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ORIGINAL PAPER

Complex relationships among environmental conditions and bill morphology in a generalist songbird

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Abstract The selective pressures acting on phenotypes are complex and can vary both spatially and temporally. To elucidate relationships among environmental conditions and selection on a complex morphological trait, we explored spatial and temporal variation in avian bill structure in a common generalist songbird, the Dark-eyed Junco (*Junco hyemalis*). We measured bill length, width, and depth, and calculated bill surface area for >800 museum specimens collected in California from 1905 to 1980. We then determined which environmental variables (precipitation, temperature, habitat type) acting over which temporal scales (seasonal, annual, hemi-decadal, decadal) explained variation in these measures of bill morphology. Although we had predicted that relationships between environmental parameters and selection on the bill structure would reflect either foraging ecology or thermoregulatory needs, the patterns that we found were more complex and varied with season and among the different bill traits examined. Temperature was consistently a more important predictor of bill morphology than precipitation, although overall support for temperature was still weak. While bill surface area was related to habitat type, linear measures of bill morphology were related to temperature maxima, minima, and variability. Bill morphology was related to temperature maxima in summer; in contrast, both temperature maxima and minima were supported in winter models. Of the climate variables identified as important in our analyses, support was strongest for the measure of decadal temperature variability. The strong relationship between vegetative community and bill surface area revealed by our analyses as well as the unexpected role of decadal temperature variability indicate that consideration of the large-scale context—ecology and climate—in which complex phenotypic traits occur may reveal important patterns of selection that are not evident from studies of more isolated components of natural systems.

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Introduction

Phenotypic traits are the product of multiple, complex, and sometimes conflicting selective pressures (Andersson 1982; Endler 1983; Schluter et al. 1991; Fleming and Gross 1994; Brooks and Endler 2001; Alcántara and Rey 2003; Gómez 2004; Templeton and Shriner 2004; Goodman et al. 2015; Heinen-Kay et al. 2015). Conflicting selection pressures may occur simultaneously, as in the case of trade-offs between mate acquisition and predation risk (Endler 1983; Heinen-Kay et al. 2015), or sequentially, when the trait value favored by selection changes over the course of an individual's or taxon's existence (Schluter et al. 1991; Rohr et al. 2003; Gómez 2004). What we observe as a current phenotype is the net consequence of multiple selective pressures acting over various time scales (Alexander et al. 2006), as current selective pressures act on phenotypes already bearing the signatures of past selection (Balmford 1996; Hansen and Orzack 2005). Understanding the interaction of multiple selection pressures across several time scales is a basic goal of evolutionary biology.

Environmental conditions can exert strong selective pressures which may vary over time (Endler 1983; Balmford 1996; Gotanda and Hendry 2014). Field and laboratory experiments in guppies (*Poecilia reticulata*) have demonstrated rapid evolution of color patterns in response to changes in predation intensity (Endler 1983; Gotanda and Hendry 2014). Long-term studies in natural populations of Darwin's finches have demonstrated selection to be variable in strength and direction over the time scale of decades, as well as documenting the long-lasting effects on phenotype of brief but extreme selective events (Grant and Grant 1993, 2002). As human activity drives changes in environmental conditions at an accelerating pace (Parmesan and Yohe 2003), it is increasingly important to understand how multiple, temporally-varying selective pressures interact to shape phenotypes (Babin-Fenske et al. 2008; Desrochers 2010).

Yet it is often difficult to tease apart these several influences on phenotype (Schluter et al. 1991; Rohr et al. 2003; Hansen and Orzack 2005). A chief challenge is obtaining sufficient breadth and depth of sampling. True patterns may be obscured if a contributing factor is not sampled: for example, conflicting selection may be masked by a correlation with an unmeasured variable (Schluter et al. 1991), and temporal variation may be mistaken for geographic variation if there is insufficient temporal range of sampling (Rohr et al. 2003). Additionally, when different selection pressures act in opposition, they may mask each other's effects (Tingley et al. 2012). In this study we use museum specimens collected over the course of decades and historical climate data to examine the effects on bill morphology of multiple environmental selection pressures across several temporal scales.

Analyses of avian bill morphology provide opportunities to explore potentially complex interactions between selective pressures and phenotypic variation across multiple spatial and temporal scales. The bill is fundamental to multiple critical aspects of avian biology such as foraging, thermoregulation, and sound production (Grant and Grant 1996; Ballentine 2006; Greenberg et al. 2012; Tattersall et al. 2016). As a result, the bill is likely to be subject to a complex suite of selective forces, the effects of which may be evident over relatively short time periods (Grant and Grant 1993, 2002; Badyaev et al. 2008) as well as longer temporal frameworks (Smith et al. 1995; Symonds and Tattersall 2010; Freed et al. 2016); multiple adaptive radiations in birds have been attributed to innovations in foraging due to variation in bill morphology (Freed et al. 1987; Burns et al. 2003; Jønsson et al. 2012). Variation in bill morphology is readily documented given that avian bills are typically preserved as part of museum specimens. Collectively, these attributes suggest that studies of avian bill morphology may shed light on the effects of multiple selective pressures of varying strengths on complex organismal phenotypes.

To explore the effects of selection on avian bill morphology, we examined spatial and temporal variation in bill morphology in a common, ecologically generalized songbird, the Dark-eyed Junco (*Junco hyemalis*). We focused our analyses on a geographically widespread generalist to capitalize on intraspecific variation in bill morphology as a measure of the outcomes of the selective pressures experienced by individuals. To focus on selection rather than genetic drift, which can also generate morphological variation, we focused on associations between environment and bill morphology across a large spatial and temporal range, so that our sample set for any given variable value includes individuals from many populations. This minimizes the impact of drift and any other stochastic process on our results. We selected a set of specimens representing a broad range of both geographic and climate space in order to maximize the likelihood of detecting competing selective pressures; while these pressures may mutually mask their effects in a subset of regions, our broad dataset is likely to include other regions in which their effects will be detectable.

