chicks frequently entered the air space (based on audible peeping call notes) a day or more before the shell was pipped. Eggs were housed in tubular, open-ended plexiglass holders (C. Vleck 1978) and did not touch. However, vocalizations within the egg were audible to humans a meter or two from the closed forced-draft incubator a day or two before hatching. In fact, chicks can be heard calling within the egg before any hairline fractures in the shell ("starring") are noted. The vocalizations may serve to accelerate development of younger eggs and retard that of older eggs (Vince 1969).

The pre-pipping $\dot{V}_{O_2}$ for all eight stilt eggs that hatched averaged 10.2 ± 0.6 $cm^3 \cdot hr^{-1}$ or 244.8 $cm^3 \cdot day^{-1}$. Pre-pipping $\dot{V}_{O_2}$ of the stilt, predicted from fresh egg mass ($\dot{V}_{O_2} = 25.2\ M^{0.73}$ from Hoyt et al. 1978), is 232.4 $cm^3 \cdot day^{-1}$. Predicted pre-pipping $\dot{V}_{O_2}$ based on water-vapor conductance ($\dot{V}_{O_2} = 51.3\ G_{H_2O}$ from Rahn et al. 1974) is 264.4 $cm^3 \cdot day^{-1}$ (N = 7), and predicted pre-pipping $\dot{V}_{O_2}$ based on egg mass and incubation time ($\dot{V}_{O_2} = 267$ M/I from Rahn et al. 1974) is 224.0 $cm^3 \cdot day^{-1}$. The predictive value of all equations are good but $\dot{V}_{O_2} = 25.2\ M^{0.73}$ best fits the measured pre-pipping oxygen consumption of stilt eggs. Hoyt et al. (1978), C. Vleck et al. (1979), and D. Vleck et al. (1980) found the best fit occurred when the prediction was based only on initial mass of the egg.

Oxygen conductance (G_{O_2}) of stilt eggs was calculated from water-vapor conductance measurements by $G_{O_2} = 1.081\ G_{H_2O}$ (Paganelli et al. 1978) and averaged 5.46 ± 0.8 (n = 7) $cm^3 \cdot day^{-1} \cdot torr^{-1}$. The partial pressure gradient of oxygen across the shell (ΔP_{O_2}) can be calculated from the Fick diffusion equation, $\Delta P_{O_2} = \dot{V}_{O_2}/G_{O_2}$ (Rahn et al. 1974). The pre-pipping rate of oxygen consumption divided by the oxygen conductance gives a partial pressure gradient of 45 torr.

Air cell oxygen tension, $P_{A_{O_2}}$ is equal to $P_{I_{O_2}} - \Delta P_{O_2}$, where $P_{I_{O_2}}$ is the effective ambient oxygen tension (Wangensteen and Rahn 1970/1971) which at 37°C averaged 147 torr. Thus, $P_{A_{O_2}} = 102$ torr in the stilt eggs. Measured $P_{A_{O_2}}$ (Rahn et al. 1974) prior to pipping in 10 species averaged 104 torr (range 98–114). Calculated pre-pipping air cell oxygen tension ranged from 72–126 torr (D. Vleck et al. 1980).

EFFECTS OF SALT AND MUD ON EGGS

As a consequence of frequent belly-soaking in saline and silt-laden waters, the eggs in some nests at the Salton Sea became covered with a thin layer of dried salt and/or mud during the course of incubation (Fig. 14). Eggs in 64 of 191 (33.5%) stilt nests at the Salton Sea were sufficiently covered with mud to warrant comments in my field notes. Eggs without mud were those in nests near clear water and in nests well lined with sticks (elevated eggs above the mud substrate). None of the eggs in 19 coastal nests had mud on it.

The soaked belly feathers of stilts, Killdeers, and avocets were frequently discolored with mud during the heat of the day if the birds were soaking in muddy or very shallow water. In some instances when a stilt left the nest, clumps of mud from the nest lining stuck to the ventral feathers. Some eggs were totally covered with mud so that none of the original shell color could be seen. In some instances the egg shape was grossly altered by irregular clumps of mud. Egg recognition does not appear to be highly developed in stilts and perhaps not in

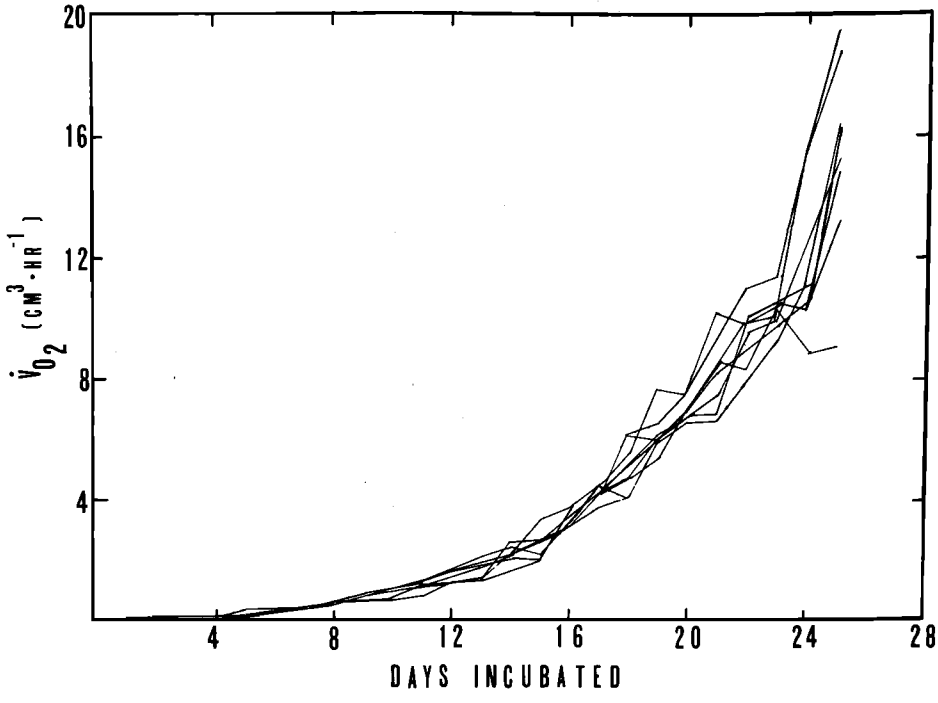

FIG. 13. The relationship between oxygen consumption by eggs of the Black-necked Stilt and days incubated; based on 181 measurements on nine eggs.

other Charadriiformes nesting at the Salton Sea. In one instance a pair of Forster's Terns incubated a round piece of pumice (about the same size as its eggs) in a nest with two eggs, and a pair of stilts incubated a clump of mud (about the same size as its eggs) in a nest with three eggs (Fig. 14). I did not test egg recognition and/or nest site recognition at the Salton Sea because of the danger to the eggs from extreme heat. Field observations indicated that eggs completely covered with mud and/or salt hatched. However, it was of interest to determine the effect of a layer of salt and/or mud on oxygen consumption, water-vapor conductance, daily mass loss, crypsis, and near-infrared reflectance of stilt eggs.

The pre-pipping rate of oxygen consumption was 10.2 $cm^3 \cdot hr^{-1}$ (N = 3) in mud-covered eggs, 10.2 $cm^3 \cdot hr^{-1}$ (N = 3) in salt-covered eggs, and 10.4 $cm^3 \cdot hr^{-1}$ (n = 2) in clean or control eggs. Thus, mud and salt did not affect embryonic oxygen consumption.

Fresh stilt, avocet, and chicken eggs were used to determine the effects of salt and mud on water-vapor conductance. The average dry mud mass applied to four chicken eggs was 1.320 ± 0.13 g. Water-vapor conductance of mud-covered eggs decreased an average of 12.9% while the conductance of the controls actually increased 2.1% (Table 10). The slight increase in conductance of the controls may have been due to the changing of the silica gel at the mid-point of this experiment (soiled and control eggs were housed in the same desiccation chamber). Conductance of salt-covered eggs decreased 1.5% (N = 2), while that of the controls

FIG. 14. Nest of the Black-necked Stilt at the Salton Sea showing three mud-covered eggs and a large clump of mud in the nest.

increased 2.1% (same controls used for both mud and salt experiments). The covering of mud decreased conductance more than a covering of salt when maintained over silica gel. However, the mud (obtained from the Salton Sea nesting environment) has a high salt content and may take up moisture from the atmosphere in the field. Mud-covered eggs removed from the desiccators increased in mass at room temperature (27°C) and a relative humidity of 36%. Four such mud-covered chicken eggs gained an average of 31.4 ± 4.5 mg of water from the ambient air in 21 minutes. The water content of the mud on the eggshell in the nest changes during the heat of the day when belly-soaking occurs but also at other times depending on nest humidity. Presumably water taken up by the mud on the eggshell does not pass through the shell because of the vapor pressure gradient.

I analyzed daily mass loss of clean and mud-covered stilt eggs at the Salton Sea to determine the consequence of mud application. Clean stilt eggs lost 162.6 ± 42.4 mg·day^{-1} (N = 157), and mud-covered stilt eggs lost 142.3 ± 36.6 mg·day^{-1} (N = 123). Thus, mud-covered stilt eggs lost significantly less mass per day (12%; $P < .001$) than clean eggs. This agrees well with the 12.9% average decrease in conductance measured in the laboratory. It also suggests that potential water-uptake by the mud layer probably is not significant, assuming that ΔP_{H_2O}, the water vapor pressure gradient, is the same in all nests (equation 1). An additional complication in the $\dot{M}_{H_2O}$ data is that the quantity of mud adhering to the eggshell from one weighing to the next may not be constant. However, the large sample size (123) probably averages the effect of variation in mud mass. Fractional mass loss (equation 3) over the course of incubation would be 17.0% and 19.4% for mud-covered and clean eggs, respectively. Thus, the fractional

TABLE 10

EFFECT OF MUD ON WATER-VAPOR CONDUCTANCE OF EGGS

Species	n	G_{H_2O} (mg·day^{-1}·torr^{-1})		
		Pre-mud[1]	Post-mud[1]	% Change
H. mexicanus	6	4.9 ± 1.1	4.4 ± 1.0	−10.2
R. americana	4	5.6 ± 2.8	4.7 ± 2.4	−16.1
G. gallus	12	12.8 ± 1.9	11.2 ± 1.6	−12.5
Control (*G. gallus*)	3	13.8 ± 1.1	14.1 ± 1.3	+2.1

[1] Mean ± one standard deviation. See text for details.

mass loss of mud-covered eggs, when evaluated over the total incubation period, does not differ from the mean fractional mass loss values of other species (Drent 1975; Rahn et al. 1976; Morgan et al. 1978; Ar and Rahn 1980). Salt-covered, mud-covered, and clean eggs hatched successfully in the laboratory and in the field, but I cannot quantify the comparative hatching success of soiled eggs in the field. The laboratory oxygen consumption data indicate that no serious problems are posed by the application of salt and mud to the eggshell.

Charadrii and Lari eggs are noted for their cryptic coloration. The main defense against predators is egg and nest camouflage (Tinbergen et al. 1962). In marshes stilt eggs are well-camouflaged, but on the light clay-sandy soils and barnacle bars at the Salton Sea, clean eggs are conspicuous to a trained human eye. However, eggs deposited in simple scrapes in the clay-sandy soils are rendered inconspicuous by a layer of salt and/or mud. As salt and mud present no known physiological hardships, perhaps they enhance survival in this nesting environment through crypsis. During the heat of the day, the only active visually-oriented egg predators are a few gulls. Almost all of the other potential egg predators are nocturnal and/or detect prey by means of olfactory cues. Such predators include the Black-crowned Night Heron (*Nycticorax nycticorax*), Coyote (*Canis latrans*), Raccoon (*Procyon lotor*), Kit Fox (*Vulpes macrotis*), Striped Skunk (*Mephitis mephitis*), Gopher Snake (*Pituophis melanoleucus*), and Red Racer (*Masticophis flagellum*). Corvids are rare at the Salton Sea, especially during the summer. I have not actually witnessed egg predation at the sea. On the few relatively cool days that occurred during the nesting season, Coyotes, Raccoons, Kit Foxes, and both snakes were seen in the study area.

One major disadvantage associated with mud from the Salton Sea on the eggshell surface is enhanced absorptivity in the near-infrared portion of the electromagnetic spectrum (Bakken, pers. comm.). Bakken et al. (1978) reported near-infrared reflectance of about 80–95% for ground nesting bird eggs (their sample included stilts, avocets, Killdeers) but only 70–73% reflectance for eggs of *S. forsteri*. Egg pigments (protoporphyrin and biliverdin) show absorption characteristics similar to melanin in the visible range, but in the near-infrared range egg pigments reflect most incident solar radiation (Bakken et al. 1978). Because mud obscures this reflective surface, mud-covered eggs should gain heat from solar radiation faster than clean eggs. The water content of the mud on the eggshell may slightly decrease the rate of heat gain from solar radiation because the water evaporates as the temperature surrounding the egg increases and as nest vapor pressure decreases when the parent leaves the nest uncovered.

INCUBATION BEHAVIOR

Aspects of the incubation behavior of 7 species of Charadriiformes and the Lesser Nighthawk were studied to determine the thermoregulatory mechanisms used to mitigate the effects of the high temperatures encountered at the Salton Sea.

Egg-covering Behavior

The intentional covering of eggs with nest material or sand has been reviewed by Maclean (1974). This behavior occurs in four families of the Charadrii, the grebes, some waterfowl, and the screamers. It has not been reported in either North American or European shorebirds but has been described in shorebirds nesting in the southern hemisphere. The primary function appears to be concealment, though in a few species, thermoregulation may be equally important (Maclean 1974). In most cases the evidence for concealment appears stronger, but adequate biophysical measurements generally have not been made.

The scarcity of reports of egg-covering in New World Charadriiformes is striking. If it occurs in response to high temperatures in the Old World, one would expect to see it at the Salton Sea. However, I found partial egg-covering in only one nest at the Salton Sea, that of a pair of Snowy Plovers with three eggs. About 50–60% of the surfaces of these eggs were embedded in the loose dirt and plant matter in the nest. It is of interest that on the previous evening, this pair of plovers attempted to distract a gopher snake away from the nest; the eggs were not covered with any material at that time. I weighed the eggs and transported the snake to a point 0.5 km from the nest (to insure that the eggs would be present the next day for additional measurements). Egg-covering in this instance probably occurred in response to the predator(s) (snake and/or human) rather than for thermoregulation. Meinertzhagen (1954) stated that the Snowy Plover often covered its eggs in Arabia.

As a crude experiment to assess the thermoregulatory effects of egg-covering, I equipped six chicken eggs (mass 52–53 g; white eggshells) with thermistors and exposed them to various conditions for nearly a full day at the Salton Sea (Fig. 15). All egg temperatures were within 1°C of each other at the initiation of the experiment at 07:10. Unfortunately light clouds were present off and on throughout the day, so the temperatures encountered were not the maximum possible. All eggs remained at temperatures higher than shaded ground. The shaded (5 × 10 cm shade platform 1 cm above egg) egg on the surface remained below lethal levels most of the day but was warmer than the ground shade probe, probably because of reradiation and conduction from the hot nearby soil. A similarly-shaded egg at the surface was watered six times (5 g each time, all water poured onto the upper surface of egg at once allowing excess to wet the ground below) between 10:05 and 14:00. These 30 g of water sufficed to keep this egg below 41°C (stilts may transport 30 g or more of water to their nests on a hot day; see section on Nest Ventilation).

One egg was buried 2.5 cm below the surface and not shaded, while another egg was partially buried such that 2 cm^2 of its surface area was exposed to the sun. Temperatures of both eggs exceeded lethal levels and were higher than that of an egg on the surface of the ground fully exposed to the sun. This surface-

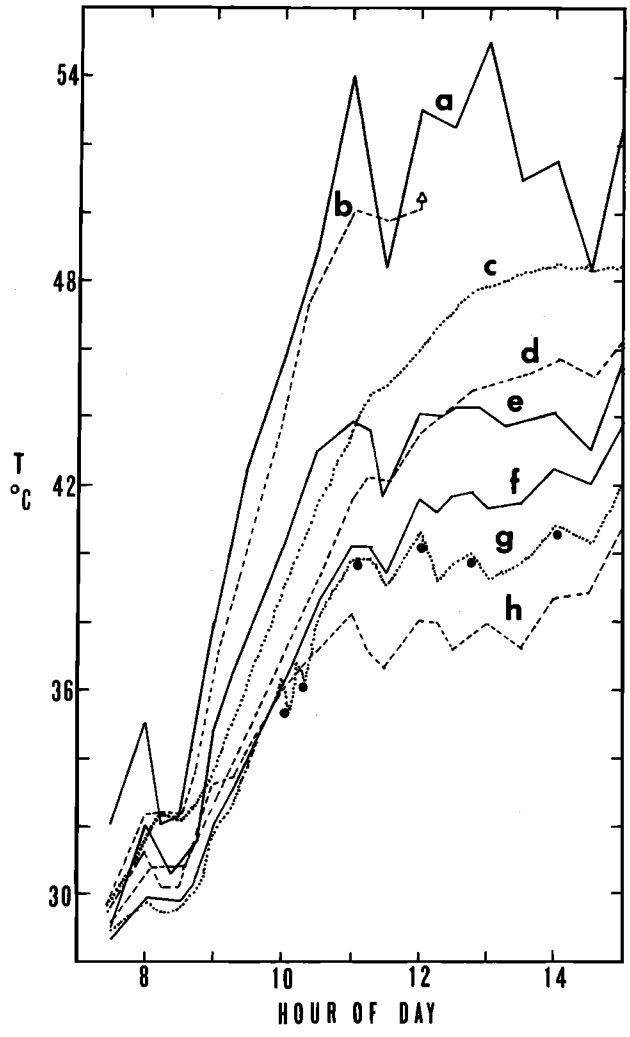

FIG. 15. Ground temperatures and temperatures of chicken eggs exposed to various environmental and experimental conditions at the Salton Sea on 15 July 1976. See text for details. a = ground in sun; b = partially buried egg with 2 cm^2 exposed above ground, unshaded; c = egg buried 2.5 cm below ground, unshaded; d = partially buried egg with 2 cm^2 exposed above ground, shaded; e = egg on surface exposed to full sun; f = egg on surface, shaded; g = egg on surface, shaded and watered; h = ground in shade; ● = wetting of egg with 5 g of water; △ = upper limit of instrument.

exposed egg was cooler than a partially buried shaded egg. These findings are anticipated in view of the cooling effect of the wind, evaporative cooling of the egg (as a result of slight water loss during this time), and the emissivity of the egg. The results of this experiment suggest that on an average day at the Salton Sea, unattended or even shaded eggs buried (partially or totally at shallow depths) in dry sand would be fatally over heated. Shaded but unattended eggs on the surface also probably would suffer lethal damage ($T_E \geq 43.7°C$). The only alternatives are tight egg-brood patch contact and/or the addition of large quantities

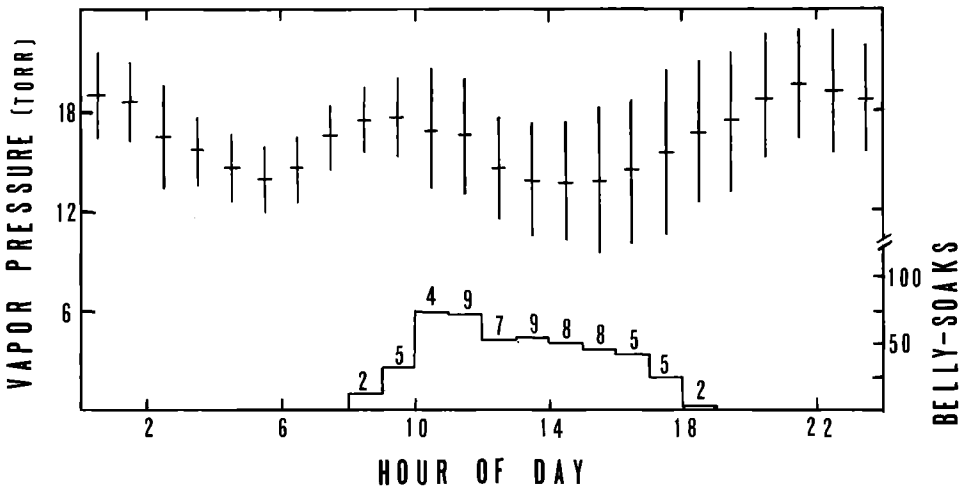

FIG. 16. Mean vapor pressure at ground level near stilt nests and mean number of belly-soaks per nest (total N = 3109) according to time of day for seven days during June and early July (1976–1978) at the Salton Sea. Numbers above the belly-soaking columns indicate total nests where complete data for that hour were gathered. Vapor pressure lines indicate means (horizontal) ± one standard deviation (vertical).

of water. The Old World Egyptian Plover (*Pluvianus aegyptius*) buries its eggs in sand, but shades them, and transports large quantities of water to them during the hottest part of the day (Howell 1979).

