

Rapid Climate Adaptation in San Francisco Bay Area Songbirds

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ABSTRACT

Museum specimens offer a unique and powerful tool for understanding the impact of climate trends and anthropogenic change on populations over time. Morphological traits tend to be impacted by many different environmental variables that are difficult to separate from one another as potential driving factors. A combination of modeling and comparative analysis between similar species experiencing certain shared variables can allow us to more confidently say what the likely driving factors are of morphological change over time. I compared the temporal changes in bill size, tarsus length, and body size between six species of songbirds from the San Francisco Bay Area over the past 150 years. Then I used linear mixed effects models to determine what climate variables are most likely contributing to the observed temporal patterns of morphological change. I found a significant increase in bill surface area across all but one species and minimum annual vapor pressure deficit was consistently the best explanatory variable of temporal change in bill surface area. This result is less intuitive than our original, temperature driven hypothesis, yet consistent with some literature and the hypothesis that bills may be used as more efficient thermoregulatory organs when subject to a more humid environment. Overall, this study has important implications for future research on the role of bills in thermoregulation and for conservation efforts based on the adaptive capacity of birds to respond to climate change.

KEY WORDS

thermoregulation, museum specimens, climate change, California, bill morphology

INTRODUCTION

Many forms of human disturbance such as urbanization, habitat destruction, and climate change have drastically altered environments around the planet (Stephens et al. 2019). These extreme changes have put pressure on many organisms to rapidly adapt (Ryding et al. 2021), shift their ranges (Thomas 2010), or go extinct (McLaughlin 2002). Understanding historic changes that species have undergone and are continuing to go through in order to adapt to their rapidly changing environments can lead to both predictions of future change and conservation insights. For this purpose, museum specimens present a resource uniquely suited to answering questions about historic and current change in species. Already, many studies are making use of natural history collections around the world and gaining insights into historic change and the adaptive capacity of many organisms to respond to anthropogenic pressures (Rocha et al. 2014). These studies primarily focus on phenotypic traits, though genetic analysis is also common. However, the phenotypic traits of an organism tend to have a variety of different functions, making it difficult to discern a single driving cause of phenotypic change (Friedman et al. 2019). When using museum specimens to understand how traits change in response to anthropogenic pressure, it is critical to understand the role that a given trait may play in the organism's adaptive response.

Birds have a number of morphological features that play a role in adaptive responses to their environment. Bird bills, body size, and tarsus length may all change in response to climate trends. Bird bills help with thermoregulation (Danner and Greenberg 2015) and have been shown to change in correlation with climate trends (Campbell-Tenant et al. 2021, LaBarbera et al. 2017). Both bill surface area and tarsus length may elongate in response to increased temperatures, which aligns with Allen's Rule (Danner and Greenberg 2015). In accordance with Bergmann's Rule (Teplitsky et al. 2008), body size may decrease as another adaptive response to heat (Weathers 1981). The effects of heat on bird morphology can be compounded by precipitation and humidity (Gardner et al. 2016). There is already ample evidence that climate trends have an impact on bird morphology, however, most studies focus on diet as the primary driving force behind bill morphology. This has created a relative lack of understanding for the ways in which bird bills have adaptively responded to human disturbance around the world. Additionally, few studies have looked at the combined changes in bills, body size, and appendages in response to climate trends.

The San Francisco Bay area is an ideal place to study the morphological response of birds to climate trends. The Bay Area has undergone rapid urbanization in the last 150 years, putting pressure on many local species, and exacerbating the effects of climate change. Aside from rapid urbanization, coastal areas are especially vulnerable to greater climate change impacts (Scavia et al. 2002). Studying local species could yield more immediate insights into adaptive responses to climate change that are yet to be detectable in less vulnerable populations. Some research has already found relationships between hotter, drier environments and both increases in bill surface area (Campbell-Tennant et al. 2021) and decreases in body size (Weathers 1981). However, there is conflicting evidence for how climate impacts bird's bills. A study on Australian honeyeaters found that larger bill surface areas were correlated with higher humidity and cooler summers (Gardner et al. 2016). Alternatively, a study on northern cardinals found that bill size decreased at higher humidities and colder winters (Miller et al. 2018). It should be noted that these studies are hard to compare because they are of different species, in vastly different environments, subject to different climates, and with much more specialized bill morphology for their very different and specialized diets. The strength of this study is that I am comparing the morphological responses of six different species that are subject to approximately the same environmental pressures and climate trends. They are also much more generalist in their diets, decreasing the potential impact and importance of diets and foraging as confounding variables. Additionally, a number of local songbird species are relatively widespread and densely sampled in museum collections, making them a good choice for a study.

