ORIGINAL ARTICLE

Agriculture induces isotopic shifts and niche contraction in Horned Larks (*Eremophila alpestris*) of the Colorado Desert

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Abstract

Agriculture can dramatically alter community composition, food webs, and resource availability, yet the impacts of agriculture on many ecosystems and their constituents remain unstudied. Here, we examined the effect of agriculture on the isotopic ecology of Horned Larks (*Eremophila alpestris*) in the Colorado Desert. Over the last century, the Imperial Valley in southeastern California has transformed from desert scrub into agricultural land, while breeding Horned Larks have persisted in the area. We compared the isotopic composition of nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and hydrogen ($\delta^{2}H$) from feathers of lark specimens from two time periods in the Imperial Valley: a historical series collected between 1916 and 1923 and more recent vouchers collected between 1984 and 2014. We also quantified $\delta^{15}N$ and $\delta^{13}C$ values from plants and soil samples in contemporary agricultural land and adjacent desert scrub to estimate isotopic baseline changes associated with agricultural intensification. Contemporary larks had lower $\delta^{15}N$ and $\delta^{13}C$ ratios compared to historical larks, while plant and soil $\delta^{15}N$ ratios were higher at agricultural sites compared to adjacent desert sites. These opposing trends suggest temporal change in isotope values that cannot be explained by shifting baselines alone. Furthermore, isotopic niche breadth ($‰^2$; $\delta^{15}N$ and $\delta^{13}C$) was lower among contemporary larks. Thus, contemporary larks in the Imperial Valley may capitalize on seeds and phytophagous insects that are abundant among crops, possibly representing an opportunistic change in diet over time in response to agriculture. Finally, $\delta^{2}H$ values did not differ between historical and contemporary larks, but contemporary larks had $\delta^{2}H$ values that differed from historical ground water, suggesting intake of water introduced by irrigational canals. Collectively, these findings highlight the power of stable isotope analyses combined with natural history collections to examine ecological change in the Anthropocene.

Keywords Alaudidae · Arid land · Diet · Farming · Food web · Imperial Valley · Natural history collection · Stable isotopes

Landwirtschaft verursacht eine Isotopenverschiebung und einen Nischenrückgang bei der Ohrenlerche (*Eremophila alpestris*) in der Colorado-Wüste

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Zusammenfassung

Die Landwirtschaft kann die Artenzusammensetzung, Nahrungsnetze und Ressourcenverfügbarkeit dramatisch verändern, doch sind die Einflüsse der Landwirtschaft auf viele Ökosysteme und ihre Bestandteile unerforscht. Hier untersuchten wir die Auswirkungen der Landwirtschaft auf die Isotopenökologie der Ohrenlerche (*Eremophila alpestris*) in der Colorado-Wüste. Im Laufe des letzten Jahrhunderts hat sich das Tal Imperial Valley im Südosten Kaliforniens von einem Wüstengestrüpp in landwirtschaftlich genutzte Flächen verwandelt, während die Ohrenlerche unverändert in dieser Landschaft überdauert hat. Wir verglichen die Isotopenzusammensetzung von Stickstoff (δ15N), Kohlenstoff (δ13C) und Wasserstoff (δ2H) aus Federn von Lerchenbälgen aus zwei Zeitabschnitten im Imperial Valley: eine historische Serie, die zwischen 1916–1923 gesammelt wurde, und neuere Belege, die zwischen 1984–2014 gesammelt wurden. Weiterhin quantifizierten wir die δ15N- und δ13C-Werte aus Pflanzen- und Bodenproben auf heutigen landwirtschaftlichen Flächen und im angrenzenden Wüstengestrüpp, um die mit der landwirtschaftlichen Intensivierung verbundene Basislinienverschiebung der Isotope abzuschätzen. Jüngere Lerchenbälge zeigten im Vergleich zu den historischen Lerchenbälgen niedrigere δ15N- und δ13C-Verhältnisse, während der δ15N-Anteil in den Pflanzen- und Bodenproben von landwirtschaftlichen Flächen höher war als vom anliegenden Wüstengestrüpp. Diese gegenläufigen Trends deuten auf eine zeitliche Veränderung der Isotopenwerte hin, die sich nicht allein durch die Verschiebung der Basislinien erklären lässt. Darüber hinaus war das Isotopenspektrum (‰2; δ15N und δ13C) bei jüngeren Lerchenbälgen geringer. Daher könnten heutige Ohrenlerchen im Imperial Valley von Sämereien und phytophagen Insekten profitieren, die unter den Nutzpflanzen reichlich vorhanden sind. Dies könnte eine opportunistische Veränderung der Ernährung im Laufe der Zeit als Anpassung auf die Landwirtschaft darstellen. Schließlich fanden wir zwischen den historischen und jüngeren Lerchenbälgen keine Unterschiede in den δ2H-Werten. Jedoch unterschieden sich die δ2H-Werte der jüngeren Bälge vom historischen Grundwasser, was auf die Aufnahme von Wasser aus eingeleiteten Bewässerungskanälen hindeutet. Insgesamt verdeutlichen diese Befunde die Leistungsfähigkeit der Stabilen Isotopenanalyse in Kombination mit naturkundlichen Sammlungen zur Untersuchung ökologischer Veränderungen im Anthropozän.

Introduction

Humans are modifying native ecosystems with increasing frequency and intensity, often with dramatic impacts on food webs and resource dynamics. Agriculture is an essential human activity that alters resource availability in native ecosystems (Tilman et al. 2002; Vellend et al. 2007), accounting for over 40% of the planet's ice-free land surface (Ramankutty et al. 2008) with large increases predicted over the next century (Ramankutty and Foley 1999; Schmitz et al. 2014). Intensified farming generally reduces abundances and restricts the geographic ranges of native birds (Donald et al. 2001; Green et al. 2005; Stanton et al. 2018). However, some avian species persist in agricultural land (Sekercioglu et al. 2007) or even benefit from agriculture (Magurran et al. 2010), which offers opportunities to study ecological change in human-modified landscapes. Understanding how birds respond to agricultural modifications of native habitat is increasingly important as farmland continues to spread.

