

- Atlantic Alcidae, p. 233–261. In D. N. Nettleship and T. R. Birkhead [eds.], *The Atlantic Alcidae*. Academic Press, New York.
- KNUDTSON, E. P., AND G. V. BYRD. 1982. Breeding biology of Crested, Least, and Whiskered Auklets on Buldir Island, Alaska. *Condor* 84:197–202.
- MANUWAL, D. A. 1979. Reproductive commitment and success of Cassin's Auklet. *Condor* 81:111–121.
- NELSON, D. A. 1985. The syntactic and semantic organization of Pigeon Guillemot (*Cephus columba*) vocal behavior. *Z. Tierpsychol.* 67:97–130.
- NELSON, D. A. 1987. Factors influencing colony attendance by Pigeon Guillemots on Southeast Farallon Island, California. *Condor* 89:340–348.
- NISBET, I.C.T. 1979. Conservation of marine birds of northern North America—a summary, p. 305–315. In J. C. Bartonek and D. N. Nettleship [eds.], *Conservation of marine birds of northern North America*. U.S. Fish and Wildlife Service, Wildlife Research Report 11, Washington, D.C.
- PIATT, J. F., B. D. ROBERTS, AND S. A. HATCH. 1990. Colony attendance and population monitoring of Least and Crested Auklets on St. Lawrence Island, Alaska. *Condor* 92:97–106.
- SEALY, S. G. 1973. Breeding biology of the Horned Puffin on St. Lawrence Island, Bering Sea, with zoogeographical notes on the north Pacific puffins. *Pac. Sci.* 27:99–119.
- SPEICH, S., AND D. A. MANUWAL. 1974. Gular pouch development and population structure of Cassin's Auklet. *Auk* 91:291–306.
- TENAZA, R. R. 1966. Pigeon guillemot banding returns. *Bird Banding* 37:288.

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SHORT-TERM VARIATIONS IN WATER-VAPOR PRESSURE IN NESTS OF COMMON CANARIES¹

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The discovery that eggs, regardless of their size, lose similar proportions of water during incubation (Ar and Rahn 1980) generated considerable interest among avian biologists in the water-vapor pressure of the nest (P_N) since it determines how much water is lost from the egg. As a result, P_N has been measured in numerous avian species (Walsberg 1980, Rahn and Paganelli 1990).

However, most of these measurements were made with egg hygrometers which provide only one value of P_N for periods of incubation typically spanning one or more days. Until recently, little information was available concerning variations in the moisture content of nests over short intervals of time. We now have descriptions of such changes, but only from nests of a few large birds, specifically those of (1) swans and geese, where P_N fluctuates as much as 9 torr during 24-hr periods (Howey et al. 1984); (2) ostriches, where it only varies about 4 torr each day (Swart et al. 1987); and (3) ptarmigans, where it scarcely changes at all (Andersen and Steen 1986). No comparable information appears to exist for other birds, particularly small ones. We attempt here to remedy this situation partially by describing short-term variations in the moisture content of Common Canary (*Serinus canarius*) nests.

MATERIALS AND METHODS

We measured P_N in 11 canary nests throughout days 1, 4, 7, and/or 10 of incubation. In all, we collected data for 28 separate days of incubation (Table 1). During 23 of these days, we measured P_N every 15 min; during the other 5 days, at hourly intervals. Our canary hens were experienced birds which had raised broods successfully in previous seasons. However, the data (see below) suggest that some of the males with which they were paired were inexperienced breeders.

Pairs were kept in standard double-brooder cages (23 × 36 × 28 cm) in an indoor aviary. They were exposed to a long daily photoperiod (16L:8D, lights on from 06:00 to 22:00 EDT), air temperatures of 20.3–25.0°C (22.8°C on average), and ambient vapor pressures (P_i) of 7.8–16.7 torr. Within any given day, P_i varied 1.4–6.5 torr (4.1 torr on average; Fig. 1). The birds had access to food and fresh water ad libitum, and received greens and vitamins once or twice a week.

Each cage contained a lined, plastic nest pan in which the hens laid and incubated clutches of 4–5 eggs. The bottom of the nest pan was fitted with a 2-cm diameter scintered bronze (dust) cap. This enabled us to plug a relative humidity probe (Solomat Model HC1) into a nest for 24-hr periods without disturbing the incubating canary. Parts of the cap other than the surface facing the eggs were taped, and the cap itself taped to the probe, so that the only air reaching the sensor came from the nest. When P_N was not being measured, we kept a plug covered with Saran Wrap® in the cap to prevent it from draining heat and moisture from the nest.

