



## **The Implications of Increased Body Size in the Song Sparrows of the California Islands**

Authors: Danner, Raymond M., Greenberg, Russell, and Sillett, T. Scott

Source: Monographs of the Western North American Naturalist, 7(1) : 348-356

Published By: Monte L. Bean Life Science Museum, Brigham Young University

URL: <https://doi.org/10.3398/042.007.0126>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## THE IMPLICATIONS OF INCREASED BODY SIZE IN THE SONG SPARROWS OF THE CALIFORNIA ISLANDS

Raymond M. Danner<sup>1,2</sup>, Russell Greenberg<sup>1,3</sup>, and T. Scott Sillett<sup>1</sup>

**ABSTRACT.**—We investigated morphological divergence between mainland and California Island populations of the Song Sparrow (*Melospiza melodia*). Body size in small terrestrial vertebrates has been hypothesized to be larger in island forms than in their mainland relatives. Previously, we established that although bill size in island populations was similar to that in mainland populations with similar climate, bill-size dimorphism averaged much greater on the islands. In this paper, we compare various measures of structural body size and body mass between the California Islands and the mainland. We found that average body mass is over 10% higher in island Song Sparrows than in comparable mainland populations. However, a lack of commensurate structural body size suggests that body condition might be better in island Song Sparrows. This higher size-corrected mass may be explained by the dominance hypothesis, greater food availability and/or reduced competition, or adaptive mass regulation in the face of reduced predation pressure on adults. Both greater sexual bill dimorphism and greater body mass suggest reduced competition for food for the island Song Sparrow: a possibility that invites further investigation.

**RESUMEN.**—Investigamos las divergencias morfológicas entre las poblaciones de la península y de las Islas de California del gorrión (*Melospiza melodia*). Se tenía la hipótesis de que el tamaño corporal de vertebrados pequeños terrestres era más grande en los individuos de las islas que el de sus parientes en la península. Con anterioridad, habíamos establecido que mientras el tamaño del pico era similar a los de poblaciones en la península con climas similares, el dimorfismo del tamaño del pico era mayor en las islas. En este informe, comparamos varias medidas del tamaño de la estructura y la masa corporal entre las Islas de California y la península. Encontramos que el promedio de masa corporal es más de un 10% superior en el gorrión de las islas en comparación con las poblaciones de la península. Sin embargo, una falta de proporcionalidad en la estructura del tamaño corporal sugiere que la condición corporal podría ser mejor en los gorrones de la isla. Este tamaño mayor (corregido por la talla) puede explicarse a través de la hipótesis de dominancia, mayor disponibilidad de comida y/o menor competencia, o regulación corporal adaptable ante una presión de depredación menor en los individuos adultos. Ambos factores, mayor dimorfismo sexual de pico y mayor masa corporal sugiere una menor competencia por la comida entre los gorrones de la isla, posibilidad que invita a más investigaciones.

Since Darwin (1859) and Wallace (1869), islands have been viewed as laboratories for studying ecological and evolutionary processes (Lack 1945, Grant 1965, MacArthur and Wilson 1967, Losos 1990). Islands are small, isolated, and relatively simple systems for studying the interaction of history, natural selection, and stochastic processes for shaping adaptation in single populations, development of faunal assemblages, and evolution of adaptive radiations. Evolutionary biologists have often focused on the factors that favor morphological divergence of island forms from mainland forms, either in size or shape (Grant 1965, Lomolino 1985, Maiorana 1990, Clegg and Owens 2002).

Most studies of morphological divergence and diversification on islands have focused on potential ecological drivers, particularly predation, variation in habitat and food resources,

and the balance between intra- and interspecific competition. These studies often focus on body size—and in birds, bill size. Among birds, decreased interspecific competition for food could select for increased body and bill size because larger size in these features is thought to be favored for a dietary generalist (Scott et al. 2003). Similarly, increased intra-specific competition due to higher density may also select for larger body and bill size (Clegg and Owens 2002). Decreased interspecific competition could select for increased diet breadth within a species, which could further select for distinct ecological morphs (Smith 1990) or divergence between the sexes (Selander 1966). Reduced need to disperse large distances and reduced risk of predation could allow body size to increase. The possible role of climate in shaping divergent adaptive

<sup>1</sup>Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20008.

<sup>2</sup>E-mail: danner.ray@gmail.com

<sup>3</sup>Deceased.

morphology has been discussed in terms of optimization of body size for reasons of energetic or temperature regulation once the constraints of competition are relaxed (Maiorana 1990, Scott et al. 2003, Greenberg et al. 2012, Greenberg and Danner 2013; but see Meiri et al. 2005, Raia et al. 2010). In North America, birds of the California Islands have been studied from a biogeographical perspective (e.g., as a test for island biogeography equilibrium theory; Jones and Diamond 1976), but very little has been done on the factors that promote morphological divergence (but see Johnson 1972, Power 1983).