Detecting ecological patterns in response to human activity requires data that span time, anthropogenic disturbance gradients, or both. Long-term monitoring projects have provided compelling evidence for changes in ecological interactions in response to anthropogenic changes to native ecosystems (Sinclair et al. 2007; Peterson et al. 2014). However, many taxa and ecosystems are not feasible subjects for long-term monitoring studies. Natural history collections offer a solution: specimens housed therein provide relevant data to quantify changes in ecology and evolution over time and space for many taxa that have not been subjected to long-term studies (Lister 2011; Holmes et al. 2016; Schmitt et al. 2019). For example, temporal studies leveraging museum specimens have revealed ecological trends over time in various birds, including Marbled Murrelets (*Brachyramphus marmoratus*; Becker and Beissinger 2006), Greater Black-backed Gulls (*Larus marinus*; Farmer and Leonard 2011), Eastern Whip-poor-wills (*Antrostomus vociferus*; English et al. 2018), Hawaiian Petrels (*Pterodroma sandwichensis*; Wiley et al. 2013), Leach's Storm-petrels (*Oceanodroma leucorhoa*; Fairhurst et al. 2015), various penguins (Spheniscidae; Jaeger and Cherel 2011), and Black-browed Albatrosses (*Thalassarche melanophris*; Mariano-Jelicich et al. 2017) among others. These studies have revealed a wide variety of temporal patterns and dynamics depending on the system in question, but collectively illustrate the power of museum specimens to study ecological change over time—often through the use of stable isotopes.

Stable isotopes are widely used in ecology, and provide insight into biotic and abiotic interactions at different spatial and temporal scales (Newsome et al. 2007; Inger and Bearhop 2008). Variation in stable isotope ratios can inform trophic relationships: isotopes of certain elements—particularly nitrogen ($\delta^{15}N$ or $^{15}N/^{14}N$)—fractionate at different rates during trophic transfer and shed light on variation in animal diets and trophic levels (Kelly 2000; Boecklen et al. 2011). Heavier ^{15}N isotopes are concentrated in consumers as amino acids and are absorbed and converted into other tissues, such as keratinous feathers,

while the lighter ^{14}N isotope is preferentially excreted in nitrogenous waste products (Sutoh et al. 1987; Kelly 2000). This fractionation, or preferential removal or retention of certain isotopes, is central to inferring the trophic level of organisms through stable isotope analysis (Tieszen et al. 1983; Hobson and Clark 1992). In contrast, while carbon (δ^{13}C or ^{13}C/^{12}C) does minimally enrich at higher trophic levels, it is a stronger reflection of the isotopic ratio of the carbon source for a given food web (Rounick and Winterbourn 1986; Peterson and Fry 1987). For example, animal species in an arid environment dominated by C_4 grasses likely have higher δ^{13}C values compared to organisms growing in temperate environmental conditions where most primary producers use C_3 photosynthesis (Post 2002a). Furthermore, differences in the isotopic ratios of other elements, namely hydrogen and oxygen, can provide information regarding the environmental conditions where a tissue originated, and can thereby estimate the geographic origin and movement patterns of sampled individuals (Rubenstein and Hobson 2004). The relative abundance of hydrogen isotopes (δ^2H, δD or ^{2}H/^{1}H) can also be used to detect variation in water intake from resources with different isotopic profiles (Wolf and Martinez del Rio 2000; McKechnie et al. 2004). Importantly, because stable isotopes are inert and do not change over time, vouchered museum specimens, such as round skins of birds, provide an accurate signal of a tissue's isotopic ratios regardless of how long ago the specimen was collected (Barrow et al. 2008). Thus, combining natural history collections with stable isotope analyses provides a powerful tool to quantify extended temporal trends in trophic ecology in response to human activity and land use.

The Imperial Valley in southeastern California has undergone a dramatic transformation from Creosote bush scrub to agricultural land over the past century (Fig. 1; Clemmings 1996). In the late 1800s and early 1900s, settlers began diverting water from the Colorado River to the Imperial Valley to irrigate crops via slipshod canals, which subsequently burst in 1905 and flooded the region for over a year to form the Salton Sea. Agriculture has continued to prosper in the region and the Imperial Valley now includes thousands of acres of agricultural land that generate over $2 billion in annual revenue, providing large quantities of cattle, vegetables, melons, and feed for the dairy industry (California Department of Food and Agriculture 2018). Despite intense changes to native habitat, the Salton Sea and the Imperial Valley sustain large populations of migratory and resident birds by providing important stopover sites along the Pacific Flyway and breeding habitat for a wide variety of species (Shuford et al. 2002; Patten et al. 2003). Persistent bird species in the Imperial Valley can, therefore, offer insight into how native populations have been impacted by intensive agricultural practices.

Here, we examine trends in the isotopic ecology of Horned Larks (*Eremophila alpestris*) of the Imperial Valley in the Colorado Desert of southeastern California via comparisons of stable isotope values between time periods and habitat types. Horned Larks are widespread, occupying deserts, meadows, tundras, grasslands, and additional open habitats on five continents (Cramp 1985; Beason 1995). Throughout their range, larks consume a wide variety of seeds and terrestrial arthropods (both phytophagous and predaceous) in different amounts across localities, seasons, and years (Wiens and Rotenberry 1979). Horned Larks also frequently associate with sparsely vegetated agricultural land, particularly unused fallow fields, across their range (Beason and Franks 1974), where they consume various seeds and insects with negligible impact on the crops themselves. In the Imperial Valley, Horned Larks are common year round in agricultural land with little to no grass, and have become darker as agriculture has spread in the area (Mason and Unitt 2018). Given their variable diets and affinities for natural and modified open habitats, Horned Larks in the Imperial Valley present an excellent system to examine the impact of agriculture on avian biology.

