

Foraging Niche and Acute Infection Inferences in Channel Island Song Sparrows (*Melospiza melodia graminea*) Across a Climate Gradient

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Abstract

Climate variation facilitates differences in community assemblages and dynamics (e.g., parasitism, predation), which may have cascading effects on foraging ecology and immunocompetence. Consequently, diet and disease prevalence are likely to vary among populations in species with broad geographic ranges. However, patterns of community assemblage can be complicated to predict across small spatial scales, and the impacts of differing assemblages on widely distributed species are not well understood. Song sparrows (*Melospiza melodia*), a North American passerine, exhibit extensive phenotypic variation across their broad range that has been found to correlate with climate. Here, we tested whether stark climate differences among isolated Channel Island song sparrow (*Melospiza melodia graminea*) populations lead to variation in foraging niche and infection rates. Specifically, we (1) used stable isotope analysis (n = 90) to infer foraging niche width among three populations (San Miguel, Santa Rosa, and Santa Cruz Islands), and (2) inferred infection rates between our two windiest and most humid islands (San Miguel and Santa Rosa Islands) using blood cell counts as a proxy (n = 47). We found $\delta^{13}\text{C}$ levels were elevated on San Miguel Island, suggesting that San Miguel Island song sparrows forage on greater amounts of CAM and C4 plants and/or on plants growing in high salinity soil. Additionally, we found elevated $\delta^{15}\text{N}$ levels on Santa Rosa Island, providing evidence for Santa Rosa Island sparrows foraging at a higher trophic level (i.e., more invertebrates, less vegetation). However, we did not find differences in either white blood cell or abnormal red blood cell counts between Santa Rosa Island and San Miguel Island birds. Collectively, our findings suggest that climate has complex effects on organismal biology among the islands, and diet and infection rates may not vary consistently with predictions of the theory of island biogeography. As habitat restoration efforts move forward, our study provides valuable insights regarding the management of this California Species of Special Concern.

Introduction

Climate varies across the globe, driving patterns of biodiversity, and consequently, regional differences in a community's species abundance and composition (community assemblage). Variation in community assemblage has cascading impacts on populations, such as on population dynamics (Hanski, 1998; Zhao et al., 2016; Fauteux et al., 2021), available resources (Zupo et al., 2017), and infection and disease rates (Sehgal, 2015; Fecchio et al., 2021). Broad-scale, climate-driven patterns of biodiversity shape variability across landscapes, often prompting adaptive responses to differential conditions experienced by populations of widely distributed species (Willig, 2001). Specifically, resource differences suggest that populations of widely distributed species will exhibit phenotypic dietary plasticity. While there are species whose diets remain highly generalist across a wide range of environmental conditions (Lehmann et al., 2013), some species exhibit localized dietary specialization across their distribution range, even if their overall foraging niche is categorized as generalist (Burstahler, 2016). For example, recent research on the Canadian Lynx (*Lynx canadensis*), using isotopic analysis of diet, has found populations to consist of facultative specialists in some regions of their range, and obligate generalists in others, depending on resource availability (Szumski et al., 2023). Regional environmental extremes tend to exacerbate local specialization, dietary or otherwise (Berthelot et al., 2023; Nishiura & Kaneko, 2021).

Other environmentally driven regional effects, such as patterns of parasite abundance, can also lead to adaptively different phenotypes across a species' range. For instance, birds inhabiting humid regions with high parasite abundance have more feather melanization, likely as a defense against infection (Burt & Ichida, 2004; Bosch, 2019). Additionally, underlying genetic differentiation in genes associated with immune function may increase resistance to common parasites in populations with strong host-parasite interactions (Nishiura & Kaneko, 2021). Yet, adaptive plastic responses such as high feather melanin content require more energy to produce (Minias et al., 2013), and phenotypic plasticity in melanin deposition may be costly to maintain (Ghalambor et al., 2007). Furthermore, local adaptation necessitates a certain degree of genetic isolation, which, while preserving locally adaptive gene complexes, also increases the chances of inbreeding depression (Marr et al., 2002; Kawecki & Ebert, 2004). Phenotypic and genotypic divergence are typically only found in regions with strong environmental selection pressures

(Nishiura & Kaneko, 2021) or among populations that are geographically separated and, consequently, have little gene flow (Kawecki & Ebert, 2004).

In island systems, rates of divergence are often high. Natal dispersal distance, the distance individuals move from natal territories to breeding territories, tends to be reduced in island populations (Blondel, 2000). Island systems are often comparatively less biodiverse than mainland systems, leading to reduced competition and more available resources, and thus a reduced need to disperse (Blondel, 2000; MacArthur & Wilson, 1967). Island populations, therefore, experience amplified effects of local climate, leading to more rapid specialization and speciation (Blondel, 2000; Vinciguerra et al., 2022). Furthermore, island size-biodiversity relationships correlate with differences in community assemblage and consequently selection pressures among islands, thereby increasing the likelihood of local adaptations (MacArthur & Wilson, 1967). While random genetic drift and small founder populations may interact to reduce genetic variation, it is directional selection that wields the most influence, facilitating phenotypic divergence in island organisms. Indeed, selection has been shown to maintain a diversity of adaptively distinct island forms and populations, often characterized by high levels of divergence over small spatial scales (Clegg et al., 2002; Scott et al., 2003; Clegg et al., 2008; Estandía et al., 2024). However, while island effects do accelerate neutral and adaptive genetic differentiation, predicting exact patterns can be difficult due to varying environmental selection pressures among islands, which can have complex impacts on locally adaptive traits (Clegg et al., 2002; Gamboa et al., 2021).