Dark-eyed Juncos are found throughout North America and feed on seeds and arthropods (Nolan et al. 2002). Ecologically, these birds range from highly seasonal boreal habitats to less seasonal semi-tropical regions. Elevationally, this species occurs from sea level to the sub-alpine tree line of montane regions. As a result, populations of Dark-eyed Juncos are expected to experience considerable variation in environmental conditions that should be associated with marked differences in the selective pressures acting on the bill morphology of members of this species.

We used data from museum specimens of Dark-eyed Juncos (hereafter "juncos") to evaluate two hypotheses regarding the effects of environmental conditions on bill morphology. The foraging ecology hypothesis asserts that bill morphology is under strong selective pressure to optimize the acquisition and processing of food (Price 1987; Grant and Grant 1996). According to this hypothesis, bill structure—in particular differences in bill width and depth, both of which have been shown to be associated with bite force in multiple avian species (Herrel et al. 2005; Badyaev et al. 2008)—should co-vary with the food resources consumed. In contrast, the heat dissipation hypothesis asserts that bill morphology is subject to selective pressures associated with the necessity of regulating heat loss to the external environment as part of thermoregulation (Symonds and Tattersall 2010; Greenberg et al. 2012; Cardilini et al. 2016; Tattersall et al. 2016). According to this hypothesis, bill structure—in particular bill surface area (Greenberg and Danner 2012)—should co-vary with differences in thermal environments. These hypotheses are not exclusive and both may contribute to variation in bill structure, particularly in geographically widespread generalist species that are likely to encounter a variety of environmental conditions.

Methods

Study species

Dark-eyed Juncos are medium-sized (~16 g) songbirds common across most of North America. Their adult diet includes arthropods (primarily coleopterans, lepidopterans and their caterpillars, hymenopterans, and dipterans), seeds (most ~0.5 mm in diameter, occasionally as large at 4.5 mm in diameter), and occasionally fruit (Nolan et al. 2002). Arthropods make up ~50% of the diet in spring and summer but <10% in fall and winter. Foraging strategies include gleaning, litter-pecking, and scratching; foraging occurs on the ground or low in vegetation (Nolan et al. 2002). Juncos occupy distinct breeding and wintering grounds, which may be a few km apart (in partially migratory populations) or hundreds to thousands of km apart [in fully migratory populations (Keiser et al. 2005)]. They exhibit site fidelity to both the breeding and wintering grounds (Nolan et al. 2002). Within breeding and wintering grounds, home range sizes are usually small; e.g. home range sizes of breeding male juncos average ≤200 m^2 (Chandler et al. 1994).

Specimens examined

We measured museum specimens of adult *Junco hyemalis* belonging to the Oregon Junco taxonomic group (*J. h. thurberi*, *J. h. shufeldti, J. h. oreganus, J. h. pinosus,* and *J. h. montanus*). The specimens examined had been captured in the state of California between 1905 and 1980, with the majority of individuals (92%) collected between 1905 and 1945. Using specimens >10 years old minimizes the cofounding effects of postmortem bill shrinkage, as shrinkage usually occurs within the first few years following specimen preservation (Summers 1976). We chose to focus on juncos from California for two reasons: first, because the state contains a large diversity of biomes within a relatively small geographic area; and second, because the early collecting expeditions mounted by the Museum of Vertebrate Zoology (MVZ), which explicitly focused on California, provide an unusually extensive record of juncos from across the state. All materials examined were held in the MVZ or the California Academy of Sciences (CAS). Although specimens held in the MVZ had been designated *Junco oreganus* instead of *Junco hyemalis* due to a historical difference in naming convention, the two taxa are considered synonymous (American Ornithologists' Union 1998). Metadata associated with each specimen (sex, subspecies, date and location of collection) were downloaded from the VertNet online search portal (http://vertnet.org).

Morphological measurements

Bill length, width, and depth are standard avian morphological measures (Symonds and Tattersall 2010; Greenberg et al. 2012) that are expected to capture the aspects of variation in bill morphology most relevant to the hypotheses considered here. Bill length was measured as the length of the exposed culmen. Bill width was measured at the base of the bill, immediately adjacent to the first feathers. Bill depth was measured at the deepest part of the bill, which typically corresponds to the area between the nares. Bill surface area was calculated from bill length, width, and depth following Greenberg et al. (2012) using the formula:

$$\text{Surface area } = \frac{width + depth}{4} \times length \times \pi$$

Wing chord length, a proxy for overall body size (McGlothlin et al. 2005), was measured from the base of the carpometacarpus to the end of the longest primary feather. All measurements were performed by the same individual (KL) using digital calipers. Only undamaged bills were measured.

Temporal variation in bill morphology

Bill morphology is known to vary over multiple temporal scales (Tattersall et al. 2016). Environmental variation over the course of years to decades—the equivalent of two-to-ten generations for most passerines—has been shown to be associated with variation in bill morphology in other passerines (Grant and Grant 2002). The generation time for juncos is approximately one year; juncos can breed at one year of age and on average breed for less than three years before dying (Nolan et al. 2002). Accordingly, to capture variation across generations, we examined potential environmental correlates of bill morphology over the following temporal scales: (1) annual (most recent year), (2) hemi-decadal (most recent five years), and (3) decadal (most recent 10 years).