Methods

Feather, plant, and soil sample acquisition

We acquired feathers from Horned Lark specimens collected in Imperial County of southeastern California (Fig. 1; Supplementary Table S1) to perform stable isotope analyses among contemporary and historical populations. Isotopic values housed in feathers reflect the diet and environmental conditions of an individual during tissue growth (Kelly 2000). In the Imperial Valley, Horned Larks are present during both breeding (March to September) and non-breeding (October to February) months (Patten et al. 2003). In non-breeding months, Horned Larks are nomadic and track food sources, yet populations in southern California do not undertake long-distance migration (Unitt 2004). Furthermore, Horned Larks undergo a single annual molt, during which they replace all their feathers in a 4–5 week period from mid-July to mid-August (Beason 1995). Thus, isotopic values from specimens collected during non-breeding months may reflect molt conditions on breeding territories. We therefore restricted our contemporary sampling ($n = 28$) to breeding months to focus on isotopic signatures associated with agricultural land in the Imperial Valley. Contemporary larks were collected by shotgun as authorized under permits issued by the US Fish and Wildlife Service and the California Department of Fish and Wildlife. To maximize our sample sizes for historical larks ($n = 16$ total), we included specimens from both breeding months ($n = 1$) and
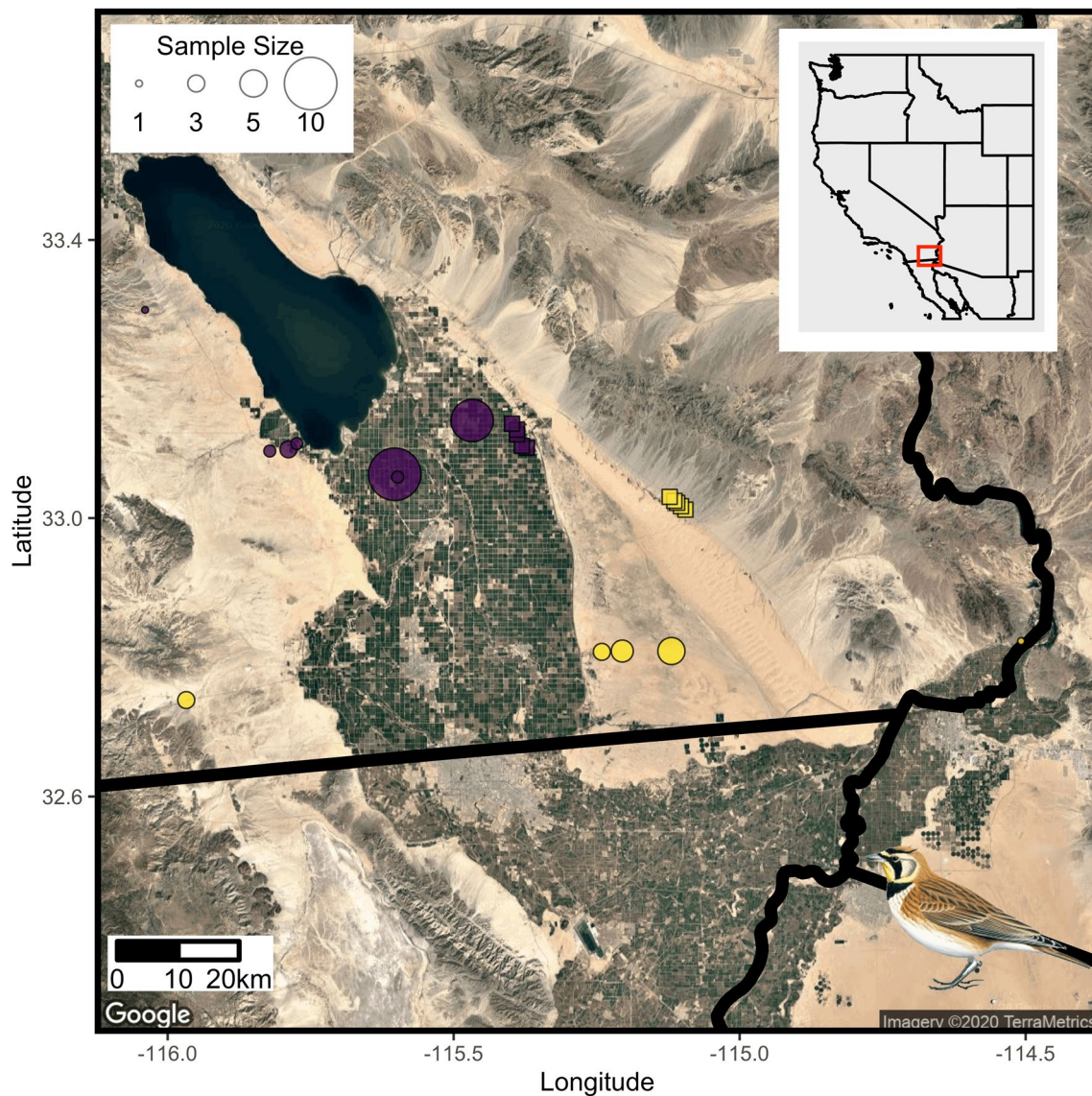
Fig. 1 Map of the Imperial Valley, California indicating localities of samples used in this study. Inset map in the top right localizes the focal area of study. Purple and yellow circles indicate contemporary and historical samples of Horned Lark feathers, respectively. Purple and yellow squares correspond to sites where soil and plant samples were taken from agricultural land and Creosote desert scrub, respectively. Horned Lark image is reproduced with permission from Lynx Edicions. Satellite imagery was generated via Google Maps with the ggmap package (Khale and Wickham 2013)

non-breeding months ($n = 15$). Historical larks were likely residents of the Creosote bush scrub, but may have not bred in the exact locality where they were collected. We, therefore, estimated the geographic origin of historical samples by comparing δ^2H values to isotopic measurements of water sources throughout the area to confirm that they bred within the Imperial Valley region (Smith et al. 1992). We subsequently compared $\delta^{15}N$, $\delta^{13}C$, and δ^2H values of the historical series from 1916 to 1923 to a contemporary series of specimens collected during the breeding season from 1984

to 2014. For isotopic analyses, we sampled between 2 and 4 breast feathers from the right side of each vouchered specimen, which were then stored in individual 1.5 mL plastic tubes until later processing.

