



Avian Behavior, Ecology, and Evolution

Wintering *Artemisiospiza* sparrows: patterns of segregation between Sagebrush Sparrow (*A. nevadensis*) and Mojave Bell's Sparrow (*A. belli canescens*) across Lower Colorado Desert vegetation assemblages, with evidence for differential migration in Mojave Bell's Sparrow

Pinzones del género *Artemisiospiza* pasando el invierno: patrones de segregación entre *A. nevadensis* y *A. belli canescens* a lo largo de ensamblajes de vegetación del Desierto del Bajo Colorado, con evidencia en favor de la migración diferencial en *A. belli canescens*

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ABSTRACT. Bell's Sparrows (*Artemisiospiza belli*) have only recently been recognized as distinct from Sagebrush Sparrows (*A. nevadensis*), and the "Mojave" subspecies (*A. b. canescens*) shares an overlapping wintering distribution with Sagebrush Sparrow in the Mojave and Sonoran deserts of southeastern California and western Arizona. We lack understanding of the two species' respective wintering habitat preferences and the degree to which they interact or segregate on their wintering grounds due to the difficulty in separating them in the field and to their previous classification as one species. We captured and sampled 74 *Artemisiospiza* sparrows from 5 sites across western Arizona, supporting field identifications with genetic analyses of mitochondrial DNA to confirm species and molecular sexing of sampled individuals. Bell's Sparrows and Sagebrush Sparrows segregated into different habitat types across our study area, with only one species detected at four of five study sites. Bell's Sparrows comprised 82% ($n = 33$) of *Artemisiospiza* sparrows captured at the 5th site at Robbins Butte. Broadly, Sagebrush Sparrows were found in more upland, well-drained locations that were less vegetated with xerophytic scrub. Bell's Sparrows were found in more vegetated locations with halophytic Mojave seablite (*Suaeda nigra*) and saltbush (*Atriplex*) adjacent to mesquite and tamarisk woodlands. Bell's Sparrow sex ratios were significantly female-biased (binomial test: $n = 56$, observed $k = 48$ females, expected $k = 28$ females for assumed $p = 0.5$, $\Pr [k < = 8 \text{ or } k > = 48] < 0.0001$; 95% CI = 0.369 – 0.631 for assumed $p = 0.5$) at Fort Mohave and Robbins Butte, the 2 sites where Bell's Sparrows were found. Our observed sex-ratios and well-documented year-round presence of Bell's Sparrows on and near the breeding grounds suggest that Bell's Sparrow males and females employ different migration strategies, a phenomenon not previously documented for this taxon.

RESUMEN. *Artemisiospiza belli* solo hasta hace poco fue reconocida como una especie diferente de *A. nevadensis*, y la subespecie *A. b. canescens* comparte una distribución de invierno que se sobrepone con la de *A. nevadensis* en los desiertos de Sonora y Mojave en el sureste de California y oeste de Arizona. Hace falta un mejor entendimiento sobre las preferencias de hábitat durante el invierno de las dos especies y el grado en el cual interactúan o se segregan en el territorio de invierno debido a la dificultad de separarlos en el campo y a su previa clasificación como una sola especie. Capturamos y muestreamos 74 pinzones del género *Artemisiospiza* en 5 sitios a lo largo del oeste de Arizona, dando soporte a las observaciones en campo con análisis genéticos de ADN mitocondrial para confirmar la especie y sexar molecularmente los individuos muestreados. *Artemisiospiza belli canescens* y *A. nevadensis* se segregaron en tipos de hábitat diferentes a lo largo de nuestra área de estudio, con una sola especie detectada en cuatro de los cinco sitios de estudio. *A. b. canescens* comprendió el 82% ($n=33$) de los pinzones del género *Artemisiospiza* capturados en el quinto sitio en Robbins Butte. En general, los individuos de *A. nevadensis* fueron encontrados en tierras más altas, en localidades con buen drenaje que tenían menos vegetación con matorrales xerofíticos. *A. b. canescens* fue encontrado en localidades con mayor vegetación caracterizada por la presencia de *Suaeda nigra* y *Atriplex* adyacentes a bosques de mezquites y tamariscos. La proporción de sexos en *A. b. canescens* estuvo significativamente sesgada hacia las hembras (Prueba binomial: $n = 56$, observados $k = 48$ hembras, esperadas $k = 28$ hembras bajo el supuesto $p = 0.5$, $\Pr [k < = 8 \text{ or } k > = 48] < 0.0001$; 95% CI = 0.369 – 0.631 asumiendo que $p = 0.5$) en Fort Mohave y Robbins Butte, los 2 sitios donde *A. b. canescens* fue encontrado. Nuestra observación sobre la proporción de sexos y la documentación de la presencia a lo largo del año entero de *A. b. canescens* en y cerca de los sitios de reproducción sugiere que las hembras y los machos de *A. b. canescens* utilizan estrategias de migración diferentes, un fenómeno que no se había documentado anteriormente en este taxon.

Key Words: *Artemisiospiza*; *Bell's Sparrow*; differential migration; Sagebrush Sparrow; wintering habitat

INTRODUCTION

The *Artemisiospiza* "Sage Sparrows" are demonstrably difficult to separate in the field (Pyle 2013), and their taxonomic status has been debated for over 120 years (Cicero 2010). Bell's Sparrow (*Artemisiospiza belli*) and Sagebrush Sparrow (*A. nevadensis*) were once grouped together as Sage Sparrow in the genus *Amphispiza*, along with Black-throated Sparrow (*A. bilineata*). Klicka and

Spellman (2007) found that the genus *Amphispiza* was not monophyletic, Sage Sparrows were not as closely related to Black-throated Sparrows as believed, and Sage Sparrows were more closely related to the clade of "grassland" sparrows (genera: *Pooecetes*, *Oriturus*, *Passerculus*, *Ammodramus* [in part, and now labeled *Ammospiza*], *Melospiza*, and *Xenospiza*; Klicka and Banks 2011). Klicka and Spellman (2007) also suggested a new

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genus name, *Artemisiospiza*, for Sage Sparrow, and Klicka and Banks (2011) formally named the new genus. The American Ornithologists' Union accepted *Artemisiospiza belli* in 2012 (Chesser et al. 2012).

Preceding this change, Johnson and Marten (1992) used morphometric and allozyme data to separate *Amphispiza belli canescens* and *A. b. nevadensis*. Patten and Unitt (2002) challenged the morphological diagnosability of these latter two taxa, but Cicero and Johnson (2006) demonstrated that Patten and Unitt had mixed breeding and nonbreeding individuals in their samples, distorting their results. Mitochondrial DNA (mtDNA) analysis by Cicero and Johnson (2006) further demonstrated genetic differences between the taxa, showing that their breeding distributions met only in a narrow (15-20 km) contact zone in the Owens Valley, near Bishop, California (Cicero and Johnson 2007). Cicero and Koo (2012) further used mtDNA, morphological differences, and ecological niche models to support a proposal for full species status for Sagebrush Sparrow, which was then added to the Check-list of North American Birds (Chesser et al. 2013). For brevity, we use hereafter use "Bell's Sparrow" when referring to *A. b. canescens*.

Both Sagebrush and Bell's sparrows winter in southeastern California and western Arizona (Phillips et al. 1964, Martin and Carlson 2020a, b). Species-specific wintering habitat preferences and the degree to which the two species segregate or interact on their wintering grounds nonetheless remains largely undescribed (Rosenberg et al. 1991). This knowledge gap is due to the species' apparent niche overlap during the nonbreeding season, the difficulty of separating the two species in the field, and to the very recent taxonomic separation of *A. b. canescens* and *A. nevadensis* into separate species.

