

## NESTS AND NEST SITES OF THE SAN MIGUEL ISLAND SONG SPARROW

MICHAEL D. KERN

*Biology Department  
The College of Wooster  
Wooster, Ohio 44691 USA*

MARK K. SOGGE<sup>1</sup>

*Cooperative National Park Resources Studies Unit  
Institute of Ecology  
University of California  
Davis, California 95616 USA*

ROBERT B. KERN

*166 8th Street  
Cresskill, New Jersey 07626 USA*

CHARLES VAN RIPER III<sup>1</sup>

*Cooperative National Park Resources Studies Unit  
Institute of Ecology  
University of California  
Davis, California 95616 USA*

**Abstract.**—Nests and nest sites of the San Miguel Island (SMI) Song Sparrow (*Melospiza melodia micronyx*) are described; nests are compared with those of 16 other races of Song Sparrows. Bush lupins (*Lupinus albifrons*), coyote brush (*Baccharis pilularis*) and golden bush (*Haplopappus venetus*) were the shrubs used most commonly as nest sites by Song Sparrows on SMI. As a result of its location, the nest was effectively concealed from gray foxes (*Urocyon littoralis*), the major predator of this sparrow. Nest and nest site also moderated the combined chilling effects of cool air temperatures and strong northwesterly winds on the eggs and nestlings. Even in the absence of these moderating effects of the nest site, the energetic cost of incubation, estimated at 41–53% of the sparrow's resting metabolic rate, was modest. Twenty-nine percent of the canopy above the nest was open and as much as 73% of the nest cup was in the sun at midday, a time when surface temperatures of foliage, nest and nestlings sometimes exceeded 40 C. Whereas this exposure did not apparently reduce fledging success, it may explain why the incidence of addled eggs was so high in this population of Song Sparrows compared to others. Significant differences existed among races of Song Sparrows in the size, porosity and insulation of the nest. In most cases, these differences were not related to the latitude of the races' nesting areas.

### NIDOS Y LUGARES DE ANIDAMIENTO DE MELOSPIZA MELODIA MICRONYX

**Sinopsis.**—Los nidos y los lugares de anidamiento del gorrión de la Isla de San Miguel (*Melospiza melodia micronyx*), son descritos y comparados con los de otras 16 razas de este tipo de gorrión. En la Isla de San Miguel los arbustos de *Lupinus albifrons*, *Baccharis pilularis* y de *Haplopappus venetus*, fueron los más utilizados por el gorrión para la construcción de nidos. Como resultado de su localización, los nidos quedaron bien escondidos y pasaron desapercibidos a la zorra gris (*Urocyon littoralis*), quien es el principal depredador del ave. Los nidos y el lugar de anidamiento, moderaron el efecto combinado del enfriamiento a huevos y pichones, causado por las bajas temperaturas del aire y los fuertes vientos del

<sup>1</sup> Current address: National Park Service, Cooperative Park Studies Unit, P.O. Box 5614, Northern Arizona University, Flagstaff, Arizona 86011 USA.

norooeste. Aun en la ausencia de los efectos de moderación causados por la localización de los nidos, el costo energético de la incubación, resultó ser modesto (estimado entre 41–53% de la taza metabólica de un gorrión en descanso). El 29% del dosel sobre el nido resultó estar abierto y hasta un 73% del nido recibió el impacto directo del sol al medio día, período cuando, en algunos casos, la temperatura excedió a los 40 C en la superficie foliar, el nido y los pichones. Aunque este tipo de exposición, aparentemente, no redujo el éxito de los pichones en dejar el nido, podría explicar la alta incidencia de huevos hueros en esta población de gorriónes. Existen diferencias significativas, entre las distintas razas de este tipo de gorrión, en lo que respecta al tamaño, porosidad e insulación del nido. En la mayoría de los casos las diferencias no pudieron atribuirse a la latitud en que anidan estas razas.

Song Sparrows (*Melospiza melodia*) are widely distributed throughout North America, breeding from Alaska to the Mexican Plateau and on islands off both the Pacific and Atlantic coasts (Austin 1968). Three subspecies currently nest on the California Channel Islands: *M. m. clementae* on Santa Rosa and Santa Cruz Islands, *M. m. coronatorum* on Los Coronados Islands and *M. m. micronyx* on San Miguel Island (Diamond and Jones 1980, Jones et al. 1985).

Relatively little is known about the ecology of the Channel Islands group. Published information consists primarily of descriptions of races, taxonomic relationships and distribution (Collins 1979, Grinnell 1928, Grinnell and Daggett 1903, Miller 1951, Oberholser 1899, Van Rossem 1924, Wright and Snyder 1913). Song Sparrows of the San Miguel Island (SMI) race occur most commonly in four plant communities on the island: *Haplopappus* scrub, island grassland, *Coreopsis* phase and canyon (as defined by Hochberg et al. 1979), of which the former two are the most important.