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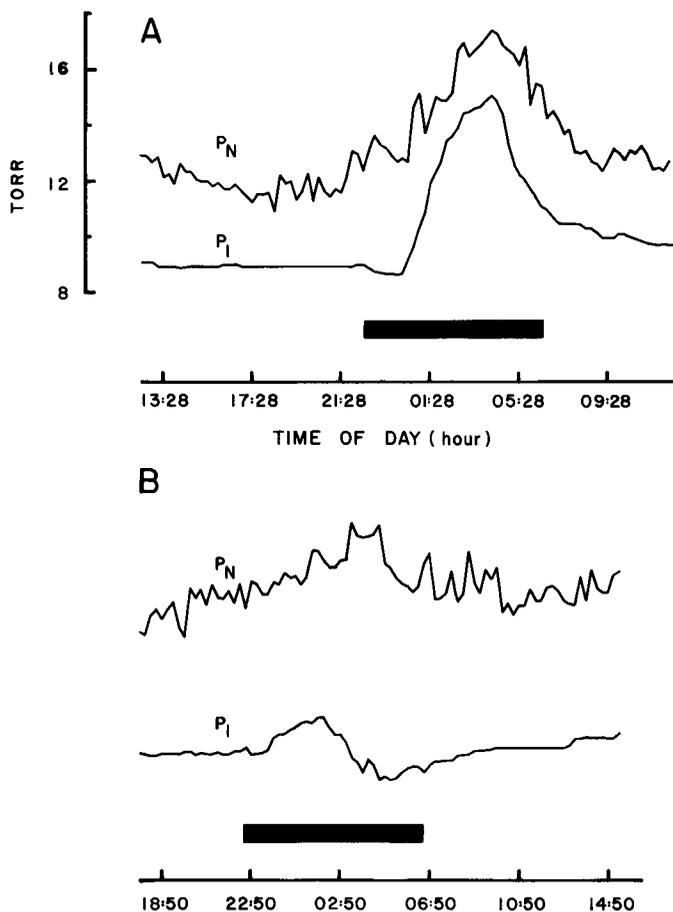


FIGURE 1. Concurrent fluctuations in nest (P_N) and ambient (P_I) humidity during individual days of incubation in two canary nests. (A) Day 4 of incubation. P_N and P_I were significantly correlated ($r^2 = 0.84$; $P < 0.001$). (B) Day 10 of incubation. P_N and P_I were not significantly correlated ($r^2 = 0.003$; $P > 0.05$). The black bar in each panel indicates when the lights were out in the aviary.

We checked the calibration of the humidity probe before, during, and after the study by exposing it to atmospheres over dry desiccant, distilled water, and $MgCl_2$ solutions of known concentrations and temperature. The probe rarely needed adjustment and its readings were always within 3% of the relative humidities expected in atmospheres above these standards.

The leads from the probe were connected to a data logger (Solomat Model MPM 2000) which automatically recorded the relative humidity of a nest (RH_N) at 15- or 60-min intervals. Data were downloaded from the logger to an Epson (Model 40) printer at the end of each 24-hr period.

We also inserted a 30-gauge, copper-constantan thermocouple (calibrated against a high-precision mercury thermometer certified by the National Bureau of Standards) among the eggs in the clutch to measure nest temperature (T_N). The leads from the thermocouple were connected to a strip chart mini-recorder (Cole-

Parmer Model R-8377-15) so that T_N could be recorded continuously while RH_N was being measured.

The continuous record of T_N made it possible for us to determine when a hen changed position in the nest and when she left it. Since the records contained considerable "noise" (i.e., small-scale variations in T_N), we considered only large, gradual declines in T_N below this noise to indicate times when the hen was away from her nest (Fig. 2). We considered other abrupt, usually small changes in T_N to represent movements of the birds while they incubated.

While measuring P_N , we also recorded the relative humidity and temperature in the aviary with a hygrothermograph (Cole-Parmer Model 8368-50) calibrated daily with a mercury thermometer and the humidity probe.

