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Article

Effects of climate on bill morphology within and across *Toxostoma* thrashers

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Bird bills possess an important thermoregulatory function as they are a site for environmental heat exchange. Previous studies have demonstrated that birds in warmer climates have larger bills than those living in colder climates, as larger bills can dissipate more heat. Because this dry heat transfer does not incur water loss, it may be additionally advantageous in water-restricted habitats. Here, we examine the influence of climate on bill morphology in *Toxostoma* thrashers, a group of 10 North American species that varied in bill morphology and occupied climate niche, with several species inhabiting arid climates. Past examinations of thrasher bill morphology have only considered foraging, leaving unanswered the role of climate in morphological divergence within this group. We photographed 476 *Toxostoma* museum specimens encompassing all 10 species and calculated bill measurements from the photos using a MATLAB-based program. For each species, we calculated occupied climate niche using data from WorldClim describing temperature and precipitation. We found no reliable significant relationships between climate variables and bill morphology across species, suggesting that other factors such as foraging behavior may be more important in shaping bill morphology in this genus. Within species, we found three *Toxostoma* species have significant relationships between bill morphology and climate that follow Allen's rule. However, we also found the relationships between climate and bill morphology varied in strength and direction across species. Notably, we found a negative relationship between maximum temperature of the hottest month and bill surface area in LeConte's thrasher, which occupies the hottest and most arid climates of the thrashers. This adds to the evidence that Allen's rule may reverse in extremely hot climates when the bill may become a heat sink instead of a heat radiator. These results demonstrate the importance of considering the generality of ecogeographical rules across lineages that occupy extreme climates.

Keywords: Allen's rule, climate niche, desert birds, foraging ecology, image analysis, thermoregulation

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Introduction

Bird bills are famously shaped by diet and foraging strategy (Boag and Grant 1984, Temeles et al. 2002, Olsen et al. 2017). Bill dimensions are predictive of bite force, which functions in processing food (Herrel et al. 2005), and novel environmental foraging pressures have been shown to lead to divergence in bill morphology (Grant and Grant 2006). However, bird bills are multifunctional. Bill morphology influences preening (Clayton and Cotgreave 1994, Barbosa 1996), vocalizations (Seddon 2005), social interactions (Navarro 2009), nest excavation (Bock 1999), tool use (Matsui et al. 2016), thermoregulation (Tattersall et al. 2009) and water retention (Greenberg et al. 2012b). Therefore, multiple selective pressures may be acting to shape bill phenotype (Cox et al. 2003, Friedman et al. 2019), and recent studies suggest that diet may account for less of the variation in bill shape across species than previously thought (Navalón et al. 2019). Because trade-offs between the bill's various functions influence its morphology, divergence in bill morphology could be related to uses other than the bill's primary function in feeding and foraging (Luther and Greenberg 2014, Navalón et al. 2019).

In recent years, researchers have begun to explore the role of thermoregulation and water retention in shaping bill morphology (Tattersall et al. 2009, Greenberg et al. 2012a, Danner et al. 2016, LaBarbera et al. 2020). Because bills are extensively vascularized, excess heat can be passively dissipated from the bill via environmental heat exchange (Hagan and Heath 1980). The size of bird bills therefore varies with local climates consistent with Allen's rule (Allen 1877, Symonds and Tattersall 2010). Populations that occupy hotter climates tend to have greater bill surface areas which may help dissipate heat (Greenberg et al. 2012a, Campbell-Tennant et al. 2015), whereas populations in colder climates tend to have smaller bills which may help retain heat (Symonds and Tattersall 2010, Friedman et al. 2017). Climate has been shown to influence bill morphology in this way both within species (Greenberg et al. 2012a, Campbell-Tennant et al. 2015, LaBarbera et al. 2020) and across diverse lineages (Symonds and Tattersall 2010, Friedman et al. 2017).

The relationship between temperature and bill morphology may be modulated by precipitation. Thermoregulatory strategies vary depending on the water vapor gradient available for evaporative cooling (Gerson et al. 2014), and studies have found that stronger relationships exist between surface area and maximum summer temperature in climates with high humidity (Gardner et al. 2016, LaBarbera et al. 2020) as humidity decreases the effectiveness of evaporative cooling (Dawson 1982, van Dyk et al. 2019). Therefore, it can be advantageous for birds in humid climates to increase avenues of dry heat loss as evaporative cooling becomes less effective (van de Ven et al. 2016). It may also be advantageous to use non-evaporative thermoregulatory strategies in water-restricted areas, where dehydration is a serious concern (McKechnie and Wolf 2009, Greenberg et al. 2012b). As the ambient temperature approaches body temperature, passerines become increasingly reliant on evaporative cooling. To decrease the need for evaporative cooling, passerines may elevate their body temperature to hyperthermic levels to maintain a favorable thermal gradient for dry heat transfer (Smith et al. 2017). However, when ambient temperature surpasses body temperature, evaporative cooling is the only cooling pathway available, and the bird must lose water to prevent lethal body temperatures (Smith et al. 2017). As birds have a limited capacity to store water, this creates a dangerous balance between hyperthermia and dehydration in hot and water-restricted habitats (Albright et al. 2017). Efficient passive heat loss could help to mitigate this effect, as it may aid in water retention by delaying the onset of evaporative cooling to higher ambient temperatures (Smith et al. 2017). This might be especially true for passerines, as evaporative water loss via panting is their primary cooling mechanism (McKechnie et al. 2021). In song sparrows, an increase in bill surface area by 13.1% is estimated to reduce water loss requirements by 7.7% (Greenberg et al. 2012b). The water savings are estimated to be even higher in California Savannah Sparrow populations, where a bill size increase of 7.37% is estimated to reduce water loss by 16.2% (Benham and Bowie 2021). Therefore, non-evaporative cooling may be especially advantageous in fresh water-restricted habitats, such as salt marshes (Greenberg et al. 2012a, Benham and Bowie 2021) and deserts (Smith et al. 2017), and we may predict climate to have a larger influence on bill morphology in these habitats.

