Communications

Rapid phenotypic change in a native bird population following conversion of the Colorado Desert to agriculture

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Humans are modifying our planet's ecosystems with increasing frequency and intensity. Exploring population responses to anthropogenic modifications of natural habitat provides insights into how species persist in the Anthropocene. Here, we leverage natural history collections to document rapid phenotypic change within a native bird population following ~80 yr of agriculture in the Colorado Desert of southeastern California. By comparing spectrophotometric measurements of horned lark *Eremophila alpestris* specimens collected in the Imperial Valley from 1918 to 1934 to those collected from 1984 to 2014, we found that more recent birds have darker backs, napes, and crowns. This dorsal darkening may have resulted from a shift in selective pressures for camouflage induced by land use: previously, the lark population nested on light-colored desert flats, whereas contemporary larks occupy darker soil associated with agricultural fields. Adaptation and/or introgression may have contributed to this instance of rapid phenotypic change following the rise of agriculture in the Imperial Valley.

Introduction

When confronted with changes to their native habitat, species must adapt, relocate, or face extinction. Since the Neolithic Revolution and the origin of agriculture, human population growth and development have revolutionized our planet's ecosystems and their constituents (Bar-Yosef 2008). Anthropogenic changes to natural habitats are often rapid and dramatic, leading to strong selective pressures that affect ecosystem function, ecological interactions, and adaptive phenotypes. Prominent examples of rapid evolutionary responses to human activity include industrial melanism in the peppered moth *Biston betularia* (Kettlewell 1955, Cook et al. 2012) and directional changes in fishes' life history following commercial over-exploitation (Conover and Munch 2002). A growing number of studies have illuminated the eco-evolutionary processes that underpin species' persistence and rapid phenotypic change amid human-mediated perturbations to native habitats (Carroll et al. 2007, Kinnison and Hairston

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2007, Lavergne et al. 2010, Ellner et al. 2011), including numerous empirical examples among vertebrates (Phillips and Shine 2006, Darimont et al. 2009, Barrett et al. 2011, Ohlberger et al. 2011, Holt and Jorgensen 2014, Phillis et al. 2015).

The specimens in natural history collections provide an invaluable source of data for studying genetic and phenotypic changes over time (Wandeler et al. 2007, Pyke and Ehrlich 2010, Buerki and Baker 2015, Holmes et al. 2016). Increasingly, biologists are leveraging these collections to quantify ecological and evolutionary responses of native populations to anthropogenic disturbances – including changes in land use – in plants (Robbirt et al. 2010, Bakker et al. 2015), vertebrates (Bi et al. 2013, Kuhn et al. 2013, DuBay and Fuldner 2017), and invertebrates (Babin-Fenske et al. 2008, Yeates et al. 2016). These comparisons provide important perspectives on the biological processes of extinction and persistence of species amid increasingly frequent and severe anthropogenic disturbances.

One striking example of modern anthropogenic disturbance is the agricultural conversion of the Imperial Valley in southeastern California. Irrigation canals began diverting water from the Colorado River in the early 1900s (Clemmings 1996). Today, over half of a million acres of land in the Imperial Valley (agcensus.usda.gov) are dedicated to irrigated agriculture, which has dramatically increased the amount of organic matter and water in the soil. Although some native species have been displaced from areas that are now dedicated to crops and livestock, others have persisted and now breed in agricultural fields. Persistent species offer the opportunity for study of the ecological and evolutionary responses of species following the conversion of native habitat to agriculture over the last century.

The horned lark *Eremophila alpestris* is a common resident of the Imperial Valley, occurring in sparsely vegetated desert, fallow fields, in pastures and fields of alfalfa and Bermuda grass (these categories accounted for 40% of the Imperial Valley's agricultural land in 2015; cdfa.ca.gov) and along roadsides bordering other crops. Across the horned lark's range, its plumage varies substantially, especially in dorsal coloration (Behle 1942). As the horned lark lives in open habitats with little vegetation, its dorsal coloration tends to match the regional substrate, presumably enhancing camouflage against avian predators (Zink and Remsen 1986, Donald et al. 2017). This background matching or crypsis has never been quantified, however. The population of the Imperial Valley and surrounding Colorado Desert has long been classified in the subspecies *E. a. leucansiptila*, the palest in dorsal plumage of all larks in North America (Behle 1942). However, Patten et al. (2003) observed that some specimens collected from the Imperial Valley since 1985 appeared darker than those collected before 1940, and that recent specimens are seemingly more variable than historical samples. Patten et al. (2003) speculated that their qualitative observations of phenotypic change in Imperial Valley larks may be related the rise of agriculture in the area and changing evolutionary pressures related to background matching

as the soil grew darker with supplemental of organic matter and irrigation.