Despite the magnitude of anthropogenic change that has occurred in the Bay Area over the past 150 years, it remains poorly understood how pressures such as climate change have impacted local songbird species and what adaptive changes may have taken place in response to these pressures. The goal of this research is to understand the morphological responses of six songbird species to climate trends in the San Francisco Bay Area in California, USA. The first objective is to determine if there are temporal patterns of morphological change in Bay Area songbirds. Based on those results I can ask how morphological changes are related to local climate trends. Due to the broadly observed increase in temperatures and the current continent-wide increase in vapor pressure deficit (Ficklin and Novick 2017), I predict that I will find an increase in bill surface area and associated bill metrics along with a decrease in body size over the past roughly 150 years. Selection for longer appendages in hotter and drier environments is thought to produce ecogeographic patterns in morphology consistent with Allen's Rule. If birds

are responding to similar selective pressures through time in the Bay Area, then I expect any observed changes in bill size to be driven by increasing temperature and decreasing humidity.

METHODS

Morphological data collection

Table 1. Sample summary. The number of males, females, and total specimens measured for each species.

Species	Male	Female	Total
Dark-eyed Juncos	65	43	108
Song sparrows	127	68	195
Savannah sparrows	229	126	355
House Finches	97	30	127
California Towhees	45	38	83
Red-winged Blackbirds	93	46	139

For 652 museum specimens I measured the bill length, width, depth, tarsus length, and unflattened wing chord length of museum specimens for six species of Bay Area songbirds: California towhees (*Melospiza crissalis*), dark-eyed juncos (*Junco hyemalis*), house finches (*Haemorhous mexicanus*), savannah sparrows (*Passerculus sandwichensis*), song sparrows (*Melospiza melodia*), and red-winged blackbirds (*Agelaius phoeniceus*). I used museum specimens from Bay Area counties (Figure 1) that are housed at the UC Berkeley Museum of Vertebrate Zoology and the California Academy of Science. All savannah sparrow data used was from Benham and Bowie (2020). All specimens were resident subspecies, but for some taxa migratory populations spend the winter in the Bay Area, so analyses were restricted to breeding season individuals. Migratory individuals were not included since they would not be subject to the Bay Area climate year round. I only included adult specimens and specimens where the sex was known. All the specimens measured had been preserved for at least four years, so they had all undergone a similar degree of shrinkage after being prepared. All measurements were taken with digital calipers to .01mm precision. I took each measurement three times and then averaged the measurements. All bill measurements were taken from the anterior end of the nares. I calculated the bill surface area with a formula for the lateral surface area of a cone (LaBarbera et al., 2017): Bill surface area = ((bill width + bill depth)/4)*bill length* π . Wing chord length was measured

from the bend of the wing to the tip of the longest primary feather. Tarsus length was measured from the intertarsal joint to the first metatarsus. I am using wing chord length as a proxy for body size (Nolan and Ketterson 1983) because body size is notoriously difficult to measure in museum specimens. The way a specimen is prepared, how old it is, and even season of collection can all have a big impact on both size and mass. Additionally, many older specimens don't have body mass data. Tarsus length is another common proxy for body size, however under my current hypothesis I was interested in how tarsus length itself could be changing as it is also an area of heat exchange in birds.

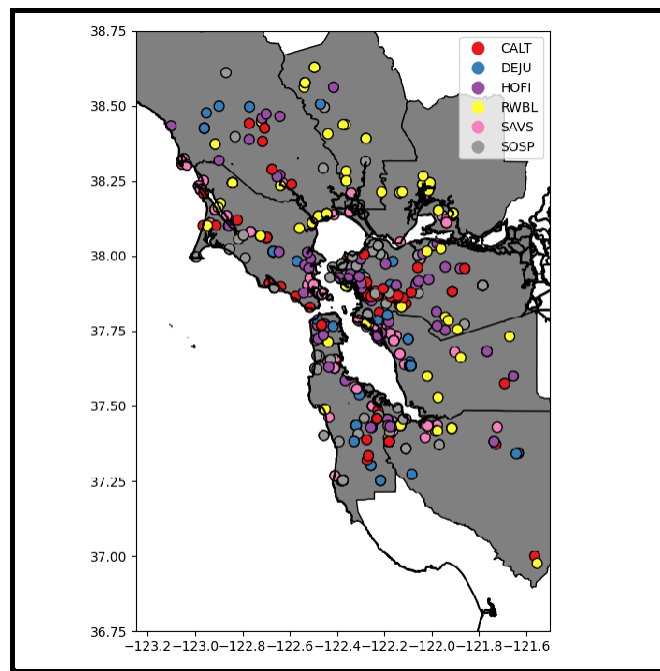


Figure 1. Museum specimen sample distribution. A map of the San Francisco Bay Area with colored points indicating the sample location over every specimen used. The species are California towhees (CALT), dark-eyed juncos (DEJU), house finches (HOFI), red-winged blackbirds (RWBL), savannah sparrows (SAVS), and song sparrows (SOSP). Bay Area counties are filled in gray.