BELLY-SOAKING AND FOOT-WETTING

Belly-soaking, as defined by Maclean (1975), is the wetting of the ventral plumage and the transport of water to the eggs or young; this excludes incidental wetting of the plumage in aquatic birds. The stereotyped motor patterns associated with this behavior differ conspicuously from those that result in incidental wetting as a result of foraging and/or resting on the water and bathing. Foot-wetting is the dipping of the feet and lower legs into the water while in flight (Turner and Gerhart 1971). Belly-soaking and foot-wetting are most pronounced in, and may even be limited to, the order Charadriiformes (Maclean 1975; Grant 1978). Seven species of Charadriiformes currently breed at the Salton Sea, and I have observed belly-soaking in all seven. I also observed foot-wetting in both species of terns and the Black Skimmer.

Black-necked Stilts belly-soak by walking into relatively deep water and flexing the legs. The lower breast usually strikes the water first, but the ventral feathers from the upper throat to the undertail coverts frequently become wet and matted during the hottest portion of the day. In its undisturbed form, belly-soaking is a series of dipping motions alternated with frequent preening of the belly feathers (water is often taken into the mouth and used to preen the ventral feathers). All of the belly-soaking data presented were gathered from undisturbed birds. Belly-soaking can be readily induced at lower temperatures by disturbing the birds. However, such belly-soaking behavior is clearly interspersed with numerous distraction displays. One distraction display employed by stilts is false incubating,

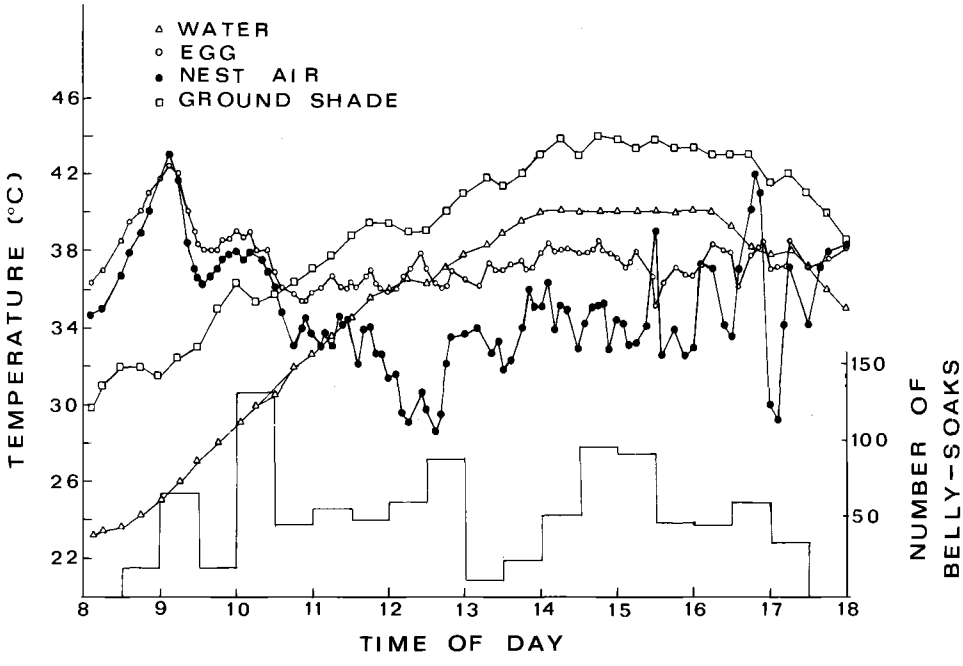

FIG. 17. Frequency of belly-soaking, and nest air, water, egg, and ground shade temperatures at one Black-necked Stilt nest at the Salton Sea, 27 June 1977.

or Displacement Brooding. In this behavior the bird flexes its legs and appears to incubate away from the nest site. If this Displacement Brooding occurs in shallow water, the motor patterns employed are indistinguishable from those used in "pure" belly-soaking. The context in which the behavior appears and the duration of sitting in the water serve to distinguish belly-soaking from Displacement Brooding. In belly-soaking, water contact lasts only a second or two while several minutes may elapse during Displacement Brooding. Nevertheless, these activities grade into one another.

I observed stilts belly-soaking between 08:00 and 19:00 (Fig. 16) at the Salton Sea. The mean number of soaks or dips per hour was highly variable. More belly-soaks occurred during midday than during the late afternoon when shaded ambient temperatures peak. The average number of belly-soaks per day (based on all-day observations at 10 nests) by nesting stilts at various ambient temperatures was 3 at 25–30°C, 40 at 30–35°C, 155 at 35–40°C, and 101 at 40–45°C. Belly-soaking is probably more frequent in the 25–30°C ambient temperature range in other areas where ambient temperatures this low are not associated with low solar radiation loads as they are at the Salton Sea.

The highest number of belly-soaks (each belly-water contact counts as one) recorded at a stilt nest was 953 on a day when ambient temperatures reached 44.0°C (Fig. 17). The numbers of belly-soaks at two nests watched simultaneously were 101 (nest #45) and 795 (#46), an eight-fold difference. These nests were less than 20 m apart along the same narrow dike, both were less than 0.3 m above water and less than 1.0 m from surface water, and both nests were similarly

FIG. 18. Black-necked Stilts at nest relief. Both birds have wet, matted belly feathers.

exposed to insolation (i.e., no shade) and wind. In addition, at nest #45 the male incubated without relief from 09:44 to 18:37 while at nest #46 both sexes relieved each other repeatedly throughout the day. Yet fewer belly-soaks occurred at the nest (#45) where only the male incubated, and the egg temperatures averaged lower (extreme upper egg temperatures were also lower) than at nest #46 where both sexes alternated, and belly-soaking was eight times more frequent.

Belly-soaking behavior is anticipatory as birds frequently belly-soaked not only upon being relieved but also when coming in to take their turn at the nest (Fig. 18). At nest #35 on the morning of 27 June 1977, a total of 85 belly-soaks (by both members of the pair) was seen before the eggs were covered by one of the parents. Stilts belly-soaked and transported water to the nests when chicks were hatching. I watched one nest with three chicks and one pipped egg for several hours while ambient temperatures ranged from 43 to 44°C. Belly-soaking was frequent, but I did not see chicks attempting to drink from the ventral plumage of the adult. Rather, the chicks seemed to move around under the adult to maximize wetting of their down and, hence, cooling. All shorebirds studied wet their feet and legs as a consequence of feeding and belly-soaking. This incidental wetting of the feet and legs does not constitute foot-wetting in the sense described above. Belly-soaking has not been previously reported for Black-necked Stilts, though it is known to occur in Black-winged Stilts, *H. himantopus* (Crossley 1964; Dharmakumarsinhji 1964).

The motor patterns of belly-soaking in the American Avocet appear very similar to those used by stilts. One pair of avocets belly-soaked 282 times on 25 June, 1976 when shaded ambient temperatures reached 44.0°C (Fig. 19). The female at

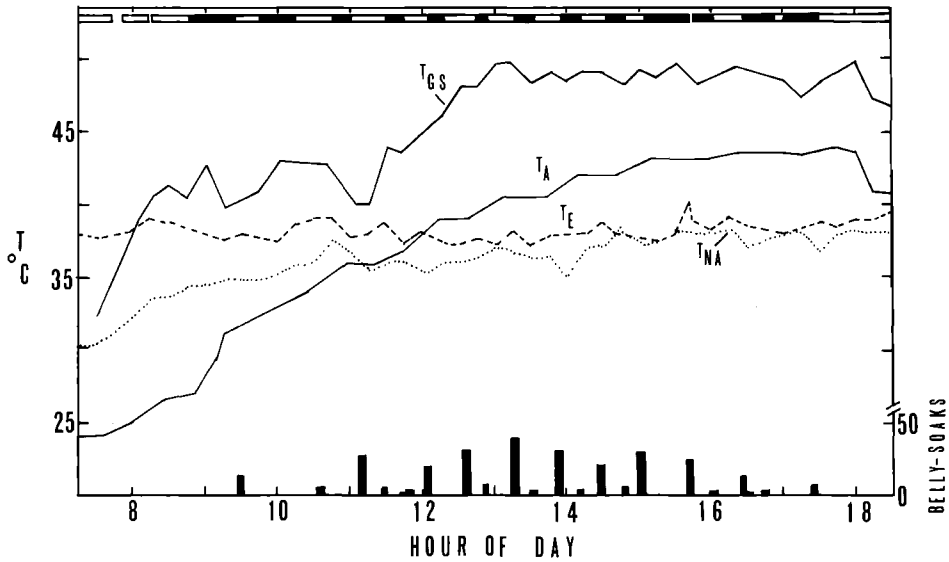

FIG. 19. Frequency of belly-soaking, attentiveness, egg (T_E), nest air (T_{NA}), ambient (T_A), and ground in sun (T_{GS}) temperatures at an American Avocet nest at the Salton Sea, 25 June, 1976. Horizontal bars: male on nest (solid), female on nest (open), eggs uncovered (gap). Vertical bars = frequency of belly-soaking. Note that the relieved bird frequently belly-soaked while its mate was incubating.

this nest frequently flew 300 m to another impoundment when relieved at the nest, so the actual number of belly-soaks was probably much higher. The male belly-soaked in the impoundment adjacent to the nest. The female performed 18 belly-soaks while the male belly-soaked 264 times between 09:30 and 16:45. Frequent nest relief coupled with frequent belly-soaking kept egg temperatures below 40°C for nearly the entire day (Fig. 19). Belly-soaking has not been described previously for the American Avocet but has been reported for *Recurvirostra avosetta* (George Kainady 1977).

Snowy Plovers belly-soak by running through relatively deep water and intermittently preening the ventral feathers. They may flex their legs, but the observation distance coupled with the relatively short legs made this difficult to confirm. Belly-soaking is less conspicuous for the same reasons, and, consequently, I do not know the frequency of this behavior. Excellent photographs of belly-soaking in the closely related *Charadrius dubius* appear in Gatter (1971). Belly-soaking also has been recorded for *C. alexandrinus* in India, the United States, and Iraq (Dharmakumarsinhji 1964; Bailey and Niedrach 1965; Boyd 1972; George Kainady and Al-Dabbagh 1976). Circumstantial evidence (mud on eggs) for belly-soaking exists for *C. alexandrinus* in Australia (Hobbs 1972).

Belly-soaking by the Killdeer is very similar to that of the Snowy Plover. In addition to being fairly inconspicuous, it often was performed relatively far from nests, making accurate determination of its frequency impossible. In general, throughout the heat of the day, the bird returning to the nest at nest relief had a wet, matted belly. Nesting Killdeers with wet bellies were seen at the Salton Sea from 09:46 until after 18:00. Belly-soaking in the Killdeer has been reported pre-

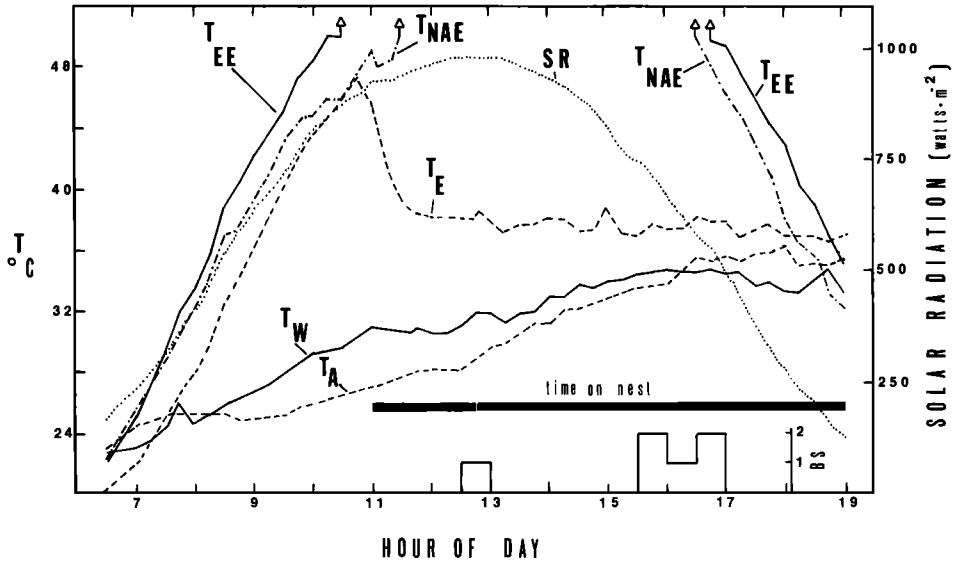

FIG. 20. Meteorological conditions, egg temperatures, and behavior at two Forster's Tern nests, 31 May, 1977. Nest no. 25 was deserted; nest no. 26 was active; T_{EE} = temperature of exposed egg (nest 25); T_{NAE} = temperature of nest air exposed to sun (nest 25); T_E = temperature of incubated egg (nest 26); T_W = temperature of water; T_A = shaded ambient temperature at ground level; SR = solar radiation; BS = frequency of belly-soaking (nest 26). Horizontal bar = tern on nest 26.

viously (Boyd 1972; Kull 1977; Schardien and Jackson 1979). Killdeer chicks generally leave the nest within 24 hours of hatching, but typically all young leave as a group. Thus, it is common to find nests with one or two pipped eggs and several recently hatched chicks. I saw adults transporting water to these nests at the Salton Sea, but I have not seen the chicks drink from the wet belly feathers.

Both Gull-billed Terns and Black Skimmers nesting at the Salton Sea foot-wetted and belly-soaked during the heat of the day (Grant and Hogg 1976; Grant 1978). Belly-soaking in the Gull-billed Tern occurred between 09:30 and 17:30 on 13 July 1976 and as late as 18:04 in Black Skimmers.

Belly-soaking by the Forster's Tern occurred throughout the heat of the day and was recorded as early as 09:22 and as late as 17:57. The number of belly-soaks by the pair at nest #26 varied from 6 on 31 May, 1977 (Fig. 20) to 109 on 1 June, 1977 (Fig. 21). Ground shade temperature did not exceed 36.4°C on 31 May but climbed to 41.0°C on 1 June. Stronger winds on 31 May depressed black-bulb temperatures (not plotted), while solar radiation recordings for the two cloudless days were nearly identical.

Foot-wetting in terns resembles "walking" on water. Terns generally expose the feet and legs whenever they approach the surface of the water. Belly-soaking in terns seems to represent a "deeper" drinking flight with the ventral surface splashing through the water, probably in response to high body temperature of the adult. On some occasions the long low belly-skimming flight is not seen, but rather the tern appears to drop vertically from the air. This superficially resembles plunge-diving, but the belly strikes the water first, and the bill is seldom submerged. Belly-soaking is generally seen only in nesting terns. However, on hot

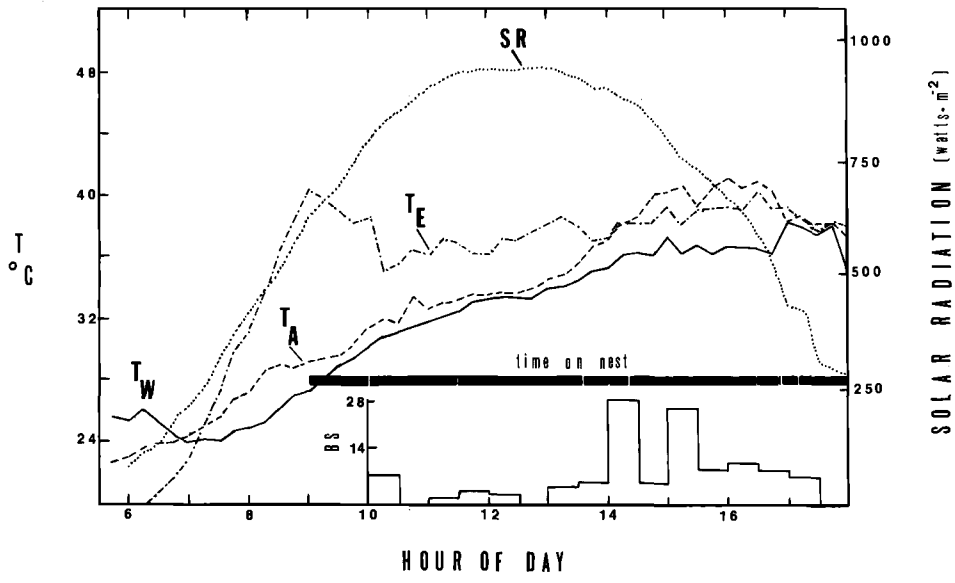

FIG. 21. Meteorological conditions, egg temperatures, and behavior of Forster's Terns at nest no. 26, 1 June, 1977. SR = solar radiation; T_E = temperature of incubated egg; T_A = shaded ambient temperature at ground level; T_W = temperature of water; BS = frequency of belly-soaking. Horizontal bar = tern on nest.

days, non-nesting Caspian (*Sterna caspia*) and Black Terns (*Chlidonias niger*) occasionally wet their bellies while on the wing. Forster's Terns may leave the nest uncovered for brief intervals (generally less than 1–2 min) to belly-soak during the hottest part of the day.

Belly-soaking and foot-wetting have not been described previously for Forster's Terns but have been reported for incubating *Sterna fuscata* (Dinsmore 1972; Stonehouse *in* Drent 1972; T. R. Howell, pers. comm., film; Grant, pers. obs.), *S. albifrons* (Mabbett 1890; Abdulali 1939; Tompkins 1942; Hardy 1957; Dharmakumarsinhji 1964; Ali and Ripley 1969), *S. acuticauda* (Currie 1916; Lowther 1949; Ali and Ripley 1969:, *S. aurantia* (Lowther 1949), *S. bergii* (Hulsman 1975), *S. hirundo* (Grant 1981), *S. maxima* (Grant 1981), and *S. sandvicensis* (Grant 1981).