Following previously published methods for morphometric and genetic analyses on the *Artemisiospiza* sparrows (Johnson and Marten 1992, Cicero and Johnson 2006, 2007, Cicero and Koo 2012) and a photographic guide to plumage differences (Pyle 2013), we sought to identify locations across western Arizona where the two *Artemisiospiza* sparrow species were found during the winter, to estimate their relative proportions at these sites and to describe the vegetation communities present at these locations.

METHODS

Study area

We compiled recent sight reports of *Artemisiospiza* sparrows in late 2013 and early 2014 to help us locate individuals to sample from 5 locations spanning approximately 250 km across western Arizona in Maricopa, Yuma, and Mohave counties (Fig. 1). Sampling sites (Table 1) were selected to represent a variety of plant assemblages that could potentially host wintering Sagebrush and Bell's sparrows. Field sampling was from 6 to 16 February 2014. Figures 2-6 depict the five study sites, with sparrow flushing areas outlined in yellow and five vegetation plots for each site depicted with yellow circles.

Robbins Butte Wildlife Area

The Robbins Butte study site (Maricopa County, AZ; 33.316°N, 112.634°W) is within the southern periphery of the Gila River floodplain in western Maricopa County, west of Arizona Highway 85. Tamarisk (*Tamarisk* sp.) riparian woodland and

small cultivated plots of winter wheat (*Triticum aestivum*) and alkali sacaton grass (*Sporobolus airoides*) planted for wildlife forage extend to the north and northwest of the site (Fig. 2). The toe of an alluvial fan that descends from the Buckeye Hills extends uphill to the south, transitioning to mixed Sonoran Desert scrub. A portion of the site appears to have once been irrigated by a small canal that bisects the site, suggesting that the area was previously used for pasture or cultivated crop production several decades ago. The LANDFIRE US 220 Existing Vegetation Type classification system (LANDFIRE 2022) classifies this site as a mix of western warm temperate fallow/idle cropland, North American warm desert ruderal and planted scrub, Sonoran Paloverde-mixed cacti, and Sonora-Mojave creosotebush-white bursage desert scrub.

Fig. 1. Sampling locations in western Arizona.

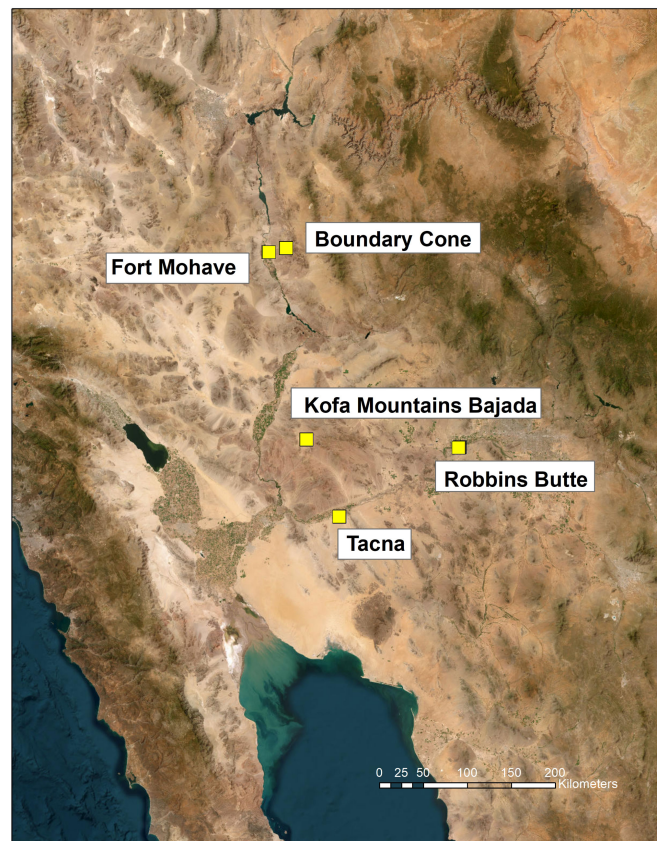


Table 1. *Artemisiospiza* sampling locations in western Arizona.

Site Name	County	Latitude	Longitude	Elevation	Sampling dates
Robbins Butte Wildlife Area	Maricopa	33.318	-112.632	250 m	6–10 Feb
Tacna	Yuma	32.727	-113.853	104 m	12 Feb
Kofa Mountains Bajada	Yuma	33.372	-114.168	472 m	13 Feb
Fort Mohave	Mohave	34.968	-114.589	148 m	14–15 Feb
Boundary Cone	Mohave	35.000	-114.408	658 m	16 Feb

Fig. 2. Vegetation sampling plots at Robbins Butte, Maricopa County, Arizona.

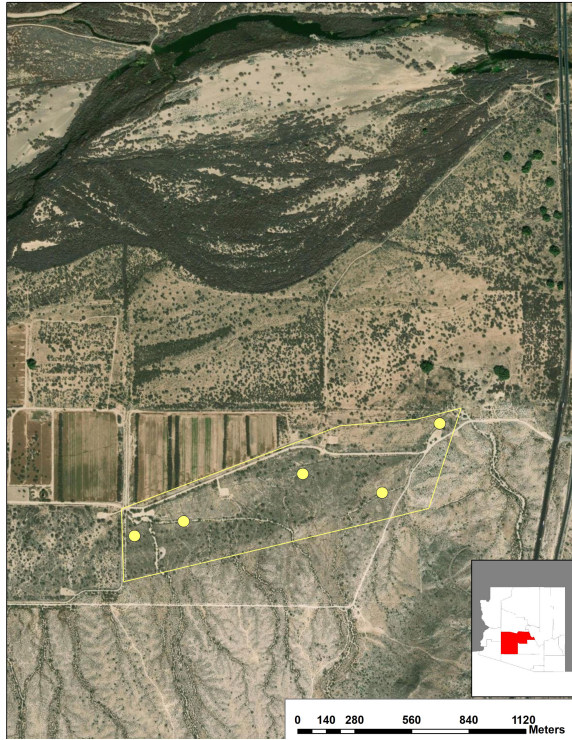


Fig. 4. Vegetation sampling plots at Kofa Mountains Bajada, Yuma County, Arizona.

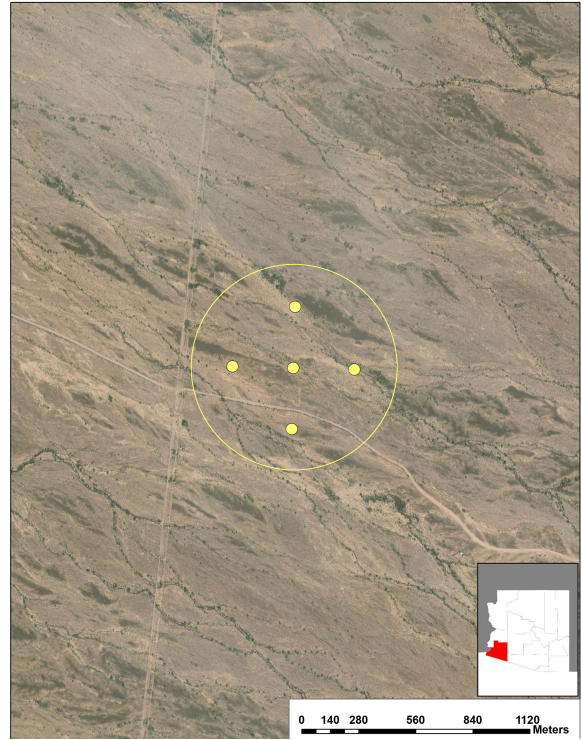


Fig. 3. Vegetation sampling plots at Tacna, Yuma County, Arizona.