Song sparrows (*Melospiza melodia*) are a widespread bird species in the United States, ranging from Alaska to Florida (Patten & Pruitt, 2009; Arcese et al., 2020). Song sparrows display a remarkable amount of phenotypic diversity across their wide geographic range, consisting of 24 diagnosed and 52 described subspecies, or “types.” High rates of polytypism are likely due to low gene flow and high selection locally (Arcese et al., 2020). Song sparrow populations follow predictable, climate-driven, broad-scale patterns of darker pigmentation and larger body size in colder, wetter regions, and lighter pigmentation and smaller body size in warmer, drier regions (Aldrich, 1984; Patten & Pruitt, 2009). Patterns of body size (Bergmann’s rule) are linked to thermoregulation, while patterns of plumage pigmentation (Gloger’s rule) are linked both to thermoregulation and parasite resistance (Burt & Ichida, 2004; Freire, 2016; Bosch, 2019; McQueen et al., 2022). Furthermore, recent research has found evidence for an

additive genetic basis that has been the target of selection and underlies the diversity of body sizes across the occupied latitudinal gradient (Carbeck et al., 2023). However, while the arrangement of phenotypes is evident across a broad scale, it is not well understood how song sparrow traits vary across heterogeneous landscapes at small spatial scales, particularly in island systems.

The island song sparrow (*Melospiza melodia graminea*) is a subspecies endemic to the northern California Channel Islands. The islands are characterized by a dramatic east-west climate and size gradient, ranging from warm, dry, large Santa Cruz Island, to wet, windy, cold, little San Miguel Island, with Santa Rosa Island having intermediate conditions (Schoenherr et al., 2003). Unlike many of their mainland relatives, island song sparrows are nonmigratory, aligning with the island syndrome of reduced dispersal distances. As a result, the island song sparrow populations of San Miguel, Santa Rosa, and Santa Cruz Islands are largely genetically distinct from each other, despite the close proximity of the islands (Gamboa et al., 2022). Remarkable phenotypic differences are found among the three island populations. Sparrows on San Miguel Island are significantly smaller and darker with smaller bills, while on Santa Cruz Island, birds are bigger, paler, and have larger bills (Gamboa, *pers. comm.*). Bigger bills are hypothesized to be adaptive to the hotter climate, as they have more surface area from which heat can be released, while the smaller bills seen in the San Miguel Island population help with heat retention (Gamboa et al., 2022). However, foraging niche has yet to be ruled out as a driver of island song sparrow bill differentiation; overall, the impact of diet on trait divergence is understudied in these populations. Although island song sparrow populations occupy similar habitat types, the exact vegetative composition differs by island, suggesting potential variation in food resources (Gamboa et al., 2021). However, given the secretive foraging strategies of song sparrows, analyzing diet by observation alone is difficult (Arcese et al., 2020).

Stable isotope analysis is a useful and common tool for inferring foraging niche. The isotopic signatures of prey are assimilated into an organism's tissues, and analysis of the stable isotope ratios in those tissues is a strong indicator of diet (Inger & Bearhop, 2008). The stable isotope $\delta^{15}\text{N}$ increases with trophic level, while $\delta^{13}\text{C}$ gauges the plant types an organism is feeding on, distinguishing between plants that use C3, C4, and CAM photosynthesis (O'Leary, 1988; Hobson & Clark, 1992). Variation in $\delta^{13}\text{C}$ may also indicate local soil salinity (Wei et al., 2008). Many widely distributed species exhibit regional dietary differences, but due to

environmental conditions, secretive foraging strategies, or risk of disturbance to the individuals, field observations of diet are often infeasible (Inger & Bearhop, 2008). Stable isotope analysis has been used to infer foraging niche differences among and inform management of populations of many secretive species (Mazariegos-Villarreal et al., 2023; Berthelot et al., 2023). Applying stable isotope analyses to song sparrows will help us determine whether island populations differ in foraging ecology, while minimizing costs and human disturbance.

In addition to diet, climate and island size are also predicted to impact the prevalence and diversity of local diseases (MacArthur & Wilson, 1967). The climate gradient of the northern Channel Islands has complex effects on community assemblage, suggesting the potential for differential levels of disease exposure among island populations. Populations with dissimilar levels of exposure to disease are likely to exhibit unique immune responses (Becker et al., 2023). Indeed, differentiation in immune-linked genetic markers is found among island song sparrow populations (Gamboa, *pers. comm.*). However, patterns of parasitism correlate inversely with humidity and wind speed, as Diptera vectors of avian blood parasites thrive under humid conditions, but have significantly lowered activity when wind speeds are high (Freire et al., 2016). Thus, there are competing hypotheses for infection rates among the northern Channel Islands given the east-west gradient of both increasing wind speed and precipitation (Freire et al., 2016). To determine which environmental factor correlates the most strongly with rates of parasite infection, high counts of white blood cells (WBCs), as well as abnormal red blood cells (abRBCs), can be used as a proxy to measure infection rates in a population due to their co-occurrence with acute parasite infections (Ricklefs & Sheldon, 2007; Deshmukh et al., 2021).

Here, using stable isotope analysis and blood cell counts, we examined how climate and community assemblage differences among islands impacted parasite interactions and foraging niche breadth in island song sparrows. We predicted that Santa Cruz Island, the largest and most resource-rich, would have the widest foraging niche breadth, while San Miguel Island, the smallest island, would have the narrowest. Additionally, we expected that San Miguel Island song sparrows would exhibit less negative $\delta^{13}\text{C}$ value due to the island's grassy (C4 plant family) composition and high soil salinity. However, regarding parasite infection, we had two competing predictions: (1) the high rainfall on San Miguel Island increased rates of infection in its population, or (2) inversely, the extreme wind speeds on San Miguel Island caused comparatively lower rates of infection. Through this study, we aimed to deepen our

understanding of how environmental interactions shape evolutionary processes in insular island song sparrow populations.