The hypothesized direct relationship between bill surface area and non-evaporative cooling potential would only hold when the bird's body temperature is greater than the ambient temperature, allowing heat to be passively lost from the body surface (Hagan and Heath 1980, Greenberg and Danner 2012). If the ambient temperature exceeds body temperature, this reversal in the temperature gradient causes the bill to function as a heat sink, instead of a heat radiator (Greenberg and Danner 2012). Therefore, at environmental temperatures approaching or exceeding body temperature, a large bill surface area could be counterproductive to cooling (Tattersall et al. 2017), and a reversal in the relationship between bill surface area and temperature has been seen in habitats where birds experience these conditions (Greenberg and Danner 2012). This makes deserts and other hot, arid habitats an interesting place to study the effects of climate on bill morphology variation.

Toxostoma thrashers (family: Mimidae) are a lineage of North American passerines that occupy a variety of habitats and climate niches across North America (Fig. 1). These habitats vary in both temperature and aridity, ranging from cool and wet temperate woodlands in the eastern United States to hot and dry scrublands, chaparral and deserts in the southwestern United States and Mexico (Billerman et al. 2020, Fig. 1, 2). The ten species within this genus also show large variation in cranial and bill morphology, with bills that vary in both size and curvature (Zink et al. 1999). Previous work on thrasher bill morphology has related this to diet and foraging substrate (Engels 1940, Zink et al. 1999). Although some work has suggested that thrashers may be

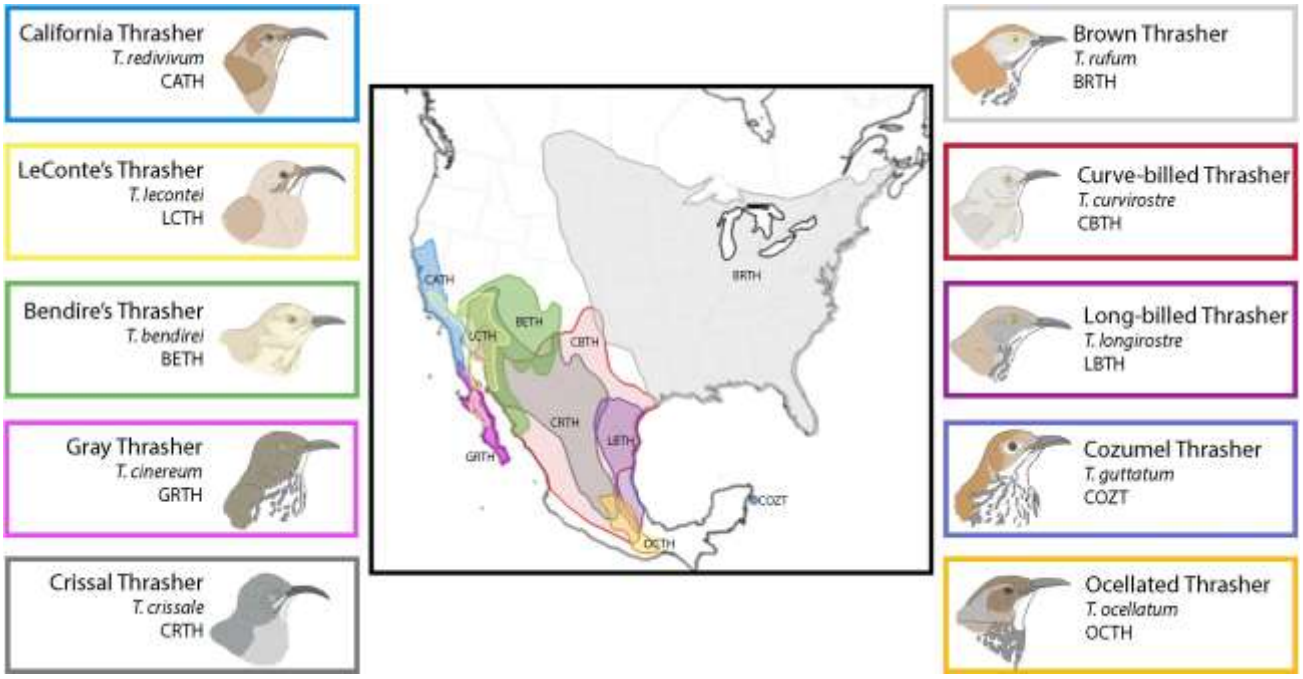

Figure 1. Geographic distribution of the ten *Toxostoma* thrashers. Colored boxes match colors on the range map and contain common name, scientific name and four-letter alpha code used to identify species in the map and in Fig. 2, 4 and 5. Depictions of each species are meant to show general variation in bill morphology across species.

better at non-evaporative cooling than other desert passerines (Smith et al. 2017), no studies have yet investigated the role of climate in shaping bill morphology across this group. Here, we test whether bill morphology is associated with climate niche in the genus *Toxostoma*. We hypothesize that species occupying hotter, more arid climate niches will have bills with greater surface area, compared to those in wetter or colder climates. We test this hypothesis across *Toxostoma* thrashers, as well as within each species. Further, we hypothesize that for species occupying the hottest and driest climate niches, this relationship will be reversed. We measured bill dimensions from museum specimens of all ten *Toxostoma*