The Song Sparrows (*Melospiza melodia*) of the California Islands comprise an excellent system for investigating intraspecific divergence. This sparrow is a widely distributed and highly polytypic species of North American songbird that breeds or has bred on San Miguel, Santa Rosa, Santa Cruz, Anacapa (recent colonist), Santa Barbara (extinct), San Clemente (extinct), and at least 2 of the 4 Coronados (extinct) Islands. These populations showed sufficient variation in plumage, size, and shape to justify the recognition of up to 4 distinct subspecies, 2 of which are extinct. However, this variation does not rise to the level of diagnosable specific units, and a recent treatment has lumped them into a single subspecies (*M. m. graminea*; Patten and Pruett 2009). Nevertheless, California Island Song Sparrows show consistent plumage differences (Patten and Pruett 2009) and a greater level of mtDNA divergence from mainland song sparrows than is found among most populations of this widely distributed species (Wilson 2008).

The purpose of this paper is to examine divergence in body size in the Song Sparrow and relate this to already described patterns in bill morphology (Greenberg and Danner 2012, 2013). In so doing, we hope to further develop hypotheses for the ecological forces that shape island adaptations in this geographically variable species. We investigate size-corrected differences in body mass, which has not been studied in island song birds, and differences in structural size. Specifically, we aim to determine if body-size divergence is a result of plasticity or selection and ultimately if this divergence is a response to resource availability, competition, or predation. Although this observational study cannot establish cause and effect, we interpret divergence mainly in

size-corrected mass as support for plasticity because the sizes of fat stores and muscle are known to change within individual birds (including in *Melospiza* sparrows) in response to climate (Danner 2012, Danner et al. 2013). In contrast, divergence mainly in structural sizes may support selection or plasticity.

## METHODS

### Body Mass

We obtained weight data for California Song Sparrows from banding stations (particularly those participating in the Monitoring Avian Productivity and Survivorship, or MAPS, program; DeSante 1992), the Museum of Vertebrate Zoology, the San Diego Museum of Natural History, and the San Bernardino County Museum, with smaller amounts of data from other museums. We amassed a sample size of 16,700 weights for Song Sparrows taken primarily during the breeding season, and the sheer size of the sample should dampen sampling variation. Of the 16,700 total weights, 6264 had data on sex and were in the age categories appropriate for analysis. Age classification follows the MAPS protocol (DeSante 1992). We collapsed the categories for hatching-year bird (excluding fledglings and juveniles) and after-hatching-year bird to “first year” and second-year and adult to “adult.” We analyzed 4087 weights from Northern California, 2067 from Southern California, and 141 from islands, totaling 6295. Island weights were from Santa Cruz (82), Santa Rosa (24), San Miguel (34), and San Clemente (1) islands.

### Specimen Measurement

Bill, tarsus, and wing measurements were taken from 1488 museum study skins by Russell Greenberg (data archived at <http://national.zoo.si.edu/scbi/migratorybirds/research/data/>). Bill length (BL), depth (BD), and width (BW) were measured at the anterior edge of the nares with digital calipers (0.01-mm precision). Tarsometatarsus length was measured from the joint of tibiotarsus and tarsometatarsus to the last complete scute before the articulation of the hallux. Collection locality, date, sex, weight, and age were recorded from the specimen tag. Bill measurements were converted to an estimate of surface area of the distal portion of the bill using the formula for the lateral

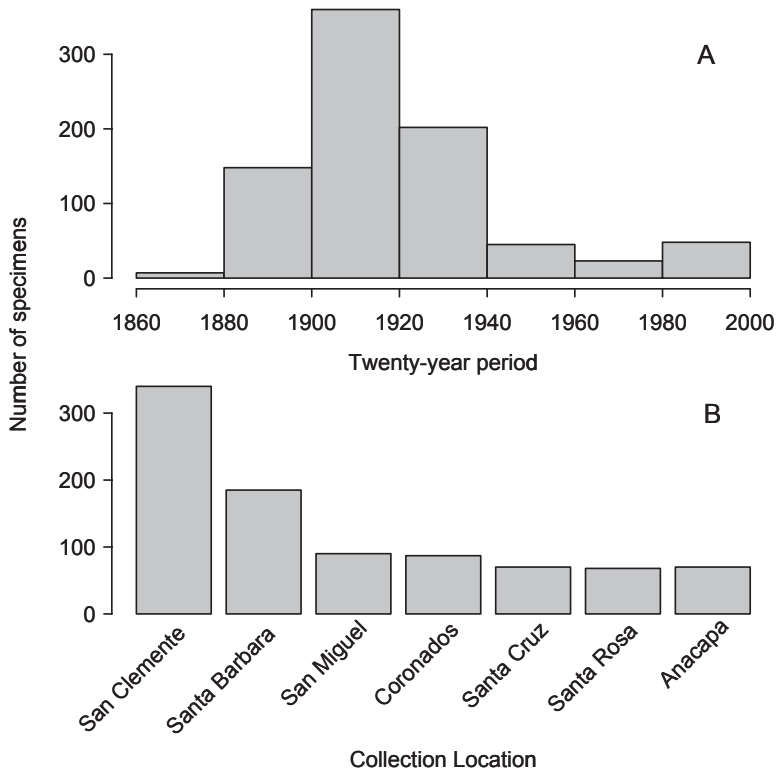


Fig. 1. Frequency of Song Sparrow specimens collected: **A**, over time; **B**, by island. Data courtesy of Paul Collins.