Song Sparrows are widely distributed on the island, probably because *Haplopappus* scrub and island grassland associations are also widespread. But the largest concentrations occur on the northeastern side of the island, particularly on terraces overlooking the sea. These terraces are covered by dense shrubbery, denser than elsewhere on the island. As a result of their location and the low elevation of the island (only 253 m), however, they are also exposed to strong northwesterly winds. Nonetheless, nesting Song Sparrows prefer these dense stands of shrubbery to pure grassland or areas where grass and shrubs are mixed. Nesting territories have significantly higher vegetation and more shrubs than nondefended areas (Sogge and van Riper 1988). The measurements in this paper were collected so that we could more closely define the vegetation in the immediate vicinity of the nest within larger *Haplopappus* scrub and island grassland vegetational communities and determine how the vegetation influenced climatic conditions at the nest.

The information about the nest in this paper also complements and extends three recent publications concerning the breeding biology of the SMI Song Sparrow (Kern et al. 1990, Sogge et al. 1991, Sogge and van Riper 1988). Nests may be simply receptacles which house eggs and chicks, but more often they (and the nest site) have additional biological importance because they conceal eggs and chicks from potential predators or ameliorate nest microclimate. This in turn reduces the energy expen-

diture of incubating parent birds and influences their nest attendance. Studies of several avian species show that variations in nest structure, including latitudinal variations, reflect differences in the climatic conditions to which birds are exposed while nesting (Collias and Collias 1984; Kern 1984; Palmgren and Palmgren 1939; Schaefer 1976, 1980). We consequently examine not only nests of the SMI race in this paper, but nests of 16 other races of Song Sparrows as well.

#### MATERIALS AND METHODS

##### *Study Site*

During 1985 and 1986, we studied the breeding activities of Song Sparrows on SMI (120°W, 34°N), the northernmost of the Channel Islands west of Santa Barbara, California. Our study site was 9.2 ha on a terrace overlooking the sea on the north-central side of the island. Vegetation on the terrace consisted of *Haplopappus* scrub and island grassland communities. The island grassland association is the most extensive community on SMI and is dominated by introduced annual grasses (particularly *Avena* and *Bromus*) among which are scattered shrubs such as *Astragalus*, *Baccharis*, *Coreopsis*, *Eriogonum*, *Haplopappus* and *Lupinus*. *Haplopappus* scrub, which is the second most widespread plant association on the island and is unique to it, consists of a large variety of shrub species of which coast goldenbush (*Haplopappus venetus*) is dominant. Several gullies extended across the site. Some contained little vegetation, but others had prominent stands of bush lupin (*Lupinus albifrons*), coyote brush (*Baccharis pilularis*) and coast goldenbush.

San Miguel Island has a Mediterranean climate, but is subject to strong northwesterly winds that sweep south around Point Concepcion (Johnson 1979). During the 1986 nesting season, we recorded windspeeds of 2–30 m·s<sup>-1</sup>. The weather during the nesting season was highly variable with extreme air temperatures ( $T_a$ ) of 4–34 C and vapor pressures of 4–13 torr. Rain and dense fog were common and sometimes heavy. Overcast days were interspersed with occasional clear sunny days. Detailed weather data have not been kept for SMI, but those available for Santa Cruz Island which is nearby illustrate just how variable weather conditions can be on the Channel Islands. At coastal sites on Santa Cruz, where the elevation (229 m) is similar to that on SMI, extreme temperatures range from 2.0–42.2 C during November–May. Sixty-five percent of the days are clear, 14% partially overcast and 21% completely overcast (Hochberg 1980).

We located Song Sparrow nests within the study area by watching territorial birds. The SMI race nests between March and June, producing 2–3 broods a year. New nests are built for each brood.

##### *Nest Site Measurements*

*Vegetation around the nest.*—We identified and measured the size of plants with nests, including: nest height above ground, distance below

the top of the plant and from the nearest edge of the plant, and compass position of the nest with respect to the center of the plant. We also identified plants and measured vegetation height at 0.25-m intervals along eight, 3-m transect lines extending out at 45° from 26 nests.

*Canopy over the nest.*—Hemispherical photographs of the vegetation above 25 nests were taken to determine canopy closure. The method is that of Walsberg and King (1978) in which photographs are taken using a camera equipped with a “fisheye” lens pointed skyward from the location of the nest in the nest plant. The amount of sky in each quadrant of the canopy was quantified by covering photographs with a 2-mm mesh grid and counting the number of intersections falling on sky and vegetation.

*Amount of light in the nest cup.*—We put discs of white paper, cut to fit, in the nest cavities of 26 nests and photographed the discs at roughly hourly intervals (0600–1900 hours PDT) on sunny days to determine when and how much of the nest cup was exposed to the solar beam. The amount of light on the paper was quantified as above.

