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Evolutionary biology

Climate, ecological release and bill dimorphism in an island songbird

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Sexual size dimorphism is expected to be more pronounced in vertebrates on islands, particularly in trophic characters, as a response to decreased inter-specific competition for food. We found (based on measurements of 1423 museum specimens) that bill size dimorphism was greater in island than mainland populations of song sparrows. However, dimorphism varied among islands and was positively correlated with high summer temperature and island size. Island song sparrow bills follow the overall positive temperature bill size relationship for California song sparrows, which includes larger bills on large, warmer islands. Large bills dissipate more heat and may be an adaptation to summer heat stress. Dimorphism increases because the slope for males is greater than females. Thus, the greater magnitude of bill dimorphism on islands with warmer summers may result from males experiencing greater thermal stress during territorial activity, creating different thermal optima. In contrast, bill dimorphism was unrelated to climate on the mainland. We hypothesize that reduced interspecific competition releases island populations from a constraint so that sex-specific physiological optima can be achieved, whereas mainland birds are constrained.

1. Introduction

Islands have fewer species compared with mainland regions and have long been studied for their ability to provide insights into evolutionary processes. Island life engenders trends in the evolution of morphology of vertebrates. Studies of morphological shifts in island forms have focused on three phenomena: overall divergence from mainland forms with small animals increasing and large animals decreasing in size from their mainland counterparts ('the island rule'; [1]); diversification between islands in an archipelago [2]; and an increase in sexual size dimorphism as sexes diverge to occupy morphological space that would otherwise be occupied by other species [3–5]. A corollary to the island rule for passerine birds is that bill size tends to be larger in island compared with mainland forms even when body size is not [1,6–8].

Explanations for divergence in island forms have focused on interspecific competition and predation, whereas the role of the physical environment, such as climate, has received less attention. An interesting possibility is that the biotic and physical are related. A reduction in interspecific competition and predation and other factors associated with species-depauperate communities might allow island organisms to achieve optimal morphological adaptation to climatic conditions that are constrained by competition for food and other resources in more complex mainland assemblages [1,8]. Previously, we reported that bill size in song sparrows (*Melospiza melodia*) varies with summer temperature on the islands and mainland of California, and we hypothesized that bills were selected by temperature for the ability to dissipate heat [9,10]. Here, we present evidence that the sexual dimorphism in bill size on islands is higher than on the mainland and the degree of sexual dimorphism on different islands is related to the same environmental variables that explain inter-island variation in bill size. These results support the hypothesis that mainland conditions constrain sparrow bills from evolving towards sex-specific sizes best adapted for local climatic conditions.

2. Material and methods

Song sparrows breed or once bred on seven islands off the Southern California and Baja California coast, and populations on different islands vary in mean bill size [9]. Recent gene flow among islands and between the islands and mainland has been negligible [11].

Bill measurements were taken from 1423 museum skins by the lead author (data archived at <http://nationalzoo.si.edu/scbi/migratorybirds/research/data/>). Specimens were from six California islands (Channel and Coronado Islands, $n = 462$), and the mainland of Southern ($32\text{--}35^\circ\text{N}$, $n = 480$) and Northern California (less than 35°N , $n = 481$; see [9]). Bill length, depth and width were used to estimate surface area anterior of the nares. Dimorphism was quantified as the percentage difference of male-to-female bill surface area (for details, see the electronic supplementary material).

To test hypotheses of dimorphism in relation to geography and temperature, we built competing linear models of bill size as functions of island or mainland origin, maximum monthly average temperature and sex, controlled by other variables known to describe bill size in this system (for details, see the electronic supplementary material and [9]). We selected the best fitting models with AIC_c [12]. If sexual dimorphism differs between the islands and mainland, we would expect a model containing the interaction of sex by island/mainland origin to be supported. On both the islands and the mainland, to test if dimorphism varied with maximum temperature, we tested for support of interactions between temperature and sex. We then tested if bill dimorphism on islands was correlated with bill size and island size (for details, see the electronic supplementary material).

3. Results

The bills of island song sparrows were more dimorphic than those sampled from the mainland, with island male bills averaging 6.0 per cent (4.4–7.0 95% CI) larger than island females as compared with 1.8 per cent (0.2–3.4) and 2.0 per cent (0.4–3.1) for the Northern and Southern California mainland, respectively. Larger dimorphism on the islands was supported, as the model including the interaction between sex and island/mainland origin garnered 95% of the model weight and the alternate model had a ΔAIC_c of 5.86 (see the electronic supplementary material, table S1). In addition, mainland populations near the islands (Southern California within 5 km from the coast) exhibited mean dimorphism of only 2.0 per cent (0.8–3.2), and the model with the sex by island/mainland origin interaction garnered 70 per cent of the model weight (see the electronic supplementary material, table S2). The coastal sample and the island sample are similar in climate and almost identical in the range of maximum temperature (21°C – 28°C), whereas the total mainland sample includes temperatures well above those found on the islands (figure 1).