Bill morphology may also vary seasonally and with changes in life history stage (Gosler 1986; Matthysen 1989; Greenberg et al. 2013). In California, much of the seasonal variation in environmental conditions occurs in the form of predictable changes in precipitation, with high precipitation in the winter and low precipitation in the summer. Seasonal temperature variation is less consistent, but the general pattern is one of mild winters and warm summers. The selection pressures acting on birds likely differ among seasons: the spring and summer months are dominated by breeding efforts, while the fall and winter are not. Additionally, because most Dark-eyed Juncos are migratory (Nolan et al. 2002), few experience the environmental conditions present at a given location year-round. To account for potential seasonal differences in the conditions experienced by individuals, we analyzed breeding and wintering birds separately. We allocated specimens to one of two seasonally-distinct analyses, "summer" or "winter," based on subspecies and date of collection: *J. h. shufeldti, J. h. oreganus,* and *J. h. montanus*, which only winter in California, were included in the winter analysis; *J. h. thurberi* and *J. h. pinosus*, which may winter and breed in California, were included in the summer analysis if they were collected between 15 March and 30 September but were otherwise included in the winter analysis. These delimitations were based on our own field observations of the timing of junco migration as well as Nolan et al. (2002). The winter analysis included only environmental data from October through February, while the summer analysis included only environmental data from April through August. This procedure ensured that each specimen was associated only with environmental data corresponding to the season of collection (Fig. 1).

Environmental correlates of bill morphology

To examine the effects of variation in abiotic environmental factors on bill morphology, we obtained records for the following monthly climate variables from the PRISM historical climate dataset (PRISM Climate Group 2015): precipitation (pptn), minimum temperature (T_{min}), and maximum temperature (T_{max}). Temperature and precipitation are standard measures of abiotic climate (Tingley et al. 2012). Temperature maxima were included because even a brief spike or drop in temperature can have large effects on small birds, e.g. through mortality due to dehydration or hypothermia, respectively (Graber and Graber 1979; McKechnie and Wolf 2010). Precipitation maxima and minima were not included because in mesic habitats, mean precipitation explains substantially ($\sim 10\times$) more variation in net primary productivity than does variation in precipitation (Guo et al. 2012). The PRISM historical dataset provides GIS raster files containing the monthly means of the four climate variables ranging from 1895 to 1990 as measured over 4 km-by-4 km grid cells across California. Geospatial processing of the data was performed with Python, and a

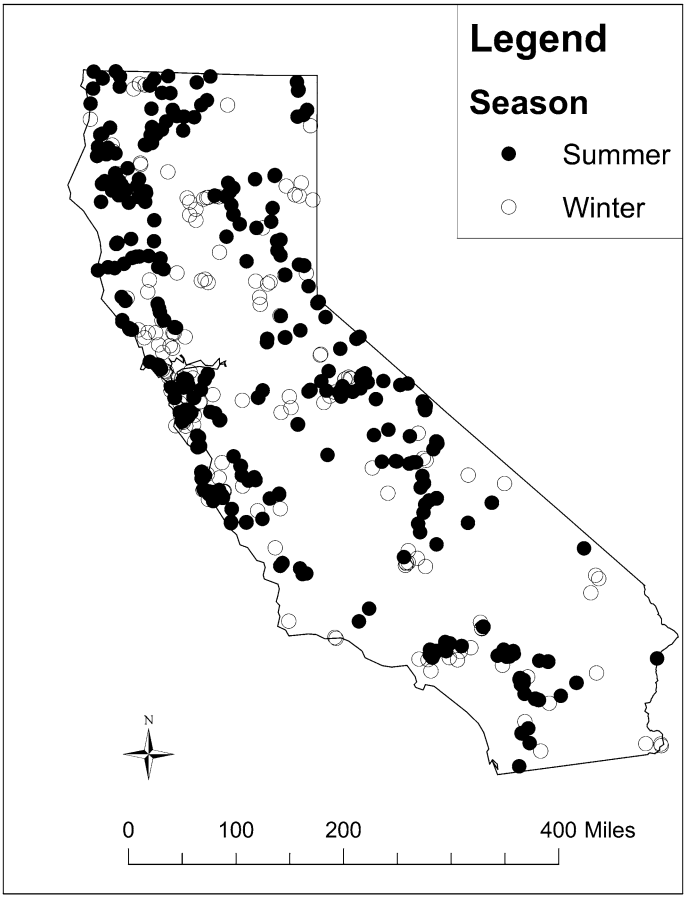

Fig. 1 Specimens collected in each season were approximately evenly distributed across the study area (California)

common Open Source library, GDAL, provided the “geo” capabilities of the script to generate geographic locations and query PRISM raster climate files for data pertaining to those locations.

We used the PRISM monthly climate data to calculate three precipitation-derived and seven temperature-derived climate variables (Table 1). These variables were chosen to maximize coverage of climatic variation while limiting the number of variables examined to a quantity that was tractable given our sample sizes.

To determine which environmental conditions were associated with a given specimen, we used the the latitude and longitude of the locality at which each specimen was collected to assign that individual to a specific raster cell. Because juncos are vagile birds whose ranges may extend beyond a single 4 km by 4 km cell (Nolan et al. 2002), a buffer code was used to convert mean environmental values for a given cell to those for a circle with a radius of 15 km centered on the collection locality for each specimen. For each calendar month, values for cells within this circle were averaged to generate a single mean value per environmental variable examined; raster cells that were only partially located within the

Table 1 Climate variables used in our analyses include measures of both precipitation and temperature at multiple temporal scales

Variable name	Description	Time span (years)	Calculated from
Pptn (1 year)	Annual mean precipitation	1	Monthly total pptn
Pptn (10 years)	Decadal mean precipitation	10	Monthly total pptn
Pptn_{sd} (10 years)	Decadal standard deviation of precipitation	10	Monthly total pptn
T_{min} (1 year)	Annual minimum temperature	1	Monthly T_{min}
T_{max} (1 year)	Annual maximum temperature	1	Monthly T_{max}
T_{min} (5 years)	Hemi-decadal minimum temperature	5	Monthly T_{min}
T_{max} (5 years)	Hemi-decadal maximum temperature	5	Monthly T_{max}
T_{min} (10 years)	Decadal minimum temperature	10	Monthly T_{min}
T_{max} (10 years)	Decadal maximum temperature	10	Monthly T_{max}
T_{sd} (10 years)	Decadal standard deviation of mean temperature	10	Monthly T_{mean}

15 km radius were not included in these analyses. This procedure was repeated for each of the 10 years prior to the collection date of a specimen.