surface area of a nearly circular elliptical cone:  $[(BW + BD)/4] * BL * \pi$ . A principal component analysis (PCA) was conducted on bill size, tarsus length, and wing chord; and the first axis was used as an indicator of body size (the factor loadings were 0.78 for both tarsus length and wing chord; the first factor explained 63.5% of the total variance). Specimens were obtained from U.S. museum collections from 3 regions: (1) the California Islands (Channel and Coronado Islands,  $n = 462$ ); (2) the Pacific coast to the outer and inner Coast Ranges and the Central Valley of Northern California ( $35.1^{\circ}$ – $38.8^{\circ}$  N,  $n = 481$ ); and (3) the Pacific coast, Coast Range, and interior valleys and deserts of Southern California ( $32^{\circ}$ – $35^{\circ}$  N,  $n = 480$ ). Available specimens tended to be old (Fig. 1a), averaging 90 years since collection. The specimens were not evenly distributed across the islands that have or had breeding populations (Fig. 1b). In fact, no museum specimen exists for Anacapa Island, which is thought to have been colonized in the past decade.

Collection date was first assigned a number between 1 and 365, with year beginning on 16 August—the approximate end of the breeding season. Date was transformed twice. First we created the variable  $dt$  in radians using the formula

$$dt = 2\pi \frac{\text{date}}{365}$$

We then transformed  $dt$  as  $\cos(dt)$  and  $\sin(dt)$ . The 2 terms  $\cos(dt)$  and  $\sin(dt)$  together comprise a single oscillating date effect that forces the predicted value for bill size to be equivalent at date = 0 and date = 365 (Zar 1999). Because  $\sin(dt)$  accounted for substantial variation in nearly all models but  $\cos(dt)$  explained almost no variation and was not significant in any model, we dropped the  $\cos(dt)$  term from the analyses to economize on parameters used to describe date.

#### Analyses

We considered the following morphological variables in our analyses: body mass, body

mass dimorphism, wing chord, wing chord dimorphism, tarsus length, and tarsus length dimorphism. First, we graphically present the mean and 95% confidence intervals for these variables for 4 data subsets: (1) the complete sample (California 32°–36° N, excluding the Sonoran Desert), (2) Southern California (32°–34° N), (3) coastal Southern California (<5 km from coast), and (4) the California Islands. Percent sexual size dimorphism was quantified by  $[(\text{male size}/\text{female size}) - 1] * 100$ , and the confidence interval was derived based on Fieller's Theorem (Fieller 1954). Second, we used model selection based on the corrected Akaike information criteria (AIC<sub>c</sub>, Burnham and Anderson 2002) to determine if mainland or island origin was important for explaining either morphological variation or sexual dimorphism. For each morphological variable, we compared 4 explanatory models: (1) a null model ("Null," sex + sin[dt] + size PCA), (2) a simple geographic model ("Geography," sex + sin[dt] + size PCA + latitude + distance from coast + [distance from coast]<sup>2</sup>), (3) the geographic model with island/mainland origin ("Island"), and (4) the geographic model with an interaction between island/mainland origin and sex ("Island \* Sex"), which could be considered the full or saturated model. All models were built in the General Linear Models module of Statistica (Version 10; Statsoft, Inc. 2011) using both categorical (island/mainland origin, sex) and continuous variables (size PCA, sin[dt], latitude, distance). We present regression statistics from the top model in which they were included. Diagnostics based on residual plots were conducted on the top models to ensure that they conformed to the assumptions of normally distributed errors, linearity, and homoscedasticity.

Body mass difference could result from structural (skeletal) features or the condition of the bird (muscle mass and fat). To determine the relative contribution of these 2 sources of variation, we used data from 204 museum skins for which we had measurements and mass data and then modeled body mass using the 4 models described above.