Methods

Study Site

Located just off the coast of southern California, the northern California Channel Islands of Santa Cruz, Santa Rosa, and San Miguel boast a maritime Mediterranean climate characterized by overall mild conditions with wet winters and warm, dry summers. An eddy formed by the California Current brings cooler, wetter, windy conditions to the outermost islands, and warmer, dryer conditions to islands closer to the mainland (Junak et al., 2007). The islands are separated by channels of no more than 9.6 km, and have a landscape of rocky coastlines, cliffs, scrub and grassland, and some woodlands (Moody, 2001; Pasciullo Boychuck et al., 2024). Historic introductions of non-native herbivores and plants by ranchers have caused significant disturbance to native vegetative communities, including the establishment of invasive grasslands (Junak et al., 2007). The westernmost and smallest (37 km²) of the three focal islands, low-lying San Miguel Island, is dominated by dunes, with vegetation consisting of grassland, scrub, invasive iceplant carpet, and a recovering population of native *Dudleya* (Gamboa, *pers. comm.*; McGlaughlin et al., 2014; Zellman, 2014). While San Miguel Island was historically lush, overgrazing combined with windy conditions has destabilized the soil, leading to the formation of sandy dunescapes (Holland, 1963). Santa Rosa Island (215 km²) is located between Santa Miguel and Santa Cruz Islands, and has a central mountain range surrounded by scrubby rugged terrain in the south, and grassy marine terraces bisected by canyons in the north. Pockets of oak woodland and pine forest are intermixed throughout (Junak et al., 2007; Pasciullo Boychuck et al., 2024). Santa Cruz Island (250 km²) is the largest of the northern Channel Islands and the closest to the mainland at only 30 km distance (McGlaughlin et al., 2014). The island has two mountain ranges surrounding a central valley, and hosts grassland, scrub, chaparral, oak woodland, and pine forest ecosystems across its topographically diverse terrain (Pasciullo Boychuck et al., 2024; Junak et al., 2007). Invasive fennel is also abundant on Santa Cruz Island, particularly in the central valley (Dash & Gliessman, 1994).

Inferences of foraging niche using stable isotope analysis

Song sparrow breast feathers were collected during the breeding season (spring) in the northern California Channel Islands at 10 sites on San Miguel Island, 6 sites on Santa Rosa Island, and 8 sites on Santa Cruz Island from 2015 to 2019 (Fig. 1). Breast feathers were collected using mist netting with the aid of targeted playback, and all samples used in this study were from male birds (Chamberlain et al., 2000). Feathers were stored in labeled manilla envelopes until use in the lab. To prepare breast feathers for analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope levels, we cut the feather's barbs from the rachis and weighed them out in 8x5mm tin capsules at masses between 0.5 and 0.6 mg (Bensch et al., 2006). All samples were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope values at the University of New Mexico Center for Stable Isotopes. Measurements were taken by Element Analyzer Continuous Flow Isotope Ratio Mass Spectrometry using a Costech ECS 4010 Element Analyzer coupled to a ThermoFisher Scientific Delta V Advantage mass spectrometer via a CONFLO IV interface. To ensure machine calibration, three laboratory standards (casein, soy protein, and house-made tuna protein) were run at the beginning of analytical sessions, at intervals between samples, and at the end. Analytical precision calculated from the standards was ± 1 standard deviation for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

To investigate the variation in stable isotope levels among islands, we ran an ANOVA test in RStudio to determine whether island song sparrows differed in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. We performed post-hoc Tukey's HSD test (Hothorn et al., 2008) to conduct pairwise comparisons among islands. Additionally, we calculated and reported means and standard deviation for each island's isotope levels. Next, we investigated isotopic niche width and overlap, with isotopic niche width acting as a proxy for foraging niche width, in the R package *SIBER* (Jackson et al., 2011). We used the parameter of a 50% ellipse to calculate the ellipse area (SEA) and % overlap of the niches using *SIBER*'s *plotSiberObject*, *groupMetricsML*, and *maxLikOverlap* functions. With the *siberDensityPlot* and *lapply* functions, we calculated SEAc to correct for small sample size, and Bayesian standard ellipse area (SEAb), which represents the average ellipse size after

running the model repeatedly to correct for error.