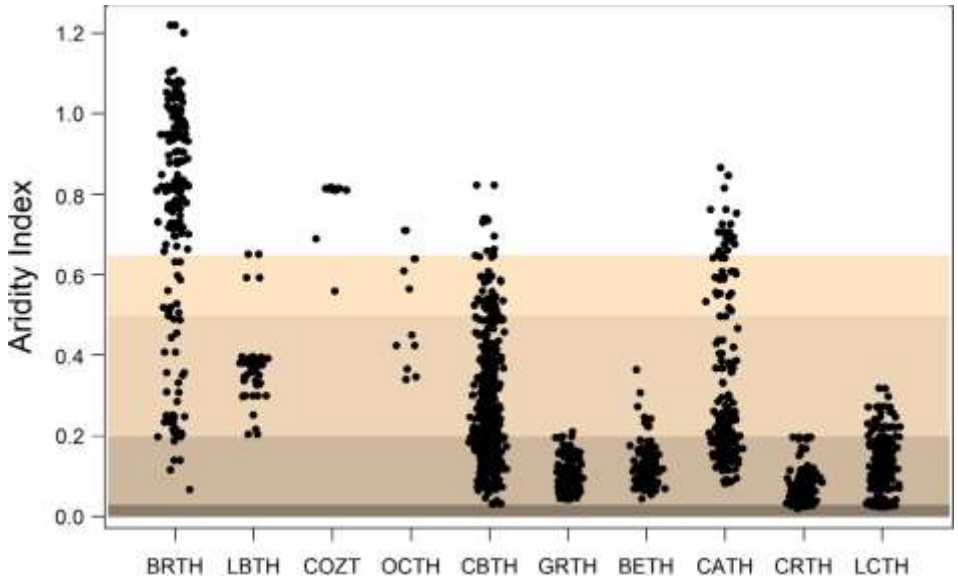

Figure 2. Distribution of aridity index at occurrences for all 10 species of *Toxostoma* thrashers. Aridity index increases on a scale from drier to more humid: values < 0.03 (dark brown) are hyper-arid; 0.03–0.20 (medium-dark brown) are arid; 0.2–0.5 (medium-light brown) are semi-arid; 0.50–0.65 (light brown) are dry sub-humid; and values > 0.65 are humid (Trabucco and Zomer 2018). Four-letter alpha codes correspond to species common names and are defined in Table 1 and Fig. 1.

thrasher species and compared bill morphology of each species to its occupied climate niche. We also compared bill morphology within each species to the climate of the location at which each specimen was collected.

Material and methods

Specimen measurements

We searched VertNet (Constable et al. 2010; <www.vertnet.org>), an online vertebrate museum specimen database, to locate *Toxostoma* thrasher specimens across each species' range. We excluded juveniles from our sample and included both males and females. We only measured specimens collected after the year 1900 to match the time frame of the available climate data. We requested specimens from all ten *Toxostoma* species from the Carnegie Museum of Natural History, Cornell University Museum of Vertebrates, Delaware Museum of Natural History, Denver Museum of Nature and Science, Field Museum of Natural History, Louisiana Museum of Natural History, Museum of Comparative Zoology, Moore Lab of Zoology, Museum of Vertebrate Zoology, San Diego Natural History Museum, Burke Museum and Yale Peabody Museum of Natural History (Supporting information).

We measured bill depth, width and length from each specimen, as well as length of the closed wing (hereafter 'wing length') (Stiles and Altshuler 2004), which we used as a proxy for individual body size. We used digital calipers to measure wing length, but because many thrasher species have curved bills, caliper measurements would not capture the full curved length of the bill (but see Subasinghe et al. 2021). Therefore, we photographed each bill from a dorsal and profile view against a gridded background using a mounted Canon Rebel DSLR camera. We then used the length measurement feature in Scientific Image Analysis (SIA), a recently developed software written in MATLAB (Ralston et al. unpubl.), to measure bill depth, width and length (Fig. 3). SIA can be used to determine the distance between selected landmarks on the digital photograph after an image has been calibrated. We calibrated our images using the gridded background to convert pixels to cm. We also used the Skew function in SIA to correct for skew in measurements that may arise from the angle at which the photograph was taken (Ralston et al. unpubl.). To best approximate the amount of exposed bill surface area available for passive heat transfer, all measurements were taken at the most proximal exposed section of the bill (Fig. 3), and not at the anterior edge of the nares as in other studies (Greenberg et al. 2012a). Because some specimens were preserved with a slightly open bill, we measured

Figure 3. Profile (top) and dorsal (bottom) bill measurement photographs for *T. crissale* analyzed in SIA. Specimens were photographed on a 1 cm scaled background, which was used to calibrate the images. Profile photographs provided bill length (sum of line segments along culmen, orange), depth (pink) and mandibular depth (green). Dorsal photographs provided bill width (blue).

bill depth as the depth of the upper mandible only. We then calculated bill surface area using a simplified equation for the lateral surface area of a nearly circular elliptical cone ((width +depth)/4) × π × length, following Greenberg et al. (2012a). Specimens with damaged bills that prevented an accurate measurement of bill length, depth or width were excluded from analysis. Sample sizes for each species are shown in Table 1.