## RESULTS

### Body Mass

California Island Song Sparrows had a substantially greater mass (Fig. 2a), but not dimor-

phism in mass, compared to mainland birds. The geographic model with island/mainland origin (Island model) had a high model weight (>0.99) when compared to the Geography model and the Null model (Table 1). Variation in mean mass was found among island samples, but sparrows from the 3 islands for which we had mass data were heavier than mainland birds (19.25 g, CI 18.91–19.59), ranging from 20.66 g (21.61–22.80) for Santa Cruz and 21.76 g (21.26–22.25) for San Miguel to 22.08 g (21.61–22.80) for Santa Rosa. Mainland and Southern California samples showed 6.0% dimorphism, whereas the south coastal mainland showed 3.5% and the islands only 3.2% dimorphism. The Island model, compared to the Island \* Sex and Null models, garnered nearly 100% of the total model weight (Table 1).

### Body Mass versus Structural Size

Our sample of museum skins with weight data showed the same larger average body mass as the sample of birds from banding stations (Fig. 3a). Though the PCA size factor was larger on the islands than on the mainland (Fig. 3b), the average residual of the PCA/mass regression (Fig. 3c) indicates that greater size-corrected body mass, an index of body condition, is the biggest difference between the island and mainland. This result is supported by the evaluation of our linear models. We modeled body mass of museum skins using the first principal component of bill size, tarsus length, and wing chord as an independent variable to control for structural size. Body mass is generally higher for a similar PCA score on the islands ( $n = 60$ ) versus the mainland ( $n = 154$ ). The Island model received over 99% of the model support and was  $2.7 * 10^4$  more likely (based on the evidence ratio of model weights) than the Geography model with the size PCA factor alone (Table 1). The Island \* Sex interaction model received no support, indicating that the increase in size-corrected body mass on the islands was not related to sex. The standardized partial regression coefficient for island/mainland origin (0.513) was over twice as large as the next largest (Table 2), further indicating that island/mainland origin is an important variable in predicting body mass.

### Wing Chord and Tarsus Length

Variation in wing chord and tarsus length showed no clear patterns with geography

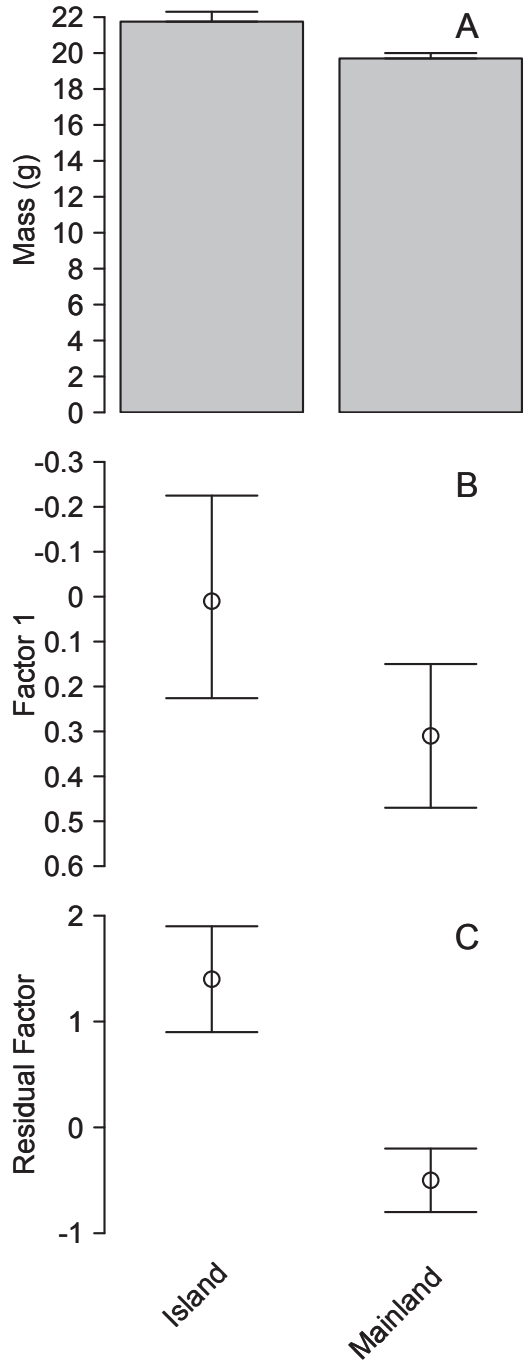
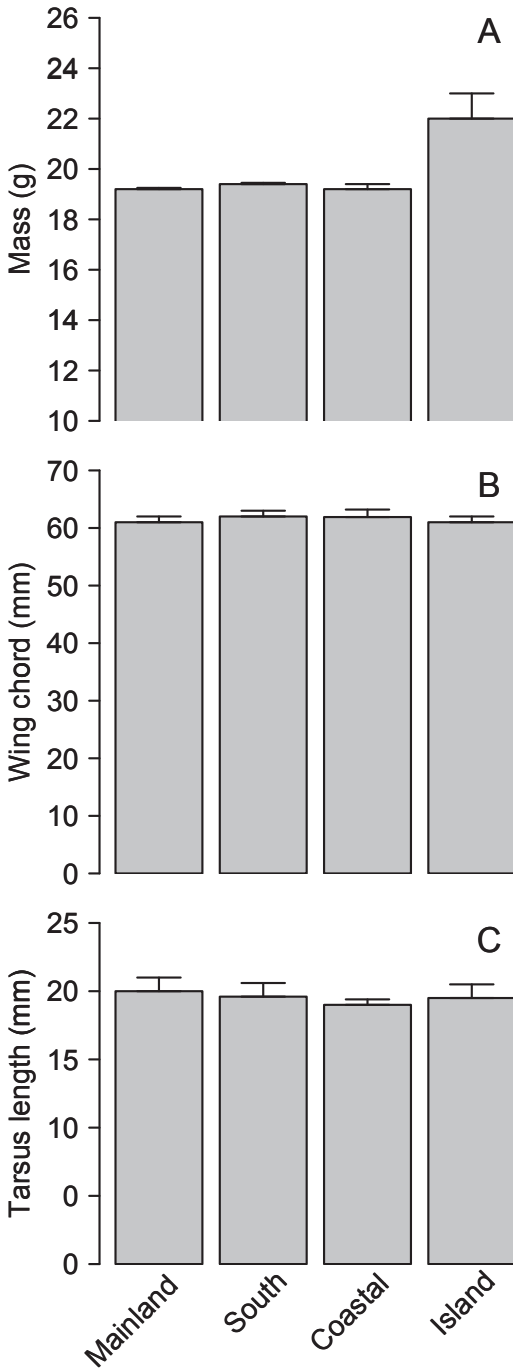