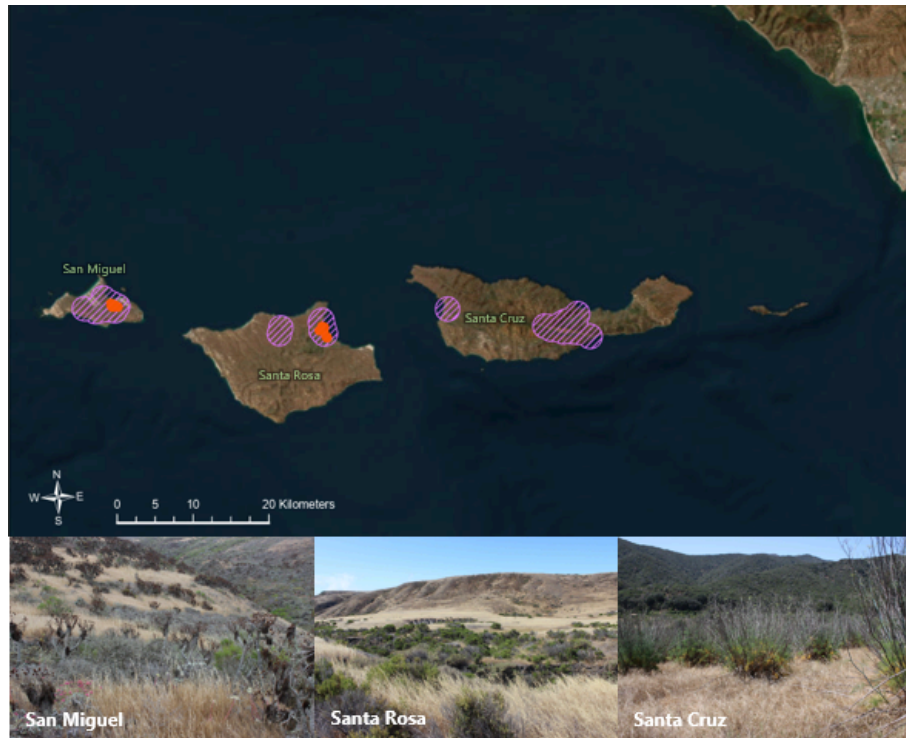


Figure 1. Map of northern Channel Islands and sample collection locations. The purple hashed regions represent breast feather sampling locations, and the orange filled regions represent blood sampling locations. Photos below are representative of the vegetation found at sampling sites.

Inferences of blood parasite presence using blood cell ratio and densities

Sparrows were captured through targeted playback and mist-netting during the 2014 breeding season on San Miguel and Santa Rosa Islands, and collection locations were centralized around field housing areas on both islands (Fig. 1). Whole blood was collected from the brachial vein with a capillary tube, and approximately 5-10 μ L of blood was used to create a thin blood smear on each microscope slide. The blood smears were dried at air temperature and fixed with pure methanol, and fixed slides were stained with 2.5% Giemsa stain for 30-60 minutes depending on smear quality and thickness (Hardian et al., 2023). We screened slides for red blood cells (RBCs), white blood cells (WBCs), and abnormal red blood cells (abRBCs) under a microscope. Cell counts were taken from three randomly selected fields per each slide using a microscope magnification of 100x (Ricklefs & Sheldon, 2007).

To quantify differences in WBCs and abRBCs between San Miguel and Santa Rosa, we calculated abRBC density and WBC:abRBC ratios. We used the *lmer* function from the *lme4*

package in R (Bates et al., 2015) to compare abRBC density and WBC:abRBC ratios between the islands, while controlling for individual samples as a random effect.

Results

We screened 27 microscope slides from Santa Rosa Island and 20 from San Miguel Island for blood cell counts, totaling 47 individual birds. For stable isotope analysis, we analyzed 96 feather samples from 90 individuals for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ levels, with all three study islands evenly represented in the sample size. Two duplicate feather samples were prepared per island to assess deviation among runs, and removed when doing statistical analysis, making the final sample size for feathers $n = 90$. From our findings, Santa Rosa Island had the most restricted isotopic foraging niche with elevated $\delta^{15}\text{N}$ levels, while San Miguel Island had a broader isotope niche with elevated $\delta^{13}\text{C}$ levels. Santa Cruz Island had the broadest isotopic niche, overlapping the niches of both San Miguel and Santa Rosa Island, but lacked elevated $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ levels. No significant differences in group means were found in blood cell levels (WBC density and abRBC:WBC ratio) between Santa Rosa and San Miguel Islands.

Stable isotope values

For both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, the ANOVA showed significant variation in isotope levels among island song sparrow populations ($P = 1.96 \times 10^{-6}$ for $\delta^{15}\text{N}$, $P = 0.0032$ for $\delta^{13}\text{C}$, $df = 2$). For $\delta^{15}\text{N}$ levels, pairwise comparison from the post-hoc Tukey's HSD test revealed that Santa Rosa Island and Santa Cruz Island varied significantly from each other ($P = 1.95 \times 10^{-5}$), and Santa Rosa Island and San Miguel Island did as well ($P = 1.95 \times 10^{-5}$). Santa Cruz Island and San Miguel Island did not vary significantly from each other in their $\delta^{15}\text{N}$ values ($P = 1.00$). The p-values indicate that $\delta^{15}\text{N}$ levels are significantly higher in the diets of song sparrows on Santa Rosa Island compared to both San Miguel Island and Santa Cruz Island (Fig. 2). For $\delta^{13}\text{C}$, Tukey's HSD test found that San Miguel Island and Santa Cruz Island varied significantly ($P = 0.00065$), and so did San Miguel Island and Santa Rosa Island ($P = 0.003$). Santa Rosa Island and Santa Cruz Island did not vary significantly in their $\delta^{13}\text{C}$ values ($P = 0.88$). Here, p-values indicated that $\delta^{13}\text{C}$ values were significantly higher in the diets of song sparrows on San Miguel Island compared to both Santa Rosa Island and Santa Cruz Island (Fig. 2).