Climate data collection

I downloaded climate data from the PRISM climate data set (<http://www.prism.oregonstate.edu>; Gibson et al., 2002) for precipitation, maximum temperature, minimum temperature, mean temperature, maximum vapor pressure deficit, minimum vapor pressure deficit, and mean dew point temperature for the years 1895 to 2018. For each specimen I extracted values from each climate parameter for the month and location of the specimen collected. The climate data for each specimen at its collection location is spatially interpolated.

Precipitation and temperature are more familiar and intuitive measurements, while vapor pressure deficit (VPD) tends to be less well known. VPD is the difference between the amount of moisture in the air and how much moisture the air can hold when saturated. Although VPD is not synonymous with humidity, it can be thought of in similar terms. A high VPD is generally associated with dryness, while a low VPD is associated with greater humidity.

Data Analysis

Temporal Patterns of Morphological Change

I analyzed temporal patterns of morphological change by species for all six study species with linear regression in Rstudio 2. Correlation coefficients and p-values were retrieved using the functions `cor()` and `rcorr()` respectively. I did this to evaluate significant trends in morphological change for each species for bill length, width, depth, surface area, wing length, and tarsus length.

Climate effects

To begin understanding the relationship between different climate variables I analyzed each of the six morphological features measured for each species using linear mixed effects (LME) models. For each trait for each species I created five LME models with precipitation, maximum temperature, minimum temperature, maximum vapor pressure deficit, and minimum vapor pressure deficit as fixed effects respectively. In all LME models wing length and sex were included as fixed effects and county was included as a random effect. For LME models analyzing variation in wing length, wing length was not included as a fixed effect. I made base models for each morphological feature for each species by simply not including a climate parameter as a fixed effect. The

base models could then be compared to the LME models with climate parameters using the Akaike Information Criterion (AIC) and from that I was able to get delta AIC values.

RESULTS

Temporal patterns of morphological change

When I performed linear regression on each of the morphological traits for each species I found that wing length was by far the most variable in terms of individual species' responses. It was found to decrease significantly in savannah sparrows, increase significantly in red-winged blackbirds, and did not show significant change in the other species.

Tarsus length was similarly variable, increasing significantly in red-winged blackbirds and song sparrows, while it decreased significantly in dark-eyed juncos (Figure 2).