Fig. 2. Morphological measurements of Song Sparrows from the California Islands and selected mainland regions (south and central California, Southern California, coastal Southern California): A, body mass; B, wing chord; C, tarsus length.

Fig. 3. Island versus mainland differences in Song Sparrows: A, mass; B, structural size (PCA Factor 1); C, residual mass.



TABLE 1. Ranked models that describe geographic variation in morphological features. Model name (variables described in Methods), log of the maximum likelihood (logL), number of parameters (k),  $AIC_c$ ,  $\Delta AIC_c$ , and model weights ( $w_i$ ) are shown for the top 3 models.

Morphological feature	Model	logL	k	$AIC_c$	$\Delta AIC_c$	$w_i$
Body mass	Island	-10305.49	8	20627.01	0.00	0.99
	Geography	-10319.63	7	20653.28	26.27	$1.97 * 10^{-6}$
	Null	-10336.40	3	20678.81	51.80	$5.64 * 10^{-12}$
Body mass dimorphism	Island	-10283.77	8	20583.56	0.00	1.00
	Island * Sex	-10305.49	7	20625.00	41.44	$1.00 * 10^{-9}$
	Null	-10336.40	3	20678.81	95.25	$2.07 * 10^{-21}$
Size-corrected body mass (museum skins)	Island	-52.68	8	122.11	0.00	1.00
	Geography	-63.99	7	142.54	20.43	$3.66 * 10^{-5}$
	Null	-90.34	4	188.89	66.77	$3.16 * 10^{-15}$
Wing chord	Geography	-1464.82	7	2943.72	0.00	0.74
	Island	-1464.84	8	2945.78	2.06	0.26
	Null	-1562.75	3	3131.51	187.79	$1.23 * 10^{-41}$
Wing chord dimorphism	Geography	-1464.82	8	2945.75	0.00	0.74
	Island	-1464.84	9	2947.81	2.06	0.26
	Null	-1562.75	3	3131.51	185.76	$3.39 * 10^{-41}$
Tarsus	Geography	349.16	7	-684.23	0.00	0.55
	Island	349.97	8	-683.84	0.39	0.45
	Null	320.21	3	-634.40	49.83	$8.30 * 10^{-12}$
Tarsus dimorphism	Island	349.97	8	-683.84	0.00	0.52
	Island * Sex	350.90	9	-683.68	0.16	0.48
	Null	320.21	3	-634.40	49.44	$9.57 * 10^{-12}$

TABLE 2. Regression statistics for models describing body mass.

	Variance inflation factor	$\beta$	Partial $r$	$t$	$P$
$\sin(dt)$	1.14	0.133	0.166	2.32	0.02
Distance	3.97	-0.116	-0.078	-1.09	0.27
Distance <sup>2</sup>	2.40	0.070	0.061	0.84	0.40
Latitude	2.83	0.065	0.052	0.72	0.47
PCA Factor 1	1.53	-0.256	-0.269	-3.86	0.0002
Sex	1.55	0.258	0.269	3.86	0.0002
Island	3.63	0.513	0.342	5.03	0.000001
Island * Sex	1.26	-0.067	-0.080	-1.11	0.27

(Fig. 2b, 2c) or sexual dimorphism (Fig. 4). The Geography model of wing chord garnered 74% of the model weight and was 4 times more likely than the model including island/mainland origin (Table 1). The Geography model of tarsus length had 52% of the model weight and was essentially no more likely than the same model with island/mainland origin added (Table 1). Coastal and island birds did have greater sexual dimorphism in tarsus length than the mainland or southern California samples (Fig. 4).