Habitat type

Because interactions among temperature and precipitation may be complex and because the impacts of these interactions on juncos may be mediated by elements of the biotic environment (e.g., vegetation), we also examined variation in bill morphology in relation to the Jepson eFlora regions of California [used with permission of the Jepson Herbarium (Jepson Flora Project 2013)]. The Jepson eFlora geographic subdivisions of California capture broad patterns of habitat variation such as differences in substrate and vegetative community. We used ArcGIS v. 10.2.2 to identify the Jepson region corresponding to each specimen in our dataset. All 10 Jepson regions of California were represented in our data; these regions consist of the Cascade Ranges Region (CaR), the Central Western California Region (CW), the Mojave Desert Region (DMoj), the Sonoran Desert Region (DSon), the Great Central Valley Region (GV), the Modoc Plateau Region (MP), the Northwestern California Region (NW), the Sierra Nevada Region (SN), the East of the Sierra Nevada Region (SNE), and the Southwestern California Region (SW).

Statistical analysis

To examine relationships among environmental parameters, Jepson regions, and bill morphology, we ran generalized additive mixed models (package gamm4) in R v. 3.1.2 (R Core Team 2014). Using additive rather than linear models allowed us to include a non-linear term to account for spatial autocorrelation; with the exception of this term, the models were implemented with linear terms comparable to those in a generalized linear mixed effects model. We ran separate models for summering and wintering birds. Each model had a single bill trait (length, width, depth, or surface area) as the dependent variable. For each bill trait, we began with a base model that included sex, subspecies, month of collection, and wing chord as linear terms, year of collection as a random effect, and the interaction term between latitude and longitude as a potentially non-linear smooth term to account for any spatial autocorrelation in bill morphology. These variables are basic parameters that may affect bill morphology and were considered important to include in all analyses. To account for a possible inflation in error rate due to multiple testing, we performed a Benjamini–Hochberg correction to hold the false discovery rate at 0.05 when determining significance (Benjamini and Hochberg 1995).

We then used AIC_C-based model selection ("dredge" in package MuMIn; Bartoń 2015) to determine the best-supported combination of the base model and any one of the following additional linear terms: Jepson region, pptn (1 year), pptn (10 years), $pptn_{sd}$ (10 years), T_{min} (1 year), T_{max} (1 year), T_{min} (5 years), T_{max} (5 years), T_{min} (10 - years), T_{max} (10 years), and T_{sd} (10 years). We considered a model to be supported if it was within the 95% confidence set of models, defined as the smallest set of models whose Akaike weights (*w)* sum to ≥ 0.95 (Burnham and Anderson 2002).

Results

Sample sizes

Sample sizes were unevenly distributed among Jepson regions and subspecies for both summer and winter analyses (Table 2). This variation in sample sizes limited our ability to compare subspecies and Jepson region categories in cases where sample sizes were small.

Note on terminology

Given the two-step modeling strategy employed, the terminology used to report our results varies. With regard to construction of the base models, because no model selection occurred (i.e. all models contained the same variables), it was appropriate to assign estimates of statistical significance to the variables included in these analyses. In contrast, because model selection was employed in analyses of Jepson regions and environmental variables, for these results we report the Akaike weights of the models examined.

Base models

The bills of *J. h. thurberi* differed from those of the other subspecies examined. Among summer birds, *J. h. thurberi* bills were significantly shorter and smaller in surface area than *J. h. pinosus* (Table 3). Among winter birds, *J. h. thurberi* bills were shorter and wider than all other subspecies (Table 4). Month, sex, and wing chord were not significantly related to any bill measure in either season.

Effects of Jepson habitat regions

For summer and winter birds, the single top-supported model for each of the three linear bill measures examined (length, width, depth) was the base model, which did not include measures of either Jepson region or climate variables (Tables 5, 6). In contrast, inclusion of Jepson region was strongly supported for models of bill surface area for both summer and winter birds.

Table 2 Sample sizes of specimens in each Jepson region (unbold values) or subspecies (bold values) were unevenly distributed, and differed between the summer and winter analyses

Jepson region or subspecies	Summer n	Winter n
CaR	23	8
CW	108	94
DMoj	12	28
DSon	2	8
GV	6	36
MP	20	30
NW	183	43
SN	70	42
SNE	37	5
SW	51	7
J. h. montanus	**NA**	**58**
J. h. oreganus	**NA**	**25**
J. h. pinosus	**90**	**36**
J. h. shufeldti	**NA**	**36**
J. h. thurberi	**422**	**146**
Total	512	301

The summer analysis did not include *J. h. montanus*, *J. h. oreganus*, or *J. h. shufeldti* because these subspecies do not inhabit the study area during the summer

Table 3 Results from the base model of the summer analysis suggest that *J. h. thurberi* has shorter bills with smaller surface area than *J. h. pinosus*

Bill	Variable	Coefficient	SE	z	p
Length	*J. h. thurberi*	-0.429	0.106	4.03	<0.001*
	month	0.004	0.015	0.284	0.777
	sex(M)	0.075	0.053	1.40	0.162
	wing	0.010	0.009	1.14	0.254
Width	*J. h. thurberi*	-0.037	0.052	0.717	0.474
	month	-0.002	0.007	0.285	0.776
	sex(M)	0.036	0.027	1.35	0.178
	wing	0.009	0.005	2.05	0.040
Depth	*J. h. thurberi*	0.049	0.044	1.11	0.266
	month	0.009	0.008	1.12	0.261
	sex(M)	0.015	0.031	0.485	0.628
	wing	0.007	0.005	1.40	0.163
SA	*J. h. thurberi*	-4.179	1.448	2.88	0.004*
	month	-0.043	0.180	0.241	0.809
	sex(M)	1.079	0.655	1.64	0.101
	wing	0.194	0.110	1.75	0.080