ORIENTATION ON THE NEST

I recorded orientation of the incubating bird with respect to the sun and wind to discern if orientation served to minimize the heat load and to determine if all species responded to heat stress in a similar fashion. Nearly 300 hrs of observations on orientation to the sun and ca. 200 hrs on orientation to the wind were obtained (Table 11). Birds were scored as facing the sun if they faced between 45° on either side of a line from the bird's head to the sun. Tail-to-the-sun orientation was scored similarly. Lateral orientation denotes that the long axis of the bird was perpendicular to the sun or wind. Even though the sun was nearly overhead during the middle of the day, orientation data were recorded because shadows were discernible. The orientation data represent the accumulated data

TABLE 11

ORIENTATION OF ADULTS ON THE NEST WITH RESPECT TO SUN AND WIND

Species	Sun[1]				Wind[1,2]			
	Lateral to (%)	Facing (%)	Tail to (%)	n (min)	Lateral to (%)	Facing (%)	Tail to (%)	n (min)
H. mexicanus	43	21	36	8384 (21)[3]	39	45*	17	5523 (21)
H. mexicanus[4]	50	19	31	533 (3)	—	—	—	—
R. americana	40	21	39	1466 (4)	26	70*	4	1854 (4)
C. alexandrinus	25	4	71*	909 (2)	40	25	35	896 (2)
C. vociferus	19	4	78*	2590 (5)	21	31	48	2394 (5)
S. forsteri	35	38*	27	2584 (5)	44	39	17	2424 (4)
C. acutipennis	32	2	66*	1296 (4)	50	7	43	588 (4)

[1] Percent of time spent by each species in each orientation.
[2] All velocities.
[3] Number of all-day (6–12 hr) nest observations in parentheses.
[4] Data from Ventura; all other data from the Salton Sea.
* Significant at $P < 0.01$ using Chi-Square determinations within species. For statistical tests, lateral orientations are divided by two, as side facing the sun or wind may be determined randomly.

from many birds observed over many continuous hours rather than individual recordings at set time intervals. I did not record which side of the bird was lateral to the sun or wind.

Orientation to the sun (Table 11) by stilts and avocets did not differ significantly from random. Stilts at the Salton Sea faced the sun as frequently as those at Ventura (χ^2 range = 0.6–3.0, df = 1, NS, $P > 0.05$). Wind data for stilts at Ventura are not available, but stilts and avocets at the Salton Sea tended to face into the wind (χ^2 range = 7.5–18.7, df = 1, $P < 0.01$). At higher wind velocities (Table 12) orientation in line with the wind increased (20.6 to 60.4% in the stilt, 36.8 to 68.5% in the avocet), while tail to wind orientation decreased (35.2 to 9.0% in the stilt and 63.2 to 1.0% in the avocet). Orientation to the sun (Table 11) by the Forster's Tern, Snowy Plover, Killdeer, and Lesser Nighthawk deviated significantly from random (χ^2 range = 18.7–49.5, df = 1, $P < 0.01$). Forster's Tern tended to face the sun while the Snowy Plover, Killdeer, and Lesser Nighthawk faced away from the sun.

Facing toward or away from the sun minimizes the surface area exposed to the

TABLE 12

ORIENTATION ON THE NEST OF BLACK-NECKED STILTS AND AMERICAN AVOCETS WITH RESPECT TO SUN AND WIND AT LOW AND HIGH WIND VELOCITIES

Species	Wind velocity[1]	Sun[2]				Wind[2]			
		Lateral to (%)	Facing (%)	Tail to (%)	n (min)	Lateral to (%)	Facing (%)	Tail to (%)	n (min)
H. mexicanus	Low	47.6	13.2	39.2	1106	44.3	20.6	35.2	472
	High	34.5	30.8	34.7	2109	30.6	60.4	9.0	2060
R. americana	Low	24.9	49.0	26.1	257	0	36.8	63.2	95
	High	64.4	32.1	3.5	623	30.5	68.5	1.0	623

[1] Low = 0–1 $m \cdot sec^{-1}$; high = >3 $m \cdot sec^{-1}$.
[2] Percent of time spent by each species in each orientation. N = 21 Black-necked Stilt nests and 4 American Avocet nests.

TABLE 13

INITIATION AND CESSATION OF PANTING AND/OR GULAR FLUTTERING WITH RESPECT TO TIME OF DAY AND SHADED AMBIENT TEMPERATURE (T_A) FOR SIX SPECIES NESTING AT THE SALTON SEA

Species	Initiation		Cessation	
	Time	T_A (°C)	Time	T_A (°C)
H. mexicanus (34)[a]	08:40	25.1	1840	34.6
R. americana (4)	08:04	25.3	1830+	41.0
C. alexandrinus (2)	08:27	29.5	1701	38.4
C. vociferus (5)	08:28	26.3	1843	32.9
S. forsteri (10)	07:50	27.9	1900	35.6
C. acutipennis (4)	10:15	35.8	1800+	41.9

[a] Number of all-day observations in parentheses.

sun and reduces shadows so the birds are less conspicuous to predators. However, facing away from the sun shades the evaporative surfaces of the mouth. Insolation impinging on the vascularized surfaces of the mouth should reduce the efficiency of evaporative cooling by warming the blood. The Snowy Plover, Killdeer, and Lesser Nighthawk faced the sun less than 5% of the time (Table 11). I observed facing the sun orientation during the heat of the day (12:00–17:00) for only 7 min (0.7% of the total time) by the Snowy Plover and for 37 min (1.4% of the total time) by the Killdeer. Lesser Nighthawks faced the sun during the heat of the day for 28 min (2.0% of the total time).

Panting Forster's Terns faced the sun nearly 50% of the time during the hottest portion (13:00–17:00) of the day and thereby exposed the evaporative surfaces of the mouth to direct insolation. This posture exposed more of the white throat to the sun while decreasing exposure of the black crown and gray mantle to incident radiation. Incubating Herring Gulls (*Larus argentatus*) tended to face the sun at low wind velocities, and Lustick et al. (1978) suggested that this is a response to reduce radiational heat gain by both reducing the exposed surface area and by presenting more reflective surface (white breast and head) to the sun. Incubating Heermann's Gulls oriented randomly with respect to the sun in the absence of moderate (> 3 m·sec^{-1}) winds (Bartholomew and Dawson 1979), and Gray Gulls (*L. modestus*) oriented randomly with respect to the sun but promptly faced into the strong afternoon wind when it began (Howell et al. 1974). Incubating Black Skimmers at the Salton Sea (Grant and Hogg 1976) faced into the wind but oriented randomly when no wind occurred. Masked Boobies (*Sula dactylatra*) faced away from the sun regardless of wind direction in their thermally stressful nesting microclimate on the Galapagos Islands (Bartholomew 1966), and *Charadrius alexandrinus* nesting in Iraq during the mid summer generally faced away from the sun (George Kainady and Al-Dabbagh 1976).

Tail-to-the-wind orientation by Lesser Nighthawks at the Salton Sea persisted at wind velocities of up to 4.5 m·sec^{-1}. Common Nighthawks (*Chordeiles minor*) nesting on a hot, gravel roof oriented with their tails to the sun on clear days and failed to orient consistently when the sky was overcast (Weller 1958). Dexter (1961) observed two incubating *C. minor* females: one predominantly faced the sun, and the other generally faced away from the sun. In the absence of direct

sunlight, one bird characteristically faced into the wind, and the other faced away from the wind. Dexter (1961) suggested that very strong wind may be more important than direction to sunlight in female orientation on the nest. Artificial shade provided by Weller (1958) impaired consistent orientation to the sun. One Lesser Nighthawk at the Salton Sea nested in a plowed field near an overhanging branch which provided some shade. Much of the lateral-to-sun orientation recorded in Table 11 was due to the female orienting under this branch in such a manner as to maximally shade her head. Shading of the head occurred throughout the heat of the day and will be discussed more fully in reference to egg-moving behavior to maximize use of shade.

In summary, some species faced into the wind (stilts and avocets) while orienting randomly to the sun, some faced the sun (Forster's Tern), and some incubated with their tail to the sun regardless of wind direction (Lesser Nighthawk, Snowy Plover, and Killdeer).

Panting and Gular Fluttering

Charadriiform birds on the nest at the Salton Sea pant almost continuously during the day. Panting has been observed as early as 07:50 (Forster's Tern) and at shaded ambient temperatures as low as 25.1°C (Black-necked Stilt). Panting may continue until nearly sundown (19:00, T_A = 35.6°C in Forster's Tern). Initiation and cessation of panting as a function of time and shaded ambient temperature appear in Table 13. Panting may cease when ambient temperatures are 40°C or greater. This usually occurs late in the afternoon when solar radiation is greatly reduced and wind is typically increasing. High temperatures may persist for a few hours after sundown. I have recorded ambient temperatures as high as 42.8°C after dark at the Salton Sea. Obviously, the times of initiation and cessation of panting are dependent upon the interaction of ambient temperature, radiation (solar and reradiated), convection (wind), and conduction. Panting becomes vigorous during the heat of the day, and rates of 250–300 pants per min probably occur. I recorded a mean rate of 271 per min in the Forster's Tern. These rates approach the maximum rate detectable by the unaided human eye.

Lesser Nighthawks show gular flutter (rates too high to count by eye) almost continuously but begin later in the day than do panting charadriiform birds nesting in the same environment. Gular flutter was seen as early as 10:15 (T_A = 35.8°C) and persisted past 18:00 (T_A = 41.9°C) at the Salton Sea (Table 13). I did not detect gular flutter in any of the Charadriiformes, but George Kainady and Al-Dabbagh (1976) reported gular flutter in *Charadrius alexandrinus*. Gaping grades into panting in Charadriiformes, and George Kainady and Al-Dabbagh may have mistaken gular flutter for vigorous panting in *C. alexandrinus*.

Pteryloerection

Dorsal pteryloerection of dark-backed birds under heat stress on nests is a conspicuous feature of behavioral thermoregulation. All Charadriiformes nesting at the Salton Sea elevate the scapular, nape, and crown feathers when heat stressed. Dorsal feather erection in stilts has been observed as early as 09:10 (T_A = 33.5°C) and at shade temperatures as low as 26.4°C (10:30). Latest stilt dorsal pteryloerection was seen at 18:29 (T_A = 41.8°C, sundown at 1930). Dorsal feathers may

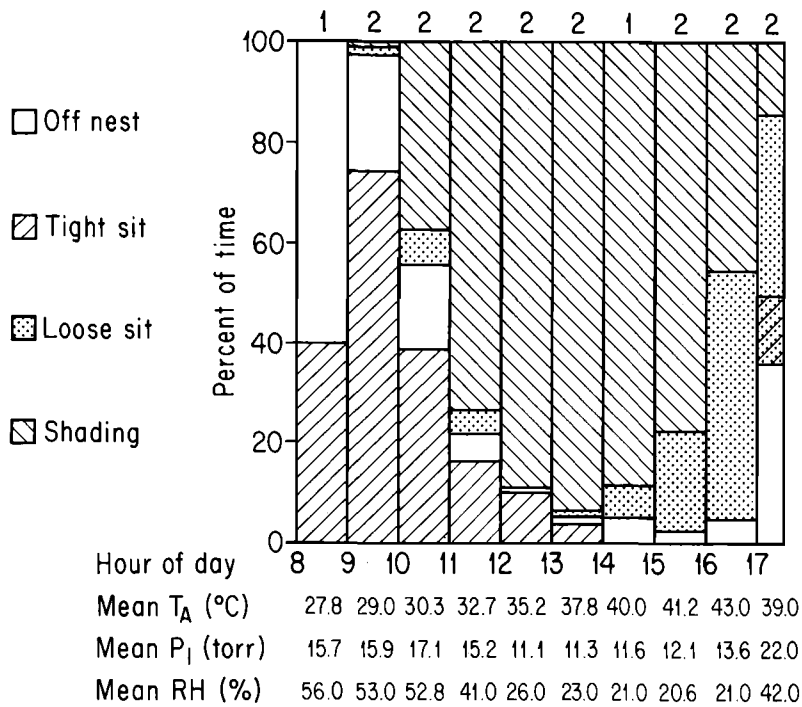

FIG. 22. Combined attentive behavior of two pairs of Snowy Plovers at their nests on 15 June, 1978 in relation to hour of day, hourly mean ambient temperature, hourly mean vapor pressure, and hourly mean relative humidity. Numbers above columns indicate the number of nests where attentive behaviors for that entire time period were recorded. The final column denotes observations from 17:00–17:30; for ca. 10% of that time, I could not distinguish between tight sit and loose sit postures.

be elevated 45–50° above the body. Degree of dorsal pteryloerection probably is correlated to some extent with body temperature in incubating birds. For example, at ambient temperatures below 38°C several minutes may elapse between the time a stilt covers the eggs at nest relief and the elevation of its dorsal feathers. A few more minutes may pass before dorsal elevation is maximal. In the afternoon, when $T_A > 40$°C, maximum dorsal elevation occurs within seconds of the bird sitting on the eggs (at nest relief). Stilts always pant prior to dorsal pteryloerection, which suggests that panting occurs at lower body temperatures than dorsal pteryloerection. Under severe heat loads, the Lesser Nighthawk elevated the dorsal plumage as a unit. Elevated charadriiform dorsal plumage presents a more ruffled appearance (Howell and Bartholomew 1962; Maclean 1967; Howell et al. 1974; Grant and Hogg 1976; Bartholomew and Dawson 1979). Walsberg et al. (1978) have shown that erection of dark plumage at all wind velocities reduces the heat reaching the skin.

In addition to maximally erecting the gray scapular feathers, the Forster's Tern elevated the gray upper wing coverts, the nape, and the white face, throat, and upper breast feathers. Erection of white face, throat, and upper breast feathers by other heat-stressed incubating Charadriiformes was not seen at the Salton Sea,

FIG. 23. Snowy Plover at the Salton Sea shading its eggs.

but stilts conspicuously elevated the white rump feathers whenever ambient temperatures approached or exceeded 40°C. At the low wind velocities generally encountered (<3 $m \cdot sec^{-1}$), erection of white feathers conferred a slight radiative heat load disadvantage over depressed white feathers in the system studied by Walsberg et al. (1978) but may serve to facilitate cutaneous evaporation by exposing the skin to the light wind. Cutaneous evaporation results in the loss of 14–20 % of the metabolic heat produced at 30–35°C by the Poorwill and Roadrunner (Lasiewski et al. 1971).

Dorsal pteryloerection is also used in other behavioral contexts (Morris 1956; Brown 1975). Among Charadriiformes, it may serve as a spacing and/or aggression diminishing mechanism. Heat-stressed incubating charadriiform birds raised the dorsal feathers in the absence of nearby conspecifics or other species and only after panting.

ATTENTIVE BEHAVIOR

The most important effect of attentive behavior at the Salton Sea is the maintenance of egg temperatures below lethal levels. In most environments, exposed eggs cool rapidly during inattentive periods, and the parent, on its return, must expend energy to rewarm eggs to the incubation temperature. In contrast, at the Salton Sea, nearly every day from approximately 09:00 to 18:00 unattended eggs gain heat (primarily from solar radiation). When the parent returns, energy must be expended to lower egg temperature without overheating the adult. Birds prevented overheating of the eggs in two ways. They reduced off-nest time to a minimum, and they belly-soaked.

Snowy Plovers tended to alternate between sitting tightly and leaving the eggs uncovered for extended periods during the cooler part of the day (Fig. 22). At

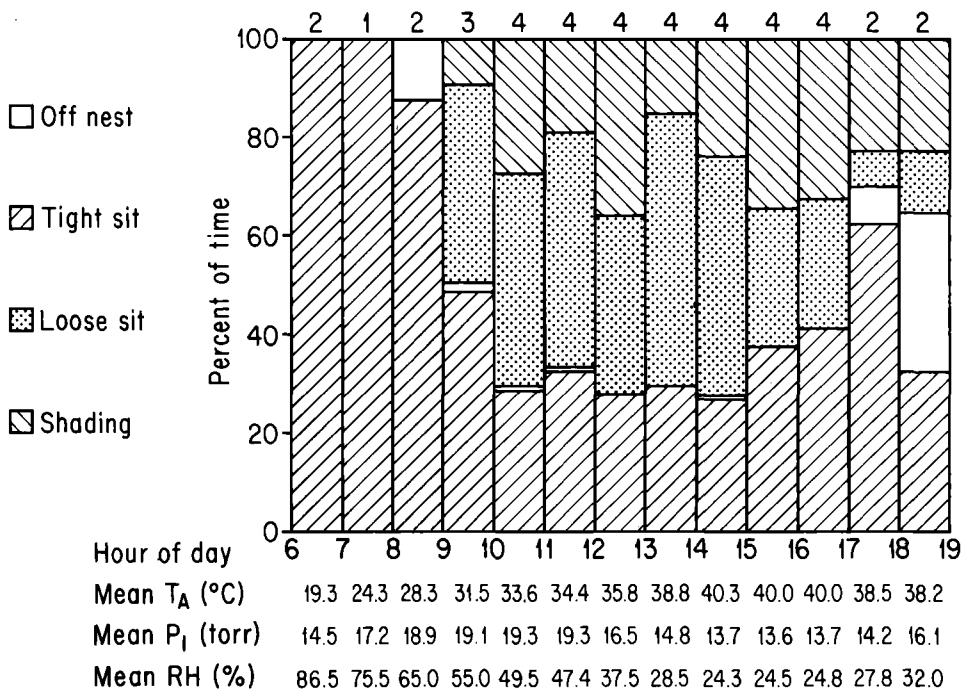

FIG. 24. Combined attentive behavior of two pairs of Killdeers at their nests on 3 and 4 June, 1978 in relation to hour of day, hourly mean ambient temperature, hourly mean vapor pressure, and hourly mean relative humidity. Numbers above columns indicate the number of nest-days when attentive behaviors for that time period were recorded.

shaded ambient temperatures greater than 30°C nearly 80% of their time at the nest was spent in shading (Fig. 23) or sitting loosely over the eggs. At the highest ambient temperatures (37–43.4°C), 90% of their time was spent in shading and sitting loosely. Between 17:00 and 17:30, as a strong, cool, and moist wind from the west (coming across the Salton Sea) began, they spent more time off the nest. Almost all of the off-nest time during the heat of the day involved belly-soaking trips (28–54 sec required for most trips) to a nearby (10 m) water source. Every 5–10 min during the hottest part of the day (14:00–17:00), the incubating bird ran or flew to water, belly-soaked, preened its wet belly, and rapidly returned to the nest.