Bill size dimorphism varied among the California islands; ranging from lowest to highest: San Miguel 1.1 per cent (0.9–1.3 95% CI), Los Coronados 2.9 per cent (0.5–5.3), Santa Barbara 3.7 per cent (1.9–5.5), Santa Rosa 5.5 per cent (3.7–7.3), Santa Cruz 7.2 per cent (4.1–10.3) and San Clemente 7.2 per cent (6.0–8.4). On the islands, dimorphism correlated with maximum temperature (figure 1). The interactive (sex by temperature) model held 94 per cent of the model weight and the additive model had a ΔAIC_c of 5.65 (see the electronic supplementary material, table S3). The increase in bill dimorphism with temperature resulted from a greater

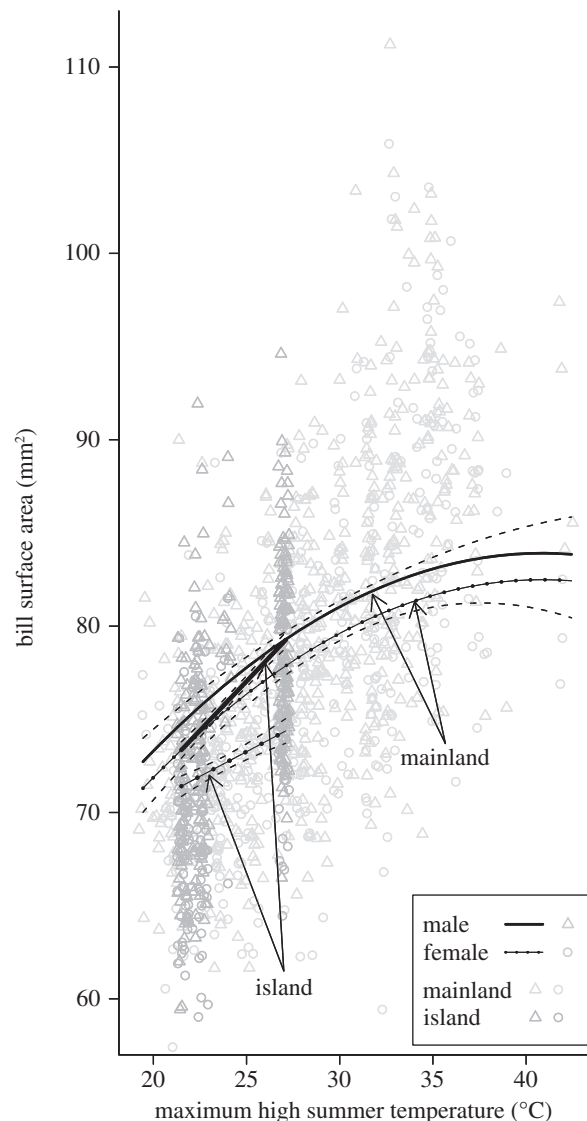


Figure 1. Bill sizes of California island and mainland song sparrows in relation to temperature. Lines are model predictions and standard errors. Open symbols are raw data. For mainland birds, only the outer error intervals of both sexes are shown to reduce clutter.

slope in bill size of males (1.05 mm^2 per 1°C , $0.82\text{--}1.28$ 95% CI) than females (0.53 , $0.20\text{--}0.86$), a significant difference ($t_{450} = -2.769$, $p = 0.006$) (figure 1). As a result of this pattern, the islands that had sparrows with the largest bill size also had the greatest dimorphism ($r = 0.94$, $p < 0.001$: σ^7 ; $r = 0.85$, $p = 0.03$: σ^8 ; $n = 6$; figure 2). In addition, because island size and temperature are related in this system [9], dimorphism was greater on larger islands ($r = 0.81$, $p = 0.05$; $n = 6$). In contrast to the islands, dimorphism on the mainland did not vary with maximum temperature; the additive model had 75 per cent of the model weight and the interactive model had a ΔAIC_c of 2.23 (see the electronic supplementary material, table S4). Thus, the slope for males and females on the mainland did not differ.