## DISCUSSION

Size-related morphological variation of California Song Sparrows can be grouped into 3 general patterns: (1) a sharp contrast between island and all mainland populations;

(2) differences between mainland coast and island populations versus total mainland populations; and (3) no consistent size variation along the mainland-coast-island gradient. The first pattern likely reflects island processes and includes body mass. Body mass data presented by Patten and Pruett (2009) also suggest that California Island Song Sparrows are heavier than their mainland equivalents. Traits showing the second pattern probably reflect the shared climatic conditions of coastal and island sites, and these include body mass and tarsus dimorphism. Traits showing no obvious relationships between geographic locations (the third pattern) include wing chord and wing-chord dimorphism. Thus, the complete analysis provides some support for hypotheses regarding morphological divergence in body size of the island form.

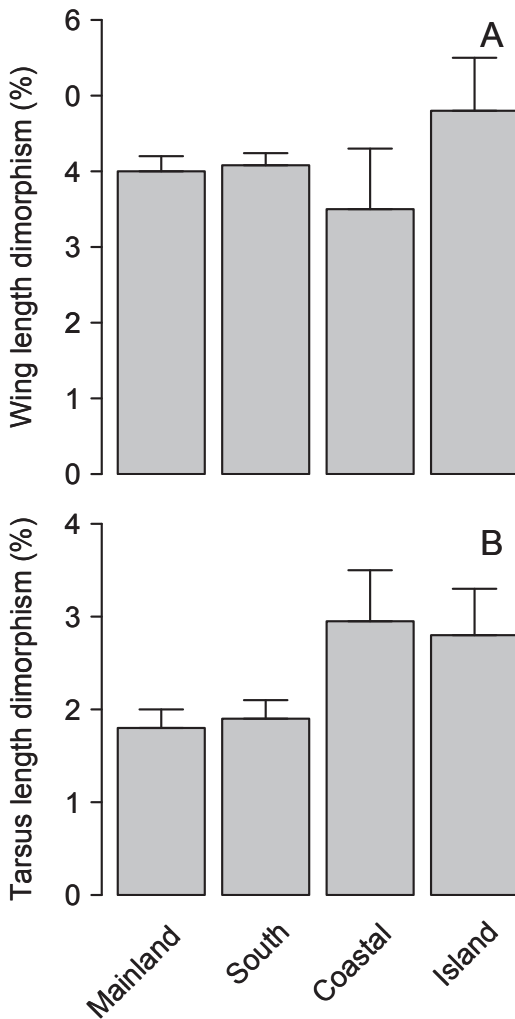


Fig. 4. Dimorphism of Song Sparrows in tarsus and wing length.

The size difference between island and mainland populations of *M. melodia* suggests a major plastic or evolutionary response in basic structural size. This pattern is especially pronounced in Alaska (Pruett and Winker 2005), where differences are an order of magnitude greater than in California. Our strongest support of island/mainland divergence in body size is found within the specimen measurements, where structural size-corrected weights are substantially higher in the island birds. However, this result is based on decades-old material. The higher mass found in our recent samples needs to be further investigated with measurements and

statistics that can evaluate conditional differences.

Despite controversy around the “island rule” as it applies across a broad range of taxa (Meiri et al. 2005, 2008), the patterns are still strongly supported within some clades. Island forms of Passerine birds still show a strong tendency toward larger body size on islands (Clegg and Owens 2002, Scott et al. 2003, Robinson-Wolrath and Owens 2003). The hypotheses for why island birds might be larger (reviewed in Clegg and Owens 2002 and Adler and Levins 1994) include (1) reduced interspecific competition allowing for the evolution of larger body size, a more trophically generalist morphology, and reduced weight-specific metabolism; (2) increased intraspecific competition selecting for body size that confers dominance and hence higher survival during times of year when food is limited; (3) lower predation threat or need to disperse, reducing the need for mobility and allowing body mass to be greater; and (4) lower predation threat creating a cascade, where higher density leads to reduced reproductive output resulting in higher body condition.

The evaluation of these hypotheses have focused almost entirely on analysis of structural body size (using PCAs to describe the collective effect of various body-size measures). However, the findings of our study suggest that size-corrected body mass may be the most diverged of body-size measures in Song Sparrows, and this phenomenon engenders a somewhat different approach to hypothesizing reasons for the island-mainland divergence. The difference in the size-corrected mass likely results from variation in fat load or muscle size, traits that show a large degree of plasticity (Danner 2012). This makes it possible that island-mainland differences in the Song Sparrows are a result of a phenotypically plastic response to immediate conditions (Clegg and Owens 2002), rather than a genetically based evolutionary response. The differences we found are robust because sparrows were collected over a 100-year period, so the increase in body mass is not simply a result of conditions during a particular year or set of years. Rather than being a weakness of the analyses, this temporal scattering of samples would seem to confer some generality to the response of island sparrows.