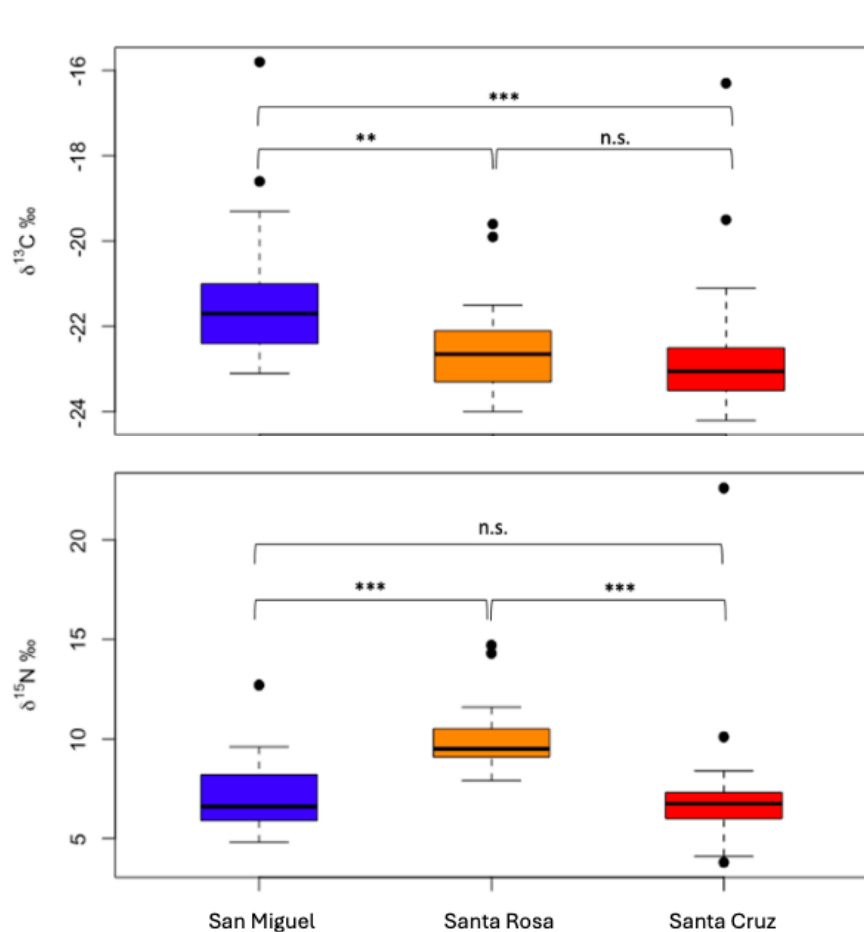


Figure 2. Boxplot representation of significant differences in isotope levels among the islands. Asterisks indicate significant relationships, with more asterisks representing a lower p-value ($* = P \leq 0.05$, $** = P \leq 0.01$, $*** = P \leq 0.001$), and n.s. indicating no significant variation. Dots above and below boxes represent outliers.

The average $\delta^{13}\text{C}$ values (mean \pm SD) per island were $-21.4 \pm 1.4\text{‰}$ for San Miguel Island, $-22.6 \pm 1.0\text{‰}$ for Santa Rosa Island, and $-22.7 \pm 1.5\text{‰}$ for Santa Cruz Island. The average $\delta^{15}\text{N}$ values (mean \pm SD) per island were $7.1 \pm 1.7\text{‰}$ for San Miguel Island, $9.9 \pm 1.5\text{‰}$ for Santa Rosa Island, and $7.1 \pm 3.2\text{‰}$ for Santa Cruz Island. The high standard deviation for Santa Cruz Island's mean $\delta^{15}\text{N}$ value is caused by a single outlying individual, which, when removed,

changed the value to $6.6‰ \pm 1.3‰$. The removal of outliers in our data overall only served to further decrease p-values and strengthen statistical relationships.

Santa Rosa Island song sparrows had the smallest niche breadth, with an SEAc of $3.34‰^2$ (95% CI = $2.26-4.63‰^2$). San Miguel Island hosted an intermediate niche breadth with an SEAc of $6.57‰^2$ (CI = $4.17-8.54‰^2$), and Santa Cruz Island hosted the widest niche breadth with an SEAc of $10.77‰^2$ (CI = $9.61-20.05‰^2$). With outliers removed, the SEAc values were $1.92‰^2$, $3.08‰^2$, and $4.18‰^2$, respectively. The percent overlap of the 50% ellipses was the highest for Santa Cruz Island and San Miguel Island ellipses at 19% (without outliers: 17%), 10% for Santa Cruz Island and Santa Rosa Island ellipses (without outliers: zero percent), and zero percent for Santa Rosa Island and San Miguel Island (without outliers: zero percent) (Fig. 3). The overlap of Santa Cruz and Santa Rosa Island's isotopic niches in our findings was driven largely by one outlying individual.

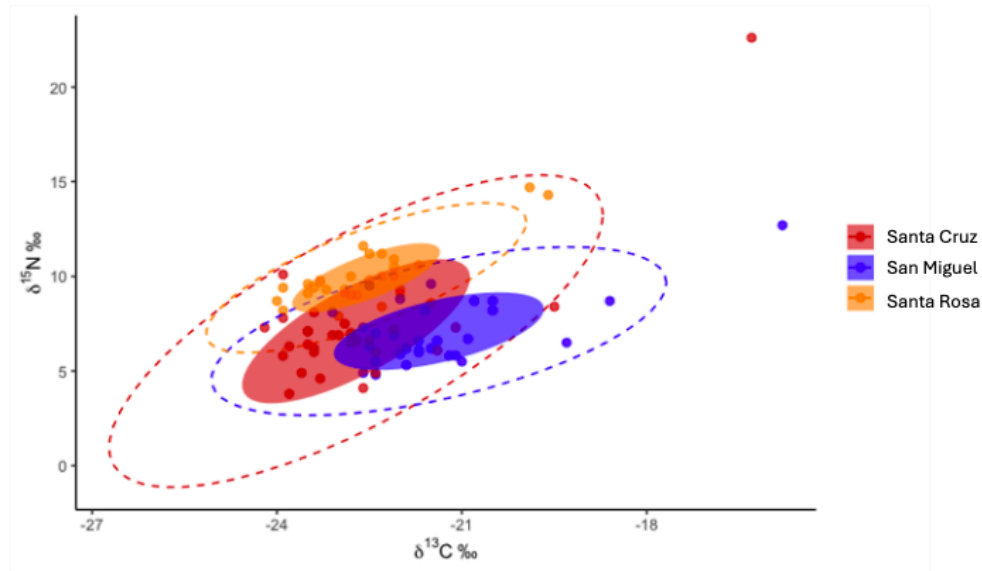


Figure 3. Ellipse graph of foraging niche width and overlap. The smaller, filled ellipses represent 50% of the data, and the dashed lines 95%, with individual data points represented as dots color-coded to their associated island.

