

1 **TITLE:** Environmental correlates and functional consequences of bill divergence in island song
2 sparrows

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29 *melodia*, California Channel Islands

30 **SUMMARY STATEMENT**

31 Island song sparrow bill differences are correlated with climate, not vegetation, and
32 experimental evidence finds no functional effect on foraging efficiency. This suggests many
33 factors shape this multifunctional trait.

34

35 **ABSTRACT**

36 Inferring the environmental selection pressures responsible for phenotypic variation is a
37 challenge in adaptation studies as traits often have multiple functions and are shaped by complex
38 selection regimes. We provide experimental evidence that morphology of the multifunctional
39 avian bill is related to climate, not foraging efficiency, in song sparrows (*Melospiza melodia*) on
40 the California Channel Islands. Our research builds on a study in song sparrow museum
41 specimens that demonstrated a positive correlation between bill surface area and maximum
42 temperature, suggesting a greater demand for dry heat dissipation in hotter, xeric environments.
43 We sampled contemporary sparrow populations across three climatically distinct islands to test
44 the alternate hypotheses that song sparrow bill morphology is either a product of vegetative
45 differences with functional consequences for foraging efficiency or related to maximum
46 temperature and, consequently, important for thermoregulation. Measurements of >500 live
47 individuals indicated a significant, positive relationship between maximum temperature and bill
48 surface area when correcting for body size. In contrast, maximum bite force, seed extraction
49 time, and vegetation on breeding territories (a proxy for food resources) were not significantly
50 associated with bill dimensions. While we cannot exclude the influence of foraging ability and
51 diet on bill morphology, our results are consistent with the hypothesis that variation in song
52 sparrows' need for thermoregulatory capacity across the northern Channel Islands selects for
53 divergence in bill surface area.

54

55 **INTRODUCTION**

56 Determining the environmental factors that drive adaptation in traits is a central goal in
57 evolutionary biology, but this is often challenging in natural populations (Kawecki and Ebert,
58 2004; MacColl, 2011; Reznick and Travis, 1996). Such challenges arise because traits may serve
59 different functions such that the observed phenotypic variation is a product of multifarious
60 selection pressures (e.g., Egea-Serrano et al., 2014; Pfrender, 2012; Shultz and Burns, 2017;

61 Templeton and Shriner, 2004; Wilkins et al., 2013). Multiple selection pressures can act either
62 synergistically, shifting the population phenotypic mean towards a predictable adaptive
63 optimum, or act antagonistically such that the observed phenotypic means represents a
64 compromise, or trade-off between different functions (Svensson and Calsbeek, 2012). This
65 concept of adaptation as a compromise between different functions is reinforced by empirical
66 studies of natural populations (e.g., Egea-Serrano et al., 2014; Ghalambor et al., 2003; Kim et al.,
67 2011; Robinson et al., 2006). Thus, testing which aspects of the environment act as important
68 selection pressures requires consideration of the different functions of a given trait and the
69 functional consequences associated with shifting trait means (Ghalambor et al., 2003; Jones et
70 al., 1977).

71 The avian bill is one of the most studied multifunctional, morphological traits. The bill is
72 involved in many fitness-related behaviors including ectoparasite removal (Clayton et al., 2005),
73 communication (Ballentine, 2006; Podos, 2001), tool creation and use (Fayet et al., 2020; Rutz et
74 al., 2016; Troscianko et al., 2012), thermoregulation (Greenberg et al., 2012; Ryeland et al.,
75 2017; Symonds and Tattersall, 2010), and, most notably, food acquisition (Barbosa and Moreno,
76 1999; Benkman, 1993; Temeles and Kress, 2003). Consequently, predicting local optima for bill
77 sizes is difficult given the potentially conflicting functional demands. For example, an increase
78 in bill morphology in the Darwin's finches is associated with improved foraging efficiency on
79 hard seeds, yet it is also predicted to cause correlated changes in syllable rate and frequency
80 bandwidth of vocal signals, which alters song production (Podos and Nowicki, 2004).
81 Furthermore, finches with increased bill surface area have greater heat dissipation, which is
82 hypothesized to improve thermoregulatory function (Tattersall et al., 2018). Similar interspecific
83 patterns of bill divergence correlated with multiple environmental drivers and resulting in
84 functional consequences have been documented in other passerines as well (Friedman et al.,
85 2019). Bill morphology in any bird species is, therefore, a product of trade-offs among multiple
86 selection pressures including, but not limited to, climate, food resources, and vocal signaling.
87 Bill dimensions also have a strong genetic component, indicating that this important trait can
88 readily evolve in response to selection (Åkesson et al., 2008; Boag, 1983; Grant, 1983; Jensen et
89 al., 2003; Keller et al., 2001). Given that the strength of selection may shift over time and space
90 (Siepielski et al., 2009; Siepielski et al., 2013), investigating avian bill morphology differences

91 among environments and populations can provide insight into how multiple selection pressures
92 act to generate and maintain variation.

93 The relationship between bill morphology and foraging ability has received extensive
94 attention, with numerous empirical studies finding correlations between bill size and
95 characteristics of available food resources or foraging ability (e.g., Langin et al., 2015; Nebel et
96 al., 2005; Temeles et al., 1993). For instance, bill depth in the medium ground finch (*Geospiza*
97 *fortis*) is positively correlated with the abundance of large, hard seeds, and evolution in response
98 to fluctuations in seed availability across years results in rapid adaptation (Grant and Grant
99 2006). Relatively small modifications in bill morphology among Darwin's finches result in
100 functional differences in bite force (Herrel et al., 2010). This strong selection pressure on bill
101 morphology for improved foraging ability has resulted in diversification and adaptive radiation
102 in several avian families (Benkman, 2003; Burns et al., 2003; Grant and Grant, 2002;
103 Lamichhaney et al., 2015; Lerner et al., 2011; Parchman et al., 2006). These striking results
104 coupled with other empirical studies suggest bill morphology should be strongly associated with
105 foraging and dietary resources. Yet, selection for foraging efficiency may not operate in isolation
106 from other environmental and ecological drivers.

107 The avian bill has also been studied in the context of thermoregulation and, specifically,
108 heat dissipation (Tattersall et al., 2016). The bird bill is an exposed, vascularized network that
109 exchanges heat directly with the environment, thereby acting as a 'thermal window' between
110 internal temperature and external, ambient temperature (Hagan and Heath, 1980; Symonds and
111 Tattersall, 2010; Tattersall et al., 2009). Increased blood flow to the vascularized region of the
112 bill results in increased heat dissipation (Tattersall et al., 2016). By dissipating dry heat through
113 radiation rather than panting, birds in arid, xeric environments may reduce evaporative water loss
114 while maintaining body temperature equilibrium (Dawson, 1981; Tattersall et al., 2016).
115 However, selection for large bills to increase thermoregulatory capacity could also impact diet
116 depending on the availability of food resources and on how strongly bill dimensions affect
117 functionality, namely in bite force and seed extraction (Herrel et al., 2010; Soons et al., 2015;
118 van der Meij and Bout, 2004). Thus, testing the relative importance of food resources and
119 climate on bill variation and evaluating the functional consequences of population shifts in bill
120 morphology allows for inferring how selection operates on integrated traits.