Changes in $\delta^{15}N$ and $\delta^{13}C$ isotope values in feathers over time may be partially due to shifting baselines of isotopic values in the environment in addition to possible changes in lark trophic ecology (Post 2002a; Casey and Post 2011; Layman et al. 2012). While a parallel comparison between time periods in soil and plant isotope profiles would provide the

most accurate quantification of baseline change over time, historical plant and soil samples for our focal area and species do not exist. Therefore, we used a "space-for-time" substitution instead of a direct temporal comparison of isotopic baselines (Fukami and Wardle 2005). Specifically, we collected plant and soil samples from fallow fields where larks were previously collected or recently observed. We then compared contemporary agricultural plant and soil samples to samples from Creosote bush scrub found outside of the agricultural area of the Imperial Valley, which represents an approximation of historical habitat prior to the onset of agriculture (Fig. 1). As an approximation of historical plant isotope values, we collected samples of the Algodones Dunes Sunflower (*Helianthus niveus tephrodes*; $n = 15$) from the Creosote bush scrub that abuts the agricultural areas of the Imperial Valley. We compared these isotope values of Common Dandelion (*Taraxacum officinale*; $n = 15$) that we sampled from fallow agricultural fields where Horned Larks had been observed (Supplementary Table S2). For both plant species, we sampled the most proximal (i.e., closest to the ground) intact leaf from each plant. To further quantify possible shifts in isotopic baselines, we also collected soil samples from the same sites as the flowering plants. We first removed 2 cm of top soil before sampling and avoided highly vegetated areas where Horned Larks were unlikely to exist. We collected soil and plant samples from 02 August 2017 to 03 August 2017, which corresponds to the molting period of Horned Larks. We also choose both agricultural and Cresote bush scrub sites for plant and soil samples based on their proximity to recent lark sightings, but acknowledge that the spatial extent they encompass is far less than the feather samples, which is a possible shortcoming of our sampling scheme.

Stable isotope analyses

We rinsed feathers in a 2:1 chloroform to methanol solution, and then air-dried the feathers under a fume hood for 48 h. We minced feathers while avoiding the rachis and placed between 0.9 and 1.1 mg of feather in a tin capsule for subsequent stable isotope analysis. We did not perform a lipid extraction since feathers have low lipid content compared to other tissue types (Post et al. 2007). We dried plant material in a drying oven for 48 h at 70 °C and then ground each sample with a mortar and pestle until it could pass through a 40 mesh screen. We then loaded 2.5–3.5 mg of leaf powder into tin capsules for SIA. Similar to plant samples, we dried soil samples in an oven for 48 h and then pulverized via liquid nitrogen combined with mortar and pestle. We then loaded 80 mg of each soil sample into tin capsules for stable isotope analysis. We choose to not acidify the soil samples to remove sources of inorganic carbon, such as shells and bones (Schlacher and Connolly 2014). Our carbon isotope values, therefore, represent both organic and inorganic carbon sources rather than purely dietary carbon. However, we were primarily interested in patterns among nitrogen isotopes, which can also be impacted by acid treatments (Schlacher and Connolly 2014), and rely more on inferences from feather isotope data with the soil and plant isotopes as supporting lines of evidence.

All feather, plant, and soil samples were run on a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific) interfaced to a NC2500 Elemental Analyzer (Carlo Erba Instruments). Stable isotope ratio values are relative to international standards of PeeDee Belemnite for carbon, atmospheric air (N_2) for nitrogen, and the Vienna Standard Mean Ocean Water for hydrogen. All analyses were conducted in the Cornell Isotope Laboratory (COIL). We report stable isotope values with the conventional δ notation (see Kelly 2000 for review), which describes differences in sample isotope values compared to the aforementioned standards ($\delta = ((R_{sample}/R_{standard}) - 1) \times 1000$), with the units being parts per thousand (‰).

We corrected $\delta^{13}C$ values for all tissues to account for the Suess effect, which represents a global decrease of ^{13}C in atmospheric CO_2 due to fossil fuel consumption over the last 150 years (Sonnerup et al. 1999). Based on ice core records (Francey et al. 1999), we applied a correction to our $\delta^{13}C$ values of -0.005‰ per year up until 1960 and applied another correction of 0.022‰ per year after 1960 (Chamberlain et al. 2005). To place δ^2H values from feathers in the context of precipitation values, we added 25‰ to our δ^2H values to account for isotopic fractionation between rainfall and feathers (Hobson et al. 2012).