A typical pattern, beginning at 15:50 on 15 June, 1978, involved a male plover that was shading two eggs. He ran to the waterhole, belly-soaked, and returned to the nest in 38 sec. While shading the eggs, he dipped down to wet the upper egg surfaces, raised up, rotated 90°, dipped down again, raised up and rotated 90°, and again dipped his wet belly feathers onto the eggs. The male then raised up again and shaded the eggs for a minute or two before returning to the waterhole at 15:56. Nest relief occurred at the waterhole or at the nest and resulted in eggs being uncovered for less than one min. The observation distance and viewing angle were such that I could not adequately determine the partitioning of incubation between the sexes. Attentive bouts were longer during the cooler parts

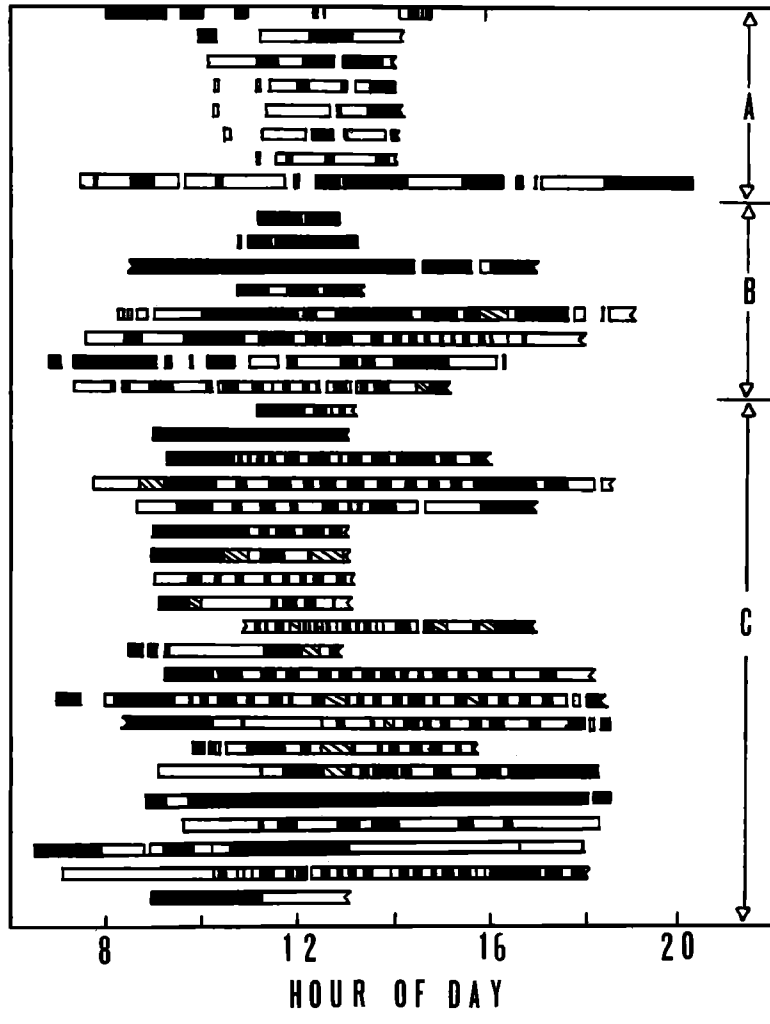

FIG. 25. Roles of male and female Black-necked Stilts during incubation. Each bar summarizes the activities of a pair at one nest. Key: male (solid bar), female (open bar), sex not determined (hatched bar), nest uncovered (gap); A = nests at Ventura, B = nests with incomplete clutches at the Salton Sea, C = nests with complete clutches at the Salton Sea. The beginning and end of the bar for each nest coincide with the beginning and end of each observation period.

of the day than during the midday heat. The male of one pair incubated primarily at its nest (behavior was monitored during the egg-laying period—third egg laid within 12 hrs after my observations), and the female of another pair seemed to be at her nest much of the day. Zimmerman (1951), Walters (1954), Rittinghaus (1956, 1961), and Boyd (1972) found that the female of a pair was on the nest most of the day while its mate incubated primarily during the early morning and evening hours.

Killdeers exhibited a similar attentive pattern at the nest, but even during the hottest part of the day, spent about 30% of the time sitting tightly over the eggs

TABLE 14

AVERAGE LENGTH IN MINUTES OF UNDISTURBED INCUBATION BOUTS BY BLACK-NECKED STILTS AT VARIOUS SHADED AMBIENT TEMPERATURES

T_A (°C)	Male	Female	Total
10–14.9	16.0 (2)[a]	31.0 (2)	23.5 (4)
15–19.9	57.4 (5)	56.6 (5)	57.0 (10)
20–24.9	50.3 (8)	30.0 (9)	39.5 (17)
25–29.9	41.8 (14)	35.6 (14)	38.7 (28)
30–34.9	28.3 (29)	17.0 (28)	22.8 (57)
35–39.9	20.6 (40)	28.2 (45)	24.6 (85)
40–44	11.7 (53)	14.3 (52)	13.0 (105)
$\bar{X} \pm 1$ SD	23.5 ± 28.7 (151)	23.2 ± 24.3 (155)	23.4 (306)

[a] Sample size in parentheses.

(Fig. 24). Because of the rough terrain between my blind and the nests under study, I was not always able to distinguish between loose sitting and tight sitting. A remotely-controlled camera positioned at a different angle about 3 m from one nest revealed that though the bird might sit low over the eggs, one or two eggs were frequently visible when the bird was orienting northward on the nest (head and shoulders frequently shaded these eggs). The Killdeers under study did not leave the nest uncovered to belly-soak, but the relieving bird frequently had a wet, soggy belly during the heat of the day. Upon being relieved the bird that had been incubating often ran or flew to water, drank, preened its breast with water, and belly-soaked by either running through relatively deep water or flexing the legs. Nest relief in Killdeers occurred about every 10–15 min during the heat of the day. I was unable to consistently sex Killdeers in the field at my observation distance (50–100 m). Bunni (1959) reported equal sharing of incubation duties by the male and female until late in the nesting season when the female typically deserted the nest.

Forster's Terns are very attentive to the eggs during the heat of the day. At nest reliefs and during belly-soaking flights, eggs generally are exposed for less than 2 min. Forster's Terns frequently alternated between shading and sitting low

TABLE 15

AVERAGE LENGTH IN MINUTES OF UNDISTURBED INCUBATION BOUTS BY AMERICAN AVOCETS AT VARIOUS SHADED AMBIENT TEMPERATURES

T_A (°C)	Male	Female	Total
10–14.9	46.0 (1)[a]	64.0 (1)	55.0 (2)
15–19.9	111.7 (6)	102.2 (6)	106.9 (12)
20–24.9	36.3 (3)	123.0 (3)	79.7 (6)
25–29.9	81.0 (5)	35.2 (5)	58.1 (10)
30–34.9	15.0 (1)	19.0 (1)	17.0 (2)
35–39.9	10.8 (6)	24.6 (5)	17.1 (11)
40–44	21.5 (11)	27.1 (11)	24.3 (22)
$\bar{X} \pm 1$ SD	46.8 ± 60.2 (33)	51.9 ± 49.2 (32)	49.4 (65)

[a] Sample size in parentheses.

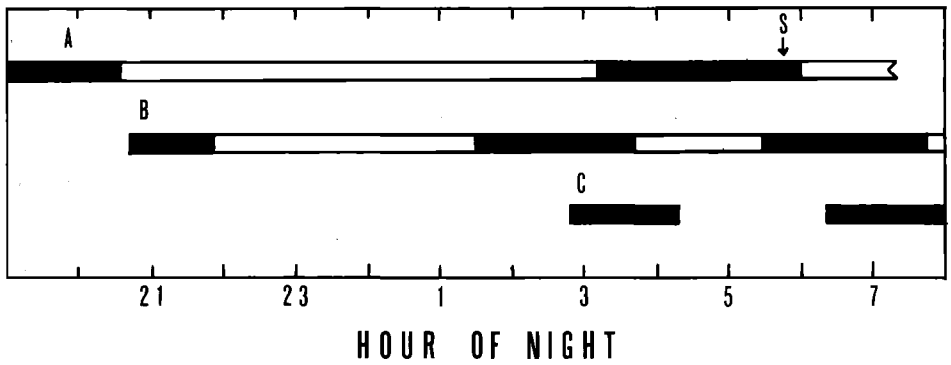

FIG. 26. Nocturnal incubation by a pair of Black-necked Stilts at the Salton Sea. Key: male on nest (solid bar), female on nest (open bar); A = night of 20–21 June, 1979, B = night of 19–20 June, C = night of 18–19 June; S = sunrise.

over their eggs during the heat of the day. Because they have short legs and a relatively deep nest cup, it was not always possible to distinguish "low" shading from tight sitting. During shading, the oval bilateral brood patches are exposed, and the distal tips of the wet belly feathers may touch the eggs. Exposed brood patches should serve as shaded thermal windows exposed to any air flow and thereby facilitating heat loss via convection (and radiation to the cooler nest). Attentive bouts were shortest during the heat of the day. I was unable to sex Forster's Terns in the field and have no data on the role of sexes in incubation other than the fact that both participate.

Attentiveness and the role of the sexes in incubation by Black Skimmers has been discussed by Grant and Hogg (1976).

Male and female Black-necked Stilts alternated in incubation duties (Fig. 25). Males appeared to incubate most during the egg-laying stage, both at coastal and Salton Sea sites. However, a male did incubate for 8 hrs without relief at a nest with a completed clutch. This male belly-soaked during the 8-hr period and was able to regulate egg temperatures within tolerable limits throughout the day (see section on Belly-soaking). Much more time was spent off the nest at the cooler coastal site than at the Salton Sea.

As a general rule, incubation bouts by each sex became shorter with increasing shaded ambient temperature (Table 14). Temperature data were not available for an additional 108 incubation bouts timed at the Salton Sea ($\bar{X}$ = 15.0 min/bout). When both sets of data for the Salton Sea are combined, incubation bouts of males average 21.3 min (N = 199) and of females, 19.4 min (N = 201). Thus, incubation bouts for male and female stilts do not differ ($P > .9$), and the duration decreased in both sexes with increasing ambient temperature. These data include only complete clutches. Incubation bouts of male stilts at coastal sites averaged 37.6 min (N = 16) and of female stilts 44.3 min (N = 16). This lengthening of incubation bouts is anticipated in view of the cooler ambient temperatures (10–20°C) at Ventura.

Inattentive bouts (neither parent at the nest) were not analyzed because during most of the day (09:00–18:00) at the Salton Sea, eggs were uncovered for intervals of 1 min or less (Fig. 25). However, careful notes on the duration of inattentive periods at nest relief were made at one stilt nest between 09:41 (T_A = 35.3°C)

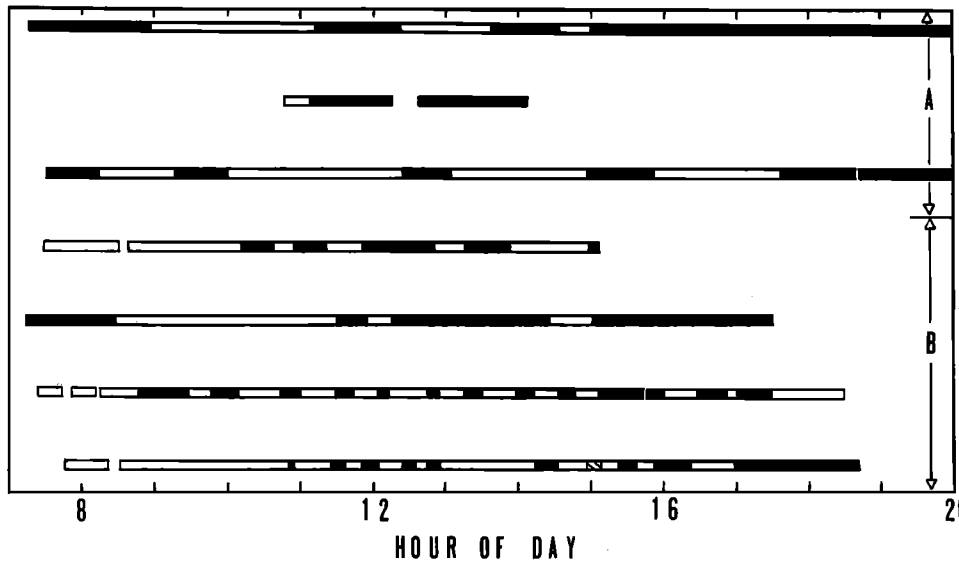

FIG. 27. Roles of male and female American Avocets during incubation. Each bar summarizes the activities of a pair at one nest. Key: male (solid bar), female (open bar), sex not determined (hatched bar), nest uncovered (gap); A = nests at Ventura, B = nests at the Salton Sea. The beginning and end of the bar for each nest coincided with the beginning and end of each observation period.

and 17:00 (T_A = 42.8°C). The eggs were uncovered for an average of 11.1 ± 10.2 sec (18 intervals), range 2.5–44.0 sec.

Attentive bouts for stilts at the Salton Sea were significantly shorter than the 64.6 (male) and 82.0 (female) min recorded by Hamilton (1975). His sample sizes were much smaller, and ambient temperatures were much lower at his study sites. Hamilton reported little variation in the length of incubation bouts, which may reflect the mild temperatures of his study area. Standard deviations for my measurements are as large or larger than the means.

Stilts do not shade their eggs. The extreme length of the legs of stilts would make shading, if employed, a conspicuous part of their thermoregulatory behavior. Many charadriiform birds shade their eggs at moderate to high ambient temperatures. The Sooty Tern, *Sterna fuscata* (Howell and Bartholomew 1962), Double-banded Courser, *Rhinoptilus africanus* (Maclean 1967), Killdeer (this study), Snowy Plover (this study), and Forster's Tern (this study) shade their eggs. However, once shaded ambient temperature exceeds incubated egg temperature, tight egg-brood patch contact or belly-soaking must occur to prevent overheating of the eggs. Even during the heat of the day (T_A = 40–44°C), tight sitting is the rule. Occasionally a stilt will stand over the nest briefly to turn or wet the eggs, or to change positions.

The roles of the sexes in nocturnal incubation are rarely known. It is generally assumed that the bird on the nest at dusk or dawn incubated throughout the night. Hamilton (1975), for example, reported that female stilts were on the nest at the time of his last observation of the day and that the first nest relief was usually a male relieving a female. He concluded that females probably incubate throughout

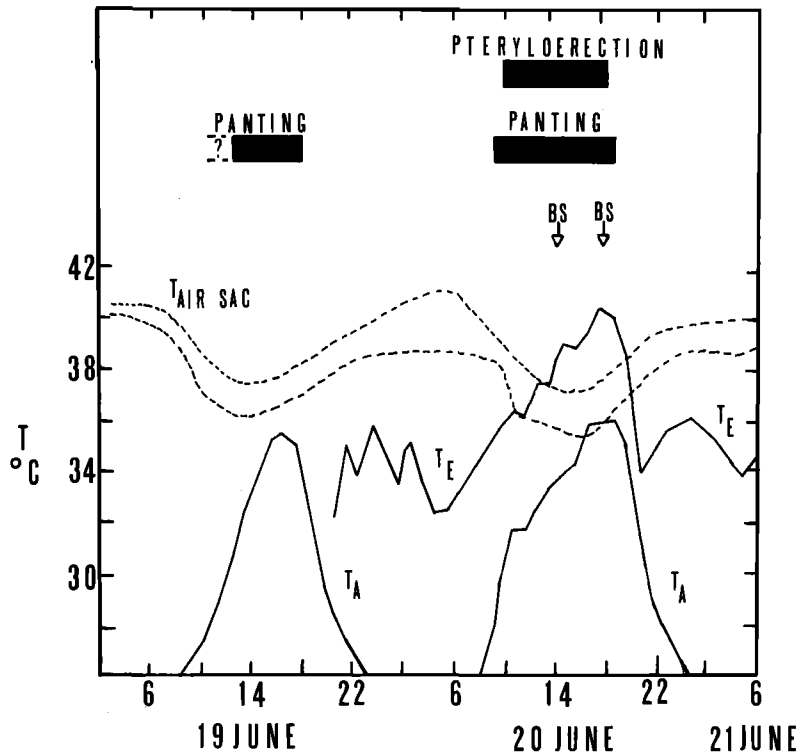

FIG. 28. The effect of panting and dorsal pteryloerection on abdominal air sac temperature of a male Black-necked Stilt. Dotted lines enclose range of air sac temperatures. Simultaneous egg (T_E) and shaded ambient air (T_A) temperatures are also presented. BS = belly-soaking.

the night. This clearly is not the case, however. I simultaneously monitored egg temperature and body temperature of a male throughout three nights (Fig. 26). The data show that incubation bouts of two hours or more occurred at night and that nest relief occurred throughout the night (egg temperature was maintained above ambient temperature throughout). This observation on a single pair of stilts casts serious doubt on previous assumptions concerning single sex incubation at night in species that are dual-sex incubators by day. The male also made comfort movements (e.g., rising and standing briefly over the eggs; volume of transmitter signal decreased with this behavior day and night) at night, however, so one cannot tell by simply monitoring egg temperature at night whether a brief temperature drop is due to a nest relief or a change in position by the incubating bird.

The sexes of the American Avocet seem to play equal roles in incubation (Fig. 27), but much variation exists. The average incubation bout for the male was 46.8 ± 60.2 min (N = 33) and for the female, 51.9 ± 49.2 min (N = 32). A general trend toward decreased bout duration with increased ambient temperature is evident (Table 15). Absence from the nest during the heat of the day is virtually unrecorded at the Salton Sea. Avocets do not shade their eggs; tight egg-brood patch contact is the rule even at the highest ambient temperatures (44.0°C) re-

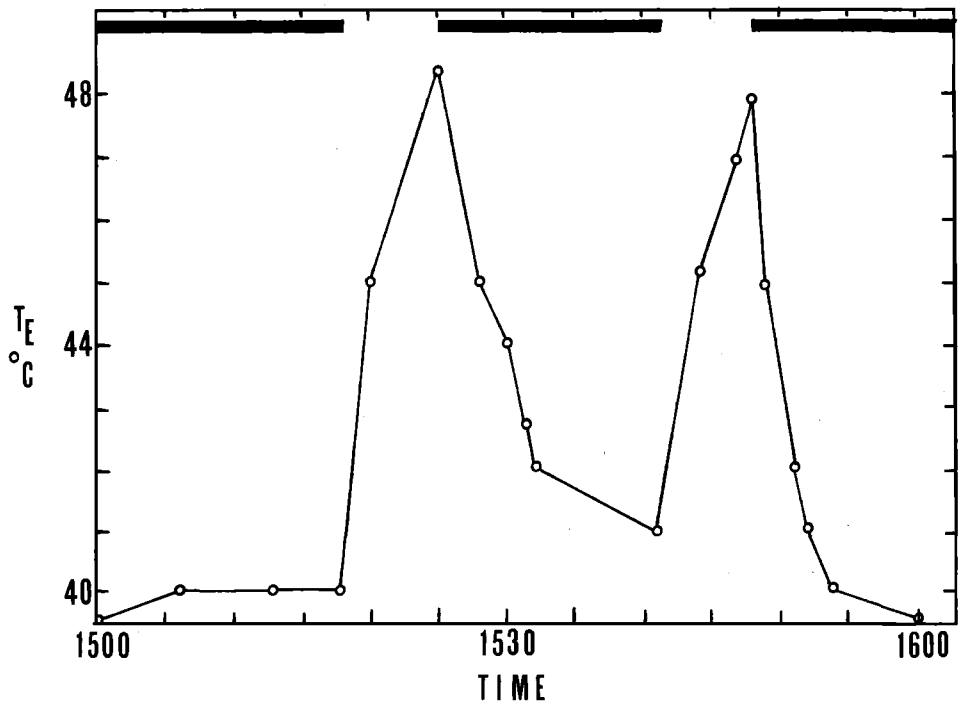

FIG. 29. The effect of brief voluntary nest exposures on egg temperatures (T_E) at a Black-necked Stilt nest at the Salton Sea on 19 July. Ambient temperature = 45°C during the interval plotted. Solid bar = male on nest, gap = nest uncovered.

corded. Avocets occasionally rise and stand over the eggs briefly (usually for less than 1 min) while changing position, turning eggs, or wetting eggs. Incubation bouts were shorter at the Salton Sea than at Hamilton's (1975) study site where bouts of males averaged 87.6 min and of females, 64.3 min. Male attentive bouts averaged 38.0 min and female bouts, 52.2 min, in central Oregon, but no temperature data were given (Gibson 1971).