Eggs in nine of the nests were cracked open after day 10 of incubation to see whether they contained developing chicks or were sterile. (We did not allow the

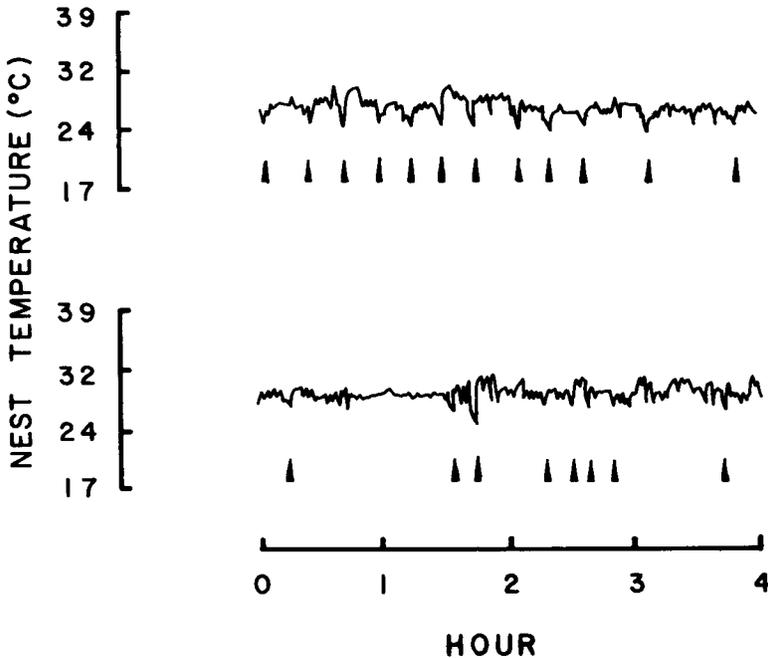


FIGURE 2. Chart recordings of nest temperature show both movements of canary hens on the nest and times when they left the nest (denoted by closed carrots). Both records were made during day 10 of incubation. The upper one is from a nest that contained fertile eggs; the lower one from a nest containing sterile eggs.

canaries to hatch the eggs because we planned to use the shells in another study.)

Data were evaluated with one-way analysis of variance (*ANOVA*), correlation analysis, and Student's *t*-tests (Zar 1974).

RESULTS

Within individual nests, P_N varied substantially during 24-hr periods on all four days of incubation (Fig. 1). On any given day, it fluctuated as little as 2.7 and as much as 9.8 torr (5.2 torr on average) depending on the nest. Recorded values of P_N ranged from 10 to 21 torr.

Incubating hens did not keep P_N constant during the upsurges of P_I that frequently occurred during early morning hours when the aviary was dark (Fig. 1). In fact, variations in P_N and P_I were significantly correlated (r^2 values between 0.06 and 0.87) during 25 of the 28 days of incubation. In these cases, changes in P_I can explain, on average, 52% of the fluctuations in P_N .

Average daily P_N differed, sometimes considerably, between nests on any specific day of incubation (Table 1), but did not change much within individual nests from one day to another. In 10 of 11 nests, it stayed between 12.3 and 15.6 torr. There was no progressive increase or decrease in average daily P_N during the 10 days of incubation (Fig. 3).

Short-term fluctuations in P_N during the 16-hr periods when the lights were on in the aviary each day

were rarely related either to (1) the hens' movements in the nest (significantly correlated during only three of 28 days of incubation: in these cases, r^2 values were between 0.24 and 0.47), or (2) the frequency with which the hens left the nest (significantly correlated during only two of 28 days: r^2 values of 0.30 and 0.46).

Three of the 11 nests contained eggs with viable and apparently normal chicks at late stages of development when they were cracked open. Six other nests contained only sterile eggs. We do not know the status of the eggs in the two remaining nests. There were no consistent differences in P_N or T_N between nests containing fertile and sterile eggs to suggest that incubation was abnormal in the latter (Figs. 2, 3). This is well illustrated in Figure 3 where in one case (panel A) fertile eggs were in the nest at the lower P_N (12.3–13.8 torr), whereas in the second case (panel B), fertile eggs were in the nest at the higher P_N (13.2–15.6 torr).

DISCUSSION

Individual values of P_N , as well as daily averages, in our study are well within the 6–26 torr range reported for other birds (Walsberg 1980) and the 5–21 torr range reported previously for canaries (Kern 1987).