Asterisks indicate p-values that are significant after Benjamini–Hochberg correction for multiple testing at a false discovery rate of 0.05

Effects of climate variables

There was substantial variation in all climate variables in our dataset (Table 7). We found no support for the inclusion of any precipitation variables in the models for any of the aspects of bill morphology examined. Inclusion of temperature variables was supported in

Table 4 Results from the base model of the winter analysis suggest that *J. h. thurberi* has shorter and wider bills with smaller surface area than *J. h. montanus, J. h. oreganus, J. h. pinosus, and J. h. shufeldti*

Bill	Variable	Coefficient	SE	z	p
Length	*J. h. oreganus*	0.088	0.124	0.706	0.480
	J. h. pinosus	0.015	0.132	0.116	0.907
	J. h. shufeldti	0.032	0.108	0.291	0.771
	J. h. thurberi	-0.324	0.088	3.65	<0.001*
	Month	-0.002	0.006	0.295	0.768
	sex(M)	0.005	0.062	0.073	0.942
	wing	0.021	0.010	2.12	0.034
Width	*J. h. oreganus*	0.070	0.059	1.19	0.234
	J. h. pinosus	0.035	0.060	0.571	0.568
	J. h. shufeldti	0.015	0.051	0.296	0.767
	J. h. thurberi	0.117	0.040	2.93	0.003*
	month	-0.003	0.003	0.949	0.343
	sex(M)	0.007	0.030	0.226	0.821
	wing	0.004	0.005	0.787	0.432
Depth	*J. h. oreganus*	0.061	0.075	0.802	0.423
	J. h. pinosus	-0.137	0.080	1.72	0.858
	J. h. shufeldti	-0.042	0.066	0.634	0.526
	J. h. thurberi	-0.132	0.053	2.50	0.012
	month	-0.002	0.004	0.540	0.590
	sex(M)	0.037	0.038	0.978	0.328
	wing	0.008	0.006	1.34	0.179
SA	*J. h. oreganus*	1.840	1.622	1.13	0.258
	J. h. pinosus	-0.476	1.711	0.277	0.782
	J. h. shufeldti	0.280	1.426	0.195	0.845
	J. h. thurberi	-2.893	1.189	2.42	0.015
	month	-0.056	0.082	0.689	0.491
	sex(M)	0.149	0.815	0.182	0.856
	wing	0.306	0.131	2.33	0.020

Asterisks indicate *p*-values that are significant after Benjamini–Hochberg correction for multiple testing at a false discovery rate of 0.05

models for some aspects of bill morphology, but not all, and the specific variables identified varied (Tables 5, 6). For example, for bill length in summer birds, there was some support for models containing each of four temperature variables: all three T_{max} variables and T_{sd} (10 years). In contrast, among winter birds, supported models of bill length contained both minimum and maximum temperature measures: all three T_{min} variables, T_{max} (1 year), T_{max} (10 years), and T_{sd} (10 years). Additionally, the level of support differed: cumulative weight of models within the 95% confidence set that contained a temperature variable was only 0.038 in models of bill length of summer birds, but was 0.455 in models of bill length of winter birds. Temperature variation [T_{sd} (10 years)] was supported when it appeared in models of bill width and bill depth in both winter and summer birds. In summer birds, supported temperature variables were positively related to bill length, positively or negatively related to bill width, and negatively related to bill depth; in winter birds, supported temperature variables were consistently negatively related to bill length, width, or depth. No models of bill surface area containing temperature variables received support in either summer or winter birds.

Table 5 Comparison of models of each bill parameter for the summer specimens

Bill	**Model**	**Coefficient**	**df**	**AIC$_{C}$**	**ΔAIC$_{C}$**	***w***
Length	Base	NA	10	703.6	0.00	0.805**
	Base + Reg	NA	19	715.7	12.13	0.002
	Base + Pptn(1yr)	-0.001	11	715.9	12.38	0.002
	Base + Pptn(10yrs)	-0.005	11	712.4	8.85	0.010
	Base + Pptnsd(10yrs)	-0.003	11	713.8	10.26	0.005
	Base + Tmin(1yr)	-0.001	11	712.8	9.24	0.008
	Base + Tmax(1yr)	0.010	11	711.9	8.37	0.012*
	Base + Tmin(5yrs)	-0.001	11	712.8	9.20	0.008
	Base + Tmax(5yrs)	0.010	11	711.8	8.29	0.013*
	Base + Tmin(10yrs)	-0.002	11	712.7	9.11	0.008
	Base + Tmax(10yrs)	0.010	11	711.8	8.24	0.013*
	Base + Tsd(10yrs)	0.070	11	707.5	3.90	0.115*
Width	Base	NA	10	8.9	0.00	0.928**
	Base + Reg	NA	19	41.9	32.98	0.000
	Base + Pptn(1yr)	0.001	11	21.7	12.78	0.002
	Base + Pptn(10yrs)	0.002	11	20.9	12.00	0.002
	Base + Pptnsd(10yrs)	0.001	11	21.6	12.75	0.002
	Base + Tmin(1yr)	-0.006	11	18.4	9.51	0.008
	Base + Tmax(1yr)	-0.006	11	17.6	8.74	0.012*
	Base + Tmin(5yrs)	-0.005	11	18.6	9.72	0.007
	Base + Tmax(5yrs)	-0.005	11	18.6	9.70	0.007
	Base + Tmin(10yrs)	-0.005	11	18.7	9.81	0.007
	Base + Tmax(10yrs)	-0.005	11	18.5	9.66	0.007
	Base + Tsd(10yrs)	0.005	11	16.7	7.84	0.018*
Depth	Base	NA	10	149.5	0.00	0.944**
	Base + Reg	NA	19	183.3	33.75	0.000
	Base + Pptn(1yr)	-0.001	11	162.9	13.38	0.001
	Base + Pptn(10yrs)	0.001	11	162.3	12.76	0.002
	Base + Pptnsd(10yrs)	0.001	11	162.9	13.41	0.001
	Base + Tmin(1yr)	0.003	11	160.0	10.49	0.005
	Base + Tmax(1yr)	-0.001	11	160.9	11.41	0.003
	Base + Tmin(5yrs)	0.005	11	159.3	10.49	0.005
	Base + Tmax(5yrs)	-0.003	11	160.5	10.98	0.004
	Base + Tmin(10yrs)	0.006	11	159.2	9.64	0.008
	Base + Tmax(10yrs)	-0.003	11	160.5	10.99	0.004
	Base + Tsd(10yrs)	-0.015	11	157.1	7.61	0.021*
SA	Base	NA	10	3222.4	21.29	0.000
	Base + Reg	NA	19	3201.1	0.00	1.000**
	Base + Pptn(1yr)	-0.011	11	3230.5	29.44	0.000
	Base + Pptn(10yrs)	-0.028	11	3228.8	27.75	0.000
	Base + Pptnsd(10yrs)	-0.018	11	3229.7	28.62	0.000
	Base + Tmin(1yr)	-0.013	11	3226.9	25.84	0.000
	Base + Tmax(1yr)	0.055	11	3227.2	26.16	0.000
	Base + Tmin(5yrs)	0.015	11	3226.9	25.79	0.000
	Base + Tmax(5yrs)	0.068	11	3227.0	25.92	0.000
	Base + Tmin(10yrs)	0.013	11	3226.8	25.75	0.000
	Base + Tmax(10yrs)	0.068	11	3227.0	25.91	0.000
	Base + Tsd(10yrs)	0.470	11	3223.1	22.03	0.000