121 Here, we investigate the relationship between variation in bill surface area, feeding
122 performance, and climate in song sparrows (*Melospiza melodia*) breeding on the California
123 Channel Islands. These island populations provide a model system for investigating how
124 environmental factors influence adaptation in bill morphology. Song sparrows are continuously
125 distributed along a climatic gradient ranging from cold, wet, and very windy on San Miguel and
126 Santa Rosa Islands to hot, arid, and less windy on Santa Cruz and Anacapa Islands (Schoennerr
127 et al., 1999; Fig. 1). In this system, maximum island temperature has been shown to be positively
128 correlated with bill surface area of song sparrow museum specimens and implicated in aiding in
129 thermoregulation (Greenberg and Danner, 2012). Yet, the islands' west-to-east climate gradient
130 is also associated with vegetation differences (Junak et al., 2007) that could affect song sparrow
131 habitat composition and food availability. We sampled contemporary sparrow populations across
132 three climatically distinct islands (San Miguel, Santa Rosa, and Santa Cruz Islands) to test two
133 hypothesized functional adaptations in song sparrow bills: thermoregulation and foraging
134 efficiency. If bill morphology is acting as a thermoregulatory trait, we predicted that variation
135 among song sparrow populations would be correlated with climatic differences across islands. If
136 foraging efficiency explained variation in bill morphology, we predicted that bite force or seed
137 extraction time would change as a function of bill dimensions, given that song sparrows
138 primarily consume seeds during the non-breeding season (Arcese et al., 2002). We additionally
139 assessed plant composition in song sparrow habitats (a proxy for food resources) across the three
140 islands. Our combined assessments of the environmental correlates and functional consequences
141 of bill variation allowed us to infer how complex selection regimes shape individual morphology
142 and feeding performance.

143

144 **MATERIALS & METHODS**

145 *Animal capture and morphological measurements*

146 We captured and measured song sparrows on San Miguel, Santa Rosa, and Santa Cruz
147 Islands during three breeding seasons (February-June 2014-2016). All birds were target-captured
148 using mist-nets and song playback in the morning (thirty minutes before sunrise to four hours
149 after sunrise) when territory defense and foraging activities are high. We measured bill
150 dimensions (depth, width, and length) from the anterior edge of the nares (Fig. 1B,C),
151 tarsometatarsus length, wing length (0.01 mm precision), and mass. Estimates of bill depth,

152 width, and length were used to generate total bill surface area, following Greenberg and Danner
153 (2012). When comparing bill surface area among populations, we used the residual of a linear
154 regression model with bill surface area as the response ($bill_{sc}$) and the first principal component
155 of an analysis of tarsometatarsus length and wing length ($PC1_{bod}$) as the predictor (Greenberg
156 and Danner, 2012). Tarsometatarsus and wing lengths are indicators of structural body size in
157 birds, and this approach allows us to control for allometry (Rising and Somers, 1989). Negative
158 values for residual bill surface area are indicative of smaller bill sizes than predicted by body
159 sizes alone and, conversely, positive values suggest larger bill sizes than predicted by body sizes
160 alone.

161 We applied nonparametric tests in R (R Core Team 2020) to determine whether raw
162 (uncorrected for body size; $bill_{raw}$) and residual (corrected for body size; $bill_{sc}$) bill surface area
163 differed by island. Specifically, we used Kruskal-Wallis tests (*kruskal.test*) to assess whether
164 island raw and residual bill surface area mean ranks differed, while accounting for unequal
165 variances. We did not include sex in our models, because body size corrections account for
166 allometric differences between males and females. To further investigate island differences, we
167 performed post-hoc, pairwise comparisons of island mean ranks and output 95% confidence
168 intervals around estimated differences using Mann-Whitney U tests (*wilcox.test*) with Bonferroni
169 corrections for multiple-testing.

170 ***Testing if song sparrows experience different thermal environments and habitats***

171 We extracted climate data at 1 km² (30s) spatial resolution from WorldClim v. 1.4
172 (Hijmans et al., 2005) for all sampling locations using ArcGIS v. 10.4 (ESRI 2011) to test if
173 birds on different islands experience different temperatures. Minimum, maximum, and mean
174 monthly temperatures were highly correlated ($r^2 > 0.7$). Based on previous work showing a
175 significant, positive correlation between residual bill surface area and maximum temperature
176 (Greenberg and Danner, 2012), we limited our analyses to maximum temperature and extracted
177 monthly temperatures in July, the hottest month of the year on average for the northern Channel
178 Islands. Extracted maximum temperature values (T) served as a proxy for climate in individual
179 song sparrow territories. As with analyses of bill dimensions, we performed a nonparametric
180 Kruskal-Wallis test to compare island mean ranks and quantified pairwise differences in island
181 mean ranks and 95% confidence intervals using post-hoc Mann-Whitney U tests.

182 Song sparrows generally occupy low shrubland and, occasionally, riparian and coastal
183 sage scrub habitat across the Channel Islands (Shuford and Gardali, 2008). To infer if sparrows
184 use different habitats with different plant species (a proxy for dietary resources), we conducted
185 vegetation surveys within a 25-meter radius of each mist-net location for sampled birds. Because
186 sampling occurred during the breeding season, these measurements were taken within the
187 approximated territories of sampled birds and, thus, reflect the plant species available. We
188 recorded dominant woody vegetation type to the species level, when possible, for all plants that
189 comprised >50% of the total area. Additionally, we identified commonly occurring vegetation
190 types and categorized the relative abundance of these vegetation types at all sparrow sampling
191 sites. Presence and coverage of vegetation types within the sampling area was recorded using a
192 ranked scale including absent (0%; 1), trace (<10%; 2), some (10-25%; 3), prominent (25-50%;
193 4), and dominant (>50%; 5). To infer island-level vegetative differences among song sparrow
194 territories, we used Fisher's exact test in R (*fisher.test*) to test for an association between ranked
195 abundance of vegetation types and island. We modeled the null distribution of the test statistic
196 using 10,000 Monte Carlo simulations, allowing us to estimate the p-value under the null
197 hypothesis that the abundance of different vegetation types is independent of the island sampled.

198 We modeled vegetation for individual sampling locations by transforming ordinal
199 vegetation data to quantitative dimensions using nonlinear principal components analysis
200 (NLPCA) implemented in the R package *Gifi* (Mair and de Leeuw, 2019). This multivariate
201 method reduced the complexity of correlated vegetation variables to two principal components in
202 ordination space while accounting for ranked abundance of each vegetation type. We visually
203 inspected NLPCA results and assessed loadings of categorical values on dimensional space to
204 infer what factors drive variation in the first two axes of variation ($PC1_{veg}$ and $PC2_{veg}$) among
205 song sparrow territories. We plotted individual sampling locations in vegetation space along
206 $PC1_{veg}$ and $PC2_{veg}$ axes and constructed 95% kernel density contours to visually assess overlap
207 among islands in vegetation space. To statistically compare these reduced vegetation descriptors
208 ($PC1_{veg}$ and $PC2_{veg}$) among islands, we again applied a nonparametric Kruskal-Wallis test to
209 account for unequal variances. We performed post-hoc Mann-Whitney U tests with Bonferroni
210 corrections and extracted estimated island means and 95% confidence intervals around these
211 differences. NLPCA dimensions ($PC1_{veg}$ and $PC2_{veg}$) were used for subsequent tests relating
212 habitat and residual bill surface area.