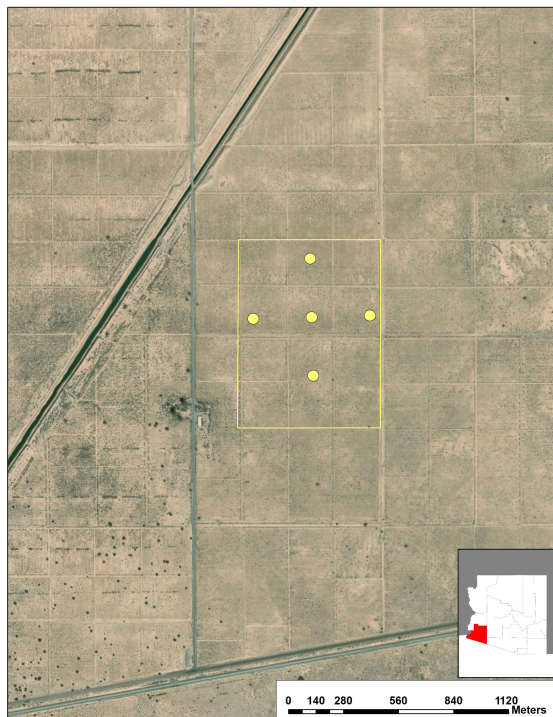
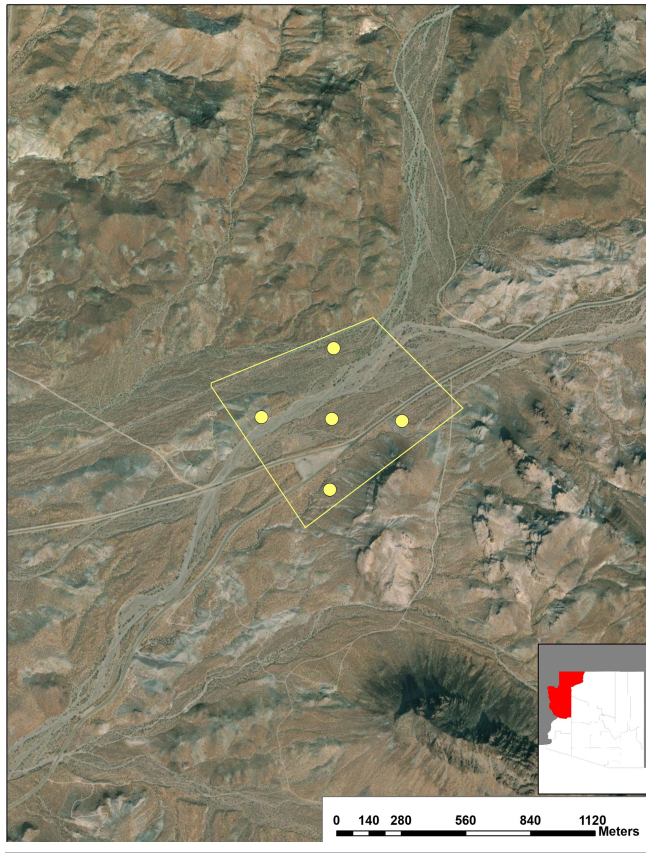


Fig. 5. Vegetation sampling plots at Fort Mohave, Mohave County, Arizona.



Fig. 6. Vegetation sampling plots at Boundary Cone, Mohave County, Arizona.



Tacna

The Tacna study site (Yuma County, AZ; 32.718°N, 113.924°W) is on a sandy mesa at the northern edge of the Mohawk Valley, approximately 2 km south of cultivated cropland in the Gila River floodplain (Fig. 3). The study site was once irrigated cropland, perhaps used for citrus production, and is in a ruderal state, not yet returned to creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) scrub that persists in untilled land with similar elevation, physiography, and soils south of the study site (December 1985 imagery housed at Google Earth <https://earth.google.com/web/>). LANDFIRE US 220 (LANDFIRE 2022) classifies this site as a mix of North American warm desert ruderal and planted scrub, western warm temperate pasture and hayland, and Sonora-Mojave creosotebush-white bursage desert scrub.

Kofa Mountains Bajada

The Kofa Mountains Bajada site (Yuma County, AZ; 33.385°N, 114.200°W) is on the lower slope of a bajada with desert pavement dissected by xeric riparian wash, approximately 8.5 km west of the mouth of Palm Canyon in the Kofa Mountains. It is mostly north of Palm Canyon Road and is approximately 1 km west of the Kofa National Wildlife Refuge (Fig. 4). LANDFIRE US 220 (LANDFIRE 2022) classifies this site as a mix of Sonoran Paloverde-mixed cacti scrub and Sonora-Mojave creosotebush-white bursage desert scrub.

Fort Mohave

The Fort Mohave site (Mohave County, AZ; 34.967°N, 114.586°W) is at the northern end of the Mohave Valley, on the eastern periphery of the Colorado River floodplain. It is between tamarisk woodland and Boundary Cone Road to the north, irrigated cropland and Arizona Highway 95 to the west, the El Rio Golf Club to the south (Fig. 5). The site does not appear to have been cultivated previously, but it was apparently cleared of vegetation around 2004, during the construction of the golf course (September 2004 imagery housed at Google Earth). LANDFIRE US 220 (LANDFIRE 2022) classifies this site poorly as a mix of western warm temperate fallow/idle cropland, western warm temperate close grown crop, and Sonoran-Mojave creosotebush-white bursage desert scrub.

Boundary Cone

The Boundary Cone site (Mohave County, AZ; 35.002°N, 114.407°W) is in a wide, shallow canyon on the western edge of the Black Mountains, on an alluvial bench bisected by xeric riparian wash. It is north of Boundary Cone Road and is approximately 2.5 km northeast of Boundary Cone Mountain and 4.3 km southwest of the town of Oatman, Arizona, near the intersection of Oatman Road and Historic U.S. Highway 66 (Fig. 6). LANDFIRE US 220 (LANDFIRE 2022) classifies this site as Sonora-Mojave creosotebush-white bursage desert scrub.

Data collection

Mist-netting

Artemisiospiza sparrows were captured following a flush-netting method described in Gordon (2000). Scouting was required at each site, given that (1) preceding reports of recent *Artemisiospiza* sightings were vague as to the precise location of potential captures, the reports occasionally dated, and (2) wintering *Artemisiospiza* are nonterritorial (Martin and Carlson 2020a). Presence of *Artemisiospiza* sparrows determined where nets were placed; all vegetation types were scouted at sites with multiple vegetation assemblages (Robbins Butte, Fort Mohave, Boundary Cone), and the yellow-outlined capture areas depicted in Figures 2-6 correspond to where *Artemisiospiza* sparrows were found and rounded up toward net lines.

Upon locating *Artemisiospiza* sparrows during scouting, we aligned 4 to 6 mist nets (2 x 10 m, 32- and 36-mm mesh) from end to end in a line near sighted birds, with care taken to hide nets in natural gaps in shrub cover when possible. We spaced ourselves and typically 8 to 15 volunteers into a large C-shaped semi-circle then slowly herded sparrows toward the net line. The net line was then dismantled and placed in a new location, contingent on where uncaptured birds moved while herding them toward nets or where new groups of potential captures were found. Occasionally the net line was left in the same location, and we herded birds toward the nets from the opposite direction. Two to approximately 12 net placements were attempted at each site, depending on the success of preceding flushing attempts.