Female Lesser Nighthawks incubated throughout the day without relief and without going to the water. Nighthawks do not belly-soak, but males and females typically fly off together (probably to drink and forage) at dusk. I do not know which sex incubates during the night, but in Common Nighthawks males do not appear to incubate (Weller 1958). Lesser Nighthawk incubation posture seems to be a tight sit, but this is difficult to ascertain due to their extremely short legs. A loose sit posture would only require standing a few millimeters higher than a tight sit, and a difference of this magnitude is not discernible at the 50 m or greater observation distance.

To summarize briefly, charadriiform parents shared incubation duties while the female nighthawk incubated continuously throughout the day. During the hottest part of the day, the terns and shorebirds relieved each other more often, thus allowing frequent trips to the relatively cool water for belly-soaking and drinking. Some species incubated tightly (stilts, avocets, and probably nighthawks), while

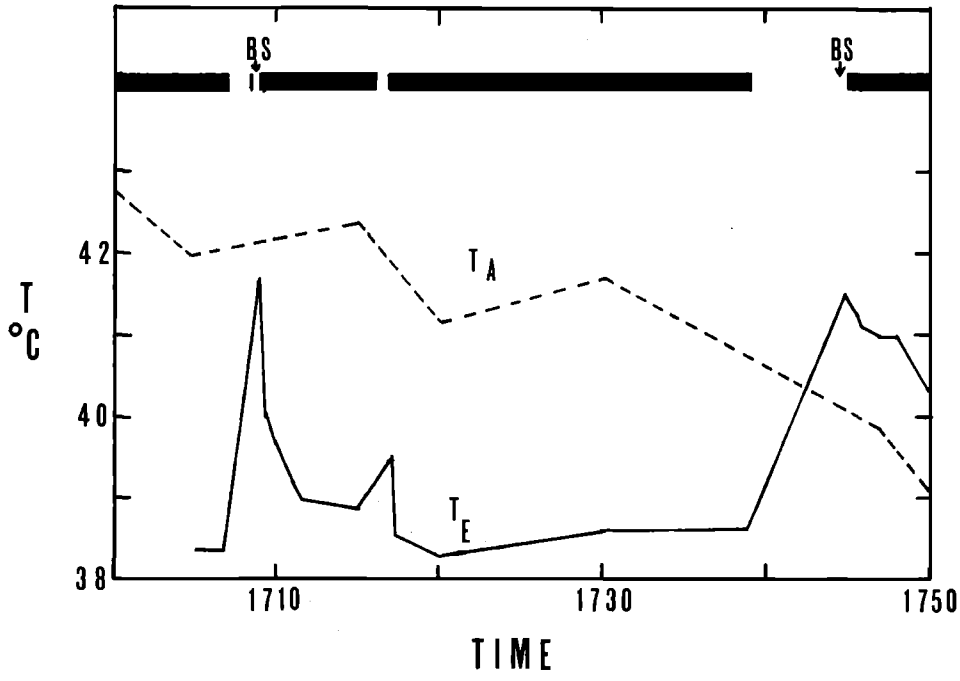

FIG. 30. The effect on egg temperature of brief nest absences of Black-necked Stilts due to territorial encounters at the Salton Sea on 28 June, 1977. Nest covered = solid bar, nest uncovered = gap; T_A = shaded ambient temperature, T_E = egg temperature; BS = belly-soaking by bird coming to the nest.

others alternated between shading, loose sitting, and sitting tightly on their eggs (Snowy Plovers, Killdeers, and Forster's Terns).

TEMPERATURE OF AN INCUBATING STILT

I simultaneously monitored the "body" temperature of a male stilt, egg temperature in its nest, and ambient temperature for nearly three days at the Salton Sea (Fig. 28). Due to the heat load encountered, one might predict highest body temperatures during the afternoon when shaded ambient and egg temperatures are highest. This is the time of day when much dorsal pteryloerection, panting, and belly-soaking occurred. However, the opposite trend (Fig. 28) is strong and consistent (3 nights and 2 days). "Body" temperatures at night (24:01–06:00) averaged 39.5 ± 0.9°C (N = 17), and those during the afternoon (12:01–18:00), only 36.6 ± 0.7°C (N = 67). Higher nocturnal body temperature may result from increased metabolism while incubating four eggs in an uninsulated nest at relatively low ambient temperatures (20–25°C). It seems unlikely, however, that this stilt, which erected its dorsal feathers and panted during the day, was experiencing core body temperatures lower than mean nocturnal body temperatures.

The most likely explanation lies with the location of the transmitter. It was surgically implanted inside the left abdominal air sac between the abdominal wall and testis. This may explain the lower temperatures recorded during panting and, more importantly, strongly suggests a major role of the abdominal air sacs in

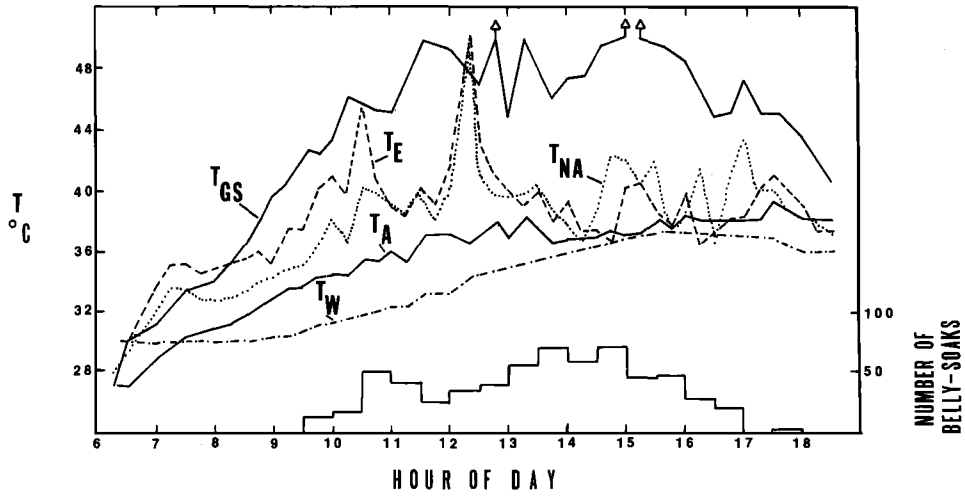

FIG. 31. The effect of exposure to the sun on egg temperatures at Forster's Tern nest # 110, total number of belly-soaks by 11 pairs of terns, and meteorological conditions. T_{GS} = ground in sun temperature, T_E = egg temperature, T_A = shaded ambient temperature at ground level, T_W = water temperature, T_{NA} = nest air temperature, and △ = off scale.

gonadal and body temperature regulation. Schmidt-Nielsen et al. (1969) reported anterior air sac temperatures of a panting Ostrich (*Struthio camelus*) 2°C lower than core body and ambient temperatures, but they did not measure abdominal air sac temperatures. Cowles and Nordstrom (1946) suggested that the abdominal air sacs may lower the temperature of the testes. More recently, Howell (*in* Cowles 1965) recorded marked fluctuations in abdominal air sac temperatures that coincide with inspiration and expiration; the low extremes were lower than cloacal temperature.

EFFECT OF BEHAVIOR ON EGG TEMPERATURE

On hot days ($T_A > 43$°C) exposed eggs rapidly gain heat. At one stilt nest at the Salton Sea egg temperature increased from 40 to 45°C 2 min after the female left the nest ($T_A = 45$°C), and a similar rise occurred after a 3 min exposure later that hour (Fig. 29). The eggs reached or exceeded 48°C as a result of these two voluntary exposures. Egg temperatures of 43°C probably cause irreversible injury to the developing chick (Baldwin and Kendeigh 1932; Moreng and Shaffner 1951; Drent 1970; Bennett and Dawson 1979), and eventually the nest was deserted. This example underscores the need for continuous egg coverage during the heat of the day as exposure of only 2 min during a 25-day incubation period may result in death of young.

Occasionally, natural situations occur that relate to the interaction between defense of the nest and feeding territory and heat load. The most detailed natural disturbance data are from a pair of stilts with three young (about 3 weeks old) who moved into the feeding territory (adjacent to nesting territory) of the pair of incubating stilts at nest #35 (for discussion of recurvirostrid territories, see Gibson 1971). At 17:07 the male and female at nest #35 left the nest uncovered in

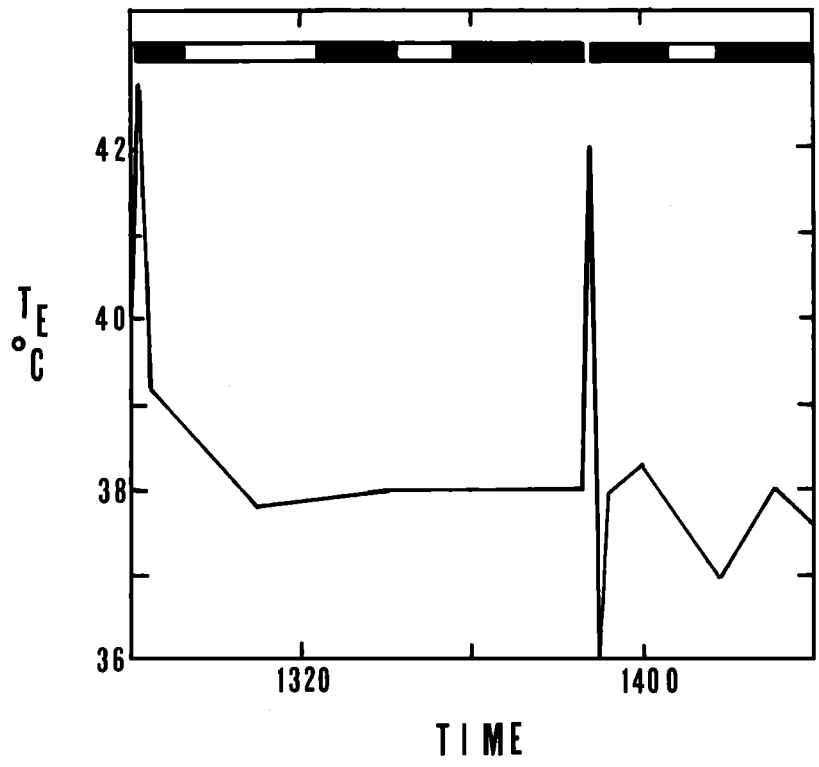

FIG. 32. The effect of exposure to the sun on egg temperatures at the nest of a Black-necked Stilt at the Salton Sea on 22 June, 1976. Ambient temperatures 34.9–36.1°C during the interval plotted. Male on nest = solid bar, female on nest = open bar, nest uncovered = gap.

an attempt to displace the pair with chicks. Egg temperature increased from 38.4 to 41.7°C (113 sec exposure) before the male of #35 belly-soaked 8 times and returned to settle on the eggs (Fig. 30). At 17:16 the eggs were uncovered for 51 sec in a repeat of the territorial scuffle. At 17:39 the female at #35 left the nest uncovered again to join her mate in defense of the territory. By 17:41 the intruders left the vicinity of nest #35, but another pair of adults stilts flew into the feeding territory and were attacked by the nesting pair. Eggs were uncovered for a total of 5 min 55 sec, and egg temperature reached 41.5°C (Fig. 30). Solar radiation (295.2–467.1 watts·m^{-2}) was greatly reduced during this late-afternoon scuffle and, therefore, contributed little to the increase in egg temperature. If this had occurred 2–3 hr earlier, the egg temperature probably would have exceeded lethal levels.

Mammalian predators have not been seen near shorebird nests during the hottest portion of the day as the heat load is probably too great for them. The effect of potential avian egg predators on egg temperature and attentive behavior was observed at a Forster's Tern nest at the Salton Sea. On 13 July, 1976 the incubating tern left the nest exposed from 10:20 until shortly after 10:30 to chase a Western Gull (*Larus occidentalis livens*) flying over the colony. Egg temperature reached 45.7°C (Fig. 31) before the tern returned. The second temperature spike occurred

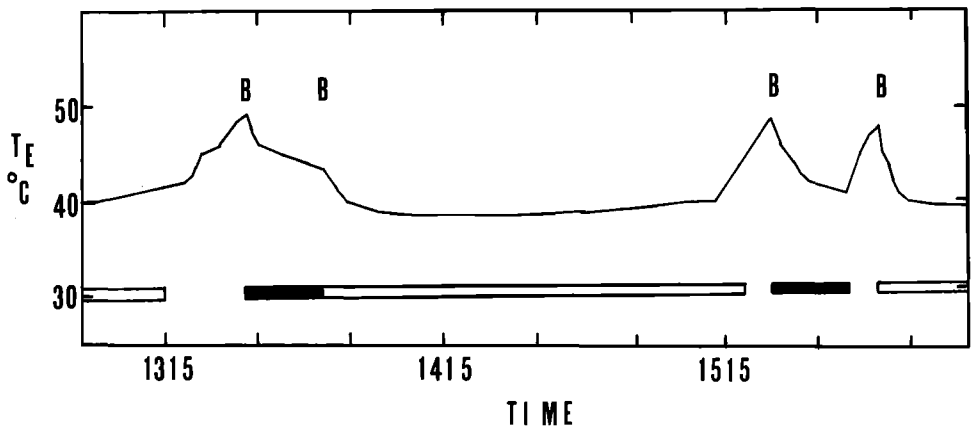

FIG. 33. The effect of nest inattentiveness and belly-soaking on egg temperature at a Black-necked Stilt nest at the Salton Sea. Ambient temperatures = 40–46°C during the interval plotted. The bird coming to the nest at each relief had wet belly feathers (B). Male on nest (solid bar), female on nest (open bar), nest uncovered (gap).

when all terns left the nests at 11:56 in apparent response to the alarm call of a stilt (Fig. 31). Most birds returned to their nests in 30–50 sec. At 11:59 all terns flushed again for unknown reasons, but most nesters returned rapidly. However, the tern at this nest did not return to its nest until shortly after 12:21 at which point the temperature of its egg had reached 50.0°C (Fig. 31). Deserted eggs exposed to full insolation on 31 May 1977 (egg # 25, Fig. 20) and 13 July 1976 exceeded 50°C for 5–6 hours during the heat of the day.

Egg temperature can change drastically during nest relief when the eggs are exposed to solar radiation and high ambient temperatures for less than 1 min (Fig. 32). The effect of a wet-bellied stilt at nest relief is also impressive; an egg temperature decrease of 3.5°C occurred in 1 min. At 13:53 the incubating male left this nest as a vehicle passed near it. In 1 min egg temperature increased 4.0°C to be followed by a decrease of 6.0°C in the next 1.5 min. In addition to returning to the nest with a wet belly, this male rose up and sat down on the eggs two to three times during this interval which maximized cooling of the eggs. Probably only the upper portion of the egg where the embryo floats undergoes such rapid temperature changes.

At another nest the inattentive periods (eggs uncovered) were longer, and time required to cool the eggs with water from the ventral feathers was longer (Fig. 33). The quantity of water transported to the nest each time may have differed, and the water temperature near this nest was about 10°C higher than that near the nest described above. These data (Figs. 32, 33) could be interpreted to mean that the primary function of belly-soaking is to decrease egg temperature rather than to cool the incubating adult. I will return to this in the discussion of the function of belly-soaking.

Single-sex incubation by ground nesting birds at the Salton Sea during the heat of the day is limited to the two species that show gular flutter (Lesser Nighthawk and Mourning Dove, *Zenaida macroura*). One wonders, thus, whether a charadriiform bird can incubate successfully during a hot day at the Salton Sea

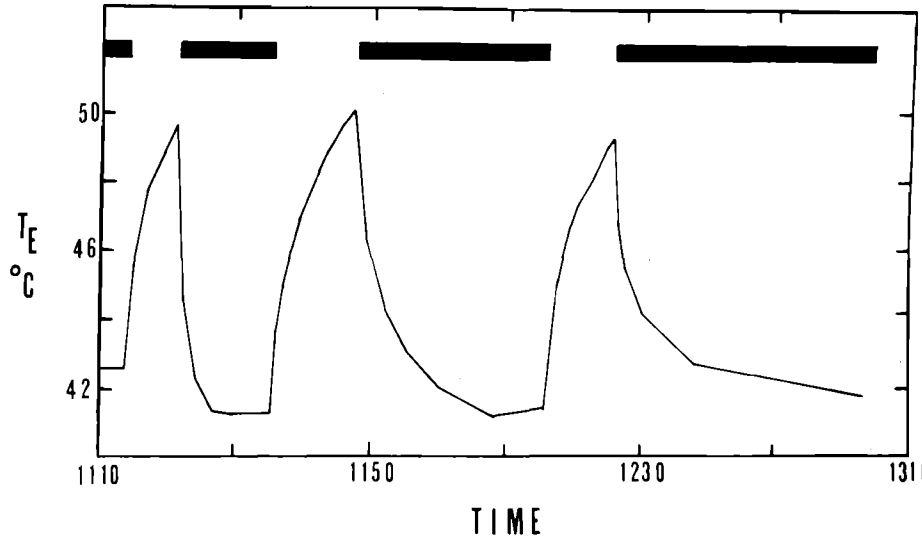

FIG. 34. Egg temperature record at a Black-necked Stilt nest after the female deserted. Shaded ambient temperatures = 36.3–39.6°C. Data recorded at the Salton Sea, 11 July, 1978. Male on nest (solid bar), nest uncovered (gap).

without being relieved. I did observe a male stilt incubating successfully at one nest from 09:44–18:37 (nest #45) on a moderately hot, clear day (maximum T_A = 40.1°C). At another stilt nest (#75), after the female deserted on a hot day, the male attempted to incubate (nest <10 m from water), but his inattentive periods were too long (Fig. 34) for egg survival. They may have been necessary, however, for his own thermoregulation. I could not quantify belly-soaking due to visual obstructions, but the male had a wet soggy belly on each return to the nest. The impact of the wet-bellied male on egg temperature depression was impressive but was nearly matched by the egg temperature elevation due to the intense midday solar radiation. Unfortunately, it is not possible to generate heating and cooling constants in the sense of Morrison and Tietz (1957) and Frost and Siegfried (1977). Ambient temperature (nest temperature in this case) is not constant because of solar radiation and because ambient air replaces nest air when the bird leaves the nest.

USE OF SHADE

Charadriiform birds nesting at the Salton Sea do not use shade. Nesting in shade would significantly reduce the heat load on the incubating bird, but shorebirds, terns, and skimmers, in general, avoid shade, presumably as an anti-predator strategy.