Blood cell ratios and density

WBC:abRBC ratio and abRBC density did not differ significantly between Santa Rosa and San Miguel Islands (Fig. 4). The ANOVA for WBC:abRBC ratio calculated an insignificant p-value of 0.27, and the ANOVA for abRBC density calculated an insignificant p-value of 0.87.

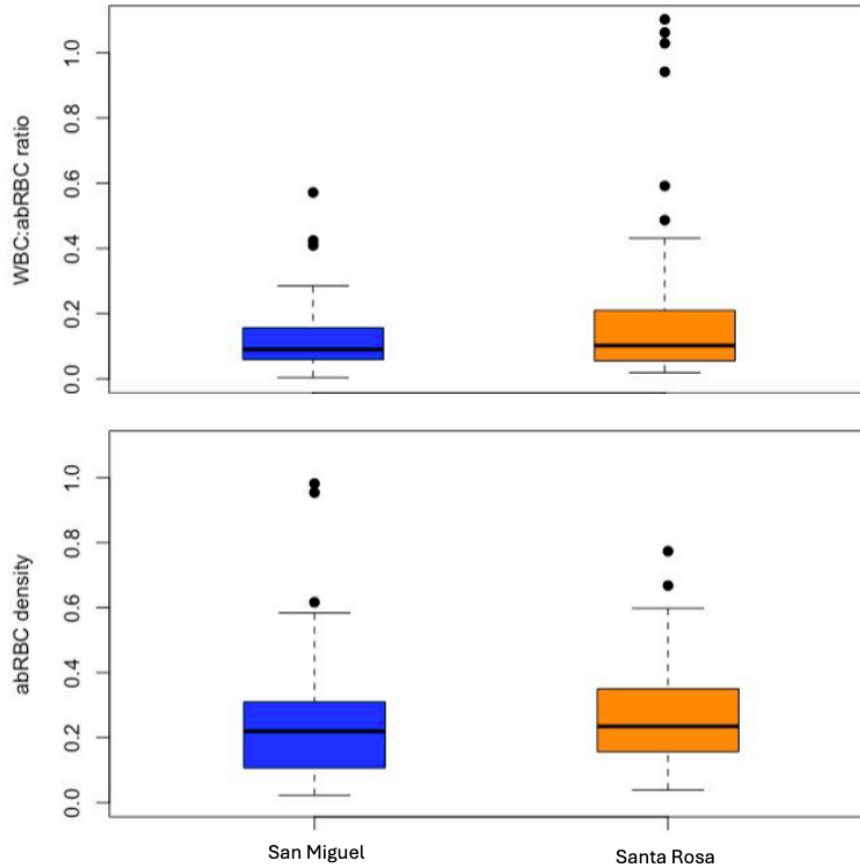


Figure 4. Boxplot representation of differences in abnormal red blood cell density and white blood cell:abnormal red blood cell ratios between San Miguel and Santa Rosa Islands. Density units are per 0.00018mm² area of a microscope slide. The dots above boxes represent outliers. All relationships are non-significant.

Discussion

Song sparrows display extensive phenotypic variation across their range, which has been shown to correlate with local climate. Thus, we hypothesized that climate and community assemblage differences among the northern California Channel Islands would correlate with phenotypic divergence among island song sparrow populations. Our study confirmed distinct, behaviorally-linked phenotypes among the island song sparrow populations, reflecting adaptations to local conditions despite the proximity of the populations. Specifically, Santa Rosa Island sparrows had elevated $\delta^{15}\text{N}$ levels and San Miguel Island sparrows had elevated $\delta^{13}\text{C}$ levels in analyzed tissue, suggesting foraging niche differentiation (Fig. 2). Variation in stable isotope levels indicates that Santa Rosa Island sparrows are foraging at a significantly higher trophic level, while the San Miguel Island population is foraging on proportionally more C4 and CAM plants, and plants grown in higher salinity soil. However, we did not find a significant difference in abRBC density or in WBC:abRBC ratios among island populations (Fig. 4). Given

other system-wide differences in community assemblage, the lack of variation in acute blood infection metrics is likely due to methodological limitations, rather than being representative of actual island community patterns.

Variation in trophic level across island populations ($\delta^{15}\text{N}$)

Our findings showed that Santa Rosa Island sparrows had significantly elevated levels of the $\delta^{15}\text{N}$ stable isotope in their breast feathers, indicating that they likely are foraging at a higher trophic level (Hussey et al., 2014) than the Santa Cruz and San Miguel Island sparrow populations (Figs. 2 & 3). Elevated $\delta^{15}\text{N}$ levels in Santa Rosa Island song sparrows may correspond with the relative lack of plant diversity found at sparrow sampling sites on Santa Rosa Island (Gamboa, *pers. comm.*). While neighboring Santa Cruz and San Miguel Islands host different plant communities, both islands have an overall greater diversity of plant species at sampling sites compared to Santa Rosa Island. In particular, Santa Cruz Island has an abundance of invasive sweet fennel (*Foeniculum vulgare*), a hypothesized important C3 food resource for its sparrows (Gamboa et al., 2021). This leads us to hypothesize that, in lieu of the abundance of plant food resources found on the other study islands, Santa Rosa Island song sparrows depend significantly more on insects to make up their diet. High dissimilarity in Santa Rosa Island's foraging niche, demonstrated by the 0% niche overlap (outliers removed) with Santa Cruz and San Miguel Islands at 50% ellipses further corroborates these findings (Fig. 3). Santa Cruz Island and San Miguel Island, while having climate-driven differences in plant community composition, both nonetheless have a diversity of plant food resources to draw from, causing those populations to depend less heavily on insects to make up their diet.