Field measurements

We banded all captured *Artemisiospiza* with uniquely numbered aluminum USGS bands and recorded a series of morphological measurements on each capture (Table 2). Specific individuals are described in text and in tables and figures with the final four digits of their band's unique number. We were constrained in the number of measurements we could take within a safe handling time

Table 2. Field measurements taken on *Artemisiospiza* captures at western Arizona sites, Feb 2014.

Measurement	Description
Wing Chord	Unflattened wing length to the nearest millimeter using a wing rule. Measurement taken while the wing was in its natural closed position, from the tip of the carpal joint to the end of the longest primary
Flat Wing Chord	Wing length as above, but with the wing gently flattened on the wing rule, producing a slightly longer measurement than unflattened wing chord
Body Molt	Assessment of the amount of molt visible in contour feathers and wing and tail coverts, with 0 representing no body molt, and 3 representing heavy body molt, with greater than 1/2 of body feathers in molt
Flight Feather Molt	Assessment of presence of molt in flight feathers of the wing and tail. Zero signified no flight feather molt, F signified regular flight feather molt, A signified adventitious molt
Wear	Degree of wear on the outer 4-5 primaries, with 0 representing no apparent wear and 5 representing excessive wear
Fade	Degree of primary tips' fade in color due to sun exposure and wear, with 0 representing no fade line present, and 3 representing pronounced fade line present in the tips of the primaries
Weight	Body weight measured to 0.1 g with an electronic scale
Tail	Measured to the nearest 0.1 mm with a clear plastic ruler inserted between the two inner rectrices of the tail
Exposed Culmen	Measured to the nearest 0.1 mm from the tip of the feathering at the base of the bill to the bill's tip
Bill Width	Bill width to the nearest 0.1 mm taken at the anterior end of the nostril
Bill Depth	Bill depth to the nearest 0.1 mm taken at the anterior end of the nostril
Primary Projection	Distance from the longest primary to the longest secondary to the 0.1 mm
Malar Streak Gap	0.1 mm from the base of the lower mandible to the uppermost extent of the malar streak

because we also wished to obtain blood samples and photographs from captured birds, and our method of capturing birds required netting several birds simultaneously. The entire suite of morphological measurements was not taken for some individuals (e.g., the bird escaped during processing, or the bird showed signs of distress and was released prior to completion of measurements).

Photographs

We photographed captured *Artemisiospiza* sparrows with a Nikon digital single lens reflex camera and a 300 mm lens. We photographed each individual's back, tail, nape, crown, profile, front, and opened wing, and all images are currently available at <https://doi.org/10.5061/dryad.gmsbcc2tp>. Additionally, notes were taken on quality and extent of dorsal streaking in the back, on malar streak color and extent, outer rectrix patterning, and coloring in the supercilium.

Blood sampling

Captured birds were gently placed in small cloth bags with drawstrings and brought to a banding station ca. 100 m from the net line. A blood sample was drawn from the brachial vein with a 27-gauge 1/2-inch needle following Owen (2011). One to two drops of blood were absorbed onto both sides of an Advantec Nobuto Blood Filter Strip. Samples were allowed to air dry and then placed into paper coin envelopes. Sample envelopes were stored outside of direct sunlight at ambient temperature and labeled with the bird's unique band number, date collected, sampling location, and suspected species. Remaining blood is archived with the Kovach Laboratory at the University of New Hampshire.

Genetic analysis

DNA was extracted from blood samples using a Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California, USA), following manufacturer's protocol. The sex of the individuals was determined using a molecular sexing protocol that leverages a length polymorphism in the CHD₁ gene of Z and W chromosomes. The CHD₁ gene was amplified using primers P2 and P8, following methods of Griffiths et al. (1996) and Fridolfsson and Ellegren (1999). Amplified products were

resolved in a 2% agarose electrophoretic gel. This assay produces two fragments of different size for females and a single fragment for males.

Species identification was performed using the mitochondrial DNA restriction fragment length polymorphism assay described in Cicero (2004). A 900-bp fragment of the cytochrome B gene was amplified with primers L14987 and H15916, as in Cicero and Johnson (2001). Restriction digests were performed in 10 µl volumes, with 1 µl of the AluI enzyme, 1 ml of enzyme-specific primer (New England Biolabs, Beverly, Massachusetts), 4 µl of DNA, and 4 µl of water, overnight at 37°F. Restriction fragment banding patterns were visualized after electrophoresis in a 2.5% agarose gel. Interpretations followed the haplotype patterns identified by Cicero and Koo (2012).

Vegetation sampling

We characterized vegetation at each study site in December 2014, following a modified protocol described in Fleishman et al. 2014, and described further in Fogarty et al. 2022. Five vegetation plots were established at each study site. At Tacna, Kofa Mountains Bajada, and Boundary Cone, the site's first net placement was used for one plot, and four additional plots were set 250 m from the first plot in each cardinal direction (Figs. 3, 4, and 6). To accommodate smaller, linear-shaped search areas at Fort Mohave and Robbins Butte: (1) 2 vegetation plots were set using the net placements used on the 2 days of sampling at Fort Mohave, and the 3 other vegetation plots were set 250 m apart heading eastward from the 2 net placements (Fig. 5); and (2) the first net placement location for each of the 5 days spent at Robbins Butte was used for that site's 5 vegetation plots (Fig. 2).

Within each plot we walked 3 30-m transects radiating from the plot's center, with the first transect direction set randomly and the following 2 transects established at 120° from the previous transect. Assessments were located at 8 m, 16 m, and 24 m along each transect to determine species presence (or in the event of no plant species present, bare ground) in each cardinal direction and along the transect line, for a total of 5 assessments per stop, 15 assessments per transect, 45 assessments per plot, and 225 assessments per site. At each assessment location, we used an

Table 3. Bell's Sparrow (*Artemisospiza belli*) and Sagebrush Sparrow (*A. nevadensis*) captures summarized by sex across five study sites in western Arizona. Captures summarized for n = 74 identifications by haplotype group and for identifications in the field using morphometric measurements and plumage characteristics. Alu-RFLP analysis does separate the taxa 100% of the time (Cicero and Koo 2012), and a capture summary that excludes six individuals with conflicting genetic and field identifications is also provided.

Species	Robbins Butte	Tacna	Kofa Mountains Bajada	Fort Mohave	Boundary Cone
By haplotype group					
Bell's Sparrow - F	23	0	0	22	0
Bell's Sparrow - M	5	0	0	4	0
Total Bell's Sparrows	28	0	0	26	0
Sagebrush Sparrow - F	4	1	6	3	1
Sagebrush Sparrow - M	1	1	2	0	1
Total Sagebrush Sparrows	5	2	8	3	2
By field identification					
Bell's Sparrow - F	23	0	0	25	0
Bell's Sparrow - M	4	0	0	4	0
Total Bell's Sparrows	27	0	0	29	0
Sagebrush Sparrow - F	4	1	6	0	1
Sagebrush Sparrow - M	2	1	2	0	1
Total Sagebrush Sparrows	6	2	8	0	2
Excluding six individuals with conflicting genetic and field identifications					
Bell's Sparrow - F	22	0	0	22	0
Bell's Sparrow - M	4	0	0	4	0
Total Bell's Sparrows	26	0	0	26	0
Sagebrush Sparrow - F	3	1	6	0	1
Sagebrush Sparrow - M	1	1	2	0	1
Total Sagebrush Sparrows	4	2	8	0	2

ocular tube approximately 11.5 cm long and 2.5 cm in diameter to take measurements at a 45° angle downward from the line of sight. A “hit” was tallied at each assessment when a perennial plant species was observed within the tube while looking downward (e.g., at assessment point 1, at 8 m on the transect tape, looking northward through the tube, only creosote bush was observed; looking eastward, only bare ground was observed through the tube; looking southward, creosote bush and boxthorn (*Lycium* spp.) were observed through the tube; looking westward, only creosote bush was observed through the tube; and looking forward on the transect tape, only white bursage was observed through the tube, totaling three creosote bush hits, one boxthorn hit, one white bursage hit, and one bare ground-only hit. All hits were aggregated by plot and then by site. Low and high heights (cm) were also recorded for each species recorded as hits on each transect.