213 We performed linear regression to determine whether vegetation and climate were
214 significant predictors of residual bill surface area. We used the R function *lm* to model residual
215 bill surface area as predicted by maximum temperature and two vegetation dimensions ($PC1_{veg}$
216 and $PC2_{veg}$) resulting from NLPCA of all vegetation sampling sites. We generated 95%
217 confidence intervals around unstandardized beta estimates using the function *confint* in the base
218 *stats* package in R and extracted standardized beta coefficients for all predictors using the R
219 package *lm.beta* (Behrendt, 2014). Unstandardized and standardized beta coefficients allowed us
220 to evaluate the relative importance of climate versus vegetation (a proxy for diet) for predicting
221 variation in song sparrow bill surface area.

222 ***Measuring maximum bite force to infer the functional consequences of bill variation***

223 To determine whether divergence in bill morphology results in functional consequences
224 for food acquisition, we compared bill functional morphology between Santa Cruz and San
225 Miguel Island song sparrows. We expected functional differences to be largest between these
226 populations based on pronounced climate differences between islands and on phenotypes
227 observed in museum specimens by Greenberg and Danner (2012). All sampling and estimates of
228 bite force were performed in early spring 2014, when birds are primarily foraging on seeds. We
229 measured maximum bite force in the field using a custom-manufactured force meter (Herrel et
230 al., 2005; van der Meij and Bout, 2004). Briefly, we used a piezoelectric isometric force
231 transducer (type 9203, Kistler, Switzerland) fitted to custom-built stainless-steel bite plates
232 (specifications in Herrel et al., 1999) and connected to a charge amplifier (type 5995, Kistler,
233 Switzerland). A micrometer head allowed adjustment of the spacing between bite plates. For
234 each measurement, we held the bird upright and positioned the bite force meter between the
235 mandible and maxilla. We positioned the ends of the plates two-thirds of the distance from the
236 bill tip to commissure, the location where song sparrows crush seeds (Danner, *pers. obs.*). The
237 meter had a precision of 0.1 Newtons. We recorded the maximum bite force over a period of 15
238 seconds. Birds were gently coaxed to open the bill by tapping on the tomia with a thin, metal
239 spade. Preliminary analyses on song sparrows indicated that bite force did not decline across
240 observations when measurements were interspersed with 15-second rest intervals (Danner, *pers.*
241 *obs.*). Thus, we recorded three measurements per bird with one-minute rest intervals to ensure
242 recovery and used the maximum bite force for all further analyses. All morphological
243 measurements were taken shortly before releasing the birds to minimize the effect of handling

244 stress on bite force and seed extraction trials. We maintained the same force meter settings for all
245 individuals.

246 To assess the relationship between bill dimensions and bite force, we performed multiple
247 regression analysis. We included bill depth and body size as predictors, because these traits have
248 been found to strongly predict bite force in other passerines (Herrel et al., 2005; Soons et al.,
249 2015; Van Der Meij and Bout, 2008). We generated a composite score of body size ($PC1_{\text{bod}}$)
250 using PCA of tarsometatarsus and wing lengths for individuals used in bite force analyses. We
251 applied linear regression in R using the function *lm* with bill depth and $PC1_{\text{bod}}$ as our predictors
252 for maximum bite force. We did not include island sampled in our analyses as this was not
253 independent of bill dimensions. We extracted standardized beta coefficients and 95% confidence
254 intervals around unstandardized beta coefficients to compare the effects of both predictors on
255 maximum bite force.

256 ***Quantifying seed extraction time to infer the functional consequences of bill variation***

257 We held a subset of captured males in 2014 for caged field trials to quantify foraging
258 efficiency. Females were excluded from trials to prevent interruption of incubating or laying
259 behaviors. Following capture, we immediately placed birds in covered trial cages for acclimation
260 to experimental conditions (*see Fig. S1 for details*). All subjects were provided with water
261 throughout the duration of the trial. We provided a two-hour acclimation and fasting period prior
262 to the initiation of each trial. During the acclimation period, we monitored activity continuously
263 via video cameras. Following acclimation, we initiated recording and slowly poured 10 grams of
264 sterilized nyjer seed (*Guizotia abyssinica*) through a funnel in a brown plastic tube, which
265 dispersed seeds across the floor of the cage. Sterilized nyjer seed is commonly used as bird feed
266 for small passerines, and sterilization ensures the subsequent germination does not occur.
267 Although *G. abyssinica* is not found on the Channel Islands and may not represent typical seed
268 resources, song sparrows are generalist, ground-foragers. Thus, we assumed that our
269 experimental food provisioning method facilitated normal foraging behavior. Trials lasted 45-
270 120 minutes depending on latency to eat. We recorded behavioral notes during both acclimation
271 and trial periods.

272 We reviewed foraging trial videos to quantify seed extraction time across multiple seeds.
273 We counted the number of frames between when a bird's bill tip lifted from the floor of the cage
274 with a seed, to when the husk fell from the tomium (van der Meij and Bout, 2006). We divided

275 the number of frames by the camera's frame capture rate (29.97 frames/second) to calculate seed
276 extraction time. The high temporal resolution of the cameras provided a precision of 0.033
277 seconds. We included only feeding events in which seed manipulation was observed throughout
278 the entire seed extraction process.

279 Seed extraction is a complex task that requires manipulation of the bill along multiple
280 axes. Consequently, we performed a PCA of bill depth, width, and length and used the first axis
281 of variation ($PC1_{\text{bill}}$) to test whether differences in bill morphology is result in differences in seed
282 extraction time. We included $PC1_{\text{bill}}$ of bill dimensions as a fixed effect in a linear mixed model
283 predicting seed extraction time using the function *lmer* in the package *lme4* (Bates et al., 2015).
284 We accounted for repeated observations of the same bird by including individual as a random
285 effect. We extracted 95% confidence intervals around the estimated coefficient for $PC1_{\text{bill}}$ using
286 the function *confint* to infer the strength of $PC1_{\text{bill}}$ in modifying seed extraction time.