Climate data extraction

For analyses across species, we constructed an estimated occupied climate niche of each species using occurrences from specimen records in VertNet. For specimens without coordinates available in VertNet, we used GEOLocate (<www.geolocate.org>) to find coordinates from the available locality data. The average occurrence sample size across species was 193 (range, 12–595; Table 1). We extracted three bioclimatic variables from WorldClim (Hijmans et al. 2005) from the year each specimen was collected: maximum temperature of the warmest month (hereafter 'maximum summer temperature'), minimum temperature of the coldest month (hereafter 'minimum winter temperature') (Symonds and Tattersall 2010, Friedman et al. 2017) and precipitation of the warmest quarter. Additionally, we calculated the aridity index for each collection location (Trabucco and Zomer 2018), which uses data from a 30-year period to quantify precipitation availability over atmospheric water demand. Aridity index values range from < 0.03, indicating a hyper-arid environment, to > 0.65, indicating a humid environment. While our focus is primarily on the need to dissipate heat in hot climates, we also included minimum winter temperature as an independent variable in our models as several studies have indicated heat conservation, rather than dissipation, is the driver of Allen's rule in bird bills (Symonds and Tattersall 2010, Friedman et al. 2017). Because brown thrasher *T. rufum* is migratory, we only extracted winter minimum temperature from specimens with a latitude less than 36.5°N. We then averaged the extracted climate data for each species to estimate the occupied climate niches (Table 1).

Across-species analyses

To test for a phylogenetic signal in our data, we estimated λ for surface area and the four climate variables in the R package geiger (Freckleton 2009, Münkemüller et al. 2012, Pennell et al. 2014), using the Mimidae phylogeny from Lovette et al. (2011). λ is a measure of phylogenetic signal; a λ near zero indicates that phylogeny does not influence the relationship between the variables, whereas a λ near one indicates that correlation in the variables is proportional to the amount of shared ancestry between the species (Freckleton et al. 2002). Because we found evidence for phylogenetic signal in some of the climate variables (Results), we used a phylogenetic generalized least squares (PGLS) regression in the R package caper (Orme et al. 2018) to control for any influence that phylogeny may have on our observed relationships. Aridity index and precipitation were log transformed to meet assumptions of normality. We then ran four PGLS models, with surface area as a function of each of our

Table 1. Study species, mean lateral bill surface areas and mean climate variables. Parentheses show SDs for each mean. Bill surface calculated from specimens with sample size shown in the specimen (n) column. Climate means calculated from sample size of occurrences shown in the occurrence (n) column.

Species	Alpha code	Specimen (n)	Occurrence (n)	Surface area (cm^2)	Maximum temperature of warmest month (°C)	Minimum temperature of coldest month (°C)	Mean precipitation of warmest quarter (mm)	Aridity index
Brown thrasher (*T. rufum*)	BRTH	72	196	1.86 (0.02)	30.4 (0.21)	−4.29 (0.48)	287.4 (8.51)	0.73 (0.02)
Long-billed thrasher (*T. longirostre*)	LBTH	49	70	2.24 (0.03)	35.27 (0.18)	8.82 (0.25)	188.09 (9.8)	0.38 (0.01)
Cozumel thrasher (*T. guttatum*)	COZT	17	13	2.28 (0.06)	33.27 (0.18)	18.21 (0.28)	430.24 (16.71)	0.78 (0.02)
Ocellated thrasher (*T. ocellatum*)	OCTH	11	12	3.26 (0.13)	27.56 (1.18)	5.45 (0.92)	239.55 (37.25)	0.52 (0.04)
Curve-billed thrasher (*T. curvirostre*)	CBTH	70	595	2.68 (0.05)	33.48 (0.16)	3.18 (0.24)	218.75 (5.32)	0.27 (0.01)
Gray thrasher (*T. cinereum*)	GRTH	51	133	2.41 (0.04)	33.52 (0.21)	7.4 (0.3)	77.25 (6.66)	0.11 (0.00)
Bendire's thrasher (*T. bendirei*)	BETH	44	201	1.98 (0.03)	36.57 (0.26)	0.24 (0.33)	112.76 (4.44)	0.12 (0.00)
California thrasher (*T. redivivum*)	CATH	51	221	3.3 (0.08)	28.44 (0.24)	3.56 (0.18)	16.24 (0.83)	0.31 (0.01)
Crissal thrasher (*T. crissale*)	CRTH	72	280	2.71 (0.04)	36.98 (0.25)	1.39 (0.22)	101.75 (4.14)	0.11 (0.00)
LeConte's thrasher (*T. lecontei*)	LCTH	39	213	2.46 (0.06)	37.38 (0.2)	2.59 (0.19)	26.13 (1.78)	0.07 (0.00)

four climate variables. We did not use wing length to control for body size in these across-species analyses as wing length may also vary across species as a function of migratory strategy, or perhaps island endemism in Cozumel thrasher *T. guttatum*. Therefore, we used the average mass of the species, taken from Billerman et al. (2020), as a covariate in each model to control for body size.

Within-species analyses

Lastly, to test for an effect of climate on bill morphology within species, we ran an all-subsets regression with bill surface area as the dependent variable and all combinations of the four climate variables as independent variables. For within-species models, which attempted to link specimen bill morphology to the environmental conditions experienced by those individuals in life, we used climate from the year prior to collection year (Campbell-Tennant et al. 2015). These models also included covariates of wing length to account for size differences across species and collection year to account for the potential for changes in morphology over time (Campbell-Tennant et al. 2015). The 16 resultant models for each species were then ranked using AICc. The model with the lowest AICc was determined to be the best model for that species. We then reran the best model for each species as a mixed-effects linear model using sex as a random variable.