Here, we expand upon Patten et al. (2003)'s anecdotal observations to test multiple hypotheses regarding phenotypic variation among larks in the Imperial Valley over time. Specifically, we test the hypothesis that mean dorsal coloration and variance in dorsal coloration have changed. We predict that contemporary larks should be darker than historical larks as a result of the rise of agriculture and background matching against darker soils. By quantifying phenotypic changes with spectrophotometry, we confirm that contemporary larks in the Imperial Valley are indeed darker than historical specimens, as first suggested by Patten et al. (2003). We discuss the various evolutionary and ecological processes that could underlie this phenomenon and consider future avenues of research that could identify the causal agents of rapid phenotypic change among larks in the Imperial Valley.

Methods

We measured dorsal plumage reflectance of 53 horned larks from the Imperial Valley, including 23 collected before 1940 and 30 collected after 1980 (for voucher and locality information, see Supplementary material Appendix 1). We used an Ocean Optics USB2000 (Dunedin, FL) spectrophotometer with a PX-2 pulsed xenon light source to measure reflectance across the avian visual spectrum. We equipped our spectrophotometer with a R200-7-UV/VIS reflection probe. We embedded our probe in a matte black box that excluded ambient light and maintained a constant distance between the probe tip and the plumage patch being measured. All measurements were taken at a 90° angle relative to the surface of the feathers, as in other spectrophotometric studies (Eaton and Lanyon 2003, Shultz and Burns 2017). Although this method does not account for the specular reflection of light that results from the 90° orientation and relies on museum specimens rather than live birds (Vaquero-Alba et al. 2016), we were consistent in using the same instrument and lighting conditions while taking all measurements (Andersson and Prager 2006). We measured reflectance of the crown, nape, and back of each specimen three times, then averaged these measurements. Back feathers from larks in the Imperial Valley have a small dark center that is surrounded by a larger, lighter area with less pigmentation. We measured the paler perimeter of back feathers rather than the central spot. We used the R package 'pavo' (Maia et al. 2013) to clean input files, average replicate spectrophotometer readings, and calculate each specimen's mean brightness, defined as the mean relative reflectance over the entire spectral range of avian vision (Montgomerie 2006). Plumage wear and feather age may also affect dorsal brightness. We therefore estimated days since molt for each specimen. Horned larks molt once per year in late July (Behle 1942, Beason 1995), so we calculated the number of days between an estimated molt date of 15 July and the date of collection. Specimen age may also influence plumage brightness. We therefore

generated a generalized linear model with mean brightness as the response variable and time period (before 1940 or after 1980), years since collection, and days since molt as predictor variables. We tested for differences in variance in brightness between historical and contemporary samples with Bartlett's test for homoscedasticity.

Data deposition

Spectrophotometry input files and processed data are available through the Dryad Data Repository <http://dx.doi.org/10.5061/dryad.708k0> (Mason and Unitt 2017). A table that includes metadata for vouchered specimens used in this study is available through the electronic supplementary material.