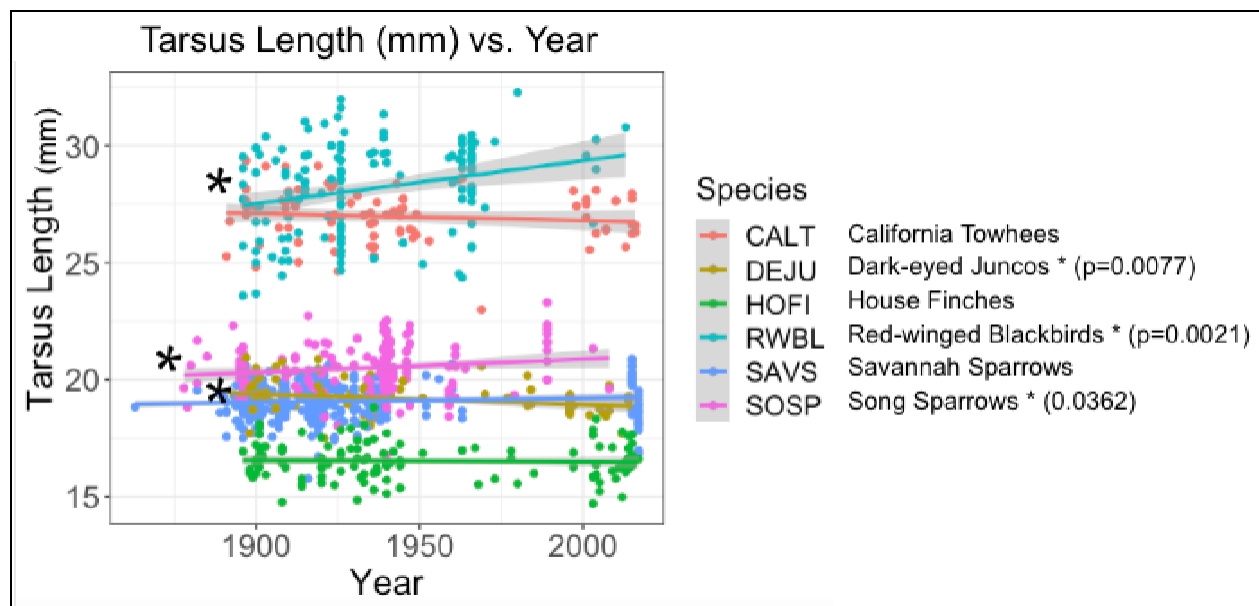


Figure 2. Linear regression of tarsus length (mm) vs. year. Asterisks indicate statistically significant results. The tarsus length of dark-eyed juncos has decreased over time, while the tarsus length of red-winged blackbirds has increased.

By far, the most consistently changing morphological trait was bill surface area (Figure 3). It was found to have increased significantly in California towhees, house finches, red-winged blackbirds, savannah sparrow, and showed a nearly significant increase in song sparrows

($p=0.0554$). The only species that didn't show a significant increase in bill surface area was dark-eyed juncos, which showed no significant change in bill surface area.

While song sparrows showed a nearly significant increase in bill surface area, it is worth noting that they did show a significant increase in both bill length and bill depth. In fact, every species except for dark-eyed juncos showed a significant increase in at least one bill metric other than surface area (length, width, or depth). This is expected given that bill surface area is derived from the other bill metrics and is therefore not an independent measurement.

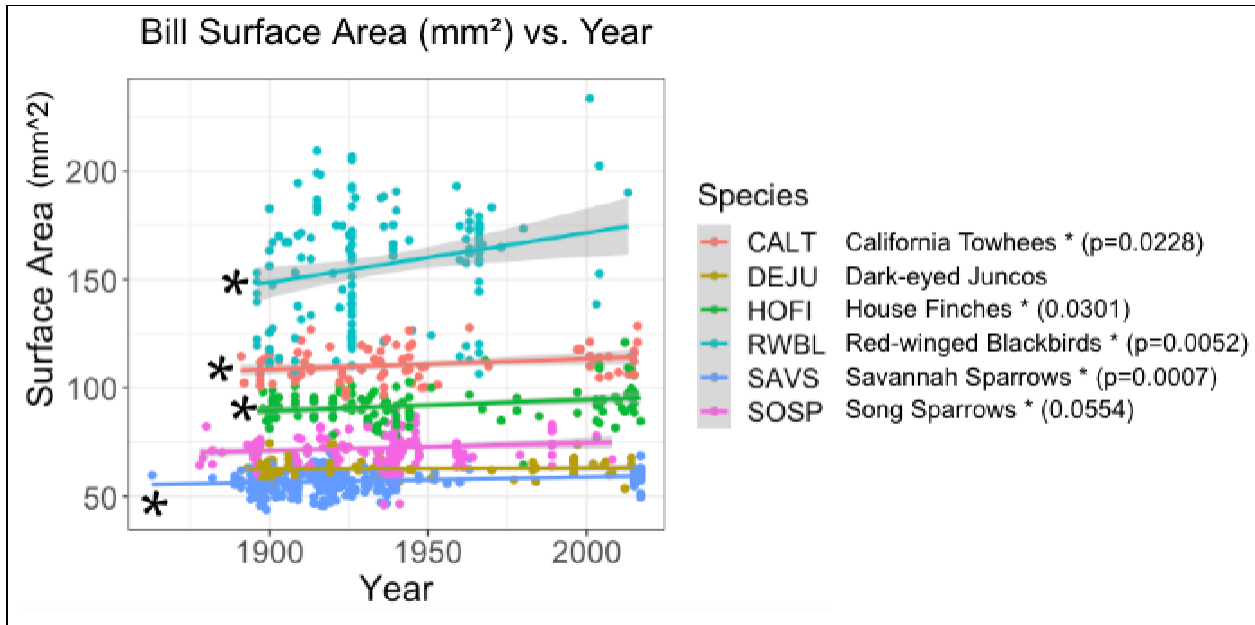


Figure 3. Linear regression of bill surface area (mm²) vs. year. Asterisks indicate statistically significant results. The bill surface area of California towhees, house finches, red-winged blackbirds, and savannah sparrows have increased over time. Song sparrows have shown a near significant increase in bill surface area ($p=0.0554$).