At the end of each transect, an 11.5 m-radius circle was set and tree canopy radius (cm), tree height (cm), and trunk diameter (cm) were recorded for each arborescent species. Diameter was typically measured at ground level or 10 cm above ground level.

We used aerial imagery provided by ESRI (2022) to estimate phreatophytic tree cover by calculating area coverage of

individually digitized trees at Robbins Butte and Kofa Mountains Bajada, the two sites with trees present. Visual comparison of historic aerial imagery stored by Google (2023) and current ESRI imagery confirmed that slow-growing tree canopies depicted in current ESRI imagery corresponded to extents depicted in 2014 Google imagery. We photographed each site and photographs are stored at <https://doi.org/10.5061/dryad.gmsbcc2tp>.

RESULTS

Species identification

We captured 86 *Artemisospiza* sparrows across the 5 study sites and analyzed blood samples from 74 unique individuals (Table 3).

Genetic results were consistent with 68 of 74 (92%) field identifications. Four of 56 individuals (7%) identified in the field as Bell's Sparrows shared the BC haplotype group consistent with Sagebrush Sparrow (Cicero and Koo 2012). Two of 18 individuals (11%) identified in the field as Sagebrush Sparrows shared the AD haplotype group associated with Bell's Sparrow.

Haplotype designations identified using the Alu RFLP approach do not distinguish the species 100% of the time (Cicero and Koo 2012). Therefore, sample totals (Table 3) are summarized by (1) all 74 individuals as identified by genetic analysis, (2) all 74 individuals as identified in the field by phenotype, and (3) for 68 individuals, excluding the 6 individuals with inconsistent field and genetic assignments. Morphometric measurements for the 6 individuals with inconsistent field and genetic assignments are provided in Table 4 and individual cases are described as follows:

- 8022: Male (Robbins Butte), identified in the field as Sagebrush Sparrow and found with the AD haplotype group. Morphometric measurements classify as Sagebrush Sparrow, notably with a wing chord outside of the range of variation for Bell's Sparrow males presented by Cicero and Johnson (2006), moderate but distinct mantle streaking through the back, and pale gray malar streaks consistent with Sagebrush Sparrow.
- 8520: Female (Robbins Butte), identified in the field as Sagebrush Sparrow and found with the AD haplotype group. Wing chord outside the range of variation for Bell's Sparrow females (Cicero and Johnson 2006), other morphometric measurements consistent with Sagebrush Sparrow, but plumage intermediate, with distinct yet lightly colored mantle streaking and relatively diminished malar streaks that were nonetheless somewhat darker than expected for Sagebrush Sparrow. Potentially a hybrid.
- 8516: Female (Robbins Butte), identified in the field as Bell's Sparrow and found with the BC haplotype group. Morphometric measurements intermediate but more suggestive of Bell's Sparrow. Dark malar streaks and lack of mantle streaking consistent with Bell's Sparrow.
- 8547, 8554, 8572: All females from Fort Mohave, identified in the field as Bell's Sparrow and found with the BC haplotype group. Morphometric measurements and plumage consistent with Bell's Sparrow. All other captures from this site were identified in the field and through genetic analysis as Bell's Sparrow.

Table 4. Morphometric measurements of six individuals with inconsistent haplotype group and field identifications at Robbins Butte and Fort Mohave, Arizona. $n = 74$ (54 assigned to the AD haplotype group, 20 to the BC haplotype group) total samples were analyzed for the study. Note: Bell's Sparrow is *Artemisiospiza belli* and Sagebrush Sparrow is *A. nevadensis*.

Band number	Location	Date	Field identification	Genetic identification	Molecular sex	Wing chord (mm)	Tail (mm)	Weight (g)	Exposed culmen (mm)	Bill depth (mm)	Bill width (mm)	Primary projection (mm)	Malar streak gap (mm)
8022	Robbins Butte	7-Feb	Sagebrush Sparrow	Bell's Sparrow	M	76.4	76.0	15.8	9.7	5.3	4.70	16.5	5.6
8520	Robbins Butte	10-Feb	Sagebrush Sparrow	Bell's Sparrow	F	72.4	69.0	13.9	9.5	5.6	4.30	14.0	3.5
8516	Robbins Butte	10-Feb	Bell's Sparrow	Sagebrush Sparrow	F	69.1	71.0	14.0	10.4	5.0	3.60	11.4	3.5
8547	Fort Mohave	14-Feb	Bell's Sparrow	Sagebrush Sparrow	F	67.0	66.5	16.0	9.3	5.2	3.80	11.0	5.0
8554	Fort Mohave	14-Feb	Bell's Sparrow	Sagebrush Sparrow	F	68.5	68.0	18.0	10.0	5.0	4.00	12.0	4.5
8572	Fort Mohave	15-Feb	Bell's Sparrow	Sagebrush Sparrow	F	67.0	67.5	15.8	9.5	4.9	3.50	10.0	1.8

Morphometric measurements of females of the two species are compared in Table 5 and measurements for all individuals are provided at <https://doi.org/10.5061/dryad.gmsbcc2tp>. We found significant differences between the two species for each measurement taken (two-sided t -test: $p < 0.05$), save weight (two-sided t -test: $p = 0.06$, $df = 58$), with Sagebrush Sparrows larger and with a wider white gap between the lower mandible and top of the malar streak. The 75th percentile for a box plot of female Bell's Sparrow wing chords fell outside the range of female Sagebrush Sparrow wing chords (Patten and Unitt 2002, Cicero and Johnson 2006). The 75th percentile for a box plot of female Sagebrush Sparrow wing chords did not fall outside of the range of female Bell's Sparrow wing chords due to two outlying female Bell's Sparrows (individual 8526 captured at Robbins Butte and individual 8543 captured at Fort Mohave). These two individuals were identified as Bell's Sparrows in the field and were found to have the Bell's Sparrow haplotype group AD.

Segregation across study sites

We found that the two species segregated across the five study sites, with only Sagebrush Sparrows found at Tacna, Kofa Mountains Bajada, and Boundary Cone (Table 3). Only Bell's Sparrows were found at Fort Mohave. Bell's Sparrows comprised approximately 82% of the individuals sampled at Robbins Butte.