*Surface temperatures.*—In 11 nests, we measured the surface temperatures ( $T_s$ ) of: leaves in the canopy above the nest, the nest rim, chicks, and the bottom of the nest cup after removing the chicks. An IR thermometer (Extech, Model 3842/1) was used and was periodically recalibrated against the  $T_s$  of a nonreflective tabletop matching the color of the nest’s interior.

*Changes in nest temperature over 24-h periods.*—To determine how the foliage around the nest influenced nest temperature ( $T_n$ ), we examined  $T_n$ , together with  $T_a$  just outside the nest bush at nest height, for 24-h periods using YSI general purpose thermistors and battery-operated Rustak recorders (Model 2133). The thermistors measuring  $T_a$  were purposely not shielded.

*Airspeed around the nest.*—As northwesterly winds constantly buffet SMI, we also examined how well the vegetation around the nest protected it from wind. Airspeed at 28 nest sites was measured with a hotwire anemometer (Thermonetics Corp., Model HWA-103) at times when the wind was blowing strongly (6–30  $\text{m}\cdot\text{s}^{-1}$ ). Over successive 1-min intervals, and in this order, airspeed was measured (1) on the windward side of the nest bush at nest height, (2) on the windward rim of the nest, (3) within the nest cup and (4) outside the nest bush at shoulder height. In the case of gully nests, we included airspeed on the terrace above the gully. In evaluating these data, we assumed that variations in ambient airspeed were the same during successive 1-min periods.

### *Nest Measurements*

Fifty nests were collected from SMI during the 1986 field season and studied in the laboratory, along with 63 museum nests representing 16 other races of Song Sparrows. Eight of the SMI nests were later dismantled so that we could record their composition.

The nests were dried and then weighed and measured. The cross-

sectional area of the nest cavity was determined with a planimeter from tracings of the nest opening. The volume of the nest cavity was measured in terms of the amount of water required to fill the nest cup.

*Nest insulation.*—Thermal conductance ( $h$ ), which is a measure of heat flux, was used to evaluate the insulation in the nests. Insulation is the reciprocal of conductance; when  $h$  is low, insulation is high, and vice versa. Measurements were made through the floor ( $h_f$ ) and walls ( $h_w$ ) of the nest. From these an average value ( $h_{w+f}$ ) was calculated for the entire nest. We used the method of Kern (1984) with one modification: the nest cavity was lined with Saranwrap® and filled with hot water. In addition, the porosity of the nest was assessed in terms of the amount of light that could penetrate the structure using the method developed by Kern and van Riper (1984).

### *Statistical Analyses*

Data were compared using standard techniques (Batschelet 1981, Zar 1974). Ratios and percentages were converted to their arcsine equivalents for analysis. Values in this paper are means  $\pm$  95% confidence limits.

## RESULTS

### *Nest Site Characteristics*

*Location of the nest.*—Eighty-four percent of the Song Sparrows on our study site nested in *Haplopappus*, *Lupinus* or *Baccharis* (Table 1), although many other species of shrubs in which they reportedly nest (Collins 1979) were also available. Shrubs containing nests averaged  $0.7 \pm 0.1$  m (range: 0.3–2.3 m) in height, and had extreme diameters of  $1.2 \pm 0.1$  m (0.4–4.1 m) and  $0.8 \pm 0.1$  m (0.3–1.9 m). On average, the nest was  $0.4 \pm 0.04$  m (0.0–1.1 m) above the ground,  $29 \pm 3$  cm (13–140 cm) below the top of the nest bush, and  $20 \pm 3$  cm (1–112 cm) from the nearest edge of the nest bush at nest height.

Thirty-seven museum nests from the mainland (those for which we had data) were built  $0.74 \pm 0.92$  m (range: 0.00–4.88 m) above ground. Fifty-three insular nests (including those from SMI) were only half ( $P < 0.01$ ) that distance from the ground:  $0.37 \pm 0.26$  m (0.00–1.22 m).

Nest height did not change significantly between first and second nests built in the study area, in contrast to reports for other races of Song Sparrows (Haldeman 1931; Nice 1937, 1943). It did increase, however, as nest plant height increased ( $r^2 = 0.60, 0.91$  and  $0.80$  for nests in *Haplopappus*, *Baccharis* and *Lupinus*, respectively;  $P < 0.001$  in each case), as it does in several other passerines (Rich 1980). In addition, the ratio of nest height to bush height was significantly different ( $P < 0.05$ ) for the three principal nest plants: 0.52 for *Haplopappus*, 0.33 for *Baccharis* and 0.68 for *Lupinus*.

Most SMI nests were on the leeward side of the shrub in which they were built, whether in an isolated bush or contiguous shrubbery. That

TABLE 1. Plants in which Song Sparrows built nests on San Miguel Island during the 1985 and 1986 breeding seasons. Numbers in parentheses are percentages of nests in each plant for the year shown.