The fact that average daily values of P_N sometimes differed considerably from one nest to another (Table 1) is also consistent with earlier reports (Walsberg 1985, Kern 1987, Kern et al. 1990), but the fact that average daily values of P_N were nearly constant within individual nests from one day to another is not. In previous

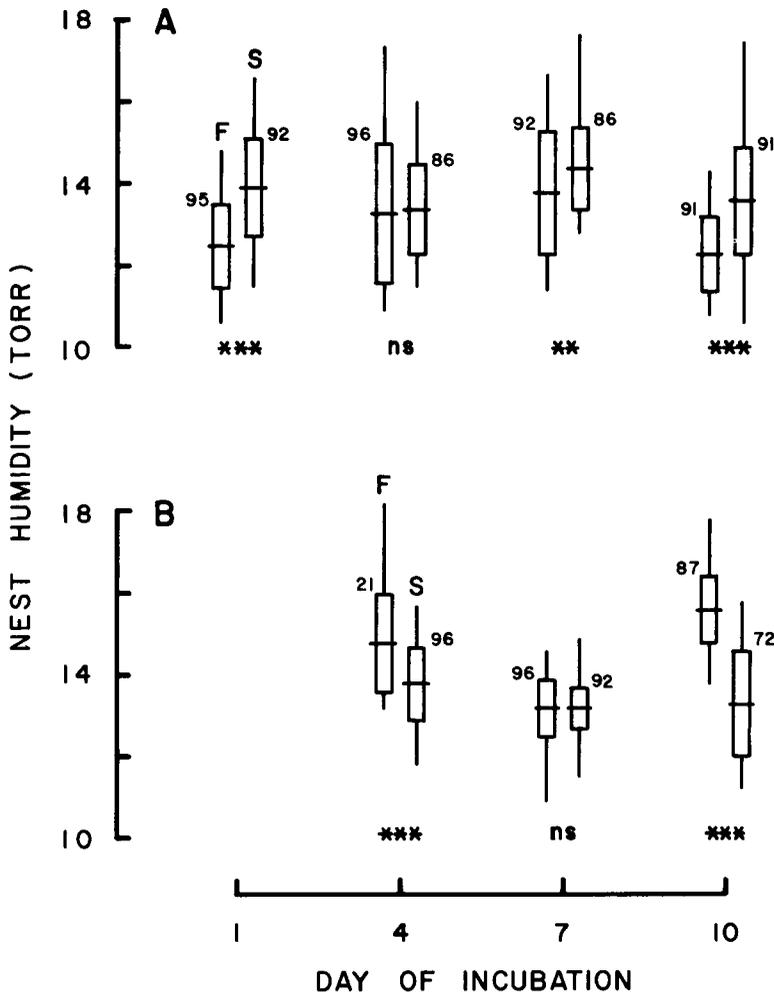


FIGURE 3. Daily variations in humidity (P_N) in two pairs (A and B) of canary nests, one nest of each pair containing fertile eggs (F) and the other sterile eggs (S). Horizontal lines are average daily values of P_N ; rectangles are ± 1 SD; vertical lines are ranges of P_N ; and superscripts are the number of times that P_N was measured during each day of incubation shown. Differences in P_N between fertile and sterile clutches were either not significantly different (ns), significant at the 0.002 level (**), or significant at the 0.001 level (***) (Student's t -tests).

studies of songbirds, average daily P_N was shown to vary as much as 9–22 torr in individual nests from one day to another (Kern 1987, Kern et al. 1990). We do not know why the changes we found are so much smaller, but perhaps they relate to the use of thermocouples and a relative humidity probe in our study and egg hygrometers in the others.

Short-term changes in P_N of canaries (Fig. 1) are similar in size to those described for ostriches (Swart et al. 1987) and anseriforms (Howey et al. 1984), but more closely resemble patterns of change in nests of the latter.

We were surprised that fluctuations in P_N were not produced by parental behavior. However, the same is

true of plovers (Grant 1982), albatrosses (Grant et al. 1982), ptarmigans (Andersen and Steen 1986), and other songbirds (Walsberg 1983). Had ventilating behavior and P_N been tightly coupled in our or other studies, we could argue that incubating birds regulate P_N by permitting accumulated moisture to escape from the nest when they move about in it or leave it. But since the two were not closely allied, other factors must also influence P_N . These may include water vapor added to nest air by the brood patch and nest material.

Although it is difficult to quantify the role of nest material, it is possible to estimate the amount of moisture provided by the brood patch since it (1) will come from the part of the brood patch that is not in contact

TABLE 1. Average daily humidity levels (torr) within individual canary nests containing fertile (*) or sterile (no asterisk) clutches on selected days of incubation.