Female-biased sex ratio for Bell's Sparrow

Sex ratios were female-biased (Table 3), particularly for Bell's Sparrow (binomial test: $n = 56$, observed $k = 48$ females, expected $k = 28$ females for assumed $p = 0.5$, $\Pr [k < 8 \text{ or } k > 48] < 0.0001$; 95% CI = 0.369-0.631 for assumed $p = 0.5$). Bell's Sparrow sex ratios at the Robbins Butte and Fort Mohave sites were similarly female-biased, with 23 females and 4 males captured at Robbins Butte (binomial test: $n = 27$, observed $k = 23$ females, expected $k = 13.5$ females for assumed $p = 0.5$, $\Pr [k < 4 \text{ or } k > 23] = 0.0003$; 95% CI = 0.311-0.689 for assumed $p = 0.5$), and 25 females and 4 males captured at Fort Mohave (binomial test: $n = 29$, observed $k = 25$ females, expected $k = 14.5$ females for assumed $p = 0.5$, $\Pr [k < 4 \text{ or } k > 22] = 0.0001$; 95% CI = 0.318-0.682 for assumed $p = 0.5$). Notably, individuals 8516, 8547, 8554, and 8572, which were all identified in the field as Bell's Sparrow yet found with the BC haplotype group, were females.

Vegetation sampling

Vegetation characterization across study sites

Species assessed included white bursage, cheesebush (*Ambrosia salsola*), allscale (*Atriplex polycarpa*), fourwing saltbush (*Atriplex canescens*), quailbush (*Atriplex lentiformis*), teddy bear cholla

(*Cylindropuntia bigelovii*), buckthorn cholla (*Cylindropuntia echinocarpa*), pencil cholla (*Cylindropuntia ramosissima*), brittlebush (*Encelia farinosa*), green mormon tea (*Ephedra viridis*), west Mojave buckwheat (*Eriogonum fasciculatum*), California barrel cactus (*Ferocactus cylindraceus*), big galleta (*Hilaria rigida*), rhatany (*Krameria* spp.), creosote bush, boxthorn (*Lycium* spp.), honey mesquite (*Prosopis glandulosa*), Mojave seablite (*Suaeda nigra* also referred to as *Suaeda moquimii*), bush seepweed, and inkbush, see Meents et al. [1982] and Sawyer et al. [2009]), catclaw acacia (*Senegalia greggii*), and desert globemallow (*Sphaeralcea ambigua*). Arborescent species included ironwood (*Olneya tesota*), blue palo verde (*Parkinsonia florida*), foothills palo verde (*Parkinsonia microphylla*), honey mesquite, catclaw acacia, and Athel tamarisk (*Tamarix aphylla*). Vegetation survey data are summarized in Table 6.

Bell's Sparrow was the predominant species found at Robbins Butte and Fort Mohave and the only species found at Fort Mohave using field identifications. Only Sagebrush Sparrows were found at Boundary Cone, the Kofa Mountains Bajada, and Tacna. Sagebrush Sparrow sites were broadly characterized as open, with well-drained soils populated with upland or facultative upland xerophytic species. Bell's Sparrow sites were within or adjacent to riparian floodplains, with less-drained, silty soils populated with wetland obligate to facultative upland perennial species (U.S. Army Corps of Engineers 2020).

Sites with Bell's Sparrow averaged more vegetation hits than those with Sagebrush Sparrows ($n_{BELLS} = 10$, $BELLS = 27.6$, $SD_{BELLS} = 11.2$; $n_{SAGEBRUSH} = 15$, $SAGEBRUSH = 17.4$, $SD_{SAGEBRUSH} = 10.2$; two-sided t -test, $t(23) = -2.3$, $p = 0.02$), despite the fact that Sagebrush Sparrow sites tended to have higher plant species richness (Table 6), potentially increasing the sites' relative number of discrete hits without necessarily increasing overall vegetation cover. Conversely, sites with Sagebrush Sparrows averaged more bare ground/annuals-only assessments than Bell's Sparrow sites ($n_{BELLS} = 10$, $BELLS = 18.9$, $SD_{BELLS} = 9.5$; $n_{SAGEBRUSH} = 15$, $SAGEBRUSH = 28.1$, $SD_{SAGEBRUSH} = 9.4$; two-sided t -test, $t(23) = -2.4$, $p = 0.03$).

Robbins Butte

The Robbins Butte site consisted nearly entirely of allscale (Table 6), with isolated honey mesquites covering 2-5% of the study area, placing it within the *Atriplex polycarpa* shrubland (allscale scrub) and the *Prosopis glandulosa* woodland (mesquite bosque, mesquite thickets) alliance (*Prosopis glandulosa*/*Atriplex* spp. association) defined by the California Native Plant Society

Table 5. Morphometric measurement of female Bell's (*Artemisiospiza belli*) and Sagebrush (*A. nevadensis*) sparrows (field-identified from plumage and morphometric measurements) at sites in western Arizona sampled in Feb 2014. Note: SD = standard deviation; CI = confidence interval; df = degrees of freedom.

Species	<i>n</i>	Mean	SD	Low CI	High CI	<i>t</i> -value	df	Two-sided <i>t</i> -test <i>p</i>
Wing chord (mm)								
Bell's Sparrow	48	68.3	1.655	67.832	68.793	-7.538	58	< 0.0001
Sagebrush Sparrow	12	73.5	3.519	71.264	75.736			
Tail (mm)								
Bell's Sparrow	47	67.0	2.488	66.270	67.730	-2.216	57	0.031
Sagebrush Sparrow	12	69.0	3.805	66.582	71.418			
Weight (g)								
Bell's Sparrow	48	15.4	1.733	14.897	15.903	-1.920	58	0.060
Sagebrush Sparrow	12	16.5	1.946	15.263	17.737			
Exposed culmen (mm)								
Bell's Sparrow	48	9.4	0.600	9.226	9.574	-2.073	57	0.017
Sagebrush Sparrow	11	9.8	0.456	9.493	10.107			
Bill depth (mm)								
Bell's Sparrow	48	5.1	0.382	4.989	5.211	-2.352	57	0.022
Sagebrush Sparrow	11	5.4	0.380	5.145	5.655			
Bill width (mm)								
Bell's Sparrow	48	3.9	0.386	3.788	4.012	-3.269	57	0.002
Sagebrush Sparrow	11	4.3	0.252	4.131	4.469			
Primary projection (mm)								
Bell's Sparrow	42	11.0	1.470	10.542	11.458	-0.514	51	< 0.0001
Sagebrush Sparrow	11	13.4	0.907	12.791	14.009			
Malar streak gap (mm)								
Bell's Sparrow	47	3.7	2.145	3.070	4.330	-2.956	56	0.005
Sagebrush Sparrow	11	5.9	2.548	4.189	7.611			

(Sawyer et al. 2009). Additional perennial species included isolated creosote bush and boxthorn that stood over 2 m in height, as well as a small number of blue palo verdes.

Fort Mohave

The Fort Mohave site consisted primarily of quailbush and Mojave seablite (also referred to as inkbush and bush seepweed) in silty, alkaline soil (Table 6), placing it within the *Suaeda moquinii* (bush seepweed scrub) shrubland alliance (Sawyer et al. 2009). Large contiguous patches of Mojave seablite and quailbush were found in lower-lying areas with potential to retain moisture after rainfall events, and the site contained patches of desert pavement largely devoid of vegetation left from clearing and grading activities in the mid 2000s. The site held an isolated cluster of 8-10 m-tall Athel tamarisk. The presence of Mojave seablite and tamarisk indicated a high-water table as well as potential for occasional flooding and additional potential hydrologic input from irrigation runoff.

Tacna

The Tacna site was the most sparsely vegetated of the five study sites, consisting primarily of isolated fourwing saltbush clumps, open sandy areas, and annual vegetation (Table 6), placing the site within the *Atriplex canescens* (fourwing saltbush scrub) shrubland alliance and also described by the fourwing saltbush (*Atriplex canescens*) shrubland association (Evens and Hartman 2007, Sawyer et al. 2009).