Although we didn't sample prey resources, research has found significant differences in $\delta^{15}\text{N}$ level to be synonymous with organisms foraging on proportionally more animal material than plant, as enrichment of $\delta^{15}\text{N}$ increases stepwise along trophic structures (Kelly, 2000; Hussey et al., 2014). Due to our small data set, explicit determination of the exact population trophic level is not possible; nonetheless, a significant difference is evident and supported by community composition data. While precipitation can contribute to a slight increase in $\delta^{15}\text{N}$ levels, Santa Rosa Island receives intermediate levels of rainfall compared to Santa Cruz and San Miguel Islands (Du et al., 2021). If precipitation was a primary driver of $\delta^{15}\text{N}$ levels in our study system, levels would instead be expected to be most elevated on San Miguel Island.

Furthermore, isotope levels in breast feathers are reflective of the individual's diet at the time they were grown in, post-yearly molt. Thus, our samples, while collected during slightly different months, represent the same period of local climatic conditions, making them a true indicator of dietary differentiation (Chamberlain et al., 2000).

Variation in $\delta^{13}\text{C}$ levels among island populations

Our findings that the San Miguel Island sparrow population had elevated levels of $\delta^{13}\text{C}$ in analyzed feathers suggests a strong foraging interaction with CAM and C4 photosynthesis-using plants, and plants grown in saline soil (Figs. 2 & 3). Due to a long history of grazing, and a relatively recent start on restoration efforts, San Miguel Island has a very grassland-dominated ecosystem. Poaceae, the grass family, uses C4 photosynthesis (Halvorson & Koske, 1987; Glebskiy et al., 2023). Additionally, San Miguel Island hosts an abundance of invasive iceplant (*Carpobrotus chilensis*) and a rebounding population of native *Dudleya* species, both of which use CAM photosynthesis (Zellman, 2014; Park et al., 2016). While there isn't currently literature on song sparrows using iceplant as a food resource, San Miguel Island song sparrows have been observed utilizing it as nesting material (Kern et al., 1993), suggesting the presence of foraging interactions with edible plant parts. However, while San Miguel Island does host the above C4 and CAM species, it still has a relative abundance of C3 plants, such as coyote brush, sage, and lupine (Gamboa et al., 2021). This leads us to hypothesize that, while sparrows on San Miguel Island likely do consume proportionally more C4 and CAM plants, high soil salinity is providing an additional boost to $\delta^{13}\text{C}$ levels (Park et al., 2019). The extreme winds on the island deposit salt from the surrounding ocean, leading to the soils having a comparatively higher salt content (Zellman, 2014). San Miguel's landscape is largely dunes, a landscape characterized by high salinity (McLachlan & Brown, 2006). Under highly salt-stressed conditions, stomatal conductance decreases, therefore decreasing carbon isotope discrimination and increasing levels of $\delta^{13}\text{C}$ in a plant's tissues. (Sandquist & Ehleringer, 1995; Park et al., 2019)

The $\delta^{13}\text{C}$ isotope signature of C3 plants lies around -28‰, while C4 plants lie around -14‰, and CAM plants range from -10‰ to -20‰ (O'Leary, 1988). The greater the proportion of C4 and CAM plants in an animal's diet, the less negative their $\delta^{13}\text{C}$ value will be skewed. The average $\delta^{13}\text{C}$ value for San Miguel lies around -21.4‰, significantly less negative than the values found on either other island (-22.6‰ and -22.7‰) (Fig. 2). Consumer tissues have only a slight

elevation in $\delta^{13}\text{C}$ levels compared to their dietary intake, making $\delta^{13}\text{C}$ levels a reliable indicator of diet (Kelly, 2000). However, $\delta^{13}\text{C}$ levels in the plants themselves can be influenced by certain factors. Research has found a positive linear relationship between $\delta^{13}\text{C}$ levels in leaves and average precipitation, indicating that the elevated $\delta^{13}\text{C}$ levels in sampled San Miguel Island song sparrows may in fact be due to the greater amounts of precipitation the island receives, rather than a significantly different foraging niche (Du et al., 2021). Future study analyzing San Miguel Island plant $\delta^{13}\text{C}$ levels is needed to determine the exact driver behind the elevated feather $\delta^{13}\text{C}$ levels in San Miguel Island song sparrows. While analysis of gut contents would be more direct, the island song sparrow is a California Species of Special Concern, making that method infeasible (Shuford & Gardali, 2008).

Blood parasite infection rates

The absence of significant variation in abRBC density and WBC:abRBC ratio among San Miguel and Santa Rosa Islands suggests equivalent infection rates (Fig. 4). Considering the distinct differences in climate between San Miguel and Santa Rosa Islands, particularly regarding average wind speed and rainfall, such comparable infection rates are unexpected (Schoenherr et al., 2003). It is noteworthy that previous research has found significant differences at immune-linked gene loci among island song sparrow populations. Even if acute infection rate may not be the primary driver, something is influencing differences in immune response (Gamboa, *pers. comm.*). It is possible that infections in our samples were largely dormant or chronic; in those cases, heightened parasitemia would not be detectable on smears, and PCR or other methods would need to be utilized (Jarvi et al., 2003; Ricklefs & Sheldon, 2007). Additionally, screening slides for actual hemoparasite levels is suggested for future studies to better substantiate the relationship of blood cell levels to infection rate and identify otherwise undetected culprits (Ricklefs & Sheldon, 2007). Furthermore, variation may be more detectable in the form of parasite species rather than abundance, as given the other differences in community assemblage among the islands, variation in parasite community assemblage would be expected. Differences in immunity-linked genetic markers may be more related to adaptive defenses to specific parasite species, rather than rates of infection (Maizels, 2009). After all, localized resistance to sympatric parasite species has been observed in both mainland song and

white-crowned sparrow populations (MacDougall-Shackleton et al., 2002; Sarquis-Adamson & MacDougall-Shackleton, 2016).