Statistical analyses

We generated linear mixed models (LMMs) to examine variation in $\delta^{15}N$, $\delta^{13}C$, and δ^2H isotope values between temporal periods and habitat types. We generated LMMs with the lme() function from the package nlme v 3.1.148 (Pinheiro et al. 2020) implemented within the R statistical language (R Core Team 2020). Our LMMs used a Gaussian (i.e., normal) distribution of residuals for our continuous isotope values with an identity link function. We grouped samples into two temporal time periods: (1) larks collected up between 1916 and 1923 (historical) and (2) larks collected between 1984 and 2014 (contemporary). We also generated LMMs to examine isotopic variation among plant and soil samples that were collected in agricultural land versus Creosote bush scrub. We included sampling localities as a random effect because many of our samples were collected from the same locality—especially plant and soil samples. We calculated the marginal and conditional coefficients of determination (R^2) to estimate the total variance explained in our models as well as the random effect of sampling sites using methods

described by Nakagawa & Schielzeth ([2013]) implemented in the R package MuMIn v1.43.17 (Bartón [2019]). To validate our assumption that the historical specimens used in our study represented breeding birds rather than wintering visitors, we also conducted a one-sample t-test to determine whether the average of our δ^2H values from the historical specimens differed from -65‰, which another study determined to be the average δ^2H value of naturally occurring water in the Imperial Valley (Smith et al. [1992]). We also conducted a one-sample *t*-test comparing contemporary δ^2H values to the same -65‰ value to determine if contemporary birds have incorporated water sources that originated outside of the Imperial Valley.

We calculated isotopic niche breadth ($‰^2$) for lark samples among time periods and habitat types by calculating Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. [2011]). This method implements a Bayesian chain to calculate the sample-size corrected 90% standard ellipsis area (SEA_C) for $\delta^{15}N$ and $\delta^{13}C$ isotope data combined, and reduces biases introduced by differing sample sizes among groups as compared to methods based on calculating convex hull polygons. We ran two chains for 2×10^4 generations and discarded the first 1×10^3 generations as burn-in. We set the precision on the normal prior on the means to 1×10^{-3} and left the remaining options at their default settings.

Results

We observed variation in stable isotope ratios among lark specimens from historical and contemporary populations of larks as well as plant and soil samples from different habitat sites (Table [1]). Contemporary lark feathers had lower $\delta^{15}N$ values compared to historical larks in the Imperial Valley (Fig. [2]; Table [1]). The marginal R^2 for the $\delta^{15}N$ LMM of feather isotope values was 0.68 and the conditional R^2 was also 0.68. Following $\delta^{13}C$ corrections for anthropogenic carbon emissions, we found lower $\delta^{13}C$ values among contemporary larks compared to historical larks (Fig. [2]; Table [1]). The marginal R^2 for the $\delta^{13}C$ LMM of feather isotope values was 0.55 and the conditional R^2 was also 0.55. In contrast, mean δ^2H values did not differ between contemporary and historical larks (Fig. [3]; Table [1]). The marginal R^2 for the δ^2H LMM of feather isotope values was 0.11 and the conditional R^2 was 0.55. Although historical and contemporary feathers did not differ in their mean values, we found that the average δ^2H value among historical larks ($-57.54‰ \pm 19.09$ standard deviation) did not differ from isotopic measurements of naturally occurring water ($\delta^2H = -65‰$) in the Imperial Valley ($t=1.56$; df$=15$; $P=0.14$), while the average contemporary δ^2H value ($-73.07‰ \pm 9.34$) did differ from $-65‰$ ($t=-4.57$; df$=27$; $P<0.001$). Finally, using the $\delta^{15}N$ and

Table 1 Results of stable isotope analysis of Horned Lark (*Eremophila alpestris*) feather, plant, and soil samples from the Imperial Valley, California

Sample type/species	Time period	Habitat type	n	$\delta^{15}N$ (‰)	P value	$\delta^{13}C$ (‰)	P value	δ^2H (‰)	P value	SEA_C (‰²)
Eremophila alpestris	Contemporary	Agricultural	28	8.0±1.3	<0.001	−22.0±1.1	<0.001	−73.1±9.3	0.19	3.9 [2.61–5.67]
Eremophila alpestris	Historical	Creosote bush	16	12.8±2.2		−19.1±1.7		−57.5±19.1		11.0 [6.36–18.43]
Taraxacum officinale	Contemporary	Agricultural	15	6.6±3.4	0.07	−28.9±1.6	0.13			
Helianthus nevius tephrodes	Contemporary	Creosote bush	15	3.4±0.9		−27.7±1.0				
Soil samples	Contemporary	Agricultural	15	6.5±1.5	<0.001	−7.9±1.1	0.77			
Soil samples	Contemporary	Creosote bush	15	1.4±1.9		−8.3±3.5				