	Day 1	Day 4	Day 7	Day 10
	12.5*	13.3*	12.6	12.3*
	13.5	13.4	13.2	13.3
	13.9	13.8	13.2*	13.5*
	13.9	14.4	13.4	13.6
	14.1	14.8*	13.8	14.7
		15.8	13.8*	15.3
			14.2*	15.6*
			14.4	18.0
			16.8	
\bar{P}_N	13.6	14.2	13.9	14.5

\bar{P}_N = grand mean P_N for each day of incubation. These grand means are not significantly different from one another ($F_{3,24} = 0.58$, $P > 0.05$; ANOVA).

with the eggs (A_{exposed}), and (2) will accumulate in the nest at a rate that depends on the water-vapor conductance of brood patch tissue (K_{bp}), the fraction of the day that the bird spends incubating (F_N), and the difference between the water-vapor pressure of brood patch tissue (P_{bp}) and nest air (P_N). In other words,

$$(\text{Water contributed by brood patch}) = (A_{\text{exposed}})(K_{\text{bp}})(F_N)(P_{\text{bp}} - P_N).$$

The canary's brood patch has an area of 6.34 cm² (Kern and Coruzzi 1979). In four-egg clutches, 21% of it is *not* in contact with the eggs, whereas in five-egg clutches only 1% is exposed (these estimates are based on the assumption that 18% of the canary egg's surface [7.65 cm²] is covered by the brood patch). Under these circumstances, A_{exposed} is (6.34)(0.21) or 1.33 cm² for a four-egg clutch; and 0.06 cm² for a five-egg clutch. Also for canaries, $F_N = 0.97$ (Ratnam and Kern, unpubl. obs.), $P_{\text{bp}} = 55.3$ torr (assuming brood patch tissue is 100% saturated with water at a temperature of 40°C), and $P_N = 14.0$ torr (the average of values in Table 1).

It is difficult to know what value of K_{bp} to assign to the canary since the only available measurements are for ptarmigans and bantams (0.25 mg H₂O·day⁻¹·cm⁻²·torr⁻¹; Andersen and Steen 1986) and penguins (2.5 mg H₂O·day⁻¹·cm⁻²·torr⁻¹; Handrich 1989). (To arrive at this value for ptarmigans and bantams, we assumed that the brood patch occupies 10% of the total skin surface; we think this is a reasonable first approximation since the brood patch occupies 8–12% of the skin in passerines [Walsberg and King 1978, Kern and Coruzzi 1979].) If K_{bp} lies between these extremes, and if the clutch consists of four eggs, the canary's brood patch will add 13–133 mg water vapor to nest air daily. On the other hand, if the clutch consists of five eggs, the patch will only add 0.6–6 mg of water vapor to the nest each day.

This is 0.1–1.3 times as much moisture as the eggs contribute (25 mg H₂O·day⁻¹·egg⁻¹; Kern 1987) when the clutch is four eggs, but a negligible amount compared to the egg's contribution when the clutch is five eggs. By way of comparison, Andersen and Steen (1986) estimated that the brood patch of bantams and ptar-

migans provided 30% of the water vapor in the nest cup.

Some of this water vapor will be trapped in the nest material and may reenter nest air later when an incubating bird moves or leaves the nest. This may explain why P_N was not usually correlated with parental behavior. However, the amount of moisture (regardless of its source—nest, egg, or brood patch) that diffuses from the nest cup into the atmosphere when the incubating bird moves or leaves the nest will still depend on P_I . This fact, as well as the large amount of activity that canaries exhibited when incubating (Fig. 2), probably explains why P_N and P_I were tightly coupled in our study.

In summary, P_N ranged from 10 to 21 torr in the nests of incubating canaries. It fluctuated 3–10 torr (the average was 5 torr) during 24-hr periods, as it does in nests of geese, swans, and ostriches (Howey et al. 1984, Swart et al. 1987). In most cases, short-term variations in P_N were related to P_I , but not to the behavior of the incubating birds. Average daily values of P_N differed considerably from one nest to another (12–18 torr), but did not change much (<2.5 torr) within individual nests from day to day. We conclude that the moisture content of nest air is not actively regulated by incubating canaries, but depends on P_I .