287

288 **RESULTS**

289 ***Patterns of bill variation in contemporary populations***

290 From 2014–2016, we measured 542 adult song sparrows (San Miguel Island, $n = 104$;
291 Santa Rosa Island, $n = 194$; Santa Cruz Island, $n = 244$) sampled from 432 unique net locations
292 (San Miguel Island, $n = 68$; Santa Rosa Island, $n = 141$; Santa Cruz Island, $n = 223$; Fig. 1).
293 Patterns of bill variation in contemporary populations aligned with our expectations based on
294 previous research using museum specimens (Greenberg and Danner 2012). Islands differed
295 significantly in mean ranks for both raw bill surface area ($H_{df=2} = 138.30, P < 0.001$) and residual
296 bill surface area ($H_{df=2} = 143.96, P < 0.001$) using Kruskal-Wallis tests. We found all Mann-
297 Whitney U pairwise comparisons of raw and residual bill surface areas between islands were
298 significant (Table 1). We confirmed larger bills were found on Santa Cruz Island, medium bills
299 were found on Santa Rosa Island, and the smallest bills were found among San Miguel Island
300 birds based on Hodges–Lehmann estimates of medians (Table 1).

301 ***Maximum temperature and vegetation within breeding territories across islands***

302 Environmental conditions within song sparrow breeding territories differed among the
303 432 unique sampling locations across islands (San Miguel Island, $n = 68$; Santa Rosa Island, $n =$
304 141; Santa Cruz Island, $n = 223$; Fig. 1). We found mean ranks in island maximum temperatures
305 were significantly different ($H_2 = 282.63, P < 0.001$). Post-hoc pairwise comparisons of

306 maximum temperature were significantly different between island pairs as expected, such that
307 Santa Cruz Island had a higher and San Miguel has lower median estimates of maximum
308 temperature in territories (Table 1). Additionally, we found ranked abundances in common
309 vegetation types were significantly associated with island sampled using 10,000 Monte Carlo
310 simulations in Fisher's exact test ($P < 0.001$). Common dominant vegetation included coyote
311 brush (*Baccharis pilularis*), toyon (*Heteromeles arbutifolia*), silver bush lupine (*Lupinus*
312 *albifrons*), introduced sweet fennel (*Foeniculum vulgare*), and a mix of annual and perennial
313 grasses (Table S1).

314 Using NLPCA, we reduced the complexity in correlated ranked abundance of vegetation
315 types among sampling locations. The first two principal components explained a total of 52.7 %
316 of the variation in vegetation. The first axis (PC1_{veg}) explained 30.5% of the variation in
317 vegetation, and the abundance of grasses and the joint effects of the abundance of lupine,
318 miscellaneous forbs, and other substrates (*i.e.*, bare ground or rock, water) loaded in opposing
319 directions (Fig. 2A). This suggests that positive values along PC1_{veg} are indicative of territories
320 with more lupine, forbs, and other substrates and less grass, and negative values represent the
321 inverse of this relationship (Fig. 2A). The second axis of variation (PC2_{veg}) explained 22.2% of
322 variation in vegetation and reflects a trade-off in fennel and coyote brush (Fig. 2A). Positive
323 values indicate more fennel and less coyote brush, and negative values represent less fennel and
324 more coyote brush (Fig. 2A). We found islands overlapped in vegetation space based on 95%
325 kernel density contours (Fig. 2B). We assessed these relationships statistically using
326 nonparametric tests and found significant differences among island mean ranks in both
327 vegetation dimensions (PC1_{veg}, $H_2 = 31.73$, $P < 0.001$; PC2_{veg}, $H_2 = 241.85$, $P < 0.001$; Table
328 1). Using post-hoc Mann-Whitney U tests, we found PC1_{veg} scores for Santa Rosa Island
329 territories were more negative, such that territories on Santa Rosa Island had more grass and less
330 miscellaneous forbs, bare ground and rock, open water, and lupine compared to Santa Cruz and
331 San Miguel Islands (Fig. 2B). In contrast, we found PC2_{veg} scores for Santa Cruz Island
332 territories were significantly greater, with Santa Cruz territories encompassing more fennel and
333 less coyote brush compared to Santa Rosa and San Miguel Islands (Fig. 2B).

334 Multiple regression analysis was used to assess the relative importance of vegetation
335 (PC1_{veg} and PC2_{veg}) and maximum temperature in driving bill differences in adult song sparrows
336 (Santa Cruz, $n = 218$ birds, Santa Rosa, $n = 146$ birds, San Miguel, $n = 81$ birds). These variables

337 together explained a significant proportion of variation in residual bill surface area ($F_{3,442} =$
338 $55.25, p < 0.001$, adjusted $R^2 = 0.27$; Fig. 3). We found residual bill surface area was
339 significantly predicted by maximum island temperatures ($\beta_{\text{standardized}} = 0.40$, $\beta_{\text{unstandardized}} = 3.06$
340 $(2.20 - 3.93)$, $t = 10.350$, $P < 0.001$). Although we found island differences in vegetation space,
341 neither $PC1_{\text{veg}}$ ($\beta_{\text{standardized}} = -0.05$, $\beta_{\text{unstandardized}} = -0.28$ $(-0.77 - 0.20)$, $t = -1.147$, $P = 0.25$) nor
342 $PC2_{\text{veg}}$ ($\beta_{\text{standardized}} = 0.04$, $\beta_{\text{unstandardized}} = 0.20$ $(-0.43 - 0.83)$, $t = 0.610$, $P = 0.54$) were
343 significant predictors. Vegetation space was used as a proxy for available food resources, and
344 these results suggest climate, not food, is likely driving differences in residual bill surface area.

345 ***Functional consequences of bill variation between island populations***

346 Contrary to predictions from the foraging efficiency hypothesis, we did not find evidence
347 that differences in bill morphology result in functional differences in bite force between birds on
348 San Miguel ($n = 28$) and Santa Cruz Island ($n = 28$). Body size ($PC1_{\text{bod}}$) and bill depth together
349 explained very little of the variation in maximum bite force ($F_{2,53} = 1.45$, $P = 0.24$, adjusted $R^2 =$
350 0.02 ; Fig. 4A). Although Santa Cruz Island birds tended to have larger structural bodies
351 ($PC_{\text{bod}(\text{Cruz})}$, $\text{mean} \pm \text{sd} = 0.22 \pm 1.09$; $PC_{\text{bod}(\text{Miguel})}$, $\text{mean} \pm \text{sd} = -0.22 \pm 1.02$), body size distributions
352 generally overlapped and did not significantly predict maximum bite force ($\beta_{\text{standardized}} = 0.17$,
353 $\beta_{\text{unstandardized}} = 0.23$ $(-0.14 - 0.59)$, $t = 1.247$, $P = 0.22$). Island sampling groups differed in bill
354 depth as expected with birds on Santa Cruz Island having deeper bills ($\text{Depth}_{(\text{Cruz})}$, $\text{mean} \pm \text{sd} =$
355 6.15 ± 0.21 ; $\text{Depth}_{(\text{Miguel})}$, $\text{mean} \pm \text{sd} = 5.54 \pm 0.20$; Fig. 4A). Yet, we found little evidence to suggest
356 that these differences in depth result in synonymous changes in maximum bite force ($\beta_{\text{standardized}} =$
357 0.17 , $\beta_{\text{unstandardized}} = -0.74$ $(-1.80 - 0.32)$, $t = -1.394$, $P = 0.17$).