Mean values and standard deviations are shown for $\delta^{15}N$, $\delta^{13}C$, and δ^2H. *P*-values are calculated from linear mixed models with either time period or habitat type as a fixed effect and sampling locality as a random effect. The estimated, size-corrected standard area of Bayesian (SEA_C) ellipses is shown as well as the 95% Highest Posterior Density of SEA_C in square brackets
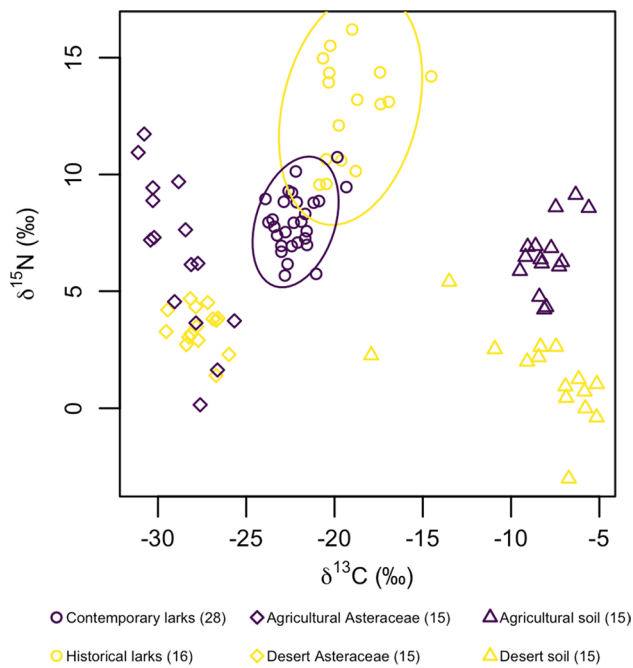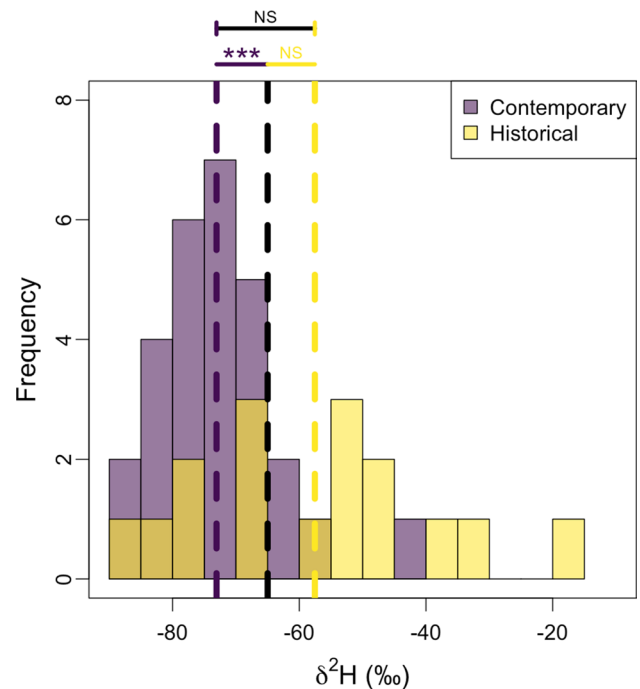
Fig. 2 Bivariate scatterplot of isotopic ratios of larks, plants, and soil, including $\delta^{13}C$ and $\delta^{15}N$. Contemporary and agricultural samples are shown in purple, while historical and Cresote bush scrub samples are shown in yellow. Standard 90% confidence interval ellipses were calculated with the R package SIBER and are displayed for the larks. Sample sizes are shown in parentheses next to each category underneath the plot

Fig. 3 Histograms of δ^2H values from contemporary (purple) and historical specimens (yellow). Vertical dotted lines indicate the mean δ^2H values for contemporary samples (purple), local ground water (i.e., not irrigational; black) from the Imperial Valley ($-65‰$; Smith et al. 1992), and historical samples (yellow). Above the plot, lower horizontal lines indicate differences in mean values for one-sample t-tests comparing historical ground water values to contemporary (purple; $P < 0.001$) and historical (yellow; $P > 0.05$) samples. Higher horizontal line indicates results of two-sample t-test comparing δ^2H between historical and contemporary samples ($P > 0.05$)

$\delta^{13}C$ data in combination, we found that Bayesian estimates of isotopic niche breadth were smaller for contemporary larks compared to historical larks (Table 1; Fig. 2), suggesting isotopic niche contraction over time.

Plant and soil isotope ratios exhibited fewer differences between agricultural land and Creosote bush desert scrub (Table 1; Fig. 2). Specifically, we found no difference in $\delta^{15}N$ or $\delta^{13}C$ values between agricultural plants and Creosote bush scrub plants (Table 1; Fig. 2). The marginal R^2 for the $\delta^{15}N$ LMM of plant isotope values was 0.28 while the conditional R^2 was 0.80. The marginal R^2 for the $\delta^{13}C$ LMM of plant isotope values was 0.16 while the conditional R^2 was 0.51. Similarly, we did not find any differences in $\delta^{13}C$ values between agricultural soil and Creosote bush scrub soil, which reflects a mixture of C_4 and calcium carbonate carbon sources (Table 1; Fig. 2). In contrast, $\delta^{15}N$ was higher in agricultural soil compared to Creosote bush scrub soil (Table 1; Fig. 2). The marginal R^2 for the $\delta^{15}N$ LMM of soil isotope values was 0.69 while the conditional R^2 was 0.88. The marginal R^2 for the $\delta^{13}C$ LMM of soil isotope values was 0.00 while the conditional R^2 was 0.28.

Discussion

The isotopic profiles of Horned Larks have changed in the Imperial Valley following conversion of Creosote bush scrub to agriculture over the last 80 years. Specifically, we observed a temporal decrease in the isotopic values of $\delta^{15}N$ and $\delta^{13}C$ among Horned Larks as agriculture has proliferated in the region (Table 1; Figs. 2, 3). In contrast, soil in agricultural land had higher $\delta^{15}N$ compared to Creosote bush scrub soil while soil $\delta^{13}C$, plant $\delta^{13}C$, and plant $\delta^{15}N$ values did not differ between habitat types (Table 1; Fig. 2). This contrast in the magnitude and directionality of isotopic change between bird, soil, and plant isotopic values suggests that shifting isotopic baselines alone cannot explain lower $\delta^{15}N$ and $\delta^{13}C$ values among contemporary birds, indicating a possible role for trophic shifts. Lower $\delta^{13}C$ values among contemporary larks could provide additional evidence for a decrease in trophic level (Fig. 3), but fractionation in $\delta^{13}C$ across trophic levels is generally smaller than trophic fractionation of $\delta^{15}N$ (McCutchan et al. 2003). Rather, a temporal decrease in $\delta^{13}C$ values may represent a dietary

increase in the intake of plants and phytophagous insects that leverage C3 photosynthetic pathways (Kelly 2000), many of which are common crops in the Imperial Valley. Additionally, contemporary larks have lower niche breadth and δ^2H values that differed from the isotopic value of historical groundwater (Table 1; Fig. 3), suggesting further changes to their trophic ecology and resource use. In what follows, we discuss each of these findings and explain any caveats or alternative interpretations of the patterns at hand.