Nest plant	# (%) of nests			
	1985		1986	
<i>Haplopappus venetus</i>	31	(61)	21	(40)
<i>Lupinus albifrons</i>	12	(23)	11	(21)
<i>Baccharis pilularis</i>	4	(8)	8	(15)
<i>Eriophyllum confertiflorum</i>	2	(4)	10	(10)
<i>Marrubium vulgare</i>	2	(4)	2	(4)
<i>Solanum douglasii</i>	—		1	(2)
Grass	—		4	(8)
Total	51		52	

is, more nests were in the southeast quadrant (mean angle = 111°) than would be expected by chance ( $P < 0.001$ , Rayleigh test,  $df = 96$  nests).

*Plants associated with the nest site.*—Three or fewer species of plants generally occurred within a 3-m radius of the nest. The one in highest numbers was commonly the same species as the nest bush. *Marrubium*, *Baccharis*, *Lupinus* and grass were commonly associated with nests in *Haplopappus* or *Lupinus*; grass and *Lupinus* with nests in *Baccharis*; *Haplopappus*, *Baccharis*, and *Lupinus* with nests in *Eriophyllum*.

Plants within 3 m of the nest were significantly taller ( $\chi^2$  test,  $P < 0.01$ ) on the windward (azimuths 270, 315 or 360°) than the leeward side of the nest bush on the terrace, but not in the gullies. At both locations, however, the shrub containing the nest (in 25 of 25 cases) and often the nest itself (in 18 of 25 cases) were significantly higher than this surrounding vegetation ( $\chi^2$  test,  $P < 0.05$ ).

*Canopy above the nest.*—The amount of visible sky in the canopy over the nest varied considerably from one nest site to another (5–68%), but averaged 29%. There were no clearcut relationships between the location of openings in the canopy and the species of shrub in which the nest was built, and there was no single quadrant of the canopy to which openings were restricted.

*Insolation.*—Forty-five percent of the nests from the terrace, and 60% from the gullies were exposed to the sun for a period of 48 or more consecutive minutes at least once a day between 0900 and 1500 hours. Peak exposure was most often at 1000–1100 hours on the terrace and 1300–1400 hours in the gullies. The maximum area of the nest cup ever exposed to sunlight averaged 52% (range: 0–73%). In both locations, exposure was greatest in the early afternoon: 30% or more of the nest was in the sun in half of the nests between 1200 and 1500 hours.

This result probably explains why the  $T_s$  of the nest reached 46 C and the  $T_s$  of the chicks 40–47 C at times when  $T_a$  was only 27–28 C (Table 2). Clouds passing overhead could quickly change the temperature in the nest cup, by as much as 1 or 2 C per min.

TABLE 2. Temperatures in and around the nests of SMI Song Sparrows. Values (other than  $n$ ) are ranges.

Location of the nest	$T_a$ and $T_s$ (C)						Changes in $T_n$ over 24 hr (C)					
	$n$	Ambient	Canopy above nest	Rim of nest	Dorsum of nestlings	$n$	Change in $T_n$ (range)	Extreme $T_n$		$T_a - T_n$ difference		
								Low	High	Minimal	Maximal	
Gully	4	14-27	10-34	10-29	17-40	2	9.2-12.0	6.0-8.5	17.7-18.0	0.2-0.3	6.6-7.8	
Terrace	7	13-28	5-41	6-46	16-47	9	3.0-20.4	10.5-14.4	15.1-34.8	0.1-0.5	2.0-12.1	