Results

Spectrophotometry confirmed that horned larks collected in the Imperial Valley after 1980 were darker than those collected before 1940 (Fig. 1A). Specifically, horned larks collected after 1980 have darker backs (mean brightness $\bar{x}_{historical} = 19.61$; $\bar{x}_{contemporary} = 13.04$; Fig. 1B, E;
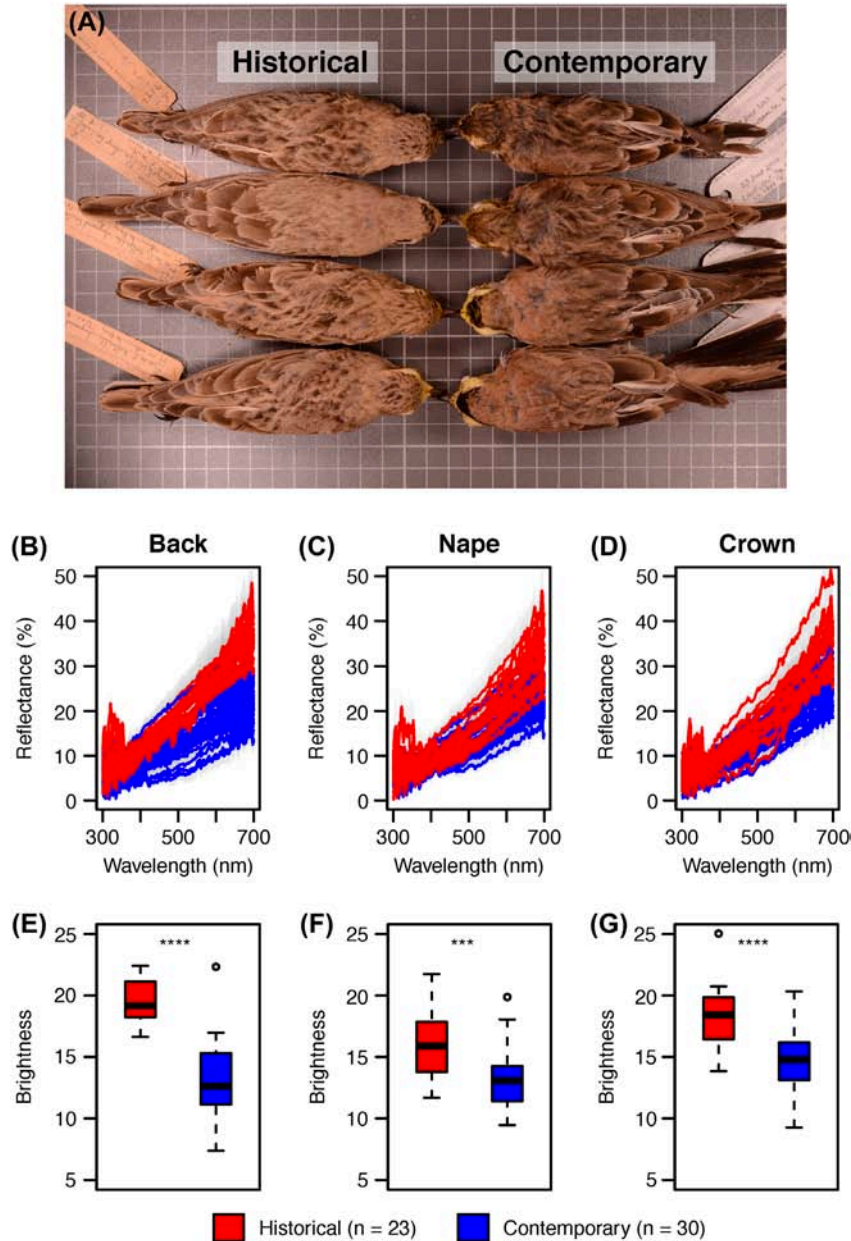

Figure 1. Historical and contemporary specimens of the horned lark *Eremophila alpestris* from the Imperial Valley, California (A). Spectrophotometric measurements and boxplots of dorsal brightness that compare historical and contemporary samples for the back (B and E), nape (C and F), and crown (D and G).

Table 1. Summary statistics of generalized linear models for examining potential associations between dorsal brightness as a response variable and time era (historical vs contemporary), days since molting, and specimen age. Asterisks indicate p values that are statistically significant (p < 0.05). Our models indicate that contemporary larks have brighter backs, napes, and crowns compared to historical specimens.

Response variable	Predictor variable	Effect size (± standard error)	p value
Back brightness	Time era	$\beta_{contemporary} = -6.60 \pm 0.75$	1.21e-11***
	Days since molt	$\beta_{days\ since\ molt} = 7.76e\text{-}3 \pm 6.53e\text{-}3$	0.24
	Specimen age	$\beta_{specimen\ age} = -6.34e\text{-}3 \pm 1.24e\text{-}2$	0.61
Nape brightness	Time era	$\beta_{contemporary} = -2.93 \pm 0.76$	3.18e-4***
	Days since molt	$\beta_{days\ since\ molt} = 1.11e\text{-}4 \pm 6.57e\text{-}3$	0.99
	Specimen age	$\beta_{specimen\ age} = -3.84e\text{-}3 \pm 1.24e\text{-}2$	0.76
Crown brightness	Time era	$\beta_{contemporary} = -3.931 \pm 0.73$	3.75e-05***
	Days since molt	$\beta_{days\ since\ molt} = 8.93e\text{-}4 \pm 6.34e\text{-}3$	0.888
	Specimen age	$\beta_{specimen\ age} = 1.81e\text{-}2 \pm 1.20e\text{-}2$	0.139