While dark-eyed juncos didn't show a significant increase in bill surface area, the fact that five out of six species showed a consistent and significant increase in the same morphological feature is strong evidence that there is likely a uniform and predictable morphological response to mutually experienced environmental pressures taking place.

Climate and morphological change

To begin analyzing the potential impact of climate on morphological change in Bay Area songbirds I performed linear regression on the specimens' extracted climate variables. The five

variables included were annual precipitation, maximum annual temperature, minimum annual temperature, maximum annual vapor pressure deficit, and minimum annual vapor pressure deficit. Out of these five climate variables, three showed significant change over time: maximum annual temperature and both maximum and minimum annual vapor pressure deficit.

Maximum annual temperature and maximum annual vapor pressure deficit showed a significant increase over time, while minimum annual vapor pressure deficit showed a significant decrease over time (Figure 4).

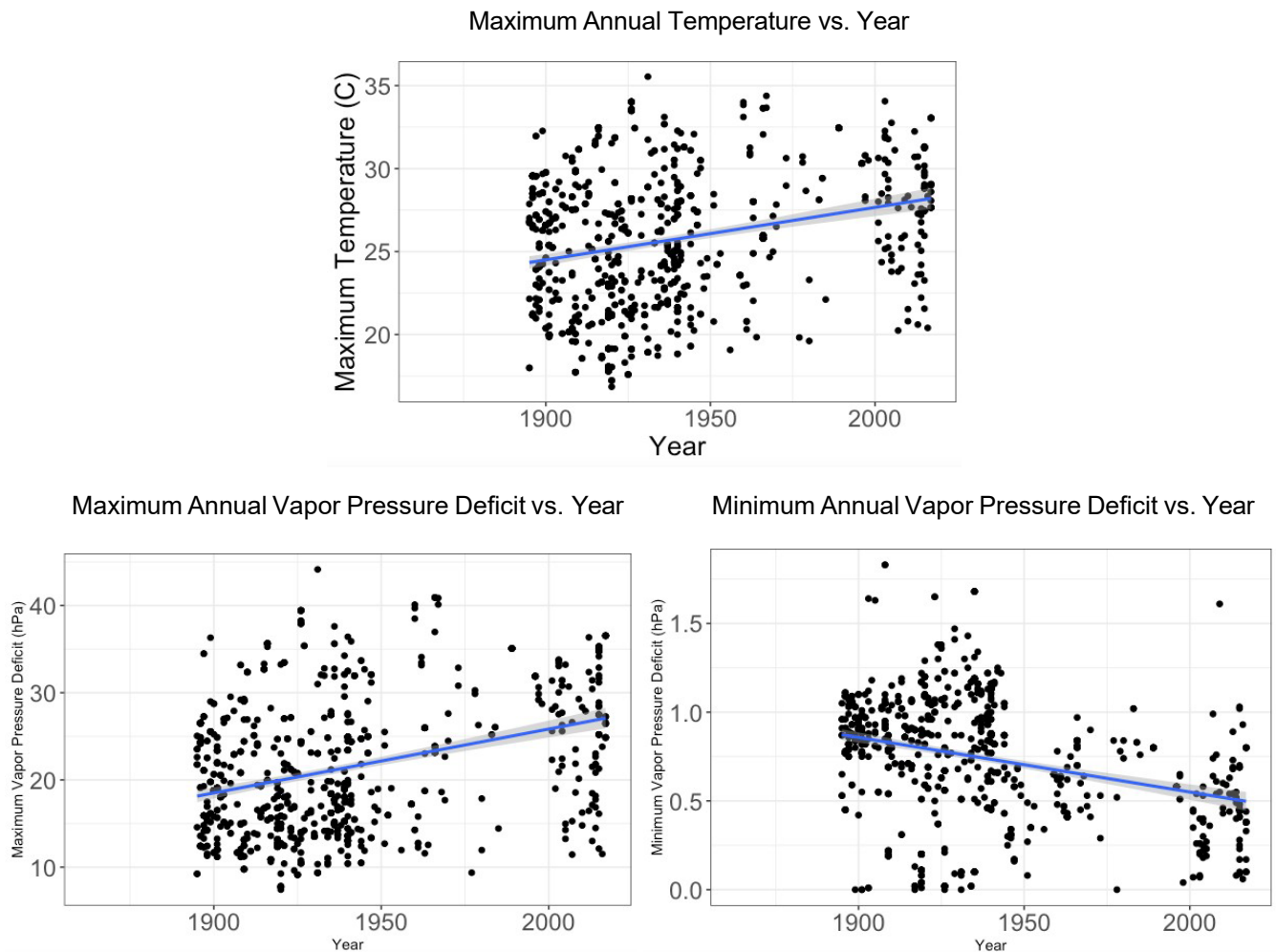


Figure 4. Linear regression of climate variables vs. year. Maximum annual temperature has increased over time, as has maximum annual vapor pressure deficit. Minimum annual vapor pressure deficit has decreased over time. The other climate variables used have not shown significant change over time.