4. Discussion

We show that (i) island song sparrows have greater bill dimorphism than mainland birds even when regions of similar climate are compared; (ii) islands differ in the degree of sexual dimorphism, whereas mainland regions do not; and (iii) factors that explain inter-island variation in sexual

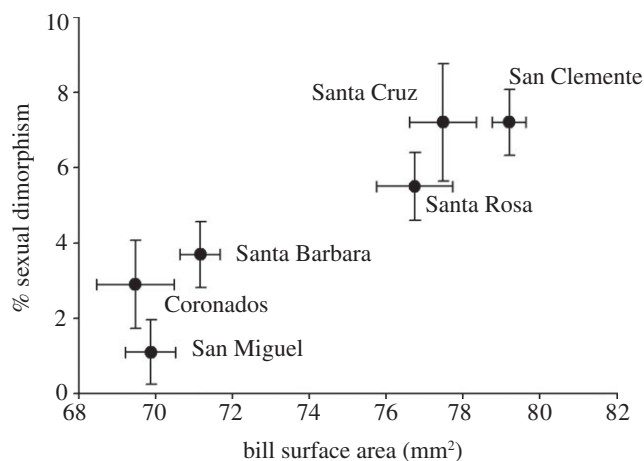


Figure 2. Bill size dimorphism on California islands in relation to mean male bill size. Bars are standard errors.

dimorphism (maximum temperature and island size) are the same as those that explain variation in bill size, whereas for mainland populations they are not. The overall greater dimorphism on islands and its sensitivity to the maximum temperature and island size gradients suggests that differential selection on male and female bill size in mainland populations may be constrained by interspecific competition from the greater diversity of species.

Bill size increases with higher summer temperatures in a similar way on the islands and mainland of California [9] consistent with the theory that heat dissipation can be important in shaping adaptation in endotherms [13]. Bill surface dissipates 'dry heat' [10,14] and bill size may track spatial variation in high temperatures [15,16], particularly in regions of water stress [9], such as the Mediterranean climate of California. Summer temperatures on the California islands are influenced by a marine layer of air chilled by the waters of the California current. The marine layer has a heterogeneous impact on different parts of large islands depending on topography and distance from the island edge [17]. The effect of the marine layer will be more homogeneous and large on the small islands with less topographic relief. We, therefore, think that the combination of maximum temperature along with island size best represents the environmental conditions that influence bill size.

Dimorphism in bill size follows the same maximum temperature + island size gradient as bill size. The two sexes respond in a similar qualitative, but different quantitative manner to the temperature gradient [16] as supported by the greater slope in males. Male fitness is related to their ability to defend a territory, which requires them to remain active and exposed, even under hot conditions. Females can remain in more buffered microhabitats. This leads us to propose the sex-specific thermal niche hypothesis where exposure to

different thermal environments related to sex roles may underlie the divergence in bill size where such divergence is not constrained by interspecific competition for food [16].

Another explanation for higher sex or shape dimorphism on islands, the sex-specific foraging hypothesis, holds that a reduction in the number of trophic competitors leads to decreased interspecific competition for food and this alone favours the divergence of the two sexes in feeding ecology [3–5]. The sex-specific foraging hypothesis as currently formulated does not, however, explain inter-island variation in dimorphism. Land bird diversity increases with island size among the California islands as expected by island size–diversity relationships ([18] and references therein). As a result, bill size dimorphism varies positively with the number of land bird species, which is opposite the direction predicted by the sex-specific foraging hypothesis. It is possible, however, that an effect of interspecific competition is more complex. Even for large islands, land bird species richness is reduced compared with similar mainland habitats [19], and the diversity of seed-producing plants also increases [18]; thus, the range of seed size and hardness (features important to the evolution of finch and sparrow bills; [20]) might increase but with fewer competing granivorous species than on the mainland. Therefore, dimorphism could be responding to increased resource diversity on larger islands in the face of a lower level of interspecific competition compared with the mainland. A more complex analysis akin to work on anoles in the Caribbean [5] would be required to evaluate how changes in resource availability and species composition might combine to influence bill dimorphism.

The sex-specific thermal niche hypothesis posits that heat dissipation and water conservation related to difference in the behaviour of the sexes is the driving force for divergence, and that a reduced diversity of trophic competitors, such as is found on islands, allows for the bill morphology of each sex to conform to its thermal optimum without suffering from competition from species with similar diets. The sex-specific foraging hypothesis does not predict the observed patterns. Based on existing data, the sex-specific thermal niche hypothesis offers the more parsimonious explanation of the among island and island/mainland patterns.

The system offers two compelling hypotheses and thus the possibility of field tests for trophic and physiological processes that drive sexual dimorphism. The results of such tests will have relevance to a much larger debate on the relative role of heat dissipation versus energy acquisition in shaping adaptations, such as sexual dimorphism, in endothermic vertebrates [12].

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