Each model includes the base set of variables (“base”: subspecies, month, sex, wing chord, and a smoothed latitude*longitude interaction term) and, in some models, an additional environmental variable. The coefficient of that additional environmental variable is given in the column labeled “coefficient”, except in the case of the one categorical variable, Jepson habitat region

Reg = Jepson habitat region; *df* degrees of freedom; *w* Akaike weight of model

Within each bill parameter, the model with the highest *w* is indicated by **, and any model(s) within the confidence set (highest *w* models that sum to $\geq$0.95) are marked by *

Table 6 Comparison of models of each bill parameter for the winter specimens

Bill	Model	Coefficient	df	AIC_C	ΔAIC_C	*w*
Length	Base	NA	13	425.8	0.00	0.502**
	Base + Reg	NA	22	440.7	14.88	0.000
	Base + Pptn(1yr)	0.001	14	437.3	11.49	0.002
	Base + Pptn(10yrs)	0.001	14	437.1	11.28	0.002
	Base + Pptnsd(10yrs)	0.002	14	436.8	10.97	0.002
	Base + Tmin(1yr)	-0.036	14	428.8	2.95	0.115*
	Base + Tmax(1yr)	-0.030	14	430.1	4.30	0.058*
	Base + Tmin(5yrs)	-0.038	14	429.0	3.23	0.100*
	Base + Tmax(5yrs)	-0.030	14	431.0	5.17	0.038
	Base + Tmin(10yrs)	-0.036	14	429.7	3.89	0.072*
	Base + Tmax(10yrs)	-0.032	14	430.6	4.78	0.046*
	Base + Tsd(10yrs)	-0.100	14	429.9	4.12	0.064*
Width	Base	NA	13	-7.9	0.00	0.790**
	Base + Reg	NA	22	31.7	39.55	0.000
	Base + Pptn(1yr)	0.000	14	9.3	17.16	0.000
	Base + Pptn(10yrs)	0.000	14	8.8	16.73	0.000
	Base + Pptnsd(10yrs)	0.000	14	8.3	16.16	0.000
	Base + Tmin(1yr)	0.004	14	2.6	10.46	0.004
	Base + Tmax(1yr)	0.001	14	3.1	11.05	0.003
	Base + Tmin(5yrs)	0.003	14	2.7	10.57	0.004
	Base + Tmax(5yrs)	0.001	14	2.9	10.77	0.004
	Base + Tmin(10yrs)	0.004	14	2.4	10.28	0.005
	Base + Tmax(10yrs)	0.001	14	2.8	10.71	0.004
	Base + Tsd(10yrs)	-0.081	14	-5.0	2.89	0.186*
Depth	Base	NA	13	133.4	0.00	0.835**
	Base + Reg	NA	22	160.5	27.10	0.000
	Base + Pptn(1yr)	0.001	14	144.1	10.68	0.004
	Base + Pptn(10yrs)	0.001	14	147.4	13.95	0.001
	Base + Pptnsd(10yrs)	0.001	14	146.9	13.44	0.001
	Base + Tmin(1yr)	-0.001	14	143.7	10.22	0.005
	Base + Tmax(1yr)	-0.005	14	143.1	9.70	0.007
	Base + Tmin(5yrs)	-0.002	14	143.4	9.99	0.006
	Base + Tmax(5yrs)	-0.006	14	143.0	9.52	0.007
	Base + Tmin(10yrs)	0.000	14	143.5	10.03	0.006
	Base + Tmax(10yrs)	-0.005	14	143.0	9.54	0.007
	Base + Tsd(10yrs)	-0.087	14	137.3	3.85	0.122*
SA	Base	NA	13	1916.7	32.75	0.000
	Base + Reg	NA	22	1884.0	0.00	1.000**
	Base + Pptn(1yr)	0.016	14	1922.0	38.01	0.000
	Base + Pptn(10yrs)	0.018	14	1922.1	38.12	0.000
	Base + Pptnsd(10yrs)	0.021	14	1921.1	37.19	0.000
	Base + Tmin(1yr)	-0.223	14	1919.1	35.10	0.000
	Base + Tmax(1yr)	-0.218	14	1918.8	34.87	0.000
	Base + Tmin(5yrs)	-0.242	14	1918.9	34.94	0.000
	Base + Tmax(5yrs)	-0.236	14	1918.8	34.88	0.000
	Base + Tmin(10yrs)	-0.199	14	1919.5	35.52	0.000
	Base + Tmax(10yrs)	-0.243	14	1918.8	34.80	0.000
	Base + Tsd(10yrs)	-2.365	14	1912.6	28.61	0.000