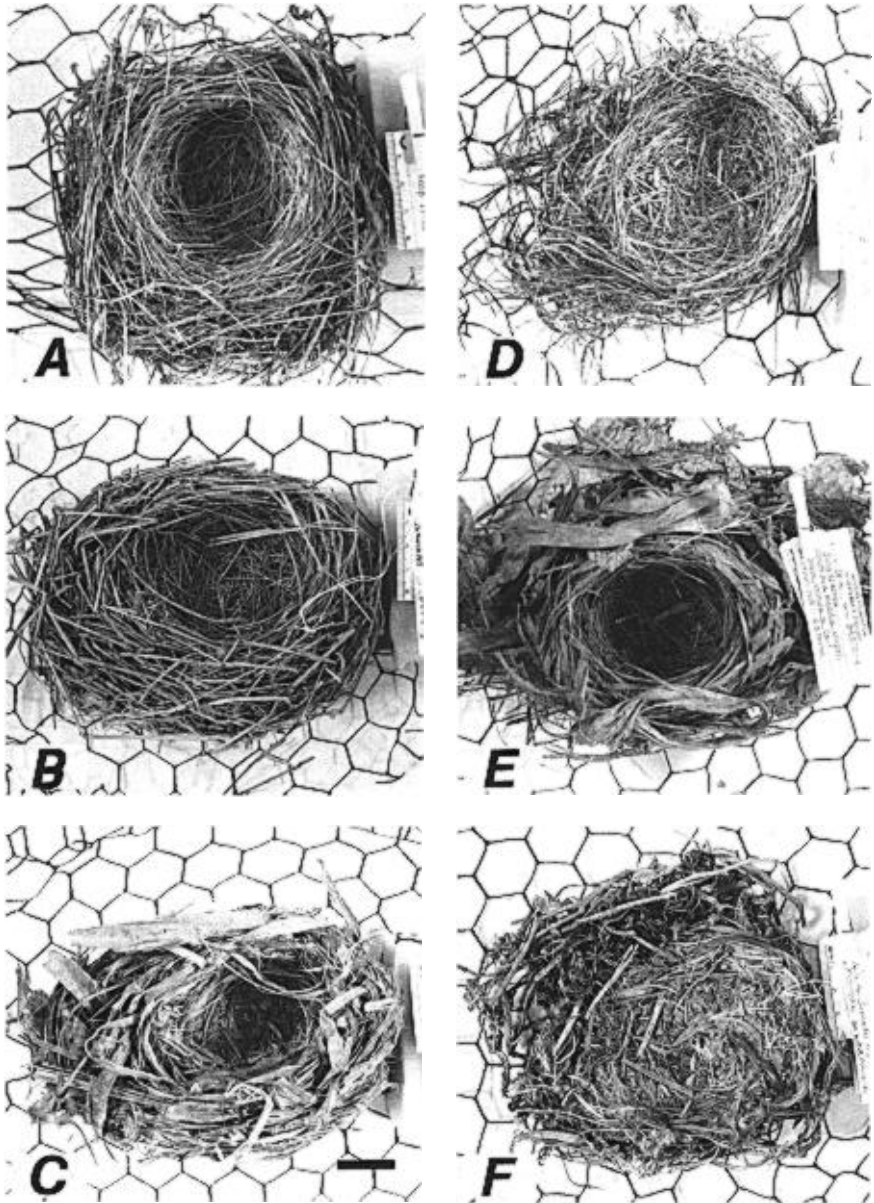


FIGURE 1. Nests of various races of Song Sparrows differ in size and composition. Nests A-C consist of weedstems of increasing size: fine stems in *M. m. micronyx* (A), medium stems in *clementae* (B), and heavy stems in *saltonis* (C). Nest D (*merrilli*) lacks an outer frame; *cooperi* (E), in contrast, has a substantial frame containing leaves and strips of vine and bark. Nest F (*coronatorum*) is a crude affair consisting largely of seaweed, feathers, and soil. All nests are approximately the size indicated by the 2-cm bar in C.



*Twenty-four-hour profiles of  $T_n$  and  $T_a$ .*—The temperature within empty nests varied as little as 3 and as much as 20 C during 24-h periods (Table 2), being coolest at night. Correlations between  $T_n$  and  $T_a$  were especially strong for nests in *Lupinus* and *Baccharis* ( $r^2 = 0.87-0.97$ ) both of which are tall and open below the canopy. Much lower correlations occurred in more prostrate shrubs such as *Haplopappus* and mint, or in grass ( $r^2 = 0.54-0.81$ ). Although maximum differences between the nest and its surroundings over 24-h periods were similar in both locations (6.9 and 7.2 C), variations in  $T_n$  were more pronounced on the terrace than in the gullies (Table 2).

*Airspeed in and around the nest.*—Shrubs around the nest reduced airspeed  $73\% \pm 4\%$  ( $n = 23$  nests). The nest bush reduced it another 20% ( $93\% \pm 1\%$  below ambient airspeed;  $n = 27$ ); and the nest itself another 5% ( $98\% \pm 0.4\%$  below ambient airspeed;  $n = 24$ ). Consequently, air currents in the nest cavity were negligible.

#### *Characteristics of the Nest*

*Composition of the nest.*—Nests from SMI (Fig. 1A) were compact open bowls consisting of twigs, herbs, parts of shrubs, weedstems, grass stems and often dry leaves. Some nest cups were unlined, whereas others were lined with fine grasses. No differences were evident between nests from terrace and gully sites. The principal items of which eight dismantled nests consisted were grass leaves and stems (7 or 8 nests); leaves of *Achillea millefolium* (6 nests), *Calystegia macrostegia* (2 nests), *Cirsium occidentale* (2 nests) or *Agoseris* (1 nest), and *Coreopsis* leaves, stems and peduncles (1 nest).