Results

We collected 1934 VertNet occurrences and measured 476 specimens across the 10 *Toxostoma* thrasher species (Table 1). Bill surface area varied across all species, with brown thrasher having the smallest surface area (1.86 cm^2) and California thrasher having the largest (3.30 cm^2). There was no phylogenetic signal in bill surface area or maximum summer temperature ($\lambda = 0.000$), and low phylogenetic signal in minimum winter temperature ($\lambda = 0.025$). However, there was a larger effect of phylogeny on both precipitation ($\lambda = 0.964$) and aridity index ($\lambda = 1.000$). While accounting for phylogeny, and using body mass as a covariate, we found no significant effect of maximum summer temperature on bill morphology, and the observed direction was opposite from our prediction ($\beta = -0.024$, $p = 0.637$, $R^2 = 0.437$, Fig. 4). We did find a significant positive correlation between relative bill surface area and minimum winter temperature ($\beta = 0.060$, $p = 0.017$, $R^2 = 0.706$), supporting our prediction. However, given the distribution of the data, we suspected this relationship was driven by a single species, Cozumel thrasher. When Cozumel thrasher was removed from this analysis, the relationship between relative bill surface area and minimum winter temperature for the remaining species was non-significant, though the slope and R^2 values were little changed ($\beta = 0.062$, $p = 0.109$, $R^2 = 0.693$). The observed slopes for both log precipitation ($\beta = -0.140$, $p = 0.296$, $R^2 = 0.508$) and log aridity index ($\beta = -0.087$, $p = 0.574$, $R^2 = 0.445$) were negative as we predicted, but neither of these relationships were statistically significant (Fig. 4).

For our within-species analyses, the observed relationships between individual relative bill surface area and climate varied by species. For five of the ten species (brown thrasher, long-billed thrasher [*T. longirostre*], Cozumel thrasher, ocellated thrasher [*T. ocellatum*] and Bendire's thrasher [*T. bendirei*]), the best model did not include any climate variables (Table 2). The best model for gray thrasher (*T. cinereum*) included maximum summer temperature, but there was no significant relationship between maximum summer temperature and relative bill surface area ($p = 0.540$) in this model. Moreover, R^2 for the best model was generally low for these species ($R^2 \leq 0.111$).

The remaining four species (curve-billed thrasher [*T. curvirostre*], crissal thrasher [*T. crissale*], California thrasher [*T. redivivum*] and LeConte's thrasher [*T. lecontei*]) each had at least one significant climate variable in their best model, though the variables and their direction of effect varied across species (Table 2, Fig. 5). Each tested climate variable was significant in the best model of at least one species. For curve-billed thrasher, there was a negative relationship between relative bill surface area and winter minimum temperature ($\beta = -0.024$, $p = 0.005$, $R^2 = 0.142$). The best model for LeConte's thrasher included a marginally significant negative relationship with summer maximum temperature ($\beta = -0.033$, $p = 0.086$, $R^2 = 0.430$), providing some limited support for our hypothesis that Allen's rule may be reversed for species occupying the hottest and driest climate niche. The LeConte's thrasher model additionally included a significant positive relationship with log summer precipitation ($\beta = 0.077$, $p = 0.046$). The best model for California thrasher included a significant positive relationship with summer maximum temperature ($\beta = 0.092$, $p = 0.005$), and log aridity index ($\beta = 0.387$, $p = 0.023$, $R^2 = 0.125$). Finally, the best model for crissal thrasher included only log aridity index, with which relative bill surface area had a significant negative relationship ($\beta = -0.133$, $p = 0.025$, $R^2 = 0.153$), following our prediction. Including sex as a random effect in linear mixed-effects models for each species' best model had no discernable effects on results. In all cases, the variance in slopes due to sex was negligible (< 0.05 in all species), and neither the direction of the slope nor the significance changed for any variable. We therefore only present results from models excluding sex.

Discussion

We predicted that species of the genus *Toxostoma* occupying hotter, drier climates would have larger bill surface areas than species occupying cooler and wetter climates. We further predicted that within each species, individuals occupying hotter, drier climates would have larger bills than their conspecifics in cooler, wetter climates. However, some results were contrary to our hypotheses. Our finding of a positive relationship between relative bill surface area and minimum winter temperature matched our hypothesis and is consistent with previous studies (Symonds and Tattersall 2010, Friedman et al.