Previous taxonomic research has found San Miguel Island sparrow's plumage to be darker, in line with Gloger's rule (Patten & Pruitt, 2009). The primary hypothesis for darker pigmentation in the San Miguel Island population is that it is an adaptive response, resistant to increased exposure to blood parasites and their Diptera vectors under the moist conditions (Gamboa, *pers. comm.*). However, given the lack of significance in our results, this may not be the case. Increased melanization, while resistant to blood parasites, is also commonly adaptive against feather-eating bacteria that similarly thrive under humid conditions (Burt & Ichida, 2004). However, unless the bacteria penetrate the skin, which is not their target, a detectable immune response is not elicited (Leclaire et al., 2015). The bacteria can however elicit an adaptive increase in feather melanin content. Song sparrows have been found to exhibit increased melanization in humid regions where feather-eating bacteria are more abundant and aggressive (Burt & Ichida, 2004). The moist conditions of San Miguel Island may be driving the same pattern, unrelated to blood parasite infections.

Conclusion

While climate-driven patterns of phenotypic variation are generally well understood across broad spatial scales, determining patterns across small spatial scales is notoriously difficult. Song sparrow phenotypic differences across a broad scale predict small-scale differences; however, the nature of this variation is not well understood. Using islands as a model system, our study provides evidence for divergence in behaviorally-linked traits among song sparrow populations occupying a heterogeneous landscape. Our study is contributing to a more comprehensive understanding of the complex interactions between local environmental factors and adaptive responses, as well as how island syndromes can exacerbate these interactions. Island effects of reduced dispersal distances serve only to heighten and quicken evolutionary processes among island populations, leading to the California Channel Islands being a laboratory for song sparrow adaptive differentiation. Furthermore, the Channel Islands are actively managed and in various stages of restoration after hundreds of years of grazing. Better understanding island song sparrow behavioral differences, especially dietary differences, is important to inform and understand the impacts of conservation management moving forward. Specifically, it informs the management

of fennel as both an invasive plant and possibly an important food resource. As both climate change and management efforts march forward, it is essential to understand drivers of current variation, as that informs our understanding of these populations' responses to future change.

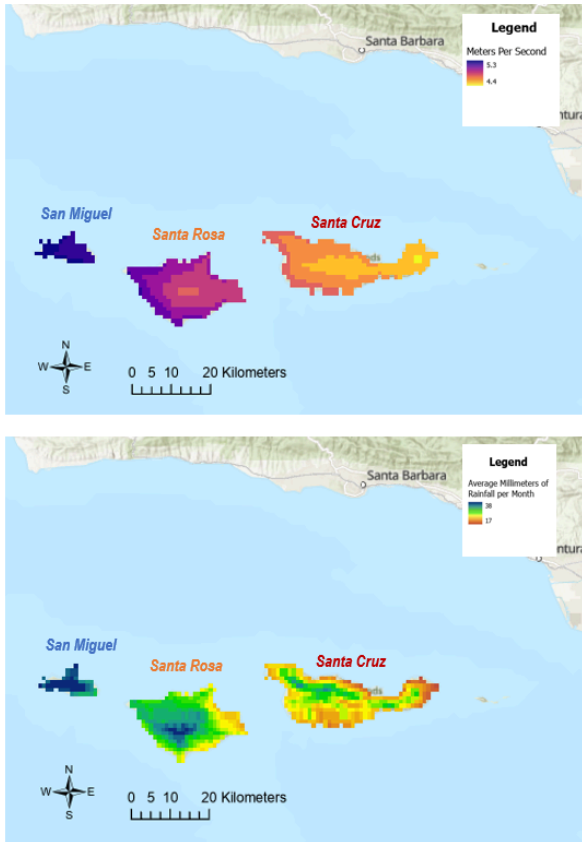
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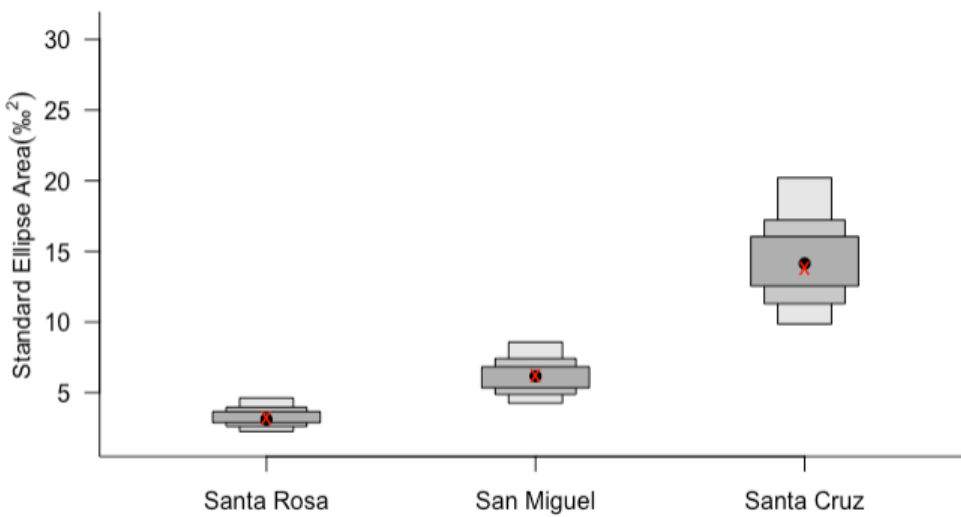
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Appendix



Appendix 1. Maps of the northern California Channel Islands showing average wind speed and precipitation. Data extracted from WorldClim.



Appendix 2. Bayesian standard ellipse area (SEAb), with boxes representing 50%, 90%, and 95% confidence intervals, respectively. The black dot represents the mode, and the red x represents the mode corrected for small sample size.

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