I can interpret this as a divergence of the extremes in which the maximum and minimum annual vapor pressure deficit are diverging and becoming more extreme. While again, VPD is not synonymous with humidity, I can generally say that the extremes of dryness are getting drier, while the extremes of humidity are becoming more humid.

After creating linear mixed effects (LME) models with each climate variable as a fixed effect for each species, I compared them to a base model (Figure 5). Dark-eyed juncos were left out because they did not show a significant change in bill surface area. For bill surface area models that incorporated minimum annual vapor pressure deficit as a fixed effect consistently explained the greatest degree of variance in bill surface area. In song sparrows there was a tie with minimum annual VPD and minimum annual temperature models performing equally well. In general, however, this is strong evidence that minimum annual vapor pressure deficit is negatively correlated with bill surface area.

Table 2. Bill surface area analysis. In every species, the linear mixed effects model that incorporated minimum annual vapor pressure deficit as a fixed effect was the best performing model. In song sparrows there was a tie between models that included minimum annual vapor pressure deficit and minimum annual temperature as fixed effects. However, it should be noted that minimum annual temperature hasn't shown significant change over time.

Bill Surface Area Analysis

Species	Climate Variable	LME Estimate	LME Std. Error	Base Model AIC	Climate Model AIC	Δ AIC
Savannah Sparrows	Minimum VPD	-2.16029	0.72146	2004.798	1903.149	101.649
Song Sparrows	Minimum VPD	-6.61E-05	1.31E-03	1277.085	1245.925	31.16
	Minimum Temp.	-6.50E-05	1.31E-03	1277.085	1245.925	31.16
House Finches	Minimum VPD	-4.0119	2.1046	874.9191	870.2745	4.6446
California Towhees	Minimum VPD	-0.3075	0.2001	561.4916	548.7573	12.7343
Red-winged Blackbirds	Minimum VPD	-3.3804	4.9733	1112.754	1109.247	3.507

DISCUSSION

While museum specimens are an incredibly powerful and valuable tool for studying morphological change over time, understanding the causes of morphological change is significantly more challenging. Many different variables could play a role in bill morphology: foraging, preening, salinity, urbanization, and many climate variables may all contribute to change over time. By testing a range of climate variables that are likely to contribute or have been found to contribute to bill morphology across a broad range of species, I can begin to weed out some of the possible confounding variables.

Broadly observed changes in bill morphology

Several recent papers have explored changes in avian morphology in the recent past. A 2021 study of five Australian parrot species found that bill surface area has increased since 1871 and that maximum summer temperatures were an indicator of this trend (Campbell-Tennant et al. 2021). Changes in bill morphology are broadly studied, but results have been somewhat conflicting. In another 2021 study evaluating Allen's Rule in relation to bill morphology, it was found that winter temperatures were a better explanation of bill size than summer heat (Danner and Greenberg 2015).

The advantage of this study is that it uses an extensive sample of museum specimens to take a broader look at a variety of Bay Area songbirds going back 150 years. In a similar study on savannah sparrows in California, Benham and Bowie 2021 found a positive association between bill surface area and maximum annual VPD. It also found that maximum annual temperature significantly explains temporal variation in bill size, but only when interacting with salinity, precipitation, and maximum annual VPD. This study in particular has the chance to expand upon their work, exploring a wider range of species experiencing the same climate trends.

Additionally, bill morphology is usually studied with respect to diet as there is evidence that foraging ecology is a primary driving factor for variation in bird bills. Considering this, I chose species of Bay Area songbirds that are roughly generalists. There is some variation in diet

with respect to preferring insects or seeds, which has the advantage of being able to compare morphological change between different species with slightly different foraging ecologies.

The results of this study align with the findings of Benham and Bowie (2021), Campbell-Tennant et al. 2021, and Danner and Greenberg (2015). There has been a significant increase in bill size across numerous dimensions in almost every species of Bay Area songbird studied. Bill surface area was by far the most commonly increasing bill metric across the species studied. This in turn aligns with our hypothesis that the bird's bill plays an important role in thermoregulation and would be the most likely trait to exhibit change over time in relation to climate trends. Since this change was so broadly observed in this study across different species with different habitats and foraging ecologies it makes it unlikely that any factor influencing a specific species would be responsible for the degree of change observed across almost all of the study species. Although this study isn't sufficient to determine why dark-eyed juncos haven't shown changes in bill surface area, it is possible that they more strictly select forested habitat and are more sheltered from climate impacts.