358 We performed foraging trials in adult, male song sparrows from Santa Cruz Island ($n =$
359 23) and San Miguel Island ($n = 10$), and, again, found little evidence for an effect of bill
360 morphology on seed extraction time. The first principal component ($PC1_{\text{bill}}$) in a PCA of bill
361 depth, width, and length explained 58% of the variation in bill dimensions and was largely
362 driven by bill depth and width (Fig. S2). San Miguel Island and Santa Cruz Island birds
363 overlapped along PC1 (Fig. 4B), but San Miguel birds loaded more positively (shallower,
364 narrower, slightly longer bills). In contrast, Santa Cruz Island birds loaded more negatively,
365 suggesting birds tended to have deeper, wider, slightly shorter bills. The mean number of
366 observed extracted seeds was 60 seeds per individual ($\text{sd} = 32$, $\text{range} = 8 - 163$), and 13% of
367 variance was explained by individual effects. $PC1_{\text{bill}}$ had a very weak to negligible effect on seed

368 extraction time ($\beta = 0.009$ (-0.14 – 0.16), $t_{32} = 0.115$, $P = 0.91$). These results combined with bite
369 force analyses suggest that morphological differences in bills do not facilitate differences in
370 foraging efficiency in island song sparrows.

371

372 **DISCUSSION**

373 Identifying the ecological correlates of phenotypic variation provides insights into the
374 selection pressures that may shape complex traits and their multiple functions. The avian bill is
375 one such complex trait that has primarily been studied in the context of foraging ability despite
376 its critical role in preening, communication, and thermoregulation. Indeed, there has been
377 growing appreciation for the role of climate in shaping variation in bill morphology, as mounting
378 evidence suggests the bill is an important tool for heat dissipation and thermoregulation (e.g.,
379 Gardner et al., 2016; Greenberg and Danner, 2013; Ryeland et al., 2017; Symonds and Tattersall,
380 2010). Here, we tested whether climate and/or vegetation composition within breeding territories
381 significantly predicted bill variation in song sparrows on the California Channel Islands (i.e., San
382 Miguel, Santa Rosa, and Santa Cruz Islands). We confirmed that bill size, maximum
383 temperature, and vegetation composition differed among islands. However, only maximum
384 temperature significantly predicted residual bill surface area in a multiple regression analysis
385 including vegetation dimensions ($PC1_{veg}$ and $PC2_{veg}$) and temperature as predictors (Fig. 3). We
386 did not find a significant relationship between bill morphology and either maximum bite force or
387 seed extraction time. This provides additional evidence against foraging efficiency as a strong
388 selective pressure in this system. Together, these results suggest that climate may be more
389 important than diet and foraging ability in the evolution of a complex phenotype in song
390 sparrows on the California Channel Islands.

391 ***Vegetation differences do not directly result in concerted changes in bill morphology***

392 Analysis of habitat composition with respect to vegetation provides key insights into the
393 potential food resources available for breeding birds. Because song sparrows on the Channel
394 Islands occupy a strong east-west climate gradient, we expected some degree of habitat
395 differences among island breeding sites. Thus, it is not surprising that ranked abundance in our
396 focal vegetation categories were significantly associated with island sampled. For example,
397 Santa Cruz Island is characterized by greater heterogeneity in topography, soil composition, and
398 climate, which is correlated with increases in species richness and diversity of plants compared

399 to Santa Rosa and San Miguel Islands (Schoennerr et al., 2003). Our results demonstrate
400 increased diversity in vegetation space ($PC1_{veg}$ and $PC2_{veg}$) within Santa Cruz Island territories
401 (Fig. 2B). Yet, 95% kernel density contours also suggest a large proportion of overlap in
402 vegetation space among islands (Fig. 2B), and similar plant taxa identifiable to the genus and
403 species level were present across all islands (Table S1). More extensive vegetation and habitat
404 sampling may allow us to parse out fine-scale habitat differentiation among islands, but whether
405 any differences in vegetation result in differences in food resources is uncertain. Direct
406 observation of foraging behavior and evaluation of the available dietary resources during the
407 non-breeding season, when song sparrows most heavily rely on seeds, would allow us to draw
408 stronger inferences regarding the relationship among foraging ability, diet, and bill morphology.
409 Nevertheless, our analyses support the hypothesis that climate may facilitate vegetative
410 differences among song sparrow territories, but differences in vegetation did not directly predict
411 bill morphology in multiple regression analyses. Hence, vegetation, a proxy for food resources
412 and diet, may not be a strong selective pressure generating bill variation across islands, and we
413 found further evidence against selection operating on foraging ability in experimental tests of
414 foraging efficiency (Figs. 4A-B).

415 ***Variation in bill morphology does not result in differences in foraging efficiency***

416 We did not find a relationship between variation in bill morphology and either bite force
417 or seed extraction time (Fig. 4A-B), despite evidence that bill dimensions affect feeding
418 performance in other passerines (Anderson et al., 2008; Herrel et al., 2005; Navalón et al., 2019).
419 Indeed, some of the most well-documented cases of specialization in resource acquisition with
420 respect to bill variation occur in island systems (Burns et al., 2003; Grant and Grant, 2002). Of
421 these cases, Darwin's ground finches (*Geospiza sp.*) are perhaps most notable and ecologically
422 similar to song sparrows in their foraging behavior and diet (De León et al., 2014). In Darwin's
423 finches, birds exhibit correlations between both bill dimensions and bite force (Herrel et al.,
424 2005; van der Meij and Bout, 2008; Soons et al., 2015) and bill dimensions and seed extraction
425 times (van der Meij and Bout, 2008). The discordance between our results and findings from
426 studies of Darwin's finches may be attributed to multiple factors.

427 First, sparrows are generalist foragers with a heavy insectivorous diet during the breeding
428 season and a transition to a granivorous diet during the non-breeding season (Arcese et al.,
429 2002), whereas Darwin's ground finches' diets consist primarily of seeds throughout the year

430 (De León et al., 2014). Specialization on seeds and food limitation in ground finches facilitate
431 competitive interactions among species that overlap in their dietary niches (De León et al.,
432 2014), resulting in strong selection on individuals to optimize bill morphology for increased
433 foraging efficiency. On the California Channel Islands, it is unclear whether food resources are
434 limited and whether food limitation imposes a strong selective pressure on song sparrow
435 populations. Mass comparisons between sparrows from the Channel Islands and nearby mainland
436 California found island sparrows to heavier than mainland sparrows when correcting for
437 structural body size, suggesting island birds may be in better condition (Danner et al., 2014).
438 Increased mass among island sparrows supports the hypotheses that food resources are not
439 limited and reduced interspecific competition for food favors the sparrows' generalist diets
440 (Blondel, 2000; Clegg, 2010; Diamond, 1970; Keast, 1970; Scott et al., 2003). As a result,
441 variation in bill morphology may be decoupled from foraging efficiency traits measured in this
442 study.