Birds are thought to regulate their weight in response to variation in food supply or as a



more complex optimization of food unpredictability and risk of depredation (adaptive mass hypotheses: Lima 1986, Houston and McNamara 1993). We have no information on the composition of the increased mass in island birds (muscle or fat), and this makes functional inference more difficult. Nonetheless, based on the natural history of the sparrows and the islands, we can propose hypotheses that might account for the greater size-corrected mass of island birds.

Interspecific competitive release may allow island Song Sparrows to acquire more food. Yeaton and Cody (1974) found support for competitive release in Song Sparrows on islands: these birds held smaller territories than birds in mainland populations with more competitors. Alternatively, greater body size may be a condition-selected trait to allow intraspecific dominance over food resources. This argument is weakened for body mass, however, by the finding that sexual dimorphism, which is also thought to be associated with higher intraspecific competition, was lower rather than higher in island samples. Greater mass may result from greater food productivity on islands, though no evidence exists for this hypothesis. Reduced competition for food and lower depredation rates resulting from lower diversity of land birds might combine to favor individuals that adaptively manage their body mass at a higher level than mainland birds. The greater bill-size dimorphism in California Island Song Sparrows also appears to suggest a role for relaxed resource specialization or increased food availability (Greenberg and Danner 2013). Therefore, both the patterns in body shape associated with trophic ecology and overall size suggest that further studies of food supply, dominance, and predation risks should show consistently different influences on the evolution of divergence in island Song Sparrow populations.

#### CONCLUSIONS

1. California Islands Song Sparrows have greater mass, after controlling for body size, than mainland song sparrows.

2. There is no evidence of structural-size difference (tarsus and wing chord) between islands and mainland specimens. This suggests that island birds are in better condition: a hypothesis that can be tested with careful

measurement of mass and structural size in the same individuals, as well as with body composition analysis.

3. Both the greater size-corrected body mass and the greater bill dimorphism are consistent with a hypothesis of reduced interspecific competition on islands. Alternatively, the greater mass might be a result of adaptive mass regulation responding to possible reduced predation threat on adults.

#### ACKNOWLEDGMENTS

We thank the following collections managers and collections for the study skins used in this study: J. Dean (Smithsonian National Museum of Natural History), M. Flannery (California Academy of Sciences), P. Unitt (San Diego Natural History Museum), K. Garrett (Los Angeles County Museum), C. Cicero (Museum of Vertebrate Zoology), K. Molina (Dickey Collection, University of California, Los Angeles), K. Fahy (Santa Barbara Museum of Natural History), and H. Fox (University of California, Santa Barbara). P. Nott provided weight data from the MAPS program. The following banders also provided weight data: P. Nieto, Y. Chan, S. Myers, A. Wilson, B. Kus, W. Sakai, J. Scullen (San Francisco Bay Bird Observatory), M. Dodge, and D. LaBerteaux. P. Collins provided information on the locations of all Channel Island specimens. A. Cruz-Angon and L. Hazard helped obtain climatological data for the Coronados Islands from SEMAR and the Scripps Institution of Oceanography. R. McKernan and E. Cardiff provided data from study skins at the San Bernardino County Museum. J. Birdsall assisted in accessing evapotranspiration data from the California Irrigation Management Information System (CIMIS). L.A. Hayek, C. Franck, and M. Etersson provided guidance on statistics. Travel to museums was supported by AirTran Airways and the Smithsonian Institution.

#### LITERATURE CITED

- ADLER, G.H., AND R. LEVINS. 1994. The island syndrome in rodent populations. *Quarterly Review of Biology* 69:473–490.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, NY.
- CLEGG, S.M., AND I.P.F. OWENS. 2002. The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B* 269:1359–1365.