Lesser Nighthawks sometimes nest in partial shade. Of 11 nighthawk nests found during this study, only four were fully exposed to the sun. A female nighthawk incubating at one of these fully exposed sites exhibited continuous gular flutter for nearly 8 hours. (Fig. 35). Shaded nests were located on the north side of small bushes, and one was in a plowed field under a branch (ca. 5 cm diam.). These female nighthawks moved their eggs during the heat of the day to take

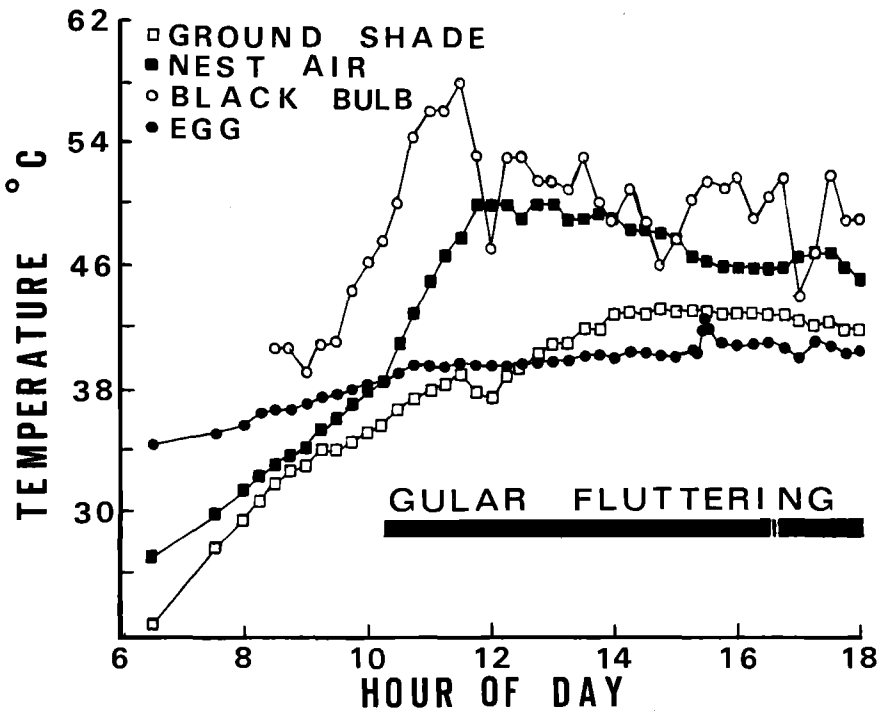

FIG. 35. Egg and environmental temperatures and duration of gular fluttering at a Lesser Nighthawk nest on 13 July, 1977 at the Salton Sea.

advantage of nearby shade. At one nest (#3) the female moved the two eggs 5 cm closer to the bush at about 14:15 on 15 May, 1976. The original nest site was shaded only until about noon each day. At 18:15 this female moved the eggs back to the original morning site. At 02:00 on 16 May these eggs were 15 cm from the original site (away from the bush). The incubating bird achieved a greater range of visibility as a result of this nocturnal movement away from the bush.

Movement to take advantage of shade also occurred at nest #41 where female orientation under a section of tree branch varied throughout two days of continuous observation. Between 10:10 and 11:42 on 12 July, 1977, female #41 incubated two eggs in full sun. At that time she oriented so that the shade cast by the overhanging branch fell across the anterior half of her head (all of the bill area) and the ventral surfaces of her neck and throat. Gular fluttering was continuous from 11:02 to at least 15:05 on this day. The female remained in this position until 15:05 when she moved the eggs and herself closer under the overhanging branch. She remained similarly shaded until 18:15 except for a brief (17:41–17:55) period when she flew off the nest in response to another nighthawk landing about 70 m from her nest. On 13 July this female incubated in full sun from 06:30 to 10:47 when she again oriented under the overhang so that the anterior portion of her body was shaded from 10:47 to 18:00. Only Woods (1924) has mentioned egg movement during the heat of the day to use existing shade near the nest. Weller (1958) provided artificial shade for an incubating female Common Nighthawk and found that she oriented to keep her head in the shaded area.

STILT CHICK THERMOREGULATION

To assess the heat load encountered by chicks at the Salton Sea, I fitted the skin of a one day old stilt chick over a thermocouple-equipped hollow copper cast of its body. It was positioned on a small wooden dowel 5 cm above dry soil near a stilt nest. This taxidermy mount has zero heat capacity and is the same size, shape, and has the same radiative properties as the stilt chick and was exposed to the same microclimate (Bakken and Gates 1975). The role of the long legs in heat balance is complex, and legs were not present on this model. In the water the legs would presumably be the greatest avenue of heat loss, and on hot dry soil, conduction (heat gain) and convection (heat gain or loss) would contribute to the total heat budget. The model was exposed to radiation and convection for a 24-hr period while I simultaneously recorded shade ground temperatures and the operative environment temperatures (Bakken 1976) of the chick model.

During the night, the stilt model radiated heat, and its temperature averaged 2.1°C ± 0.4 (n = 24 readings) lower than shaded ground temperature. During the day, the operative environmental temperature reached 40.7°C by 09:09. Chick model temperatures above 45°C were recorded from 10:00 until 18:55, with temperatures consistently above 50°C (off scale) between 12:43 to 17:39. Chick model temperatures did not fall below 40°C until shortly after 19:06. The highest shaded ambient temperature recorded during the day was 36.2°C. The operative environmental temperature of the chick model was 15–20+ C° higher than the shaded ambient temperature during the heat of the day. For 3 hrs during the hottest part of the day the temperature needle on the indicator dial bounced off the high end of the scale each time the instrument was turned on. These data show that a stilt chick continuously exposed to the sun on dry ground near a nest at the Salton Sea would have to lose large quantities of heat through evaporation for about 10 hrs a day (assuming its body temperature remained at or below 40°C; heat storage capacity for a 14 g chick is minimal). Metabolic heat production would add further to the heat load. It should be noted that this experiment was conducted on a day relatively cool (36.2°C) by local standards, and much greater heat loads would be imposed during a day with shade temperatures reaching 44°C or more.

It, thus, is not surprising that small stilt chicks generally do not walk around on dry soil during the heat of the day. If all eggs hatch during the day, chicks typically remain in the nest (covered and cooled by the wet-bellied parents) until late in the evening. Chicks hatching during the night are typically led from the nest by 08:00 the following morning. Chicks foraging in shallow water during the heat of the day do not appear to be heat stressed. Panting is seldom seen in chicks standing in water. Brooding occurs away from the nests on cool days, which are rare at the Salton Sea. In cooler regions Hamilton (1975) observed brooding up to one week of age in stilts and avocets, and Gilliard (1958) reported brooding for up to 11 days in avocets (locality not specified). I have no data on the duration of brooding at the Salton Sea.

DISCUSSION

Even though the nesting environment at the Salton Sea is one of the harshest in the world, several species of Charadriiformes and the Lesser Nighthawk breed successfully there. An obvious means of avoiding the thermal stresses of the summer at the Salton Sea would be to initiate nesting either earlier in the spring

or later in the fall. However, the nesting season used by these birds is the same as that used by these species in more moderate climates. As only the nighthawk selects nest-sites with shade, incubating birds of the other species are subject to severe heat loads. The mechanisms used by the different species to mitigate the effects of these high temperatures on the eggs, chicks, and adults are varied.

Thermoregulation of Eggs, Chicks, and Adults

For embryos to develop properly, eggs must be maintained within a narrow range of temperatures during the course of incubation. Embryos are resistant to chilling, especially early in incubation (Matthews 1954; Romanoff 1960), but tolerate very little overheating. Chicken eggs failed to hatch following continuous exposure to temperatures above 40.5°C and below 35°C (Lundy 1969; Drent 1973). Eggs maintained between physiological zero (25–27°C, temperature at which no development occurs) and the minimum optimal incubation temperature develop various anomalies (Lundy 1969; Drent 1973). Ambient temperatures at the Salton Sea seldom fall below 20°C (at night), and eggs are generally covered at night except during the egg-laying period. However, because of the extremely high ambient temperatures encountered at the Salton Sea, eggs are very close to overheating at all times. Thus, I will focus on the role the parent plays in maintaining eggs below lethal temperatures while, at the same time, avoiding overheating itself.

Incubating birds are noticeably more reluctant to leave their nests at the Salton Sea during the heat of the day. Bartholomew and Dawson (1979) demonstrated a similar behavior pattern in Heermann's Gulls under heat stress. At the Salton Sea any disturbance during the heat of the day is typically followed by frequent belly-soaking and a rapid return to the nest as soon as the source of disturbance has departed. Disturbances usually are associated with human activities.

Adult Charadriiformes nesting at the Salton Sea seem to maintain egg temperatures below lethal limits during the heat of the day primarily by (1) continuous attentiveness, (2) minimum exposure time at nest relief, and (3) belly-soaking (which adds large quantities of water to the nest for direct and evaporative cooling). Conditions 1 and 2 are mandatory if eggs are to survive, as an exposure of just two minutes may cause lethal overheating. Condition 3 is optional. Eggs can be maintained below lethal limits without belly-soaking if the parents can dissipate the heat load encountered.

Egg temperatures are maintained below high shaded ambient temperatures in the Charadriiformes primarily by frequent application of water to the nest (Figs. 17, 19, 21). I measured temperatures at the surface of an egg (brood patch temperatures) at a stilt nest and could detect no consistent difference between internal egg temperature and "brood patch" temperature because of the copius quantities of evaporating water between the brood patch and the upper surface of the egg. Therefore, I cannot demonstrate that charadriiform birds act as heat sinks for the eggs as is apparently the case with White-winged Doves, *Zenaida asiatica* (Russell 1969). From 12:45 to 18:00 on 13 July 1977, a female Lesser Nighthawk maintained egg temperature nearly 2° below shaded ambient temperature (Fig. 35). Probes for shaded ground temperature under both the bird and in the bottomless meteorological box had not been exposed to the sun since sundown the previous day. I do not know how the female was able to maintain egg temperature

2° below that of the shaded ground temperature without the addition of water. Nighthawks do not belly-soak or obviously urinate on the eggs, i.e., the eggs never appear soiled with uric acid. Body temperatures of nighthawks were not measured during this study, but Cowles and Dawson (1951) reported that Lesser Nighthawks commenced gular fluttering at body temperatues of about 42°C. As eggs averaged about 41°C during the five hours of the afternoon, and fluttering was virtually continuous (Fig. 35) during this time, the eggs may be cooler than either the body temperature or the ground in the shade. Nighthawk eggs lose 0.96 calories·hr^{-1} of heat (= 580 cal/g H_2O × 39.6 mg·day^{-1} loss of egg mass × 1/24 day) which is insignificant in depressing egg temperature. I have no data on emissivity of nighthawk eggs, but, presumably, there is no heat sink to which the eggs can emit thermal radiation when under a female with the conditions described above. Abdominal air sacs may function to cool the eggs slightly if the eggs are positioned near where these air sacs closely underlie the abdominal wall. Alternatively, the female may gular flutter at body temperatures lower than that reported by Cowles and Dawson (1951).

Belly-soaking can be interpreted to function in cooling the eggs, cooling the parent, and/or increasing nest humidity. The cooling effect of 3 g of water brought to the nest by a stilt is obvious. The evaporation of 3 g of water takes up 1740 calories (3 × 580 cal/g) of heat. It is not possible to partition the quantity of heat dissipated from each of the surfaces the water contacts (incubation patch and surrounding skin, feet and legs, ventral feathers, egg, and nest floor). Many birds rise and stand half-crouched over their eggs under high heat loads, and this behavior can serve both to cool the adult and the eggs by convection if there is wind (reviewed by Drent 1970). However, once shaded ambient temperature exceeds egg temperature, continuous shading is not adequate to prevent a rise in egg temperature. At this point the parent must initiate tight egg-brood patch contact or belly-soak to bring egg temperatures down. Maclean (1967) reported that *Rhinoptilus africanus* shaded its eggs at ambient temperatures between 30–36°C in the shade but incubated tightly at temperatures above and below that range. White-winged Doves maintained egg temperatures considerably below ambient temperatures by tight egg-brood patch contact (Russell 1969). Surface water was not available for either of the above two species. Male doves seem to incubate without relief throughout the heat of the day (Russell pers. comm.; Grant pers. obs.); leaving the nest uncovered to fly to distant water sources would be detrimental to the eggs.

Stilt, avocet, Killdeer, and Snowy Plover chicks remain in the nest for about a day after hatching. Water for evaporative cooling is brought to the nest via belly-soaking while chicks are present. Hatchlings of these species typically leave the nest in the early morning or late afternoon and forage in or near water during the nestling stage. They cope with the thermal stress by panting and wading in water. Tern and nighthawk chicks remain in the nest or nest area until fledging. Adult terns shade panting nestlings while nighthawk chicks gular flutter and seek shade. I did not study Forster's Terns during the nestling stage, so I am uncertain if the parents transport water via the ventral feathers to chicks exposed to high temperatures.

Maintenance of body temperature of incubating birds below damaging levels is more complex. Several factors seem important here: (1) frequent change-overs

at the nest, (2) standing in water between incubation bouts (excluding nighthawks), (3) panting or gular fluttering, (4) dorsal (and ventral in Forster's Tern) pteryloerection, (5) orientation on the nest with respect to the sun and wind, (6) shading, tight sitting, loose sitting (depending on the species), and (7) belly-soaking. The first six factors have already been discussed in previous sections, and all can be interpreted as adult behavioral/physiological thermoregulatory mechanisms with the eggs benefitting as an extension of the core of the parent's body (Drent 1970).

All Charadriiformes studied at the Salton Sea seem to pant, not gular flutter. In contrast, the Lesser Nighthawk and Mourning Dove gular flutter and probably are able to dissipate most of the heat gained from the environment in this way. Evaporative heat loss through gular flutter (expressed as a percentage of heat production) in related species is 118% (*Columba livia*), 148 % (*Chordeiles minor*), and 175% (*Phalaenoptilus nuttallii*) at air temperatures between 43.5 and 44.5°C (reviewed by Whittow 1976). The highest rates of evaporative water loss measured by Lasiewski (1969) for the Poorwill were 30.8–33.4 mg H_2O/min. At T_A = 47°C Poorwills evaporated sufficient water by continuous gular flutter to account for an average of 352% of their metabolic heat production. If this rate were maintained, it would equal a loss of 90–97 % of the body mass per day (Lasiewski 1969).

Eight hours of continuous gular flutter by a female Lesser Nighthawk occurred on a day at the Salton Sea when maximum shaded ambient temperature reached 43.2°C (Fig. 35). The difficulty of equating laboratory chamber studies (no solar radiation, no wind, plus stress of captivity) to the field (intense solar radiation, variable wind, orientation of the bird, no captivity stress, incubating two eggs), even when shaded ambient temperatures are similar, is nearly overwhelming. The number of assumptions necessary make such an effort of questionable significance. However, if we extrapolate from the Poorwill data, eight hours of gular flutter by an incubating nighthawk should result in a loss of about 30% of its body mass. It is doubtful that a nighthawk could survive a mass loss of that magnitude, though water losses amounting to 15% of body mass per day are tolerated by other birds at rest (Bartholomew and Dawson 1954; Bartholomew and Cade 1956; Berger and Hart 1971).

Pteryloerection of the dorsal plumage may aid in convective and evaporative cooling of heat-stressed birds during incubation. Orientation on the nest with respect to the sun and wind varied between species nesting under similar thermal stress. Why species differed in this aspect of behavioral thermoregulation is not known. Perhaps the behavior, morphology, and physiology of these species differed, and they oriented appropriately to minimize the heat stress. Similarly, some species incubated tightly (stilt, avocet, and probably nighthawk) while others alternated between shading, loose sitting, and tight sitting (Forster's Tern, Killdeer, Snowy Plover) under similar thermal stress. The function of belly-soaking will be discussed later.

Regulation of Nest Humidity

Eggs have been shown to lose water at a fairly constant rate during the course of incubation (Drent 1975; Rahn et al. 1976; Morgan et al. 1978; Rahn and Dawson 1979). This moisture, coupled with cutaneous losses from the incubating parent,

elevates the vapor pressure within the nest above that of the surrounding ambient air. In order for the eggs to continue losing water, the water vapor within the nest must be vented to the relatively drier atmosphere. The relative roles of convective and/or diffusive water transport have not been adequately quantified, but it is generally assumed that the bulk of water vapor is removed by convection from the nest. Ventilation necessary to facilitate water loss from the nest and, ultimately, the egg is thought to be achieved by exposing the eggs to ambient air periodically at nest relief and/or by briefly standing over the eggs. Periodic postural changes while sitting have been reported in the Herring Gull by Drent (1970), Black-headed Gull (*L. ridibundus*) by Beer (1961), Adelie Penguin (*Pygoscelis adeliae*) by Derksen (1977), Heermann's Gull by Rahn and Dawson (1979), and Laysan (*Diomedea immutabilis*) and Black-footed Albatross (*D. nigripes*) by Grant et al. (in press). These are species in which one member of the pair incubates continuously (except for postural changes) for hours to weeks before being relieved.

At the Salton Sea, incubation bouts and behavior vary with the species and ambient temperature. Nest relief may be as frequent as every 5 min (Snowy Plover, stilt, avocet) or as infrequent as 10 hrs or more in the nighthawk (female leaves the nest in late afternoon without relief). In addition, some species sit tightly while others alternate between tight sit, loose sit, and shading. Nest humidity and ventilation rates have been determined and/or calculated for five species nesting in close proximity at the Salton Sea (Table 8). A major complication is measuring the amount of water transported to the nest by those species that belly-soak during the day. Nest vapor pressure for all species studied at the Salton Sea ranged from 20.4 to 25.2 torr, and ventilation (per nest = full clutch) ranged from 12.8 to 92.4 $l \cdot day^{-1}$ (Table 8).

Nest vapor pressure and ventilation for stilts and avocets were very similar, and both species sit tightly over their eggs. Ventilation rates of these recurvirostrids were seven times higher than that of the only other tight sitter, the Lesser Nighthawk. Since nighthawks build no nest, an imperceptible rise in posture of only a few millimeters would flush the nest air rapidly. The relative role of shading and tight sitting cannot be quantified in the Forster's Tern due to the short legs and relatively deep nest cup. Both species of the genus *Charadrius* employ tight sitting, loose sitting, and shading during the heat of the day. Tight sitters should require greater ventilation rates to flush the water vapor periodically from the nest air.

The role of attentive postures and belly-soaking in relation to short-term changes in ambient vapor pressure and relative humidity were investigated in the Killdeer and Snowy Plover to discern if these behavior patterns regulate nest humidity. One might expect tight sitting coupled with belly-soaking to occur at the lowest ambient humidities or vapor pressures to prevent excessive water loss from the eggs. Mean hourly ambient vapor pressure ranged from 11.1 to 23.2 torr near Snowy Plover nests and 11.8 to 19.7 torr near Killdeer nests. Ambient relative humidities ranged from 20.6 to 65.0% near Snowy Plover nests and 19.8 to 88.0% near Killdeer nests. The lowest hourly ambient vapor pressure for the Snowy Plover nests occurred between 12:00 and 13:00 (11.1 torr), but ambient vapor pressure from 05:00 to 07:00 averaged 12.0 torr. Belly-soaking was first noted at 11:23 but probably occurred earlier as my view of the area where birds belly-

soaked was partially obstructed. I have no attentiveness data for 05:00–07:00 at these plover nests, but probably most of the time the birds were tight sitting or off the nest. I have not observed belly-soaking prior to 07:00 in any charadriiform nesting at the Salton Sea. For the interval 12:00–13:00, the eggs were shaded by the birds almost 90% of the time (Fig. 22). This posture allowed unobstructed flow of ambient air of low relative humidity (20.6%) around the eggs for 90% of that hour.