Each model includes the base set of variables ("base": subspecies, month, sex, wing chord, and a smoothed latitude*longitude interaction term) and, in some models, an additional environmental variable. The coefficient of that additional environmental variable is given in the column labeled "coefficient", except in the case of the one categorical variable, Jepson habitat region

Reg = Jepson habitat region; *df* degrees of freedom; *w* Akaike weight of model

Within each bill parameter, the model with the highest *w* is indicated by **, and any model(s) within the confidence set (highest *w* models that sum to $\geq$0.95) are marked by *

Table 7 Descriptive statistics of the climate variables used in our analyses, illustrating the range of conditions experienced by the individuals in our sample

Variable	Summer		Winter	
	Mean ± SD	Range	Mean ± SD	Range
Pptn (1 year)	26.6 ± 23.3 mm/mo	0.1–147 mm	86.4 ± 69.0 mm	2.9–299 mm
Pptn (10 years)	25.8 ± 16.1 mm/mo	3.3–82.6 mm	86.0 ± 62.7 mm	9.0–296 mm
Pptnsd (10 years)	35.0 ± 20.5 mm/mo	5.6–98.0 mm	75.2 ± 50.8 mm	9.6–245 mm
T_{min} (1 year)	6.9 ± 3.2 °C	−2.5–18.5 °C	2.7 ± 4.0 °C	−9.0–9.0 °C
T_{max} (1 year)	23.1 ± 3.7 °C	12.5–37.3 °C	15.0 ± 3.7 °C	4.8–25.3 °C
T_{min} (5 years)	6.8 ± 3.1 °C	−2.3–18.3 °C	2.7 ± 3.9 °C	−9.3–8.2 °C
T_{max} (5 years)	23.2 ± 3.5 °C	12.3–37.2 °C	14.9 ± 3.4 °C	5.0–24.0 °C
T_{min} (10 years)	6.9 ± 3.0 °C	−1.6–18.2 °C	2.8 ± 3.9 °C	−8.9–8.2 °C
T_{max} (10 years)	23.2 ± 3.6 °C	11.9–37.7 °C	15.0 ± 3.4 °C	5.3–23.9 °C
T_{sd} (10 years)	4.3 ± 1.0 °C	1.2–5.8 °C	3.5 ± 0.8 °C	1.6–4.9 °C

Discussion

Our analyses suggest that the selective pressures acting on bill morphology in Dark-eyed Juncos are complex and temporally dynamic. The effects of the environmental factors examined varied with season and with the specific morphological traits considered. Measures of overall habitat type (i.e. Jepson regions) were associated with different aspects of bill morphology than were individual climate variables. Temperature was consistently a more important predictor of bill morphology than precipitation, but the support for temperature was generally weak, with temperature variables appearing in the 95% confidence set of models but never in a top-supported model. The strongest support for temperature appeared in the model of bill length in winter birds. Measures of temperature maxima were more supported in summer birds, while both temperature maxima and minima were supported in winter birds. Of the climate variables identified as important in our analyses, only the measure of long-term temperature variability was supported across multiple bill traits, implying a complex relationship between morphology and environmental conditions.

Subspecies differences

The subspecies *J. h. thurberi* had significantly different bill morphology from the other examined subspecies in both seasons. This difference may be partly due to climate effects on bill morphology, as *J. h. thurberi* in our study occupied a broader range of climate space than *J. h. pinosus* or *J. h. oreganus*; however, they occupied a similar range to that occupied by *J. h. montanus* and *J. h. shufeldti* (see supp. info., Fig. S1). Alternatively, the difference may be due to nonadaptive effects such as genetic drift. Junco subspecies exhibit many morphological differences that have not been explained in adaptive terms (Nolan et al. 2002).

Temporal variation

Correlates of bill morphology varied with the temporal scale over which environmental factors were examined. For example, we found relationships between environmental parameters and bill length that were consistent across seasons as well as relationships that clearly differed between seasons. Across seasons, bill length was associated with a larger number of environmental variables than bill width or depth, and bill surface area was related to vegetative community. Temperature variability was important for models of bill width and depth in both seasons; however, the direction of the effects of temperature variability differed between summer and winter birds. While both temperature maxima and minima were supported for models for bill length among winter birds, only temperature maxima were supported among summer birds. The support for temperature maxima and temperature minima in winter is consistent with the "critical season" hypothesis presented in Danner and Greenberg (2015), which proposes that the more extreme climate variable of the more extreme season (i.e. cold in areas with very cold winters; heat in areas with very hot summers) has the greatest effect on bill morphology. However, this hypothesis does not explain either the similar support for temperature maxima, or the greater overall support for temperature, in models of winter birds when compared with summer birds.

Habitat conditions, including food resources, may vary substantially between the summer and winter and that variation may underlie the seasonal differences in results detected here. Bird bill size is known to vary seasonally within individuals (Greenberg et al. 2013). Additionally, the heterospecific community of potential competitors with juncos likely differed between seasons, and competition has been shown to play a large role in bill morphological evolution (Smith et al. 1995; Jønsson et al. 2012; Freed et al. 2016). Seasonal differences are probably not due to subspecies differences: while our summer and winter analyses differed in their make-up of subspecies, our analyses found no evidence for differences in bill morphology among subspecies, with the exception of *J. h. thurberi*, which was present in both seasons.