- DANNER, R.M. 2012. The effects of limited winter food availability on the population dynamics, energy reserves, and feather molt of the Swamp Sparrow. Doctoral dissertation, Virginia Tech, Blacksburg, VA.
- DANNER, R.M., R.S. GREENBERG, J.E. DANNER, L.T. KIRKPATRICK, AND J.R. WALTERS. 2013. Experimental support for food limitation of a short-distance migratory bird wintering in the temperate zone. *Ecology* 94:2803–2816.
- DARWIN, C. 1859. *The origin of species*. J. Murray, London, UK.
- DESANTE, D.F. 1992. Monitoring Avian Productivity and Survivorship (MAPS): a sharp, rather than blunt, tool for monitoring and assessing landbird populations. Pages 511–521 in D.R. McCullough and R.H. Barrett, editors, *Wildlife 2001: populations*. Elsevier, London, United Kingdom.
- FIELLER, E.C. 1954. Some problems in interval estimation. *Journal of the Royal Statistical Society B* 16:175–185.
- GRANT, P.R. 1965. The adaptive significance of some size trends in island birds. *Evolution* 19:355–367.
- GREENBERG, R., AND R. M. DANNER. 2012. The influence of the California marine layer on bill size in a generalist songbird. *Evolution* 66:3825–3835.
- GREENBERG, R., AND R.M. DANNER. 2013. Climate, ecological release, and bill dimorphism in an island songbird. *Biology Letters* 9(3). <http://dx.doi.org/10.1098/rsbl.2013.0118>
- GREENBERG, R., R. DANNER, B.J. OLSEN, AND D. LUTHER. 2012. High summer temperature explains bill size variation in salt marsh sparrows. *Ecography* 35: 146–152.
- HOUSTON, A.I., AND J.M. MCNAMARA. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* 24: 205–219.
- JOHNSON, N.K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. *Condor* 74:295–315.
- JONES, H.L., AND J.M. DIAMOND. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526–549.
- LACK, D.L. 1945. The Galapagos finches (Geospizinae) a study in variation. *Occasional Papers of the California Academy of Sciences*. 21:1–181.
- LIMA, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377–385.
- LOMOLINO, M.V. 1985. Body size of mammals on islands: the island rule reexamined. *American Naturalist* 12:310–316.
- LOSOS, J.B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution* 40:558–569.
- MACARTHUR, R.W., AND E.O. WILSON. 1967. The theory of island biogeography. *Monographs in Population Biology* 1:1–203.
- MAIORANA, V.C. 1990. Evolutionary strategies and body size in a guild of mammals. Pages 69–102 in J. Damuth and B.J. MacFadden, editors, *Body size in mammalian paleobiology*. Cambridge University Press, Cambridge.
- MEIRI, S., N. COOPER, AND A. PURVIS. 2008. The island rule: made to be broken? *Proceedings of the Royal Society B—Biological Sciences* 275:141–148.
- MEIRI, S., D. SIMBERLOFF, AND T. DAYAN. 2005. Body size of insular carnivores: little support for the island rule. *American Naturalist* 165:505–514
- PATTEN, M.A., AND C.L. PRUETT. 2009. The Song Sparrow, *Melospiza melodia*, as a ring species: patterns of geographic variation, a revision of subspecies, and implications for speciation. *Systematics and Biodiversity* 7:33–62.
- POWER, D.M. 1983. Variability in island populations of the House Finch. *Auk* 100:180–187.
- PRUETT, C.L., AND K. WINKER. 2005. Northwestern Song Sparrow populations show genetic effects of sequential colonization. *Molecular Ecology* 14:1421–1434.
- RAIA, P., F. CAROTENUTO, AND S. MEIRI. 2010. One size does not fit all: no evidence for an optimal body size on islands. *Global Ecology and Biogeography* 19(4): 475–484.
- ROBINSON-WOLRATH, S.I., AND I.P.F. OWENS. 2003. Large size in an island-dwelling bird: intraspecific competition and the Dominance Hypothesis. *Journal of Evolutionary Biology* 16:1106–1114. <http://dx.doi.org/10.1420/9101.2003.00615.x>
- SCOTT, S.N., S.M. CLEGG, S.P. BLOMBERG, J. KIKAWA, AND I.P.F. OWENS. 2003. Morphological shifts in island-dwelling birds: the role of generalized foraging niche and niche expansion. *Evolution* 9:2147–2156.
- SELANDER, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.
- SMITH, T.B. 1990. Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* 71:1246–1257.
- STATSOFT, INC. 2011. STATISTICA (data analysis software system), version 10. Available from: <http://www.statsoft.com>
- WALLACE, A.R. 1869. *The Malay Archipelago: the land of the orang-utan, and the bird of paradise: a narrative of travel with studies of man and nature*. Macmillan, London, United Kingdom.
- WILSON, A. 2008. The role of insularity in promoting intraspecific differentiation in Song Sparrows. Doctoral dissertation, University of British Columbia, Vancouver, Canada.
- WILSON, A., P. ARCESE, L.F. KELLER, C.L. PRUETT, K. WINKER, M.A. PATTEN, AND Y. CHAN. 2009. The contribution of island populations to in situ genetic conservation. *Conservation Genetics* 10:419–430.
- YEATON, R.I., AND M.L. CODY. 1974. Competitive release in island Song Sparrow populations. *Theoretical Population Biology* 5:42–58.
- ZAR, J.H. 1999. *Biostatistical analysis*. 4th edition. Prentice Hall, Upper Saddle River, NJ.

Received 26 April 2013  
Accepted 16 February 2014