Contemporary larks in the Imperial Valley had lower $\delta^{15}N$ values than their historical counterparts, suggesting a possible trophic shift over time. To our knowledge, the organism-specific rate of fractionation is not known for Horned Larks, which precludes an exact calculation of the degree of trophic change via $\delta^{15}N$ values. However, the observed decrease in $\delta^{15}N$ of ~4.8‰ is substantial and comparable to an entire trophic level in other avian systems, which range from 1.5 to 4.0‰ (Ponsard and Averbuch 1999; Kelly 2000). Horned Larks outside of the Imperial Valley tend to eat a mixture of seeds and insects, averaging 50–60% arthropods during July and August (Rotenberry 1980). In contrast, our observed decrease in $\delta^{15}N$ among contemporary larks suggests higher consumption of seeds, young plants, and phytophagous insects during this time of the year compared to their historical counterparts (Boecklen et al. 2011). In support of a dietary shift, stomach content surveys of contemporary larks from the Lower Colorado River Valley ($n = 48$) indicated that insects accounted for only 38% of their diet (dominant insect prey including aphids, caterpillars, weevils, and wasp pupae), while the remaining diet consisted of plant matter (Rosenberg et al. 1991). Horned Larks have also been observed taking seeds and seedlings of newly planted lettuce, wheat, and soybean in the Lower Colorado River Valley (Rosenberg et al. 1991)—both of which are abundant crops in the nearby Imperial Valley—further supporting a potential shift in lark diet following the regional rise in agriculture. An examination of stomach contents would be an excellent way to support or refute the isotopic evidence we have documented here (Polito et al. 2011), but are unfortunately unavailable for the specimens included in this study. While our isotopic data are suggestive of a possible change in trophic position, they are far from conclusive. Recently, compound-specific nitrogen isotope analyses of amino acids (CSIA-AA) present a promising new tool that may more accurately estimate changes in trophic position compared to classic stable isotope analyses (Nielsen et al. 2018; Ishikawa 2018; Whiteman et al. 2019). Future studies could leverage compound-specific isotopic analyses to more accurately estimate changes in trophic position and amino acid-derived baselines of $\delta^{15}N$ and $\delta^{13}C$, as was recently done in Short-tailed Albatross (*Phoebastria albatrus*; Vokhshoori et al. 2019).

Increased consumption of seeds and seedlings of wheat, alfalfa, soybean and lettuce (as well as phytophagous insects associated with those crops) may have also contributed to decreased $\delta^{13}C$ values among contemporary larks (Fig. 1). All of the aforementioned crops are C3 plants with lower $\delta^{13}C$ values than arid C4 or CAM grasses and non-woody shrubs that inhabit the arid Creosote bush scrub that characterized lark habitat prior to the rise of agriculture in the Imperial Valley (Teeri and Stowe 1976; Connin et al. 1997). Horned Larks are opportunistic in their consumption of seeds and insects (Wiens and Rotenberry 1979; Rotenberry 1980), such that contemporary larks may have capitalized on an abundant food source represented by agricultural crops and their associated arthropods that did not exist eighty years ago, as has been demonstrated in other avian taxa that persist in novel, anthropogenic ecosystems (Greenberg et al. 2000; Sekercioglu 2012). Furthermore, a related lark species has been known to alter its foraging behavior in response to food and water supplementation (Tieleman and Williams 2002), suggesting Horned Larks could have also exploited novel food and water resources in agricultural land.

Many of the crops in the Imperial Valley are nitrogen-fixing plants, which may also have contributed to decreases in $\delta^{15}N$ values because nitrogen-fixing plants typically discriminate the heavier ^{15}N isotope during biochemical and physiological processes associated with N_2 fixing (He et al. 2009; Unkovich 2013). Cover crops, such as clover and other common crops, in the Imperial Valley, such as alfalfa and soy beans, are nitrogen-fixing plants with $\delta^{15}N$ values that are likely lower than native plants from arid historical habitats of the Imperial Valley (Vance et al. 1979). If contemporary Horned Larks in the Imperial Valley preferentially ate seeds, seedlings, and insects associated with N-fixing plants, then the drop in $\delta^{15}N$ among contemporary larks could have been indicative of a shift in the plant-based portion of their diet rather than, or in addition to, a drop in trophic level and a reduction in the proportion of non-phytophagous insects consumed (Kelly 2000).

Decreased $\delta^{15}N$ isotope ratios among contemporary larks may alternatively reflect a contraction of the food chain under Horned Larks in the Imperial Valley rather than a shift in the diet of Horned Larks themselves (Pimm and Kitching 1987). Food chain length is related to various aspects of ecological communities, including resource availability and ecosystem stability, among other factors (Post 2002b). Agricultural practices in arid lands like the Imperial Valley increase the availability of nutrients and water that support the base of the food web and may, therefore, increase food chain complexity and length (Doi 2012). However, agriculture also involves frequent and intense disturbances to native systems that may disrupt ecological interactions that underlie longer, more complex food webs (Jonsson et al. 2012).

Estimates of stable isotope niche breadth were smaller among contemporary larks compared to historical larks from the Imperial Valley (Table 1; Fig. 1). Agriculture tends to homogenize plant and insect communities (Vellend et al. 2007; Ekroos et al. 2010), such that contemporary larks may have opportunistically preyed on a less diverse assemblage of plant and insect species that are abundant among lettuce, alfalfa, and soybean fields among other common crops compared to their historical counterparts. A similar contraction of isotopic niche breadth was observed among invasive rats (*Rattus* spp.) that occupied agricultural regions in eastern Madagascar (Dammhahn et al. 2017), while American White Ibises (*Eudocimus albus*) also have reduced isotopic niche breadth in anthropogenically modified habitats (Murray et al. 2018). Thus, reduced variance in isotope values among Horned Larks in the Imperial Valley could reflect a broader trend of generalists capitalizing on locally abundant yet homogenous food sources in anthropogenically modified biomes, such as agricultural land (Clavel et al. 2011; Hautier et al. 2015). However, local seasonal movements and limitations of our seasonal and geographic sampling may have also contributed to reduced isotopic niche breadth among contemporary larks. Our historical series was mostly limited to non-breeding months, when larks tend to aggregate in larger flocks and are less territorial. Thus, historical individuals that were collected at the same non-breeding locality likely bred on different territories within the range of seasonal lark movement that may have spanned a greater breadth of local resources compared to breeding birds collected at the same locality.