443 Additionally, methodological limitations may have prevented us from quantifying key
444 traits associated with foraging. For example, previous research in Darwin's finches identify a
445 link between muscle mass and maximum bite force (Herrel et al., 2005; Herrel et al., 2010;
446 Soons et al., 2015), and other skeletal features are correlated with bite force and closing velocity
447 (Corbin et al., 2015). These methods require analysis of euthanized individuals, which we were
448 unable perform. Here, we evaluated bite force differences elicited from the posterior section of
449 the bill, not from the anterior (the tip) where functional differences in grasping and object
450 manipulation occur across avian families (Clayton et al., 2005; Demery et al., 2011; Gentle et al.,
451 1982; Sustaita, 2007). Although skeletal structures associated with foraging traits are highly-
452 correlated (Van Der Meij and Bout, 2008) and our measures adequately estimate a large
453 proportion of variation in overall bill morphology, future studies may examine unmeasured
454 phenotypic traits in this study to better estimate the functional consequences of craniofacial
455 variation. Finally, we were limited to using readily available bird seed for foraging trials to
456 increase our ability to observe detailed manipulation of the food resource. We did not compare
457 nyjer seed characteristics with those used by song sparrows on the Channel Islands during the
458 winter months. Yet, seed availability during winter months were likely similar given that non-
459 native, seed-producing plant species (e.g., annual grasses) are widespread (Junak et al., 2007)
460 and were present at most sampling locations (Table S1). Sample size does not appear to be an

461 issue, as a power analysis suggests that our sample sizes were sufficient to detect a biologically
462 relevant difference in maximum bite force given our experimental design (Fig. S3). Although we
463 did not find evidence that foraging efficiency is an important driver of variation in bill shape in
464 our study populations, further research is needed to definitively exclude the possibility that
465 differing food resources among islands is a selective force. Our experimental design provides a
466 framework for future studies to test how bill dimensions influence multiple components of
467 foraging efficiency (i.e., both bite force and seed extraction).

468 ***Evidence for the bill as a thermoregulatory trait in island sparrows***

469 Our results are consistent with the hypothesis that selection operates on the bill to
470 improve thermoregulatory ability in passerines occupying xeric environments. Increasing
471 empirical evidence demonstrate a relationship between climate and bill morphology that aligns
472 with the thermoregulatory hypothesis (reviewed by Tattersall et al., 2016), and this relationship
473 may be traced over evolutionary time (Campbell-Tennant et al., 2015). The ability to radiate heat
474 from unfeathered structures is particularly important for small passerines, including song
475 sparrows, which are more vulnerable to dehydration from evaporative water loss and, thus, more
476 susceptible to adverse effects of thermal stress (Mckechnie and Wolf, 2010; Whitfield et al.,
477 2015). Indeed, our results are consistent with previous research that identified a significant,
478 positive correlation between climate and bill morphology in eastern and Atlantic song sparrows
479 (Danner and Greenberg, 2014). A similar pattern has been described in Darwin's finches
480 (Tattersall et al., 2018) and other similarly-sized passerines (Greenberg and Danner, 2012;
481 LaBarbera et al., 2017; Laiolo and Rolando, 2001). The magnitude of the effect of climate in
482 predicting bill morphology may change according to seasonality (Greenberg et al., 2013),
483 environmental variation during development (Burness et al., 2013; Labarbera et al., 2020),
484 habitat type (Luther and Greenberg, 2014), and sex (Greenberg and Danner, 2013). Importantly,
485 selection may act simultaneously on other traits to facilitate thermoregulation, including internal
486 nasal structures (Danner et al., 2017), plumage (Wolf and Walsberg, 2000), and physiological
487 performance (e.g., Noakes et al., 2016; Tieleman et al., 2003; White et al., 2007; Whitfield et al.,
488 2015). Thus, further research that explores the complex relationship between temperature,
489 humidity, and other morphological and physiological traits is needed to better understand how
490 climate facilitates and maintains phenotypic variation.

491 ***Conclusions***

492 Consistent with previous studies using museum specimens, variation in bill morphology
493 among contemporary song sparrow populations on the California Channel Island is correlated
494 with maximum temperature, suggesting an important thermoregulatory function. Differences in
495 the vegetation and habitats used by sparrows on different islands were not strongly predictive of
496 observed bill divergence. Variation in bill morphology was also not correlated with bite force or
497 seed extraction, perhaps because song sparrows are generalist foragers. We hope that our results
498 encourage future research about how different environmental agents of selection simultaneously
499 act on avian bills to optimize the multiple, fitness-related functions of foraging,
500 thermoregulation, preening, and vocalization.

501

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516

517 **COMPETING INTERESTS**

518 The authors declare no competing or financial interests.

519

520 **AUTHOR CONTRIBUTIONS**

521 R.M.D., J.F.H., and T.S.S. designed the study. R.M.D. and M.P.G. collected field data with
522 additional support from T.S.S. J.F.H. provided instrumentation for field data collection. R.A.F.

523 extracted foraging data from videos. M.P.G. conducted all analyses with support from R.M.D.
524 The article was written by M.P.G. with additional input from C.A.M., W.C.F., T.S.S., J.F.H., and
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526

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532

533 **DATA AVAILABILITY**

534 Phenotypic and environmental data used for all analyses are available on Dryad
535 (<https://doi.org/10.5061/dryad.wwpzgmsjc>)

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537

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- 774

775 **LIST OF SYMBOLS AND ABBREVIATIONS**

776

PC1_{bod}	body size; composite score of body size based on PCA of tarsometatarsus and wing lengths used to estimate residual bill surface area
PC1_{veg}	primary axis of variation in vegetation; composite score of vegetation based on NLPCA of common vegetation types in sampling locations
PC2_{veg}	secondary axis of variation in vegetation; composite score of vegetation based on NLPCA of common vegetation types in sampling locations
PC1_{bill}	primary axis of variation in bill dimensions; composite score of bill depth, width, and length used in analysis of foraging efficiency
T	maximum environmental temperature (in July) of sampling location

777

778

779 **TABLE & FIGURE LEGENDS**

780

781 **Table 1. Nonparametric pairwise island comparisons (median±c.i.) for song sparrow raw**
782 **(uncorrected for body size) and residual (corrected for body size) bill surface areas,**
783 **maximum environmental temperatures (T), and vegetation dimensions (PC1, PC2).**

784 Pairwise comparisons were estimated using the Hodges-Lehmann method for bill surface areas
785 in 542 birds (San Miguel Island, $n = 104$; Santa Rosa Island, $n = 194$; Santa Cruz Island, $n =$
786 244) and for temperature and vegetation characteristics across 432 unique sampling locations
787 (San Miguel Island, $n = 68$; Santa Rosa Island, $n = 141$; Santa Cruz Island, $n = 223$). Vegetation
788 dimensions include PC1 and PC2 from nonlinear PCA of ranked abundance in vegetation
789 categories within breeding song sparrow territories. All islands had significantly different ($P <$
790 0.05) mean ranks in all bill and environmental variables based on nonparametric Kruskal-Wallis
791 tests. Post-hoc Mann-Whitney U 95% confidence intervals around differences in mean ranks are
792 shown in parentheses. Bill surface area analyses include only adult, breeding, territorial birds
793 with complete phenotype measurements, and maximum temperature was extracted only for these
794 unique sampling locations. Vegetation sampling occurred at most of these temperature sampling
795 locations and at locations for territorial birds that did not have complete phenotype
796 measurements.