The impacts of climate on bill morphology

This study specifically focussed on the effects of climate variables on bill morphology. This leaves out salinity and urbanization as potential factors. While they both may compound the effects of climate on bill morphology, the most widely and directly relevant factors that birds across many similar studies experience are climate trends.

Within climate trends, temperature is by far the most studied in relation to bill morphology. However there is evidence that temperature and humidity may both play a large role in influencing change over time. Evaporative cooling is less effective at high humidities so birds may rely more on their bills for thermoregulation at higher humidities.

My results support this hypothesis since changes in surface area were inversely related to the minimum annual vapor pressure deficit. A decrease in minimum vapor pressure deficit is tied to increased humidity, making it potentially adaptive for birds to rely on an increased bill surface area to aid in thermoregulation. Although maximum annual temperature and maximum annual VPD were not found to contribute as heavily to variation in bill surface area, they have both significantly increased over time and may play a role in compounding the impact of a declining

minimum annual VPD. Using bills for thermoregulation has been found to be more effective at conserving water than evaporative cooling. Increasing maximum annual temperatures could increase the need for thermoregulation while an increasing maximum annual VPD, and the associated dryness, could increase the importance of bill thermoregulation as an alternative to evaporative cooling. While the results of this study clearly point to minimum annual VPD being the driving force behind increasing bill surface areas, I would not be quick to discount the potential for other interconnected variables like maximum annual temperature and VPD to also play a role. The linear mixed effects models I used are somewhat limited in their ability to analyze the impact of interrelated variables or the way in which multiple variables could be interacting with one another.

LIMITATIONS AND FUTURE DIRECTIONS

This study is most limited by the museum specimens available. While the museum collections leveraged in this study are quite extensive and go back over a hundred years, there is very limited recent data available after 1980. Of the specimens available, I am further limited to birds that are adult residents collected from Bay Area counties.

While confounding variables and the inherent difficulty of determining causality make it challenging to unequivocally say that climate change is driving rapid morphological change in Bay Area songbirds, there is strong evidence that climate is a driving force behind the observed rapid adaptation. Many of the other studies cited have found similar links between morphological change and climate trends. This pattern isn't limited to birds. Many other animals, including desert mammals have been found to be undergoing rapid morphological changes to cope with climate stressors.

While some may find the remarkable ability of organisms to adapt encouraging, it begs the question: is there a limit to the adaptive capacity of these species? At what point will the environment change too quickly for species to adapt? These are important questions that need to be studied to help inform the future conservation of impacted species.

CONCLUSIONS

In this study I used a vast collection of museum specimens to study if (1) Bay Area songbirds had undergone morphological change over the past 150+ years and (2) how those changes may be related to Bay Area climate trends. I found that there has been broad and significant morphological change across a variety of Bay Area songbird species with the most consistent change being an increase in bill metrics, specifically bill surface area. This prompts us to consider what other species in the Bay Area, all of California, or the rest of the world may be undergoing rapid morphological changes in response to climate trends.

Climate analysis suggests that the observed morphological changes can be best explained by the decreasing minimum vapor pressure deficit. These findings underscore the potential importance of the bill for thermoregulation as an alternative to evaporative cooling. This study adds to the growing body of evidence that suggests that climate trends and anthropogenic climate change are linked to rapid adaptation in many animals.