Kofa Mountains Bajada

The Kofa Mountains Bajada site consisted of undisturbed, sparsely vegetated desert pavement populated primarily by creosote bush, with white bursage, brittlebush, big galleta grass, and rhatany associated with small, shallow channels with alluvial

soils that cut into the desert pavement (Table 6). Isolated trees (foothills palo verde, ironwood, and catclaw acacia) and saguaro covered less than 1% of the site and were found along larger channels that descended the bajada. The site's vegetation composition is consistent with the *Larrea tridentata* - *Ambrosia dumosa* shrubland alliance (creosote bush - white bursage scrub) and the creosote bush - burro bush/big galleta (*Larrea tridentata* - *Ambrosia dumosa* - *Pleuraphis rigida*) shrubland association (Evens and Hartman 2007, Sawyer et al. 2009). Aspects of the *Carnegiea gigantea* - *Parkinsonia microphylla* - *Prosopis velutina* provisional shrubland alliance (saguaro - foothills palo verde - velvet mesquite desert scrub) were associated with the larger wash channels with emergent arborescent vegetation (California Native Plant Society 2022).

Boundary Cone

The Boundary Cone site consisted of a wide valley of alluvial soil, gravel, and small boulders. Its vegetation composition was similar to the Kofa Mountains Bajada site, with creosote bush, white bursage, brittlebush, and rhatany (Table 6), also placing it within the *Larrea tridentata* - *Ambrosia dumosa* shrubland alliance. A large wash that bisected the site also held cheesebush and catclaw acacia. The Boundary Cone site was more typical of Mojave Desert creosote bush - white bursage scrub, lacking arborescent tree species and saguaro found on the Kofa Mountains Bajada that are associated with the Sonoran Desert.

DISCUSSION

We sampled wintering *Artemisiospiza* sparrows across a variety of common, widespread vegetation community types in western Arizona, obtaining blood samples from 74 individuals to provide genetic context for our field identifications. Our sample set was

Table 6. Vegetation summary for five *Artemisiospiza* sites in western Arizona. Perennial species “hits” equals the number of times the plant species was encountered across 45 assessments for each plot. Totals for each site’s four most frequently encountered species, as well as number of instances no perennial species were encountered (bare ground/annuals), and average low and high heights are provided. Overall, four shrub species were encountered during Robbins Butte assessments, two species at Fort Mohave, three species at Tacna, nine species at Kofa Mountains Bajada, and nine species at Boundary Cone.

Site	Bare ground/ annuals	Four most frequently encountered perennial species				Total perennial species hits
		1	2	3	4	
Bell’s Sparrow (<i>Artemisiospiza belli</i>) sites						
Robbins Butte						
		<i>Atriplex polycarpa</i>	<i>Larrea tridentata</i>	<i>Lycium</i>	<i>Prosopis glandulosa</i>	
Plot 1	20	24	0	0	0	24
Plot 2	25	10	6	1	0	17
Plot 3	7	38	0	0	0	38
Plot 4	24	21	3	0	0	24
Plot 5	19	25	0	0	1	26
Total	95	118	9	1	1	129
Mean high height (cm)		128	265	200	265	
Mean low height (cm)		10	60	200	265	
Fort Mohave						
		<i>Suaeda nigra</i>	<i>Atriplex lentiformis</i>		Only 2 species encountered	
Plot 1	27	18	0			18
Plot 2	24	23	1			24
Plot 3	0	20	31			51
Plot 4	13	19	19			38
Plot 5	30	13	3			16
Total	94	93	54			147
Mean high height (cm)		158	179			
Mean low height (cm)		20	52			
Sagebrush Sparrow (<i>A. nevadensis</i>) sites						
Tacna						
		<i>Atriplex canescens</i>	<i>A. polycarpa</i>	<i>Sphaeralcea ambigua</i>	Only 3 species encountered	
Plot 1	40	5	0	0		5
Plot 2	38	5	2	0		7
Plot 3	39	4	0	2		6
Plot 4	40	5	0	0		5
Plot 5	41	0	0	2		2
Total	198	19	2	4		25
Mean high height (cm)		133	105	70		
Mean low height (cm)		25	99	32		
Kofa Mts. Bajada						
		<i>L. tridentata</i>	<i>Ambrosia dumosa</i>	<i>Pleuraphis rigida</i>	<i>Krameria</i>	
Plot 1	18	12	7	3	6	28
Plot 2	23	13	3	1	3	20
Plot 3	33	4	5	0	0	9
Plot 4	24	17	6	0	0	23
Plot 5	13	24	6	6	0	36
Total	111	70	27	10	9	116
Mean high height (cm)		149	61	102	83	
Mean low height (cm)		72	33	53	48	
Boundary Cone						
		<i>L. tridentata</i>	<i>A. dumosa</i>	<i>Encelia farinosa</i>	<i>Krameria</i>	
Plot 1	24	7	10	0	3	20
Plot 2	22	8	8	2	9	27
Plot 3	24	18	2	1	0	21
Plot 4	23	5	2	15	0	22
Plot 5	20	6	12	0	5	23
Total	113	44	34	18	17	113
Mean high height (cm)		178	41	59	80	
Mean low height (cm)		51	24	10	30	

not an exhaustive representation of all habitats within the overlapping Sagebrush and Bell’s Sparrow distributions, but our study provides a first examination of differences in wintering habitat selection between two species that are difficult to separate in the winter without assessments in the hand.

With the aid of previous reports of plumage differences (Pyle 2013) and morphometric differences (Cicero and Johnson 2006), we found that Bell’s Sparrows and Sagebrush Sparrows are readily separable in the hand, and 68 of 74 field identifications (92%) were consistent with genetic results. Cicero and Koo (2012) reported a potential for shared haplotype markers between the

species, with a small number of *A. b. canescens* found with the Hap10 BC type haplotype, and one *A. nevadensis* in their sample set found with the AD haplotype. Four of our six individuals with inconsistent field and genetic assignments were consistent with Bell's Sparrow in size and plumage characteristics but were found to have the Hap10 BC type haplotype. One individual was consistent with Sagebrush Sparrow in size and plumage but had the AD type haplotype, and one individual was consistent with Sagebrush Sparrow in size, intermediate in plumage, and had the AD type haplotype.

We found Bell's Sparrow sex ratios to be significantly female biased at our Arizona study sites. Fort Mohave and, in particular, Robbins Butte are on the southeastern periphery of the Bell's Sparrow wintering distribution. However, the sites are 250 km apart, suggesting a widespread regional pattern of differential migration at the Bell's Sparrow wintering distribution's southeastern periphery. This suggests different wintering strategies between male and female *A. b. canescens* Bell's Sparrows, with females disproportionately migrating southeastward from Mojave Desert breeding grounds. Our Bell's Sparrow sex ratio is consistent with the sex ratio of specimen records from southeastern portion of the Bell's Sparrow wintering range. Females comprised 46 of 58 (79%) winter-season (October-February) Bell's Sparrow specimens from Arizona, the Colorado River (AZ and CA), the Salton Sink and Coachella Valley, CA, Borrego Springs, CA, Laguna Salada, BCN, and the Little San Bernardino Mountains, CA, which are housed by the Museum of Vertebrate Zoology, Berkeley, CA, the San Diego Natural History Museum, and the University of Michigan Museum of Zoology and compiled at VertNet (<http://www.vertnet.org/index.html>; Appendix 1).