The lowest hourly ambient vapor pressure near Killdeer nests occurred between 05:00–06:00 (11.8 torr, 84.5% RH). Tight sitting and off nest were the only behavior patterns observed. Ambient vapor pressures and humidities averaged 13.7 torr and 24.5%, respectively, between 14:00 and 17:00 near Killdeer nests (Fig. 24). For this time interval, incubation postures were almost equally divided between shading, loose sitting, and tight sitting. Belly-soaking was first noted at 09:46 and continued until after 18:00. At the lowest ambient vapor pressure (11.8 torr) and very high relative humidity (84.5%) belly-soaking did not occur. At the very low ambient vapor pressure (13.7 torr) and lowest relative humidity (24.5%), belly-soaking occurred, but relatively dry air flowed over the eggs for about 65% of the time (shading plus loose sitting from 14:00–17:00).

Tracy and Sotherland (1979) and Spotila et al. (1981) have argued that movement of air across the surface of eggs should not significantly affect the rate of water loss from the eggs. The vapor pressure gradient was constant in both experiments (Tracy and Sotherland 1979; Spotila et al. 1981) but varies in the field situation at the Salton Sea described here. However, belly-soaking occurred during the hours when some of the highest ambient vapor pressures occurred (10:00–12:00, P_I = 19.2–19.3 torr). If incubation posture and belly-soaking were more closely tied to nest humidity than to egg-adult thermoregulation, one would predict a tight sit over the eggs and frequent belly-soaking during the intervals of lowest ambient vapor pressures and relative humidities to insure greater absolute humidity around the eggs and hence reduced water loss. Ambient vapor pressures (as a consequence of the lowered ambient temperatures) are frequently as low during the last few hours of darkness as during the mid-afternoon (Fig. 16). Nocturnal belly-soaking has not been observed.

Additional support for the idea that attentive postures are not an immediate response to ambient vapor pressure nor relative humidity comes from the observed asynchrony of postures of birds at two nests watched simultaneously. For example, attentive postures over the eggs at two Snowy Plover nests were not synchronized between 16:00 and 17:00 on 15 June 1978. The pair at one nest spent 90% of its time shading the eggs while the pair at the other nest (25 m north of the first) spent 100% of the hour sitting loosely over the eggs. Similarly, on 3 June, 1978 at 12:00, a Killdeer at one nest shaded its eggs while at another nest (100 m south of the first along the same dirt road), the bird was sitting tight. Both nests were equally exposed to wind and solar radiation.

Walsberg (1980) did not find a correlation between nest humidity and breeding habitat or ambient humidity. He (1980:371) suggested that "short-term behavioral and physiological adjustments during the course of incubation may be both unnecessary and ineffective as means of regulating egg water loss." Rahn et al. (1976) suggested that active ventilation is necessary to prevent excessive buildup of moisture in the nest. Empirical data for incubating Laysan and Black-footed

Albatrosses (Grant et al., in press) support Walsberg's (1980) hypothesis that parental "ventilation" behaviors are neither effective nor necessary in regulating egg water loss.

The attentive behaviors may be a function of body temperature rather than either egg temperature or nest or ambient humidity. Body temperature is probably correlated with how long the bird has been on the nest without relief and with the solar heat load. In general (much variation was seen), the early part of a Killdeer incubation bout was spent in tight or loose sit posture, while near the end of a bout, loose sit and shading were more frequently observed. One pair of Snowy Plovers shaded its eggs while the other pair spent more time in the loose sit posture. One could argue that, in terms of humidity regulation, belly-soaking compensates for shading (and continuous flow of dry air over eggs). However, understanding the tight sitting and frequent belly-soaking of stilts and avocets then becomes a problem.

Ventilation does not have to occur at regular intervals to achieve a nearly constant daily mass loss of the eggs. Mass loss for 24 eggs (7 nests) of the stilt was determined for two consecutive 12-hr periods. Diurnal mass loss was 85.6 ± 11.8 mg/12 hrs, and nocturnal mass loss was 73.2 ± 16.5 mg/12 hrs. I have no egg or nest air temperatures nor attentive behavior and posture data for these seven nests during this single 24-hr period. Mass loss data strongly suggest, however, that "ventilation" occurs day and night such that eggs lose nearly as much water at night as during the day. Mean nocturnal (19:00–07:00) ambient vapor pressure was 17.2 ± 2.1 torr (N = 12) and mean diurnal (07:00–19:00) ambient vapor pressure, 15.6 ± 1.5 (N = 12) torr (Fig. 16). As ambient vapor pressure is greater at night, less of a gradient exists between nest air and ambient vapor pressure and consequently $\dot{M}_{H_2O}$ should decrease if $\dot{V}_N$ remains constant (see equation 5). Alternatively, if $\dot{M}_{H_2O}$ remained constant, the ventilation rate would have to increase at night to account for these data. A rigorous experimental approach is needed to manipulate various components of these equations while carefully monitoring the behavior of the birds to determine if active nest ventilation occurs.

A role of temperature sensors on the incubation patch has been demonstrated in one passerine in which tightness of sit and duration of incubation bouts were altered by the application of a local anesthetic (White and Kinney 1974). Rahn et al. (1977) have suggested the presence of humidity and nest air temperature sensors on the incubation patch, but it is difficult to see how they may work in a species that routinely belly-soaks during the heat of the day. Active regulation of nest humidity requires integration of nest air temperature and vapor pressure or relative humidity not only while the incubator is present, but also during periods when it is absent. In dual sex incubators some knowledge of the conditions present while the mate was on the nest would seem to be necessary to achieve the nearly uniform rate of water loss from the eggs that we measure. It is easier to postulate that nest humidity and ventilation are achieved secondarily to egg temperature maintenance and comfort of the bird on the nest.

Function and Origin of Belly-soaking

Belly-soaking involves the transport of water in the ventral feathers to the eggs and chicks. Possible functions include: (1) cooling the incubating bird exposed to

intense solar radiation, (2) supplementing water intake of the chicks (Cade and Maclean 1967), (3) cooling the eggs and chicks, (4) increasing nest air humidity, or (5) some combination of the above (Maclean 1975; Grant 1978).

Belly-soaking for the purpose of transporting drinking water to chicks has been demonstrated only for sandgrouse, family Pteroclidae (Cade and Maclean 1967; Maclean 1968) and Egyptian Plovers (Howell 1979), though Gatter (1971) suggested that the young of *Charadrius dubius* also may drink from the wet feathers of the adults. Intensive watches at nests of Killdeers and stilts with young showed that young did not drink from the belly feathers but rather scrambled around in the nest to maximize wetting of the down. Maclean (1975) reviewed the occurrence of belly-soaking in Charadriiformes and reported that the nesting localities where belly-soaking occurs are generally hot and humid. The Salton Sea nesting environment is very hot and relatively humid (near surface water where nesting occurs).

Many of the other possible functions of belly-soaking are not mutually exclusive. Thus, it could serve simultaneously to cool the adult and eggs or chicks, and to increase nest air humidity. Mean vapor pressure for June at coastal sites was about 11.6 torr and at the U.S. Weather Service station nearest the Salton Sea was about 8.6 torr (Table 8). Actual ambient vapor pressure at nest level and within 50 m of nests ranged from 13.4 to 20.8 torr (Table 8) at both sites. Coastal ambient vapor pressure for stilts was 16.3 torr and for stilts at the Salton Sea was 16.0 torr. Thus, coastal and the Salton Sea ambient vapor pressures were approximately equal, but no belly-soaking was observed at coastal sites. If belly-soaking occurred solely in response to ambient vapor pressure, one would expect equal amounts of belly-soaking at the coastal and Salton Sea sites. However, means and standard deviations tell us very little about what may happen behaviorally when extreme values are encountered.

Similar results are obtained when one considers the frequency of belly-soaking (N = 3109 belly-soaks) by stilts in relation to mean hourly ambient vapor pressure (Fig. 16). Belly-soaking occurred between 08:00 and 19:00 and peaked at about 11:00. Hourly ambient vapor pressure shows a bimodal pattern with peaks at about 10:00 and 22:00 and lowest values at about 14:00 and 05:00. Most belly-soaking occurred at peak ambient pressures during the day with substantial numbers of belly-soaks also occurring during the mid-afternoon low ambient vapor pressures. I have already discussed the lack of a positive correlation between belly-soaking and hourly ambient vapor pressure and relative humidity in Killdeers and Snowy Plovers. Thus, a proximate cue for belly-soaking does not seem to be low ambient vapor pressure. If belly-soaking occurred solely in response to low nest vapor pressure, one would expect most belly-soaking in coastal stilts (Table 8) and least in Killdeers, avocets and stilts at the Salton Sea. This is not the case. Coastal stilts do not belly-soak, but all Charadriiformes at the Salton Sea do.

I was unable to monitor nest vapor pressure on a short-term basis. Hourly mass gain by the small, silica gel-filled eggshell hygrometers would not be great enough to measure accurately in the field. In addition, the normal eggs could not safely be disturbed during the heat of the day. Mean nest air temperature and egg temperature (Table 2) are similar for all species for all locations and do not differ greatly from those of other species elsewhere.

High egg temperature, by itself, does not appear to induce belly-soaking. This was demonstrated with the use of egg heaters placed in stilt nests and also by comparing temperatures at which belly-soaking did and did not occur (Figs. 17, 19–21). In all instances, belly-soaking occurred when egg temperatures were fairly constant and within the normal daytime range. Obviously, belly-soaking played a large role in keeping egg temperatures within this normal temperature range. The anticipatory role of belly-soaking and the impressive effect of belly-soaking on "correcting" an overheated clutch have been discussed. Belly-soaking occurs with egg temperatures at "normal" values, and, thus, hot eggs, by themselves, are not the proximate stimulus for belly-soaking. Hot eggs are frequently the result of too long an absence (although belly-soaking may occur during this absence) of the adult from a nest (Figs. 32–34). Nest air temperature (Figs. 17, 19) is frequently lower than egg temperature and may be as much as 10°C (Fig. 17) lower than shade ground temperature, but belly-soaking still occurs. Ultimately, belly-soaking cools the adult and prevents overheating of the eggs and chicks without further overheating the adults.

A proximate factor that cannot be ruled out without further rigorous experimental work is that of decreasing nest air humidity. Not enough is known about the mechanics of humidifying and ventilating the nest in the absence of belly-soaking, so any attempt to assign relative humidifying contributions to the nest by the incubating birds using or not using belly-soaking would be premature. The vapor pressure gradient is maintained at about 27–35 torr in birds nesting in diverse environments (Rahn et al. 1976, 1977; Morgan et al. 1978; Rahn and Dawson 1979). At the Salton Sea the vapor pressure gradient of nighthawks' eggs-nest (29.4 torr) is virtually identical to those of stilts (28.4 torr) and Snowy Plovers (29.9 torr) nesting within a few hundred meters of each other (Table 7). How the nighthawk maintains such a gradient without belly-soaking while the latter two species may put more water into their nests on a daily basis than a fresh egg weighs was not determined. Subtle postural changes, water loss of eggs, water lost by the incubation patch, belly-soaking, and probably many other factors interact in a complex manner.

Belly-soaking is highly correlated with ambient temperature in stilts. High ambient temperatures, however, do not, by themselves, induce belly-soaking. Belly-soaking generally does not occur during the last hour of daylight (at dusk) even with ambient temperatures of 40–42°C. I was unable to measure the highest ground-in-sun temperatures as they exceeded the upper limit (50°C) of the YSI thermistor. Bartholomew and Dawson (1979) demonstrated a very high correlation between ground-in-sun temperatures and behavioral thermoregulation postures in Heermann's Gulls. Ground-in-sun temperatures were typically off scale for 5–7 hrs each day at the Salton Sea.

The only unexplored short-term or proximate factor that may stimulate belly-soaking is the body temperature of the incubating bird, which behavioral thermoregulatory events suggest may be important. Panting occurred first, followed by increasing degrees of dorsal pteryloerection, and finally belly-soaking (Fig. 28). However, efforts to demonstrate the role of body temperature in belly-soaking failed. Air sac temperatures may differ significantly from core body temperatures during panting (Schmidt-Nielsen et al. 1969; this study).

Cade and Maclean (1967) suggested that in sandgrouse belly-soaking may have

been derived from bathing. The rocking motion of sandgrouse is strongly suggestive of bathing. I suggested (Grant 1978) that belly-soaking in Black Skimmers may be derived from a distraction display (injury feigning) rather than bathing. Human disturbance at shade temperatures greater than about 32°C on sunny days often induced a flurry of belly-soaking and foot-wetting activities at the Salton Sea skimmer colonies. Tompkins (1942) suggested that the origin of tern belly-soaking "may be merely the wish of the bird to cool herself." Belly-soaking in terns seems to be derived from drinking on the wing and simply represents a deeper descent. However, the belly-first belly-soaking behavior of terns is quite unlike any other behavior pattern except, perhaps, plunge diving. Forster's Terns bathe by landing at the water's edge or in shallow water and wading into deeper water where the typical head and wing motions and rocking are seen. The long skimming and plunge diving belly-soaking and foot-wetting by terns are probably simply adult cooling mechanisms. On very hot days non-nesting terns wet their bellies while on the wing or float for long intervals on the surface of the water.

Belly-soaking in the Charadriidae and Recurvirostridae may be derived from a distraction display. These shorebirds seem to belly-soak by flexing the legs as in displacement brooding while the smaller, shorter-legged species mix leg flexing with running through relatively deep water. Very little to no rocking occurs, and none of the wing and head motions of bathing are seen in undisturbed belly-soaking Both bathing and belly-soaking in the long-legged shorebirds require flexing of the legs. In belly-soaking, after flexing and wetting the belly, the bird extends its legs and preens its venter (frequently with water in its bill), while in bathing, flexing is followed by vigorous wing and head motions and rocking motions to wet the dorsal as well as the ventral plumage.

As I mentioned under belly-soaking in stilts, during disturbance, belly-soaking may grade into any segment of the distraction behavioral repertoire including bathing, Displacement Brooding, Wing-flapping Crouch-run or Crouch-walk, and Dihedral wing flight. Bathing in nesting stilts has been seen only in early morning and late afternoon. Non-nesting stilts may be seen bathing at any time of the day. Bathing, in general, seems to be a cold-temperature phenomenon. I have seen more species bathe in the cooler parts of the day and during the cooler parts of the year than during the midday heat. Maclean (1975), during his extensive field work in southern Africa, also has noted more frequent bathing in cold weather than in hot.

It seems puzzling that belly-soaking has been recorded only in the Charadriiformes (including Pteroclidae) with the exception of one questionable occurrence each in the Least Bittern, *Ixobrychus exilis* (Weller 1961), and the Osprey, *Pandion haliaetus* (Nickell 1967). If the origin of belly-soaking is in bathing, why do other taxa that bathe and nest in hot environments not belly-soak? An attractive hypothesis for the Charadriidae and Recurvirostridae is the false incubation origin, since this behavior, as far as I am aware, only occurs within some of the Charadrii. Belly-soaking has not been recorded within the Scolopacidae (in the broad sense of Jehl 1968). Most Scolopacidae breed in the cooler, high latitude environments. Two species (Spotted Sandpiper, *Actitis macularia* and Willet, *Catoptrophorus semipalmatus*) breed in temperate North America and may occasionally be exposed to high heat loads. Both species select shaded nest sites, and neither shows false incubation behavior. Both bathe but do not appear to

belly-soak. This observation serves to strengthen further my suggestion that belly-soaking in the Recurvirostridae and Charadriidae (includes Vanellinae in the sense of Jehl 1968) may be derived from the false incubation or Displacement Brooding distraction display. Other taxa use distraction displays to lead predators from the nests but do not belly-soak (e.g., nighthawk and Mourning Dove). To my knowledge neither species shows false incubation or Displacement Brooding.

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SUMMARY

Open ground-nesting Charadriiformes and Lesser Nighthawks are exposed to intense heat loads at the Salton Sea. The major problems are the regulation of egg temperatures below lethal levels, the prevention of overheating of the adult bird on the nest, and the regulation of nest humidity. For successful hatching, eggs must be maintained within a narrow range of temperature during the course of incubation. Egg temperature seems to be maintained below lethal levels during the heat of the day by (1) 100% attentiveness, (2) minimum exposure time at nest relief, and (3) belly-soaking (by Charadriiformes but not by nighthawks). Brief exposures (2 min) to high temperatures and solar radiation can destroy a clutch of eggs.

Regulation of body temperature of the incubating birds below damaging levels is more complex. Several important factors are: (1) frequent change-overs at the nest, allowing the relieved bird to go and stand in water, (2) panting or gular fluttering, (3) dorsal pteryloerection, (4) orientation on the nest with respect to the sun (minimize heat gain) and wind (maximize convective cooling), (5) shading, tight sitting, and loose sitting (depending on the species), and (6) belly-soaking.

The regulation of nest humidity is complex, and our understanding of it

confounded by our lack of knowledge of nest ventilation methods and the frequent application of water to the nest by belly-soaking. Belly-soaking in Charadriiformes studied at the Salton Sea may function in cooling the incubating bird exposed to intense solar radiation, cooling the eggs and chicks, and increasing nest humidity. The proximate stimulus for inducing belly-soaking may be the body temperature of the adult. Hot eggs, low nest vapor pressure, high nest air temperature, low ambient vapor pressure, high ambient temperature, or high solar radiation loads, by themselves, do not induce belly-soaking. Belly-soaking by the Charadriidae and Recurvirostridae may be derived from the false incubation or Displacement Brooding distraction display.

As a consequence of frequent belly-soaking in saline and silt-laden water, the eggs become soiled with salt and/or mud during the course of incubation. A layer of dried salt has no significant effect on water-vapor conductance, daily water loss, or oxygen consumption of stilt eggs. A layer of mud decreases water-vapor conductance and daily water loss but has no effect on oxygen consumption of stilt eggs. Successful nesting by Charadriiformes at the Salton Sea is possible through the interaction of behavioral and physiological adaptations. Belly-soaking is perhaps the most important adaptation used by open, ground nesting Charadriiformes at the Salton Sea.

LITERATURE CITED

ABDULALI, H. 1939. The sun as a mortality factor among young birds. J. Bombay Nat. Hist. Soc. 41:433–434.

ALI, S., AND S. D. RIPLEY. 1969. Handbook of the birds of India and Pakistan. Vol. 3. Oxford University Press, London.

AR, A, C. V. PAGANELLI, R. B. REEVES, D. G. GREENE, AND H. RAHN. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. Condor 76:153–158.

AR, A., AND H. RAHN. 1978. Interdependence of gas conductance, incubation length, and weight of the avian egg. Pp. 227–236, *In* J. Piiper (ed.), Respiratory function in birds, adult and embryonic. Springer-Verlag, New York.

AR, A., AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. Am. Zool. 20: 373–384.

BAILEY, A. M., AND R. J. NIEDERACH. 1965. The birds of Colorado, Vol. 1. Denver Mus. Nat. Hist., Denver, Colorado.

BAKKEN, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. J. Theoret. Biol. 60:337–384.

BAKKEN, G. S., AND D. M. GATES. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. Pp. 255–289, *In* D. M. Gates and R. B. Schmerl (eds.), Perspectives in biophysical ecology. Springer-Verlag, New York.

BAKKEN, G. S., V. C. VANDERBILT, W. A. BUTTEMER, AND W. R. DAWSON. 1978. Avian eggs: thermoregulatory value of very high near-infrared reflectance. Science 200:321–323.

BALDWIN, S. P., AND S. C. KENDEIGH. 1932. Physiology of the temperature of birds. Cleveland Mus. Nat. Hist. Sci. Publ. 3.