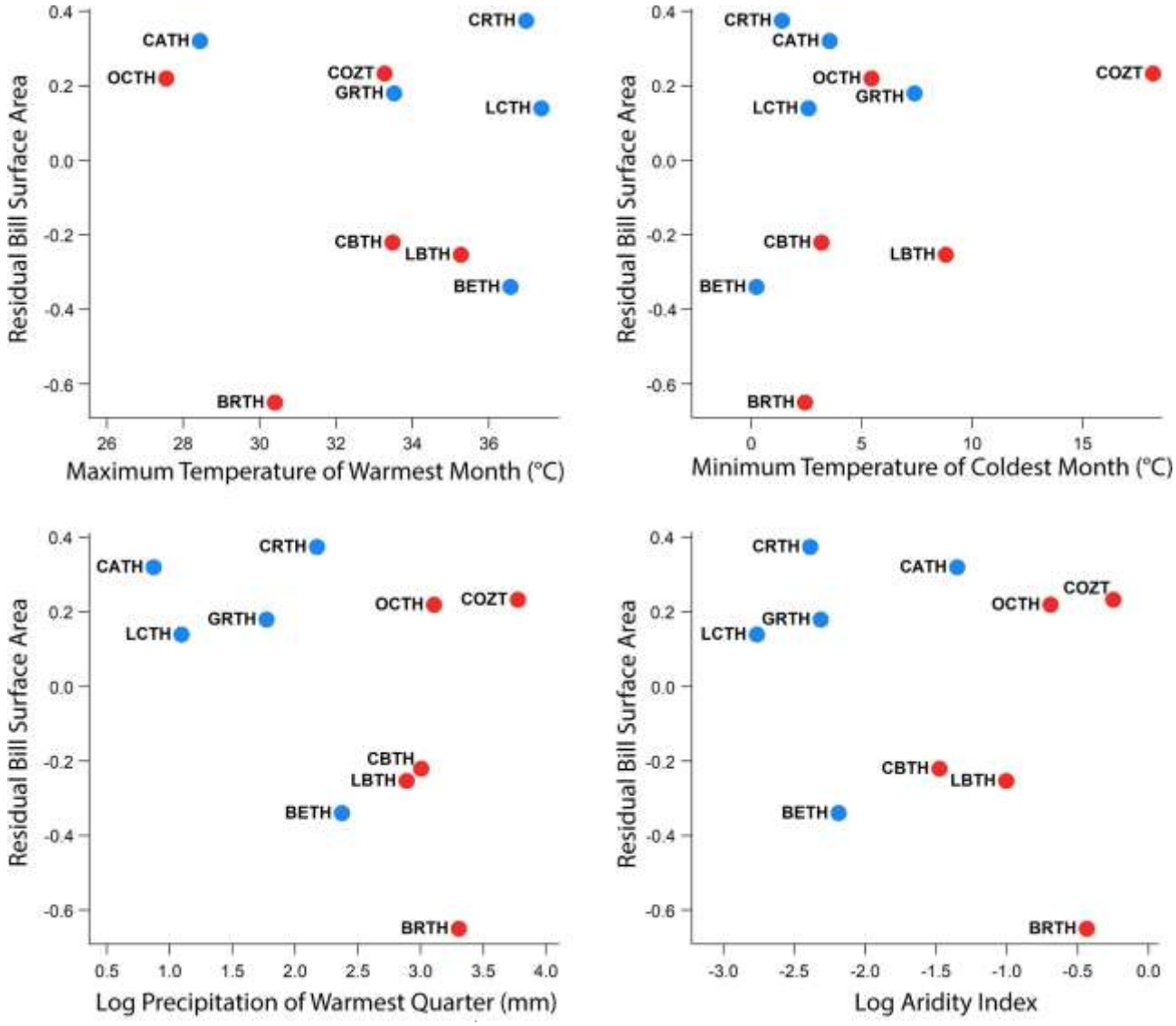

Figure 4. Relationship between bill surface area and climate variables across ten thrasher species. Residual bill surface areas are used, following regression on species mass. Blue and red points represent the two main clades within the *Toxostoma* genus. Four-letter alpha codes correspond to species common names and are defined in Table 1 and Fig. 1. The relationship between residual bill surface area and minimum temperature of the coldest month was significant ($p = 0.002$). All other relationships were non-significant.

2017). These results may suggest that Allen's rule in this genus is driven by heat conservation rather than heat dissipation, and that heat conservation may be an important selective pressure even in species that occupy generally warm climates. However, it is possible that this relationship is influenced by a single outlier species, the Cozumel thrasher, which experienced much warmer winter temperatures than all other species (Fig. 4). Removing Cozumel thrasher from this analysis resulted in a non-significant relationship between bill surface area and minimum winter temperature. Similarly, the finding of a non-significant negative relationship between bill surface area and maximum summer temperature across species may also have been influenced by two species with larger bills than expected given their relatively colder summer temperatures (California thrasher and ocellated thrasher, Fig. 4).

Altogether, our results fail to support previous studies which show birds living in hotter or more water-restricted habitats exhibit larger bills (Greenberg et al. 2012a, b, Campbell-Tennant et al. 2015), and instead align with previous studies documenting a lack of relationship between bill surface area and maximum summer temperature in desert-dwelling taxa (Gardner et al. 2016, Friedman et al. 2017).

Our results suggest that the differences in bill surface areas across species in the genus *Toxostoma* are likely not heavily influenced by climatic factors, and therefore that temperature constraints may not play a strong role in influencing the variation in *Toxostoma* bill morphologies. Other functions of the bill, such as its role in foraging ecology, may be more important (Zink et al. 1999). For instance, *Toxostoma* species with shorter, straighter bills (such as brown thrasher or

Table 2. Best model for each species as determined by lowest AICc value. Surface area was the response variable for each model, and wing length and year were used as a covariate in all models. bio5 = maximum temperature of warmest month; bio 6 = minimum temperature of coldest month; bio18 = mean precipitation of warmest quarter (log transformed); ai = aridity index (log transformed). Bold terms were significant ($p < 0.05$).

Species	Best model
Brown thrasher	**wing** + year
Long-billed thrasher	wing + year
Cozumel thrasher	wing + year
Ocellated thrasher	wing + year
Curve-billed thrasher	wing + year + **bio6**
Gray thrasher	wing + **year** + bio5
Bendire's thrasher	wing + year
California thrasher	wing + year + **bio5** + **ai**
Crissal thrasher	wing + year + **ai**
LeConte's thrasher	wing + **year** + bio5 + **bio18**

Bendire's thrasher) tend to peck or probe, whereas species with longer, more curved bills (such as California thrasher or crissal thrasher) dig (Engels 1940). It might be, then, that factors such as soil substrate are linked to the degree of curvature in a bill and have a stronger role in producing the diverse bill morphologies observed in this genus. A role in foraging may be further supported by the observation that thrasher species with overlapping distributions tend to occupy distinct habitat niches, and when habitat co-occupancy does occur, it tends to be between species of differing bill morphologies (Cody 2020). This may indicate that variation in bill morphologies in *Toxostoma* thrashers is primarily the result of differentiation in foraging niche, and not divergent climate niches. Therefore, foraging ecology may help explain why *Toxostoma* thrashers do not conform to predictions from Allen's rule as other taxa do. Friedman et al. (2019) found that multiple selective pressures act on a single bill dimension, and the evolution of bill size and shape in Australian honeyeaters (superfamily: Meliphagoidae) could be seen as a trade-off between thermoregulation and foraging ecology. In *Toxostoma*, it may be that the importance of foraging prevails over thermoregulation in shaping bill morphology. Dry heat loss through the bill could be modified by mechanisms other than increased surface area, such as ontogenetically increased vascular density (Burness et al. 2013) or vasodilation (Hagan and Heath 1980). Future studies that investigate the influence of ecology on the outcomes of Allen's rule may help untangle the roles of foraging and climate on bill morphologies in natural populations.