Table 1), darker napes (mean brightness $\bar{x}_{historical} = 16.14$; $\bar{x}_{contemporary} = 13.27$; Fig. 1C, F; Table 1), and darker crowns (mean brightness $\bar{x}_{historical} = 18.19$; $\bar{x}_{contemporary} = 14.57$; Fig. 1D, G; Table 1) than those collected before 1940. Neither the number of days since molting nor the number of years since collection were associated with our three measurements of dorsal brightness (Table 1).

The back plumage of specimens collected since 1980 was more variable (Bartlett's $K^2 = 6.55$, df = 1, p = 0.01) than specimens collected before 1940. In contrast, variances for the nape (Bartlett's $K^2 = 0.21$, df = 1, p = 0.65) and crown (Bartlett's $K^2 = 0.025$, df = 1, p = 0.87) of contemporary and historical samples did not differ significantly.

Discussion

After ~80 yr of intensive agriculture in the Imperial Valley, the region's breeding horned larks have become darker. This finding adds to a growing number of empirical studies that document rapid phenotypic change and contemporary evolution on ecological time scales in native populations (Reznick and Ghalambor 2001, Kinnison and Hairston 2007, Ellner et al. 2011, DuBay and Fuldner 2017). Multiple ecological and evolutionary processes may underlie rapid darkening in this population of larks. First, intensive irrigation and the addition of organic matter to the soil have made the substrate of agricultural lands darker than that of the adjacent desert (USDASCS 1981). This environmental change may have altered selective pressures to favor darker dorsal plumage for background matching. Natural selection could have favored the survival of darker individuals that already existed prior to the onset of irrigation; so-called 'soft sweeps', in which selection acts on existing alleles latent in multiple individuals rather than de novo mutations, are common in nature and often underlie episodes of rapid evolution (Barrett and Schluter 2008, Messer and Petrov 2013). However, we note that no darker individuals are represented in pre-1940 collections. Alternatively, novel mutation(s) that darken dorsal plumage and/or increase the size of dark central spots on dorsal feathers may have arisen since the Imperial Valley's conversion to agriculture (Pritchard et al. 2010). If these mutations conferred a selective advantage on darker individuals, then natural selection may have rapidly increased the frequency of advantageous alleles.

In addition to natural selection acting on standing phenotypic variation or novel mutants, immigration may also have contributed to rapid phenotypic change among the Imperial Valley's larks. Various subspecies with darker plumage may have served as source populations for rapid phenotypic change in the Imperial Valley. Several subspecies of horned lark that vary in dorsal coloration and brightness have been recorded as winter visitors in the Imperial Valley (Patten et al. 2003). Introgression from other populations may have introduced new phenotypic and genetic variation into the locally breeding population, as has been observed in other partially migratory songbirds (Yeh 2004). Horned larks from the Channel Islands off southern California are somewhat similar in phenotype to some recent specimens collected in the Imperial Valley (Patten et al. 2003), and molecular (Mason et al. 2014) and phenotypic (Behle 1942) evidence suggest that larks from the Channel Islands disperse regularly to the California mainland.

Finally, body parts can change colors at different rates due to exposure to sunlight and degradation over time since molting and also as a specimen ages over time since collection (Gabrielson and Lincoln 1951, McNett and Marchetti 2005, Armenta et al. 2008). However, we found no effect of time since molting or years since collection on dorsal brightness in our generalized linear models (Table 1). Unlike carotenoid-based and ultraviolet-reflective patches of plumage, melanin-based coloration such as that of the horned lark tends to change little if at all in brightness with a specimen's age (McNett and Marchetti 2005, Armenta et al. 2008, Doucet and Hill 2009), even in species where the hue shifts in the direction of red and yellow. Thus, specimen fading due to time since molt or collection cannot have contributed substantially to the pattern we observed.

In conclusion, our study adds to a growing number of empirical examples of rapid phenotypic change over contemporary time scales in vertebrates (Reznick and Ghalambor 2001). Future work that integrates high-throughput sequencing of historic and current populations combined with phenotypic analyses will further clarify the contributions of

selection and gene flow toward rapid dorsal darkening following decades of desert agriculture in the southwestern United States.

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