Across temporal scales, we found no consistent pattern to the environmental variables supported by our models. Recent, hemi-decadal, and decadal temperature measures were all supported in our analyses, but in different contexts. For example, decadal measures were supported in both seasons for all linear bill measures, while recent and hemi-decadal measures were only supported in models of bill length for both seasons, and in the summer model of bill width. Over decadal scales, temperature variability was associated with longer, wider, and shallower bills in summer birds, but with shorter, narrower, and shallower bills in winter birds. Collectively, these findings suggest that seasonal relationships among environmental parameters and bill morphology are complex and vary over larger temporal scales. Bill morphology appears to reflect recent conditions as well as to display signatures of environmental conditions over the past several generations.

Multiple selection pressures

Bill morphology differed with the environmental parameters considered here, but not in the ways that we had predicted. We had expected that bill width and bill depth would be associated with resource-related environmental variables, namely precipitation, which affects both the seed and arthropod food available (Grant and Grant 1989). However, precipitation variables did not explain variation in any of the measures of bill morphology examined. Instead, bill width and depth were most clearly associated to temperature variation. That these bill traits were characterized by similar environmental relationships may reflect their functional linkage: both are strongly indicative of bite force in passerines (Herrel et al. 2005; Badyaev et al. 2008). The absence of relationships between bill structure and precipitation, however, suggests that interactions between environmental conditions, food resources, and bill morphology are more complex than outlined by the foraging ecology hypothesis.

We had also predicted that bill surface area would be related to variation in temperature; again, this prediction was not supported. Instead, vegetative community emerged as the best predictor of bill surface area. Temperature variables were supported for models for bill length. The direction of this relationship was not consistent with the heat dissipation hypothesis in wintering birds (higher temperatures were associated with shorter bills), in contrast to the findings of Danner and Greenberg (2015) in Song Sparrows. This difference in outcomes may reflect the difference in severity between winter conditions at their highly-seasonal study site and those in California. Even so, it is not clear why moderate winter conditions should favor an inverse relationship between temperature and bill length; and this unexplained outcome suggests that relationships between temperature and bill morphology are more complex than predicted by the heat dissipation hypothesis.

Notably, in all cases the support for effects of climate on bill morphology were weak. A number of factors that probably contribute to bill morphology could not be included in our models, and may be masking some of the effects of climate. Some variation in bills may be due to the conditions experienced during the prior season; for example, a wintering bird's bill is likely to have been influenced by the previous summer's conditions at the bird's breeding grounds. Assuming that the conditions in the location where the birds spent the previous season are unlinked to the conditions they experience in California, the influence of the other season would reduce our observed effect size of the current season's conditions. Similarly, early life conditions are known to have potentially long-term effects on many aspects of the animal (Tilgar et al. 2010), but we were not able to obtain information about the early life conditions of our focal individuals.

To our surprise, models for bill surface area strongly supported the inclusion of Jepson habitat region. This was contrary to our expectation that surface area would be more affected by temperature variables than by vegetation, as surface area is closely linked to capacity for heat dissipation (Greenberg and Danner 2012; Cardilini et al. 2016). Jepson region is an integrative measure that captures information regarding multiple aspects of environmental variation, including but not limited to the other climatic variables in this study (see supp. info.). Similarly, bill surface area is a composite measure that integrates multiple linear bill dimensions (i.e. length, width, depth), and is thus likely to reflect the net outcome of multiple selective pressures acting on the bill. It is possible that integrative measures that capture multiple environmental factors (e.g., Jepson regions) or multiple morphological traits (e.g., bill surface area) are best suited to providing an overview of the selective pressures acting on morphological phenotypes. For example, a recent study of Madagascan vangas (Vangidae) found that a principal component axis corresponding to bill width and depth was related to composite measures of habitat type and foraging strategy (Jønsson et al. 2012). Although use of such composite measures may not allow a clear resolution of the effects of specific selective pressures, they may provide an integrative view of multiple selective pressures that better reflects the actual selective regimes experienced by complex morphological traits.

Alternatively, the importance of Jepson habitat region in models of bill surface area could be due to genetic drift, as individuals sharing the same region will tend to be closer to each other geographically. However, this seems an unlikely explanation as region does not appear in any of the models of linear bill traits, and it is not clear why genetic drift would impact an integrative bill trait but not its components.

Conclusions

Variation in bill morphology among Dark-eyed Juncos differed from patterns reported for other granivorous songbirds (Galápagos finches: Grant and Grant 1993, 2002; Song Sparrows: Greenberg and Danner 2012; Greenberg et al. 2012; Danner and Greenberg 2015) in that no single environmental variable was consistently associated with variability in the aspects of bill morphology examined. Neither the foraging nor the heat dissipation hypothesis was fully supported. Instead, our analyses indicated that junco bills are complex phenotypic traits and that variation in bill morphology is influenced by multiple variables over multiple temporal scales. A critical difference between our analyses and those of Galápagos finches and Song Sparrows is that we did not focus on a specific selective event or abrupt, catastrophic change in environmental conditions. As a result, our findings may be more indicative of typical interactions between environment, selection, and bill morphology. However, our results are also more likely to be influenced by other processes with moderate effect sizes, such as genetic drift, which may have obscured some environmental influences on bill morphology.

In the absence of extreme selective forces, we expect that our study animals were subject to relatively moderate fluctuations in environmental parameters. Our results suggest that under such conditions, using integrative measures of environmental conditions and phenotypes may be more informative than univariate analyses of either set of parameters. In particular, analyses of such integrative measures may reveal previously unknown relationships between environment and phenotype. This is perhaps not surprising given that, at the level of differential reproduction, selection acts on complete phenotypes, not individual phenotypic traits. As a result, understanding the factors that shape variation in phenotypic traits requires analyses of multiple environmental factors and their composite effects on organisms. This perspective may be particularly relevant for analyses of climate variables such as precipitation and temperature, common measures which tend not to be integrative and thus likely do not represent the most relevant estimates of conditions experienced by free-living organisms.

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