Within species, we found that one or more climate variables significantly predicted bill surface area in four species: curve-billed thrasher, California thrasher, crissal thrasher and LeConte's thrasher (Fig. 5). However, which variables were significant and the direction of the relationships varied considerably among species. Two relationships matched our predictions. California thrasher exhibited a positive

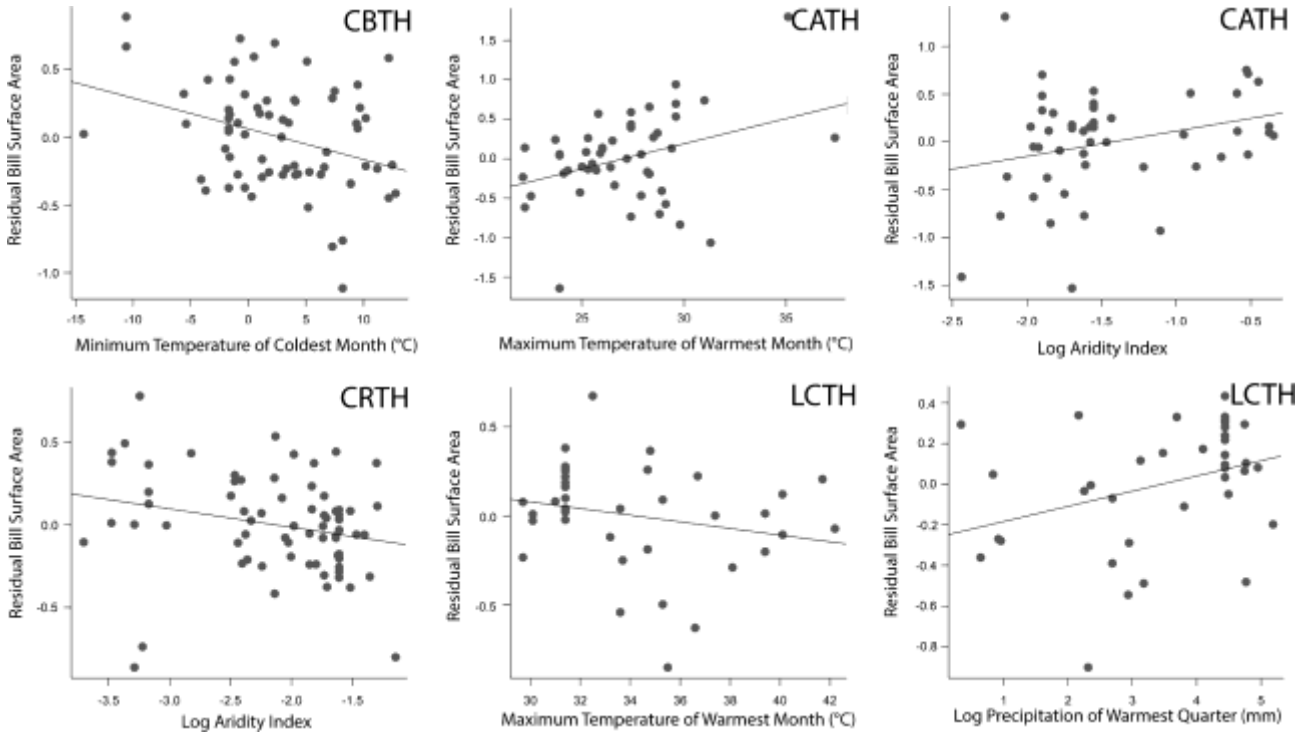

Figure 5. Significant relationships between bill surface area and climate variables taken from best models for each species. Residual bill surface area is used following regression on specimen wing length and year. All relationships shown have slopes significantly different from 0 ($p < 0.05$), except maximum temperature of warmest month for LeConte's thrasher, which was marginally significant ($p = 0.086$). Four-letter alpha codes correspond to species common names and are defined in Table 1 and Fig. 1.

relationship between maximum summer temperature and bill size, suggesting that thermoregulatory pressures may be influencing bill morphology in this species. Bill surface area in crissal thrasher was negatively associated with the aridity index, indicating that individuals in more arid habitats had larger bills. This may give additional support to the role that larger bills and non-evaporative cooling may play in water conservation.