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REFERENCES

- Benham, P.M., and R.C.K. Bowie. 2020. The influence of spatially heterogeneous anthropogenic change on bill size evolution in a coastal songbird. *Evolutionary Applications* 14(2):607-624.
- Campbell-Tennant, D.J.E., J.L. Gardener, M.R. Kearney, and M.R.E. Symonds. 2021. Climate-related spatial and temporal variation in bill morphology over the past century in Australian parrots. *Journal of Biogeography* 42:1163-1175.
- Danner, R.M., and R. Greenberg. 2015. A critical season approach to Allen's rule: bill size declines with winter temperature in a cold temperate environment. *Journal of Biogeography* 42:114-120.
- Ficklin, D.L., and K.A. Novick. 2017. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. *Journal of Geophysical Research: Atmospheres* 122:2061-2079.
- Friedman, N.R., E.T. Miller, J.R. Ball, H. Kasuga, V. Remes, and E. Economo. 2019. Evolution of a multifunctional trait: shared effects of foraging ecology and thermoregulation on beak morphology with consequences for song evolution. *Proceedings of the Royal Society B* 286: 1 - 10.
- Gardner, J.L., M.R.E. Symonds, L. Joseph, K. Ikin, J. Stein, and L.E.B. Kruuk. 2016. Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. *Climate Change Responses* 3:1-12.
- LaBarbera, K., K.R. Hayes, K.J. Marsh, and E.A. Lacey. 2017. Complex relationships among environmental conditions and bill morphology in a generalist songbird. *Evolutionary Ecology* 31:707-724.
- McLaughlin, J.F., J.J. Hellmann, C.L. Boggs, and P.R. Ehrlich. 2002. Climate change hastens population extinctions. *PNAS* 99:6070-6074.
- Nolan, V., and E.D. Ketterson. 1983. An analysis of body mass, wing length, and visible fat deposits of dark-eyed juncos wintering at different latitudes. *Wilson Ornithological Society* 95:603-620.
- Rocha, L.A., A. Aleixo, G. Allen, F. Almeda, C.C. Baldwin, M.V.L. Barclay, J.M. Bates, A.M. Bauer, F. Benzoni, C.M. Berns, M.L. Berumen, D.C. Blackburn, S. Blum, F. Bolaños, R.C.K. Bowie, R. Britz, R.M. Brown, C.D. Cadena, K. Carpenter, L.M. Ceriaco, P. Chakrabarty, G. Chaves, J.H. Choat, K.D. Clements, B.B. Collette, A. Collins, J. Coyne, J. Cracraft, T. Daniel, M.R. de Carvalho, K. de Quieroz, F. Di Dario, R. Drewes, J. P. Dumbacher, A. Engilis Jr., M.V. Erdmann, W. Eschmeyer, C. R. Feldman, B. L. Fisher, J. Fjeldså, P.W. Fritsch, J. Fuchs, A. Getahun, A.Gill, M. Gomon, T. Gosliner, G. R. Graves, C. E. Griswold, R. Guralnick, K. Hartel, K. M. Helgen, H. Ho, D. T. Iskandar, T.

- Iwamoto, Z. Jaafar, H.F. James, D. Johnson, D. Kavanaugh, N. Knowlton, E. Lacey, H. K. Larson, P. Last, J. M. Leis, H. Lessios, J. Liebherr, M. Lowman, D. L. Mahler, V. Mamonekene, K. Matsuura, G. C. Mayer, H. Mays Jr., J. McCosker, R. W. McDiarmid, J. McGuire, M. J. Miller, R. Mooi, R. D. Mooi, C. Moritz, P. Myers, M. W. Nachman, R. A. Nussbaum, D. Ó Foighil, L. R. Parenti, J. F. Parham, E. Paul, G. Paulay, J. Pérez-Emán, A. Pérez-Matus, S. Poe, J. Pogonoski, D. L. Rabosky, J. E. Randall, J. D. Reimer, D. R. Robertson, M.-O. Rödel, M. T. Rodrigues, P. Roopnarine, L. Rüber, M. J. Ryan, F. Sheldon, G. Shinohara, A. Short, W.B. Simison, W. F. Smith-Vaniz, V. G. Springer, M. Stiassny, J. G. Tello, C.W. Thompson, T. Trnski, P. Tucker, T. Valqui, M. Vecchione, E. Verheyen, P. C. Wainwright, T. A. Wheeler, W.T. White, K. Will, J. T. Williams, G. Williams, E. O. Wilson, K. Winker, R. Winterbottom, C. C. Witt. 2014. Specimen collection: An essential tool. *Science* 344:814-816.
- Ryding, S., M. Klaassen, G.J. Tattersall, J.L. Gardner, and M.R.E. Symonds. 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends in Ecology & Evolution* 2888:1-13.
- Scavia, D., J.C. Field, D.F. Boesch R.W. Buddemeier, V. Burkett, D.R. Cayan, M. Fogarty, M.A. Harwell, R.W. Howarth, C. Mason, D.J. Reed, T.C. Royer, and A.H. Sallenger. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25:149-164.
- Stephens, L. et al. 2019. Archaeological assessment reveals Earth's early transformation through land use. *Science* 365:897-902.
- Teplitsky, C., J.A. Mills, J.S. Alho, J.W. Yarrall, and J. Merila. 2008. Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *PNAS* 105:13492-13496.
- Thomas, C.D. 2010. Climate, climate change and range boundaries. *Diversity and Distributions* 16:488-495.
- Weathers, W.W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiological Zoology* 54:345-361.