Museum nests of other races of Song Sparrows often differed from one another and from SMI nests (Fig. 1). Some consisted entirely of weed and grass stems (*M. m. melodia* and *rufina*). Some contained strips of bark (*M. m. cooperi* and *fisherella*) or leaves (*M. m. cooperi*, *saltonis* and *morphna*). Those from Baja California (*M. m. coronatorium*) were constructed of ice plant, seaweed and feathers (Fig. 1F). Some had thick linings of animal hair (*M. m. cooperi* and *morphna*). Museum slips indicate that tules, ferns and rushes are also found in some nests, and that linings may consist of plant down (*M. m. heermanni*).

*Nest size, insulation and porosity.*—Among the seven races of Song Sparrows for which we had adequate samples for statistical analysis, those of the nominate race, *M. m. melodia*, tended to be the smallest; those of *M. m. morphna*, *cleonensis* and *micronyx* the largest (Table 3).

The floor of nests of all seven races had similar degrees of heat flux ( $2.9-4.0 \text{ W} \cdot \text{m}^{-2} \cdot \text{C}^{-1}$ ). But the nests separated into three groups in terms of their overall insulation ( $h_{w+t}$ ) and the insulation value of their wall ( $h_w$ ; Table 4): those of *M. m. micronyx*, *cleonensis* and *melodia* had the least insulation, those of *M. m. morphna* the most, and those of the other three races moderate amounts.

With the exception of *M. m. melodia*, the floor of the nest was so tightly constructed that almost no light could penetrate it (Table 4). The walls

TABLE 3. Size and dimensions of nests from 17 subspecies of Song Sparrows.

Subspecies <sup>1</sup>	Latitudes where nests were collected (°N)	# nests	Nest <sup>2,3</sup>				Nest cup <sup>2,3</sup>	
			Mass (g)	Height (cm)	Diameter (cm)	X-sectional area (cm <sup>2</sup> )	Volume (ml)	
<i>M. m. melodia</i>	41-48	4	9 ± 6 a	4.8 ± 1.1 a	6.0 ± 0.5 a	32 ± 6 a	56 ± 21 a	
<i>M. m. saltonis</i>	32-34	2-4	41	7.8 ± 3.3 bc	6.0 ± 1.5 a	37 ± 34 ab	62 ± 15 ab	
<i>M. m. heermanni</i>	35-37	5	15 ± 2 a	5.8 ± 1.3 ab	6.3 ± 0.6 a	35 ± 3 ab	65 ± 14 ab	
<i>M. m. morphna</i>	45-49	10	24 ± 6 a	7.4 ± 0.7 bc	7.1 ± 0.5 b	45 ± 7 b	96 ± 12 b	
<i>M. m. cooperi</i>	25-34	16	21 ± 0.1 a	6.7 ± 0.6 bc	6.2 ± 0.3 a	34 ± 3 a	77 ± 9 ab	
<i>M. m. cleonensis</i>	40-41	3-4	26	7.7 ± 1.8 bc	6.6 ± 0.7 ab	37 ± 11 ab	89 ± 47 ab	
<i>M. m. microryx</i>	34	37	33 ± 4 b	8.0 ± 0.4 c	6.4 ± 0.2 ab	29 ± 2 a	88 ± 7 ab	
Others	32-61	1-3 per race	8-43	4.8-9.2	5.2-8.4	22-62	46-100	

<sup>1</sup> Subspecies to which "others" refers: *montana*, [*rufina*], [*clementae*], [*juddi*, *merrilli*, [*sanaka*], *euphonis*, *fisherella*, [*coronatorum*], and *fallax*. Brackets = insular races. Although populations of *M. m. juddi* occur on the mainland and on islands, our nests are from mainland sites.

<sup>2</sup> No significant subspecific differences were found in the diameter of the nest (range for the 7 named subspecies = 11.3-13.6 cm; for "other" subspecies = 10.3-15.0 cm); minimal thickness of the nest wall (1.3-2.3 cm; 0.9-2.6 cm); maximal thickness of the nest wall (3.4-4.4 cm; 2.6-5.8 cm); average thickness of the nest wall (2.4-3.1 cm; 1.8-3.8 cm); or depth of the nest cavity (2.9-4.2 cm; 2.6-4.4 cm).

<sup>3</sup> For the 7 named subspecies in each column of the table, values followed by different letters are significantly different at the 0.05 or a higher level; values followed by the same letter are not significantly different ( $P > 0.05$ ; ANOVA followed by Student-Newman-Keuls tests).

TABLE 4. Insulation and porosity of nests from 17 subspecies of Song Sparrows.