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LITERATURE CITED

- ANDERSEN, O., AND J. B. STEEN. 1986. Water economy in bird nests. *J. Comp. Physiol.* 156B:823–828.
- AR, A. AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. *Am. Zool.* 20:373–384.
- GRANT, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithol. Monogr.* No. 30. American Ornithologists' Union, Washington, DC.
- GRANT, G. S., T. N. PETTIT, H. RAHN, G. C. WHITTO, AND C. V. PAGANELLI. 1982. Water loss from Laysan and Black-footed Albatross eggs. *Physiol. Zool.* 55:405–414.
- HANDRICH, Y. 1989. Incubation water loss in King Penguin egg. II. Does the brood patch interfere with eggshell conductance? *Physiol. Zool.* 62:119–132.
- HOWEY, P., R. G. BOARD, D. H. DAVIS, AND J. KEAR. 1984. The microclimate of the nests of water fowl. *Ibis* 126:16–32.
- KERN, M. D. 1987. Humidity levels in the nests of incubating canaries (*Serinus canarius*). *Comp. Biochem. Physiol.* 87A:721–725.
- KERN, M. D., AND L. CORUZZI. 1979. The structure of the canary's incubation patch. *J. Morph.* 162: 425–452.
- KERN, M. D., M. K. SOGGE, AND C. VAN RIPER III. 1990. Water-vapor pressure in nests of the San Miguel Island Song Sparrow. *Condor* 92:761–767.

- RAHN, H., AND C. V. PAGANELLI. 1990. Gas fluxes in avian eggs: driving forces and the pathway for exchange. *Comp. Biochem. Physiol.* 95A:1-15.
- SWART, D., H. RAHN, AND J. DE KOCK. 1987. Nest microclimate and incubation water loss of eggs of the African Ostrich (*Struthio camelus* var. *domesticus*). *J. Exp. Zool. Suppl.* 1:239-246.
- WALSBERG, G. E. 1980. The gaseous microclimate of the avian nest during incubation. *Am. Zool.* 20: 363-372.
- WALSBERG, G. E. 1983. A test for regulation of nest humidity in two bird species. *Physiol. Zool.* 56: 231-235.
- WALSBERG, G. E. 1985. A test for regulation of egg dehydration by control of shell conductance in Mourning Doves. *Physiol. Zool.* 58:473-477.
- WALSBERG, G. E., AND J. R. KING. 1978. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. *Physiol. Zool.* 51:92-103.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.

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GROWTH AND DEVELOPMENT OF THERMOREGULATION IN NESTLING SAN MIGUEL ISLAND SONG SPARROWS¹

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Key words: Nestling growth; thermogenesis; *Melospiza melodia micronyx*; Channel Islands.

Patterns of growth (reviewed by Ricklefs 1968, 1969; O'Connor 1984) and the development of endothermy (reviewed by Dawson and Hudson 1970, Dunn 1975, Hill and Beaver 1982) have been well-studied in altricial wild birds, especially passerines. But few studies compare growth and thermogenesis in separate populations of the same species. Results of such studies with emberizids varied among species. King and Hubbard (1981), for example, found that nestlings from subarctic, subalpine, and low-altitude montane populations of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) grew at similar rates. In contrast, Rogers (1985) reported that the growth rates of nestlings in different populations of Savannah Sparrows (*Passerculus sandwichensis*) varied in response to the different environmental constraints of the localities in which they were reared. Nice (1937) and Smith et al. (1982) documented patterns of nestling growth in mainland (Ohio) and insular (Mandarte Island, British Columbia, Canada) populations of Song Sparrows

(*Melospiza melodia*), respectively, and found that they were similar to those reported for most other passerines by Ricklefs (1968, 1969) and O'Connor (1984).

In 1985-1986, we had the opportunity to examine the growth of nestlings from a third race of Song Sparrows, *M. m. micronyx*, which is endemic to San Miguel Island near Santa Barbara, California. We also studied the development of endothermy in these young birds, a process not hitherto described for nestling Song Sparrows. We report both in this paper.

STUDY AREA AND METHODS

San Miguel Island (120°W, 34°N) is the northwesternmost of the California Channel Islands and lies 42 km from the southern California coastline, almost due south of Point Conception. It is 37 km² in area and has a maximum elevation of 253 m. It supports four major types of vegetation: coastal bluff, coastal sage scrub, foothill and valley grassland, and southern coastal dune (Philbrick and Haller 1977); and has large unstable sand dunes. Strong northwesterly winds are a dominant part of the island's Mediterranean climate, which features warm, dry summers and cool, wet winters.

Our study area was a 9.2-ha plot of grassland bisected by two large gullies on the north-central plateau of San Miguel Island. The gullies were more or less filled with

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