Beyond changes in diet, the temporal trends that we observe in lark feather isotope values in the Imperial Valley could have also been driven in part by changes in water availability. Specifically, isotopic retention of ^{15}N is greater in the production of highly concentrated uric acid, such that individuals in xeric conditions with little water tend to have higher δ^{15}N values (Ambrose 1991; Cormie and Schwarcz 1994). Larks in arid environments exhibit various physiological and metabolic adaptations to arid environments (Dean and Williams 2004), while irrigation has created novel sources of water that did not exist prior to the rise of agriculture in the Imperial Valley. Thus, a reduction in osmoregulatory stress through increased water availability may have also contributed to decreased δ^{15}N values among contemporary larks (Heaton 1987). However, the contributions of water balance to δ^{15}N values are generally thought to be smaller than the contributions of trophic interactions and vary substantially among taxa (Sponheimer et al. 2003; Murphy and Bowman 2006).

We used comparisons among soil and plant samples of agricultural (present conditions) and Creosote scrub habitat (historical conditions) to approximate baseline trends in isotopic values (Ekroos et al. 2010). However, there may

still have been changes to isotopic baselines that our sampling design does not address. For example, our estimates of isotopic baselines in plants were limited to a single species and a small geographic extent from both habitat types and may, therefore, not fully capture temporal changes in isotopic composition at the base of food webs in the Imperial Valley (Layman et al. 2012). However, other systems have documented higher δ^{15}N values as agricultural intensity increases (Hebert and Wassenaar 2001; Aranibar et al. 2008; Stevenson et al. 2010), suggesting that our soil and plant samples capture a general baseline trend observed in other agricultural systems (Fig. 3). Furthermore, temporal changes in rainfall and anthropogenic reactive nitrogen emissions may have also impacted baseline isotope values over the time (Li et al. 2016). Trends from lake sediment cores (Holtgrieve et al. 2011) and ice cores (Felix and Elliott 2013) indicate a temporal decrease in δ^{15}N values over the last century, which may have also contributed to decreases in contemporary lark δ^{15}N values.

Lastly, in addition to temporal changes in δ^{15}N and δ^{13}C, contemporary larks had lower δ^{2}H compared to ground water estimates for the Imperial Valley (Fig. 3), suggesting a possible change in water source at the base of the lark food web (McKechnie et al. 2004). Rain and ground water that originated in southeastern California have δ^{2}H values (approximately − 65‰ δ^{2}H; Smith et al. 1992) that differ from the deuterium-poor water from the Colorado River that fills irrigational canals (approximately − 100‰ δ^{2}H; Guay et al. 2006). The decrease in δ^{2}H values among contemporary larks may reflect the intake of irrigation water directly or indirectly through application of irrigation water to the plants and crops that form the base of the food web for larks in the Imperial Valley. However, we note that mean δ^{2}H values among contemporary and historical larks did not differ, due to large variance observed in historical values (Table 1; Fig. 3). Thus, contemporary larks may be specializing on a currently abundant water source (i.e. irrigation canals) that was present, but not prevalent among historical populations. While the stark difference in δ^{2}H between irrigation water and ground water in the Imperial Valley may not be present in other systems, our findings highlight the utility of hydrogen isotopes to detect shifts in water sources over time (Hobson et al. 1999; Wolf and Martinez del Rio 2000; Bowen et al. 2005).

In summary, we observe temporal declines in δ^{15}N, δ^{13}C, and δ^{2}H among Horned Lark feathers from the Imperial Valley of southeastern California that are coincident with the agricultural intensification of the Colorado Desert. These isotopic shifts are in the opposite direction of comparisons between isotopic values of soil (and plants to a lesser extent) from agricultural land and Creosote bush scrub, suggesting that baseline changes in the isotopic composition of the base of the food web are

not solely responsible for these patterns. Thus, contemporary Horned Larks may shifted to a lower trophic level, in which they eat more phytophagous insects and C3 plants than their historical predecessors. In addition to dietary shifts, frequent disturbances induced by agriculture may have shortened the food chain beneath larks in the Imperial Valley, while supplemental water via irrigation canals may have reduced water stress, both of which could have contributed to the isotopic changes we observed. We also observed decreases in δ^2H values that likely indicate the incorporation of irrigation water from the Colorado River into the lark food web. Finally, isotopic niche breadth of larks decreased with the rise of agriculture, suggesting the larks may have capitalized on an abundant but less diverse food source associated with popular crops in the area. These isotopic changes may be the product of dietary shifts of larks that have stayed in the Imperial Valley, or could be the result of new populations moving into the area that differ in their foraging behavior. Contemporary larks in the Imperial Valley are darker than their historical counterparts (Mason and Unitt 2018), resembling populations from the Channel Islands off of southern California that are dispersing inland (Mason et al. 2014). Future studies could leverage new genomic resources for the Horned Lark (Mason et al. 2020) to disentangle the contributions of immigration and in situ change toward temporal change in both stable isotopes and dorsal coloration. Taken together, our study illustrates how stable isotope analyses can be used in conjunction with temporal and spatial series of natural history collections to examine how native species respond to agriculture and other forms of human activity.

Data accessibility All data and code used to conduct the analyses presented in this manuscript are available via GitHub (https://github.com/mason-lab/IVLarkIsotopesJoO).

Compliance with ethical standards

Conflict of interest The authors have no conflict of interests to declare.

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