Subspecies	# nests	Thermal conductance <sup>2,4</sup> (W·m <sup>-2</sup> ·C <sup>-1</sup> )		Porosity of nest <sup>3,4</sup>	
		Wall of nest (h <sub>w</sub> )	Entire nest (h <sub>w+t</sub> )	Floor	Wall
<i>M. m. melodia</i>	4	6.7 ± 3.4 a	5.3 ± 1.3 a	0.143 a	1.39 a
<i>M. m. saltonis</i>	4	4.5 ± 0.6 ab	4.1 ± 1.1 ab	0.009 b	0.01 c
<i>M. m. heermanni</i>	5	3.8 ± 0.8 ab	3.6 ± 1.0 ab	0.002 b	0.40 b
<i>M. m. morphna</i>	10	3.4 ± 0.5 b	3.2 ± 0.4 b	0.001 b	0.05 c
<i>M. m. cooperi</i>	16	4.1 ± 0.6 ab	3.7 ± 0.3 ab	0.004 b	0.17 c
<i>M. m. cleonensis</i>	4	6.5 ± 1.5 a	4.8 ± 1.0 a	0.021 b	0.83 b
<i>M. m. micronyx</i>	36-37	6.6 ± 0.7 a	4.8 ± 0.4 a	0.005 b	0.03 c
Others <sup>1</sup>	1-3 per race	3.5-8.0	3.1-6.3	0.000-0.327	0.000-2.09

<sup>1</sup> See Table 3 for the 10 subspecies composing "others."

<sup>2</sup> No significant differences exist among the subspecies with regard to the thermal conductance of the floor of the nest (h<sub>f</sub>): values for the 7 named races = 2.9 to 4.0 W·m<sup>-2</sup>·C<sup>-1</sup>; for "other" races = 1.9 to 6.6 W·m<sup>-2</sup>·C<sup>-1</sup>.

<sup>3</sup> % light penetration = [(lux when nest present)/(lux when nest absent)] × 100.

<sup>4</sup> See footnote 3 in Table 3.

of the nest were more loosely woven, however, to the greatest extent in *M. m. melodia* (1% light penetration) and the least extent in *M. m. saltonis*, *morphna*, *cooperi* and *micronyx* (0.01-0.17% light penetration).

On SMI, there were no significant differences in size, insulation or porosity between nests from the terrace and gullies; or between nests that were depredated, abandoned and from which broods fledged successfully.

#### DISCUSSION

*Ways in which nest and nest site affect fitness.*—At least four factors potentially reduce the nesting success of Song Sparrows on SMI. These include (1) strong northwesterly winds, which batter the island constantly and produce windchills as low as -14 C on cool days during the nesting season (Kern, pers. obs.); (2) SMI foxes, which destroyed 23% of the nestlings during 1985 and 1986 (Sogge and van Riper 1988); (3) cool, overcast conditions that prevail during the nesting period with T<sub>a</sub>s as low as 4 C; and (4) high levels of insolation on days which are clear and sunny.

Vegetation prevents high winds from reaching the nest, as does the nest's leeward position in the nest bush (not previously described in Song Sparrows). On the exposed terrace (but not in the gullies) vegetation on the windward side of the nest was significantly taller than that on the other side of the nest. On SMI, the nests themselves are also significantly heavier than those of most other races of Song Sparrows (Table 3). This difference may be an adaptive response to the windy situation in which the birds find themselves, because nest mass and the ability of the nest wall to block out light are significantly related ( $r = 0.56$ ,  $P < 0.001$ ). In the two years of this study, only one of 103 nests was destroyed by wind.

Nests were deep within the nest plant and well concealed by a more or less closed canopy from aerial (as well as ground) predators, of which the most important is the SMI gray fox (*Urocyon littoralis*; Sogge and van Riper 1988). The nest bush and the nest within it were frequently somewhat higher than the surrounding vegetation. This may improve the birds' ability to see approaching predators, particularly those coming from downwind of the nest, although it does increase the exposure of the nest to wind. The fact that SMI Song Sparrows build their nests in many species of plants (Table 1) may also deter predation. In 1985, foxes took Song Sparrow chicks from nests in one mint, five goldenbushes, three lupines and one coyote brush (Sogge and van Riper 1988). This is the frequency with which the same shrubs were used as nest sites in our study area that year. If foxes cannot rely on a specific species of plant in which to find Song Sparrow nests, their impact on the species' reproductive success may be reduced.

Many birds use vegetation to minimize thermal extremes at the nest (Collias and Collias 1984, Kern 1984). White-crowned Sparrows (*Zonotrichia leucophrys*) and Warbling Vireos (*Vireo gilvus*), for example, use openings in the canopy to this end (Walsberg 1981, Walsberg and King 1978). On SMI, however, Song Sparrows did not position their nests so that openings in the canopy were restricted to one specific quadrant of the sky, and on clear days as much as 73% of the nest cup was in the sun near midday, sometimes elevating  $T_s$ s of the nest and chicks above 40 C (Table 2). Such conditions, although often transient, may explain why the percentage of nest failures due to addled eggs (38% of hatching failure; Sogge and van Riper 1988) is so much higher on SMI than elsewhere (Dixon 1978, Johnston 1956, Means and Goertz 1983, Nice 1937, Ricklefs 1969). This is a sedentary insular population of Song Sparrows, however, and small population size with inbreeding depression could account for such high hatching failure, particularly since one would expect females to shade their eggs on sunny days and thereby prevent the clutch from overheating. We do not think this is the case because the population of Song Sparrows on SMI in 1986 was estimated (from survey data) at more than 2000 birds (Sogge, unpubl. obs.). In 1985 and 1986, spring densities of adults in our study area were 7.1 and 10/ha, respectively (Sogge and van Riper 1988). Furthermore, nest attentiveness did not increase near midday, but averaged 62% of each hour at all times of day, during 206 h of observation at five SMI nests (Sogge, pers. obs.). On SMI, attentive periods and the overall percentage of time that the female spent on the nest were shorter than those reported for populations of Song Sparrows in Ohio (Nice 1943) and on Mandarte Island (Smith et al. 1982) where hatching success is higher.