LeConte's thrasher exhibited a marginally significant negative relationship between maximum summer temperature and bill surface area, providing some support for our hypothesis that Allen's rule may be reversed in the hottest climates when temperatures exceed body temperature. LeConte's thrasher occupies the hottest and driest habitats of the ten *Toxostoma* species (Table 1, Fig. 2), with temperatures reaching up to 48°C during the summer (Sheppard 2020). The body temperature of LeConte's thrasher is unknown, but no bird is known to have a body temperature regularly exceeding 48°C (Prinzinger et al. 1991), and avian critical thermal maxima are usually below 46°C (McKechnie and Wolf 2019). This suggests that summer temperatures may regularly exceed the body temperature of LeConte's thrasher, reversing the thermal gradient between the bill and the environment. This may result in a selective pressure for a smaller bill that absorbs less heat from the environment. Although other thrasher species (crissal thrasher, California thrasher, gray thrasher, Bendire's thrasher and curve-billed thrasher) may overlap with parts of LeConte's thrasher's range, these other species tend to occupy more riparian habitats with taller vegetation, whereas LeConte's thrasher occupies sparsely vegetated areas with little surface water (Sheppard 2020). If LeConte's thrasher is therefore more exposed to the intense summer heat, that may explain why a negative relationship between bill surface area and maximum summer temperature is found only in this species. The high R^2 value of the model for LeConte's thrasher ($R^2 = 0.430$) may also indicate that climate is more influential in shaping the bill surface area in LeConte's thrasher than in other species. It should be noted that our sample of LeConte's thrashers includes both subspecies, *T. l. lecontei* and *T. l. arenicola*. Some have proposed that *T. l. arenicola*, which occurs in Baja California (Fig. 1), is genetically distinct enough from *T. l. lecontei* to warrant recognition as a separate species (Zink et al. 1997, Vásquez-Miranda et al. 2017). As the American Ornithological Society currently does not recognize *T. l. arenicola* as an additional *Toxostoma* species (Chesser et al. 2020), we combined the two subspecies in our analyses. We found that *T. l. arenicola* tended to occupy milder climates with cooler and wetter summers. *T. l. arenicola* also tended to have larger relative bill surface area (Supporting information), perhaps influencing the climate–bill relationships we see within LeConte's thrasher. Future work may investigate the role that climate plays in driving morphological differentiation between these closely related taxa.

Several of our other within-species results contradicted our predictions. For example, we predicted that individuals occupying more water-restricted areas would have larger bills, as non-evaporative cooling may promote water retention. However, LeConte's thrasher displayed a significant positive relationship with precipitation, indicating individuals in wetter climates had larger bills. Similarly, California thrasher displayed a significant positive relationship with aridity index, indicating that individuals in more humid climates had larger bills. This may be because high humidity can decrease the efficacy of evaporative cooling, leading to selection of larger bills that can take advantage of non-evaporative cooling strategies (Gardner et al. 2016). California thrasher occupies a greater range in aridity than the other thrashers that occupy the American southwest (Fig. 1, 2), potentially indicating that high humidity may be acting as a selective pressure in some portions of its range. Grinnell (1917) also notes that differences in rainfall correspond closely with the ranges of California thrasher subspecies, suggesting a role for rainfall in influencing variation within this species. The best model for curve-billed thrasher included a negative relationship with minimum winter temperature, opposite to our predictions. However, this trend cannot be explained by thermoregulation, as there is no thermoregulatory advantage to having a larger bill in a colder climate (LaBarbera et al. 2020). For these contrary results in LeConte's, California and curve-billed thrasher, it may be that bill size does not vary with climate per se, but with other factors affected by climate. These factors might include food type and abundance (Boag and Grant 1984, Smith 1990, LaBarbera et al. 2020), vegetation (Durant et al. 2003), parasite abundance (Moyer et al. 2002, Clayton et al. 2005) or foraging substrate (Gerretsen and Van Heezik 1984).

Climate variables were not significant in the models of six species: Cozumel thrasher, ocellated thrasher, long-billed thrasher, Bendire's thrasher, gray thrasher and brown thrasher. A possible explanation for this in Cozumel and ocellated thrashers is low sample size; few museum specimens were available for these species. Furthermore, the range of Cozumel thrasher is extremely restricted, as it is endemic to a single, small island. Previous studies examining the relationship between climate and bill morphology found that climate variables were not significant in species with a restricted range, likely due to low climate variability (Luther and Greenberg 2014, Campbell-Tennant et al. 2015). The lack of climate variability between individuals would preclude finding any relationship between bill surface area and climate. This effect similarly could impact gray thrasher, which occupies only the Baja California peninsula, and ocellated thrasher, which occupies a small range in south-central Mexico. Brown thrasher may have had no significant climate variables due to weak selective pressure for non-evaporative cooling, as this species faces little water restriction or extreme heat in the majority of its range. For species like brown thrasher with large ranges, it may also be that selection is only acting at the periphery of its range, where climatic pressures are expected to be stronger (Hardie and Hutchings 2010). However, this selection at the periphery would be obscured in our results by the greater amount of variation present in the birds occupying the center of the range (Hardie and Hutchings 2010). A final possibility

for all species is that competing selective pressures on bill morphology, such as foraging ecology, may be stronger than the thermoregulatory pressure imposed by climate.

Avian bill diversification is shaped not by a single selective pressure but by multiple trade-offs and constraints (Friedman et al. 2019, Navalón et al. 2019). When a single morphological trait performs multiple tasks that each contribute to fitness, fitness can be viewed as an increasing function of the performance at all tasks, with the fittest phenotype having the best aggregate performance (Shoval et al. 2012). However, which of the trait's many tasks is most influential in determining fitness will vary by ecological context, producing different phenotypes in different species (Shoval et al. 2012). The varied relationships between climate and bill morphology in the ten *Toxostoma* species suggest that thermoregulatory constraints may exert a greater influence on fitness in some species than others.

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Charlotte Probst: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Joel Ralston**: Conceptualization (equal); Formal analysis (equal); Investigation (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Ian Bentley**: Funding acquisition (lead); Methodology (supporting); Software (lead); Writing – review and editing (supporting).

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