797

798 **Figure 1. Sampling locations for comparison of song sparrow bill morphology (grey**
799 **circles), seed extraction time (red triangles), and maximum bite force (red boxed regions)**
800 **across three climatically-distinct islands (A) and measurements of bill length, depth (B),**
801 **and width (C) used for quantifying bill morphology. Bill length (l), depth (d), and width (w)**
802 **were taken from the anterior edge of the nares and used to calculate residual (body-size**
803 **corrected) bill surface area following Greenberg and Danner (2012). All sampling was conducted**
804 **during the breeding season (February-June) from 2014-2016. Inset shows the location of the**
805 **northern Channel Islands with respect to California.**

806

807 **Figure 2. Variable loadings (A) and PC1, PC2, and 95% kernel density contours by island**
808 **(B) from nonlinear PCA of vegetation within song sparrow territories. Sampling of 432**

809 unique sampling locations occurred during the breeding season from 2014-2016 on San Miguel
810 Island (blue; $n = 68$), Santa Rosa Island (orange; $n = 141$), and Santa Cruz Island (red; $n = 223$).

811

812 **Figure 3. Residual bill surface area predicted by maximum temperature in song sparrows**

813 **($n = 446$) on the California Channel Islands.** Residual bill surface area is total bill surface area

814 corrected for skeletal body size and calculated from measures of bill depth, width, and length,

815 tarsometatarsus length, and wing length in adult song sparrows on San Miguel Island ($n = 81$),

816 Santa Rosa Island (orange, $n = 147$), and Santa Cruz Island (red, $n = 218$). Primary and

817 secondary axes of variation from nonlinear PCA of vegetation ($PC1_{veg}$ and $PC2_{veg}$) were included

818 in the linear regression analysis and were not significant predictors of residual bill surface area.

819

820 **Figure 4. Relationship between song sparrow bill dimensions and foraging traits**

821 **[maximum bite force (A) and seed extraction time (B)] between birds on Santa Cruz Island**

822 **(red; $n_A = 28$, $n_B = 23$) and San Miguel Island (blue; $n_A = 28$, $n_B = 10$).** $PC1_{bill}$ is the first

823 orthogonal axis in a PCA of bill depth, width, and length taken from the anterior edge of the

824 nares.

825

826 **Table 1. Nonparametric pairwise island comparisons (median±c.i.) for song sparrow raw (uncorrected for body size) and**
 827 **residual (corrected for body size) bill surface areas, maximum environmental temperatures (T), and vegetation dimensions**
 828 **(PC1, PC2).** Pairwise comparisons were estimated using the Hodges-Lehmann method for bill surface areas in 542 birds (San Miguel
 829 Island, $n = 104$; Santa Rosa Island, $n = 194$; Santa Cruz Island, $n = 244$) and for temperature and vegetation characteristics across 432
 830 unique sampling locations (San Miguel Island, $n = 68$; Santa Rosa Island, $n = 141$; Santa Cruz Island, $n = 223$). Vegetation dimensions
 831 include PC1 and PC2 from nonlinear PCA of ranked abundance in vegetation categories within breeding song sparrow territories. All
 832 islands had significantly different ($P < 0.05$) mean ranks in all bill and environmental variables based on nonparametric Kruskal-
 833 Wallis tests. Post-hoc Mann-Whitney U 95% confidence intervals around differences in mean ranks are shown in parentheses. Bill
 834 surface area analyses include only adult, breeding, territorial birds with complete phenotype measurements, and maximum
 835 temperature was extracted only for these unique sampling locations. Vegetation sampling occurred at most of these temperature
 836 sampling locations and at locations for territorial birds that did not have complete phenotype measurements.

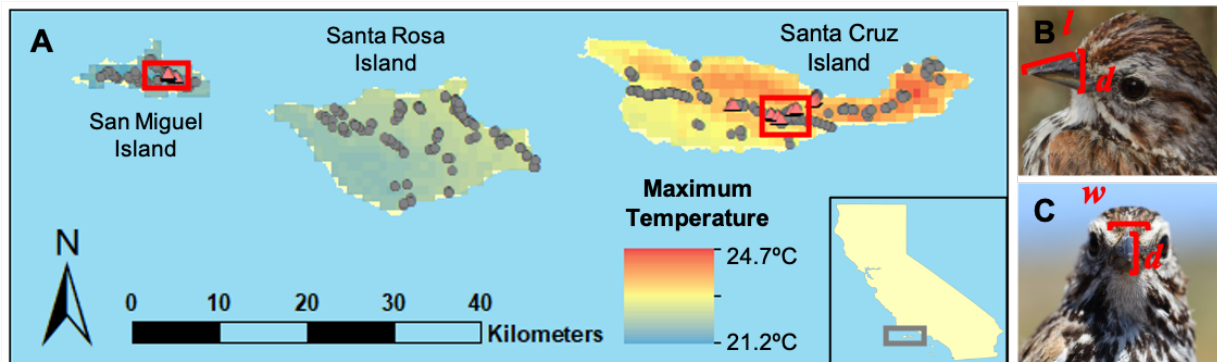
Island Comparison	Bill Surface Area		Maximum T	Vegetation	
	Raw (mm ²)	Residual	T (°C)	PC1 _{veg} (30.4%)	PC2 _{veg} (22.2%)
	2.32 ^{***}	2.72 ^{***}	1.00 ^{***}	0.35 ^{***}	1.38 ^{***}
Santa Cruz – Santa Rosa	(1.33 - 3.28)	(1.77 - 3.70)	(0.80 - 1.10)	(0.22 - 0.54)	(1.20 - 1.55)
	7.67 ^{***}	7.67 ^{***}	1.80 ^{***}	-0.34	1.36 ^{***}
Santa Cruz – San Miguel	(6.58 - 8.76)	(6.58 - 8.76)	(1.70 - 1.90)	(-0.67 - 0.00)	(1.13 - 1.59)
	5.49 ^{***}	5.03 ^{***}	0.80 ^{***}	-0.81 ^{***}	0.00
Santa Rosa – San Miguel	(4.35 - 6.58)	(3.93 - 6.11)	(0.70 - 0.80)	(-1.12 - -0.51)	(-0.10 - 0.11)

*Significant difference ($P < 0.05$) in population distributions between islands based on Mann-Whitney U tests