In contrast to effects on the clutch, solar heat loads did not apparently increase nestling mortality beyond normal levels, even though chicks were not brooded much after 7 d of age (Sogge and van Riper 1988). Fledging success on SMI (67%) was similar to that in Song Sparrow populations elsewhere (Nice 1937, Smith et al. 1982).

Nestlings and incubating or brooding adults probably do not experience the low  $T_a$ s and windchills typical of the island's terraces thanks to the nest's sheltered location. During 24-h periods of continuous monitoring,  $T_n$  at 11 nest sites averaged a mild 15.8 C and did not go below 6–14 C at night (Table 2), even though variations between  $T_n$  and  $T_a$  were tightly correlated, particularly in tall shrubs. Such mild  $T_n$ s coupled with the low insulation value of SMI nests (Table 4) and the modest estimated energetic cost of incubation (see below), suggest that  $T_a$  does not affect breeding success greatly.

*Energetic cost of incubation.*—Kern and van Riper (1984) developed a way of estimating the energetic cost of incubation ( $\dot{H}_p$  in W) from the nest's  $h_{w+f}$  with the formula:

$$\dot{H}_p = (h_{w+f})(A_{bp})(T_n - T_a)(t_n) + (\dot{H}_R)(t_r).$$

We used this approach to estimate cost for SMI Song Sparrows. Here,  $h_{w+f} = 4.8 \text{ W} \cdot \text{m}^{-2} \cdot \text{C}^{-1}$  (Table 4);  $A_{bp}$  = the area of the Song Sparrow's brood patch, which is about 12% of its surface area (Walsberg and King 1978) or 9.3 cm<sup>2</sup>;  $T_n$  = nest temperature during incubation or about 33.6 C (Drent 1975);  $T_a = 15.8 \text{ C}$ ;  $t_n$  = the amount of time the bird is on the nest daily or 78.9% (Sogge and van Riper 1988);  $\dot{H}_R$  = the energy required for a bird to rewarm a clutch of eggs after being absent from the nest, or 3.3 J · g<sup>-1</sup> · C<sup>-1</sup> per egg (Ricklefs 1974); and  $t_r$  = the number of times the bird leaves the nest each day, or 60 (Sogge and van Riper 1988). For the 2- and 3-egg clutches of Song Sparrows on SMI,  $\dot{H}_p$  is 0.14 and 0.18 W, respectively. This represents only 41–53% of the Song Sparrow's resting metabolic rate based on the equation of Aschoff and Pohl (1970).

*Latitudinal variations in Song Sparrow nests.*—Surprisingly few differences in Song Sparrow nests can be attributed to latitudinal differences in the breeding areas of the subspecies, assuming our museum nests accurately represent nest structure in various subspecific groups. Among five insular races, whose nests ( $n = 44$ ) were collected between 32 and 61°N latitude, the only significant latitudinal trends are both very weak ( $r^2 = 0.11$ –0.12) and in unexpected directions: (1) nest mass and the thickness of the nest floor were both inversely related to latitude, whereas (2)  $h_f$  was directly related to latitude. Among 12 mainland races, whose nests ( $n = 49$ –55) came from 25–54°N latitude, the only significant correlations were for (1) the diameter and cross-sectional area of the nest cup, both of which were larger at higher latitudes ( $r^2 = 0.35$  and 0.29), and (2) the porosity of the nest wall, which increased at higher latitudes ( $r^2 = 0.09$ ). These findings contrast with those reported for some other passerines whose nests tend to be larger and more highly insulated in more northerly regions (Collias and Collias 1984; Palmgren and Palmgren 1939; Schaeffer 1976, 1980).

As (1) only six of 20 measured characteristics of Song Sparrow nests showed significant changes with latitude, (2) significant latitudinal trends were often in unexpected directions and weak, (3) significant changes in nest insulation with latitude were generally absent, and (4) insulation in

these nests was highly variable, we tentatively suggest that the nest site is more important than the nest for protecting eggs and chicks and especially for maintaining a microclimate suitable for embryonic and nestling development.

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