BARTHOLOMEW, G. A. 1966. The role of behavior in the temperature regulation of the Masked Booby. Condor 68:523–535.

BARTHOLOMEW, G. A., AND T. J. CADE. 1956. Water consumption of House Finches. Condor 58: 406–412.

BARTHOLOMEW, G. A., AND W. R. DAWSON. 1954. Body temperature and water requirements of the Mourning Dove, *Zenaidura macroura marginella*. Ecology 35:181–187.

BARTHOLOMEW, G. A., AND W. R. DAWSON. 1979. Thermoregulatory behavior during incubation in Heermann's Gulls. Physiol. Zool. 52:422–437.

BEER, C. G. 1961. Incubation and nest building behaviour of black-headed gulls. I. Incubation behaviour in the incubation period. Behaviour 18:62–106.

BENNETT, A. F., AND W. R. DAWSON. 1979. Physiological responses of embryonic Heermann's Gulls to temperature. Physiol. Zool. 52:413–421.

BENNETT, C. L., JR. 1975. Climate of the Southeast Air Basin. California Air Resources Board, Sacramento.

BENT, A. C. 1927. Life histories of North American shorebirds. Part 1. U.S. Natl. Mus. Bull. 142.

BENT, A. C. 1929. Life histories of North American shorebirds. Part 2. U.S. Natl. Mus. Bull. 142.

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull. 176.

BERGER, M., AND J. S. HART. 1971. Physiology and energetics of flight. Pp. 415–477, *In* D. S. Farner, J. R. King, and K. C. Parkes (eds.), Avian biology, Vol. 4. Academic Press, New York.

BERGMAN, R. D., P. SWAIN, AND M. W. WELLER. 1970. A comparative study of nesting Forster's and Black Terns. Wilson Bull. 82:435–444.

BERNSTEIN, M. H. 1971. Cutaneous water loss in small birds. Condor 73:468–469.

BOYD, R. L. 1972. Breeding biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. Unpubl. MS thesis. Kansas State Teachers College, Emporia.

BROWN, J. 1975. The evolution of behavior. W. W. Norton and Co., New York.

BUNNI, M. K. 1959. The Killdeer, *Charadrius v. vociferus* Linnaeus, in the breeding season: ecology, behavior, and the development of homoiothermism. Unpubl. Ph.D. dissert. University of Michigan, Ann Arbor.

CADE, T. J., AND G. L. MACLEAN. 1967. Transport of water by adult sandgrouse to their young. Condor 69:323–343.

CALIFORNIA DEPARTMENT WATER RESOURCES. 1970. Geothermal wastes and the water resources of the Salton Sea area. Bull. No. 143-7.

CHATTOCK, A. P. 1925. On the physics of incubation. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 213:397–450.

COWLES, R. B. 1965. Hyperthermia, aspermia, mutation rates and evolution. Q. Rev. Biol. 49:341–367.

COWLES, R. B., AND A. NORDSTRAM. 1946. A possible avian homologue of the scrotum. Science 104:586–587.

COWLES, R. B., AND W. R. DAWSON. 1951. A cooling mechanism of the Texas Nighthawk. Condor 53:19–22.

CROSSLEY, R. 1964. Spur-winged Plovers wetting their feathers before incubating. Br. Birds 57: 515–516.

CURRIE, A. J. 1916. The birds of Lahore and the vicinity. J. Bombay Nat. Hist. Soc. 24:561–577.

DERKSEN, D. V. 1977. A quantitative analysis of the incubation behavior of the Adelie Penguin. Auk 94:552–566.

DEXTER, R. W. 1961. Further studies on nesting of the Common Nighthawk. Bird-banding 32: 79–85.

DHARMAKUMARSINHJI, R. S. 1964. Some observations on the Small Indian Pratincole (*Glareola lactea* Temminck) and some other waders breeding in Bhavnagar, Gujarat. Pavo 2:1–11.

DINSMORE, J. J. 1972. Sooty Tern behavior. Bull. Fla. State Mus. Bio. Sci. 16:129–179.

DRENT, R. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Suppl. 17:1–132.

DRENT, R. 1972. Adaptive aspects of the physiology of incubation. Proc. 15th Int. Ornithol. Congr., pp. 255–280.

DRENT, R. 1973. The natural history of incubation. Pp. 262–311, *In* D. S. Farner (ed.), Breeding biology of birds. Natl. Acad. Sci., Washington, D.C.

DRENT, R. 1975. Incubation. Pp. 333–420, *In* D. S. Farner, J. R. King, and K. C. Parkes (eds.), Avian Biology, Vol. 5. Academic Press, New York.

ERMAK, D., M. BUCHANAN, AND D. LAYTON. 1976. Land and air resources. Pp. 7–21, *In* D. Layton and D. Ermak, A description of Imperial Valley, California for the assessment of impacts of geothermal energy development. Lawrence Livermore Laboratory UCRL-52121, University of California, Livermore.

FREEMAN, B. M., AND M. A. VINCE. 1974. Development of the avian embryo. John Wiley and Sons, New York.

FROST, P. G. H., AND W. R. SIEGFRIED. 1977. The cooling rate of eggs of Moorhen *Gallinula chloropus* in single and multi-egg clutches. Ibis 119:77–80.

GATTER, W. 1971. Wassertransport beim Flussregenpfeifer (*Charadrius dubius*). Die Vogelwelt 92: 100–103.

GEORGE KAINADY, P. V. 1977. Wetting of belly feathers in White-tailed Lapwing and Avocet. Bull. Basrah Nat. Hist. Mus. 4:79–81.

GEORGE KAINADY, P. V., AND K. L. AL-DABBAGH. 1976. Some observations on the behaviour of incubating *Charadrius alexandrinus* on hot summer days. Bull. Basrah Nat. Hist. Mus. 3:121–137.

GIBSON, F. 1971. The breeding biology of the American Avocet (*Recurvirostra americana*) in central Oregon. Condor 73:444–454.

GILLIARD, E. T. 1958. Living birds of the world. Doubleday and Co., Garden City, New York.

GRANT, G. S. 1978. Foot-wetting and belly-soaking by incubating Gull-billed Terns and Black Skimmers. J. Bombay Nat. Hist. Soc. 75:148–152.

GRANT, G. S. 1979. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Unpubl. Ph.D. dissert. University of California, Los Angeles.

GRANT, G. S. 1981. Belly-soaking by incubating Common, Sandwich, and Royal Terns. J. Field Ornithol. 52:244.

GRANT, G. S., AND N. HOGG. 1976. Behavior of late-nesting Black Skimmers at Salton Sea, California. Western Birds 7:73–80.

GRANT, G. S., C. V. PAGANELLI, T. N. PETTIT, G. C. WHITTOW, AND H. RAHN. 1982. Determination of fresh egg mass during natural incubation. Condor 84:121–122.

GRANT, G. S., T. N. PETTIT, H. RAHN, G. C. WHITTOW, AND C. V. PAGANELLI. In press. Water loss from Laysan and Black-footed Albatross eggs. Physiol. Zool.

HAMILTON, R. B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae). Ornithol. Monogr. No. 17.

HARDY, J. W. 1957. The Least Tern in the Mississippi Valley. Publ. Mus. Michigan State Univ. Biol. Ser. 1:1–60.

HOBBS, J. N. 1972. Breeding of the Red-capped Dotterel at Fletcher's Lake, Dareton, NSW. Emu 72:121–125.

HOLGERSEN, N. E. 1971. Black-necked Stilt nesting in Delaware. Wilson Bull. 83:100.

HOWELL, T. R. 1979. Breeding biology of the Egyptian Plover, *Pluvianus aegyptius* (Aves: Glareolidae). Univ. Calif. Publ. Zool. 113:1–76.

HOWELL, T. R., AND G. A. BARTHOLOMEW. 1962. Temperature regulation in the Sooty Tern *Sterna fuscata*. Ibis 104:98–105.

HOWELL, T. R., B. ARAYA, AND W. R. MILLIE. 1974. Breeding biology of the Gray Gull, *Larus modestus*. Univ. Calif. Publ. Zool. 104:1–57.

HOYT, D. F. 1976. The effect of shape on the surface-volume relationship of birds' eggs. Condor 78:343–349.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh egg weight of bird eggs. Auk 96:73–77.

HOYT, D. F., D. VLECK, AND C. M. VLECK. 1978. Metabolism of avian embryos: ontogeny and temperature effects in the Ostrich. Condor 80:265–271.

HUGGINS, R. A. 1941. Egg temperature of wild birds under natural conditions. Ecology 22:148–157.

HULSMAN, K. 1975. The skimming behaviour of terns. Sunbird 6:41–43.

JAYAKAR, S. D., AND H. SPURWAY. 1965. The Yellow-wattled Lapwing *Vanellus malabaricus* (Boddaert) a tropical dry-season nester. J. Bombay Nat. Hist. Soc. 62:1–14.

JEHL, J. R., JR. 1968. Relationships in the Charadrii (shorebirds): a taxonomic study based on color patterns of the downy young. San Diego Soc. Nat. Hist. Memoir 3.

KERCHER, J. R., AND M. BUCHANAN. 1976. Biological resources. Pp. 34–93, *In* D. Layton and D. Ermak (eds.), A description of Imperial Valley, California for the assessment of impacts of geothermal energy development. Lawrence Livermore Laboratory UCRL-52121, University of California, Livermore.

KULL, R. C., JR. 1977. Color selection of nesting material by Killdeer. Auk 94:602–604.

LAMB, C., AND A. B. HOWELL. 1913. Notes from Buena Vista Lake and Fort Tejon. Condor 15: 115–120.

LASIEWSKI, R. C. 1969. Physiological responses to heat stress in the Poorwill. Am. J. Physiol. 217: 1504–1509.

LASIEWSKI, R. C., M. H. BERNSTEIN, AND R. D. OHMART. 1971. Cutaneous water loss in the Roadrunner and Poor-will. Condor 73:470–472.

LIND, H. 1961. Studies on the behaviour of the Black-tailed Godwit (*Limosa limosa*) (L.). Maddelelse Naturfredningsradets reservatudvalg No. 66. Munksgaard, Copenhagen.

LINT, K. C. 1959. Stilts in the spotlight. Zoonooz 32:3–5.

LOWTHER, E. H. N. 1949. A bird photographer in India. Oxford Univ. Press, London.

LUNDY, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. Pp. 243–276, *In* T. C. Carter and B. M. Freeman (eds.), The fertility and hatchability of the hen's egg. Oliver and Boyd, Edinburgh.

LUSTICK, S., B. BATTERSBY, AND M. KELTY. 1978. Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200:81–83.

MABBETT, G. 1890. A query in regard to the Least Tern. Auk 7:410–411.

MACDOUGAL, D. T. 1914. The Salton Sea. Carnegie Inst. Wash., Publ. No. 193.

MACLEAN, G. L. 1967. The breeding biology and behavior of the Double-banded Courser, *Rhinoptilus africanus* (Temminck). Ibis 109:556–569.

MACLEAN, G. L. 1968. Field studies on the sandgrouse of the Kalahari Desert. Living Bird 7:209–235.

MACLEAN, G. L. 1974. Egg-covering in the Charadrii. Ostrich 45:167–174.

MACLEAN, G. L. 1975. Belly-soaking in the Charadriiformes. J. Bombay Nat. Hist. Soc. 72:74–82.

MATTHEWS, G. V. T. 1954. Some aspects of incubation in the Manx Shearwater *Procellaria puffinus*, with particular reference to chilling resistance in the embryo. Ibis 96:432–440.

MCGILP, J. N., AND A. M. MORGAN. 1931. The nesting of the Banded Stilt (*Cladorhynchus leucocephalus*). South Australian Ornithol. 11:37–53.

MEINERTZHAGEN, R. 1954. Birds of Arabia. Oliver and Boyd, Edinburgh.

MITCHELL, H. H. 1917. Peculiar nesting habits of the avocet. Condor 19:101.

MORENG, R. E., AND C. S. SHAFFNER. 1951. Lethal internal temperatures for the chicken, from fertile egg to mature bird. Poultry Sci. 30:255–266.

MORGAN, K. R., C. V. PAGANELLI, AND H. RAHN. 1978. Egg weight loss and nest humidity during incubation in two Alaskan gulls. Condor 80:272–275.

MORRIS, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour 9:75–113.

MORRISON, P. R., AND W. J. TIETZ. 1957. Cooling and thermal conductivity in three small Alaskan mammals. J. Mammalogy 38:78–86.

NICKELL, W. P. 1967. Breast-wetting behavior of the Osprey at the nest. Jack-Pine Warbler 45: 96–97.

NOAA. 1974. Climates of the states. Vol. II. Western states. U.S. Dept. Commerce, Washington, D.C.

PAGANELLI, C. V., R. A. ACKERMAN, AND H. RAHN. 1978. The avian egg: *in vivo* conductance to oxygen, carbon dioxide, and water vapor in late development. Pp. 212–218, *In* J. Piiper (ed.), Respiratory function in birds, adult and embryonic. Springer-Verlag, New York.

PAGANELLI, C. V., A. AR, AND E. H. LANPHIER. 1971. The influence of pressure and gas composition on water vapor conductance. Proc. Int. Union Physiol. Sci. 9:436.

PAGANELLI, C. V., A. OLSZOWKA, AND A. AR. 1974. The avian egg: surface area, volume, and density. Condor 76:319–325.

PICKWELL, G., AND E. SMITH. 1938. The Texas Nighthawk in its summer home. Condor 40:193–215.

PIIPER, J. P., P. DEJOURS, P. HAAB, AND H. RAHN. 1971. Concepts and basic quantities in gas exchange physiology. Respir. Physiol. 13:292–304.

PURDUE, J. R. 1976. Thermal environment of the nest and related parental behavior in Snowy Plovers, *Charadrius alexandrinus*. Condor 78:180–185.

RAHN, H., R. A. ACKERMAN, AND C. V. PAGANELLI. 1977. Humidity in the avian nest and egg water loss during incubation. Physiol. Zool. 50:269–283.

RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. Condor 76:147–152.

RAHN, H., AND W. R. DAWSON. 1979. Incubation water loss in eggs of Heermann's and Western Gulls. Physiol. Zool. 52:451–460.

RAHN, H., C. V. PAGANELLI, AND A. AR. 1974. The avian egg: air cell gas tension, metabolism and incubation time. Respir. Physiol. 22:297–309.

RAHN, H., C. V. PAGANELLI, I. C. T. NISBET, AND G. C. WHITTOW. 1976. Regulation of incubation water loss in eggs of seven species of terns. Physiol. Zool. 49:245–259.

RITTINGHAUS, H. 1956. Untersuchungen am Seeregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeoog. J. Ornithol. 97:117–155.

RITTINGHAUS, H. 1961. Der Seeregenpfeifer. Die Neue Brehm-Bücherei. A. Ziemsen Verlag, Wittenberg, Lutherstadt.

ROMANOFF, A. L. 1960. The avian embryo, structural and functional development. MacMillan, New York.

RUFFNER, J. A., AND F. E. BLAIR (EDS.). 1974. The Weather Almanac. Gale Research Co., Book Tower, Detroit, Michigan.

RUSSELL, S. M. 1969. Regulation of egg temperatures by incubating White-winged Doves. Pp. 107–112, *In* C. C. Hoff and M. L. Riedesel (eds.), Physiological systems in semiarid environments. University of New Mexico Press, Albuquerque.

SCHARDIEN, B. J., AND J. A. JACKSON. 1979. Belly-soaking as a thermoregulatory mechanism in nesting Killdeers. Auk 96:604–606.

SCHMIDT-NIELSEN, K., J. KANWISHER, R. C. LASIEWSKI, J. E. COHN, AND W. L. BRETZ. 1969. Temperature regulation and respiration in the Ostrich. Condor 71:341–352.

SCHÖNWETTER, M. 1967. Handbuch der Oologie, lief. 1–13. Akad. Verlag, Berlin.

SIBSON, R. B., AND H. R. MCKENZIE. 1943. Some observations on stilts in the Firth of Thames. New Zealand Bird Notes 1:51–57.

SPOTILA, J. R., C. J. WEINHEIMER, AND C. V. PAGANELLI. 1981. Shell resistance and evaporative water loss from bird eggs: effects of wind speed and egg size. Physiol. Zool. 54:195–202.

TINBERGEN, N., G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUUK, AND E. SZULC. 1962. Eggshell removal by the Black-headed Gull, *Larus ridibundus* L.; a behaviour component of camouflage. Behaviour 19:74–117.

TOMPKINS, I. R. 1942. Least Tern watering eggs: Gideon Mabbett's query. Auk 59:308.

TRACY, C. R., AND P. R. SOTHERLAND. 1979. Boundary layers of bird eggs: do they ever constitute a significant barrier to water loss? Physiol. Zool. 52:63–66.

TURNER, D. A., AND J. GERHART. 1971. "Foot-wetting" by incubating African Skimmers *Rynchops flavirostris*. Ibis 113:244.

VERMEER, K. 1971. Large American Avocet clutches at Dowling Lake, Alberta. Blue Jay 29:88.

VINCE, M. A. 1969. Embryonic communication, respiration and the synchronization of hatching. Pp. 233–260, *In* R. A. Hinde (ed.), Bird vocalizations, their relation to current problems in biology and psychology. Cambridge University Press, London.

VLECK, C. 1978. Metabolism of avian embryos: patterns in altricial and precocial birds. Unpubl. Ph.D. dissert., University of California, Los Angeles.

VLECK, C. M., D. F. HOYT, AND D. VLECK. 1979. Metabolism of avian embryos: patterns in altricial and precocial birds. Physiol. Zool. 52:363–377.

VLECK, D. 1978. Measurement of oxygen consumption, carbon dioxide, and evaporative water loss in a closed system. Unpubl. Ph.D. dissert. University of California, Los Angeles.

VLECK, D., C. M. VLECK, AND D. F. HOYT. 1980. Metabolism of avian embryos: ontogeny of oxygen consumption in the Rhea and Emu. Physiol. Zool. 53:125–135.

WALSBERG, G. E. 1980. The gaseous microclimate of the avian nest during incubation. Am. Zool. 20:363–372.

WALSBERG, G. E., G. S. CAMPBELL, AND J. R. KING. 1978. Animal coat color and radiative heat gain: a re-evaluation. J. Comp. Physiol. B. 126:211–222.

WALTERS, J. 1954. Der Brutanteil Geschlechter beim Seeregenpfeifer (*Leucopolius alexandrinus* L.). Limosa 27:19–24.

WANGENSTEEN, O. D., AND H. RAHN. 1970/71. Respiratory gas exchange by the avian embryo. Respir. Physiol. 11:31–45.

WELLER, M. W. 1958. Observations on the incubation behavior of a Common Nighthawk. Auk 75: 48–59.

WELLER, M. W. 1961. Breeding biology of the Least Bittern. Wilson Bull. 73:11–35.

WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. Science 186:107–115.

WHITTOW, G. C. 1976. Regulation of body temperature. Pp. 154–173, *In* P. D. Sturkie (ed.), Avian physiology. Springer-Verlag, New York.

WOODS, R. S. 1924. Notes on the life history of the Texas Nighthawk. Condor 26:3–6.

ZIMMERMAN, H. 1951. Zur Brutbiologie des Seeregenpfeifer (*Charadrius a. alexandrinus* L.). Ornithol. Mitteil. 3:270–273.

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