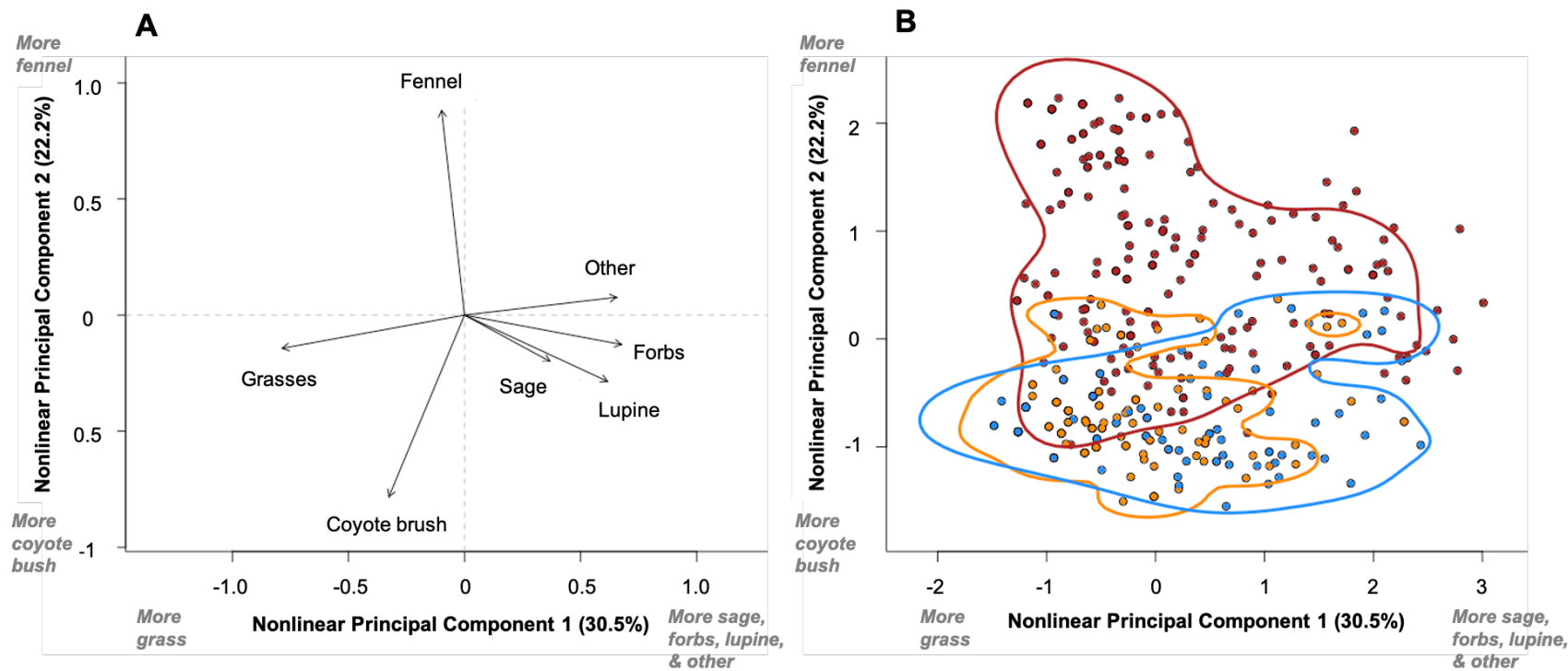
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839 **circles), seed extraction time (red triangles), and maximum bite force (red boxed regions)**
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841 **and width (C) used for quantifying bill morphology. Bill length (l), depth (d), and width (w)**
842 **were taken from the anterior edge of the nares and used to calculate residual (body-size**
843 **corrected) bill surface area following Greenberg and Danner (2012). All sampling was conducted**
844 **during the breeding season (February-June) from 2014-2016. Inset shows the location of the**
845 **northern Channel Islands with respect to California.**

846

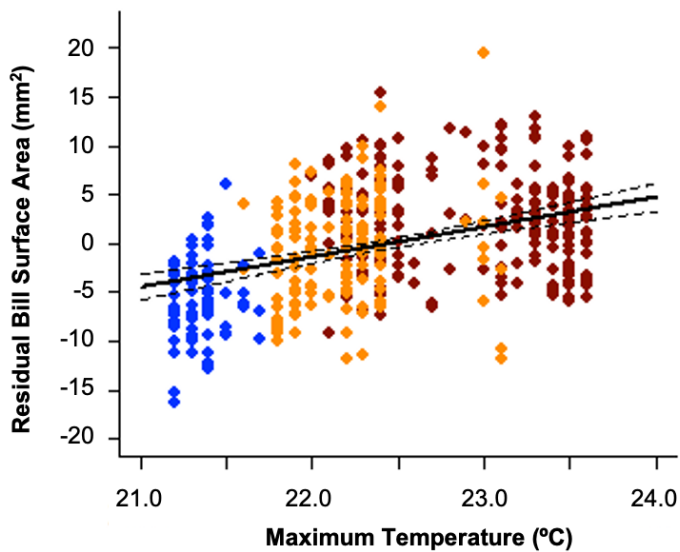


847 **Figure 2. Variable loadings (A) and PC1, PC2, and 95% kernel density contours by island (B) from nonlinear PCA of**
 848 **vegetation within song sparrow territories.** Sampling of 432 unique sampling locations occurred during the breeding season from
 849 2014-2016 on San Miguel Island (blue; $n = 68$), Santa Rosa Island (orange; $n = 141$), and Santa Cruz Island (red; $n = 223$).



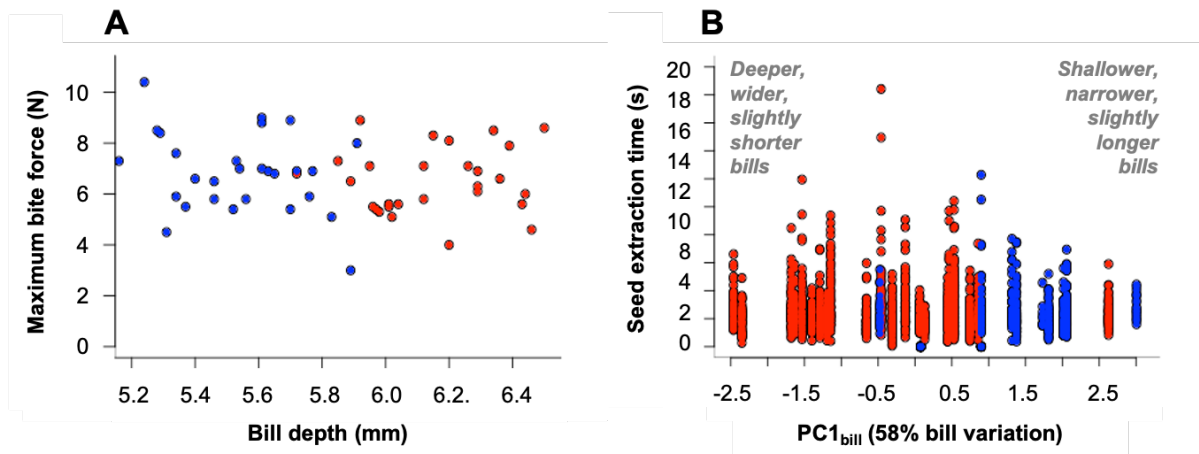
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864