As differential migration has not been reported for Bell's Sparrow, thus we recommend additional winter sampling of *A. b. canescens*, both outside its breeding distribution and in particular within the breeding grounds in the western Mojave Desert to test this pattern. Museum specimens collected from October through February within and near the Bell's Sparrow breeding distribution are less numerous and slightly male biased, with 10 males among 16 (63%) records compiled at VertNet (<http://www.vertnet.org/index.html>; Appendix 2). A portion of the *A. b. canescens* population remains within the breeding distribution year round, with males frequently reported singing in the winter (Sullivan et al. 2009). We suspect that wintering Bell's Sparrow sex ratios in the western Mojave Desert will be found to be male-biased (Ketterson and Nolan 1976, Cristol et al. 1999).

Prior to this study, little information existed on differences in habitat selection by Bell's and Sagebrush sparrows within their overlapping wintering distributions. We found wintering populations of Bell's and Sagebrush sparrows segregated across different vegetation communities within our study area, with mingling between the two species to be the exception and not the norm. Broadly, Sagebrush Sparrows were found at less vegetated, more xerophytic upland scrub than Bell's Sparrows, whereas the latter were found in more heavily vegetated, halophytic allscale and quailbush-seablite scrub with silty soils that were within or adjacent to mesquite or tamarisk woodlands. The two species only co-occurred at Robbins Butte, near the eastern perimeter of the Bell's Sparrow wintering distribution, where the sample was biased toward Bell's Sparrow (26 of 30 individuals with consistent genetic and field identifications). We did not record visual observations of the species

interacting or foraging together at Robbins Butte, only that a small number of Sagebrush Sparrows were swept up in our large round ups that flushed birds into net lines.

Garrett and Dunn (1981) noted Bell's Sparrow's affinity for *Suaeda* on the Colorado River, as did Meents et al. (1982), although Meents et al. did not differentiate between Sagebrush and Bell's sparrows. Patten et al. (2003) also reported that *Artemisiospiza* sparrows could be found in inkbush and saltbush habitats in the Salton Sink, but they did not recognize a separation between *Artemisiospiza belli nevadensis* and *A. b. canescens*, classifying the reports as *A. b. nevadensis* (see Patten and Unitt 2002, Cicero and Johnson 2006). Our findings suggest that the great majority of the *Artemisiospiza* sparrows previously reported at *Suaeda* sites in western Arizona and the Salton Sink were Bell's Sparrows, and that most were females.

Georeferenced photographs from locations within the lower Colorado River riparian corridor and the Salton Sink submitted to online citizen science platforms such as eBird and iNaturalist are consistent with this pattern, with identifiable photographed reports from the Salton Sink and the Colorado and Gila river valleys consisting typically of Bell's Sparrows, with uncommon (e.g., at a settling ponds site near Borrego Springs, California, and around Robbins Butte) to only sporadic instances of photographic documentation of Sagebrush Sparrows in expected Bell's Sparrow habitat in southeastern California and western Arizona (Sullivan et al. 2009, GBIF 2023; <https://www.inaturalist.org>).

Meents et al. also found temporal changes in diet across the wintering season, with *Artemisiospiza* sparrows consuming more seeds later in the winter as invertebrate food sources presumably became scarcer, resulting in birds clustering at study sites with Mojave seablite later in the season (1982). Our study period occurred during the first half of February, leaving open the possibility that Bell's Sparrows may be found to be more dispersed across the landscape earlier in the wintering season. Declines in available food, such as during prolonged drought, may produce conditions in which wintering Sagebrush Sparrows will be compelled to abandon xerophytic upland scrub with ephemeral food sources and be more likely to be found in Bell's Sparrow-associated wintering habitats, mixing with Bell's Sparrows. Notably, unlike our other study sites, Robbins Butte was in the midst of moderate to severe drought in early February 2014 (NDMC et al. 2014), perhaps an explanation for the sympatric occurrence of the two species at this site (27:6 Bell's to Sagebrush capture ratio).

We suspect that our observed patterns in wintering Bell's Sparrows' habitat selection may be more specific to sites outside of the Bell's Sparrow breeding distribution, given (1) that a portion of the Bell's Sparrow population remains on the breeding grounds through the winter (Sullivan et al. 2009), and (2) *A. b. canescens* nest in a variety of upland scrub habitats more similar to the desert scrub habitats in which we encountered Sagebrush Sparrows while sampling in western Arizona (Martin and Carlson 2020a). This appears consistent with photographed reports in eBird and iNaturalist that provide widespread georeferenced photographic documentation of wintering Bell's Sparrows across a variety of habitats within the Bell's Sparrow breeding distribution in the western Mojave Desert (Sullivan et al. 2009, GBIF 2023).

Wintering Sagebrush Sparrow reports from within the *A. b. canescens* breeding distribution in the western Mojave Desert are notably uncommon (Garrett 2020; https://www.youtube.com/watch?v=6RjC_fpietw), particularly given that a large amount of apparently available Sagebrush Sparrow wintering habitat exists here. This raises the intriguing possibility that Bell's Sparrows may exclude wintering Sagebrush Sparrows from habitats within the Bell's Sparrow breeding distribution or that wintering Sagebrush Sparrows may avoid the Bell's Sparrow breeding distribution in some fashion. We recommend additional winter sampling in the western Mojave Desert to document the two species' presence, habitat use, and sex ratios in this region.

Rosenberg et al. (2019) reported large scale declines in North American bird populations, and there is increasing awareness that birds are exposed to different threats across their life cycles (North American Bird Conservation Initiative 2022). Our study has identified different patterns in desert scrub selection by two taxa of *Artemisiospiza* sparrows that were once considered the same species with the same life cycle. These different vegetation types face different types and degrees of threats from climate change, fire disturbance, and conversion to solar, urban, and agricultural development. Our study also provides evidence that *A. b. canescens* Bell's Sparrows may employ differential migration, a strategy previously undocumented for the species. If occurring, sex-based differential migration will present additional conservation challenges and opportunities for this taxon.

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Data Availability:

Dryad links for captures data and photographs now included in text, as recommended by review.

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Appendix 1. Bell's Sparrows collected during the winter season (Oct–Feb) outside the breeding range and housed at the San Diego Natural History Museum (SDNHM), the Museum of Vertebrate Zoology (MVZ), and the University of Michigan Museum of Zoology (UMMZ) (Records compiled at VertNet <http://portal.vertnet.org/search?q=artemisiospiza+belli+canescens>).

Specimen	Taxon	Location	Collector	Sex	Date
		ARIZONA			
SDNHM Birds 1076	Aves: <i>Amphispiza belli canescens</i>	United States, Arizona, Maricopa: 80 mi. E Yuma	F. Stephens	female	11/19/1876
		COLORADO RIVER			
MVZ Bird specimens MVZ:Bird:13228	Aves: <i>Artemisiospiza belli canescens</i>	United States, California, San Bernardino County: Colorado River, 5 mi...	Collector(s): Joseph Grinnell	male	2/10/1910
MVZ Bird specimens MVZ:Bird:13231	Aves: <i>Artemisiospiza belli canescens</i>	United States, Arizona, Mohave County: Colorado River, Mellen	Collector(s): Joseph Grinnell	female	2/28/1910
MVZ Bird specimens MVZ:Bird:30756	Aves: <i>Artemisiospiza belli canescens</i>	United States, California, Imperial County: 1 mi W Palo Verde	Collector(s): Leo Wiley	male	2/18/1916
MVZ Bird specimens MVZ:Bird:64289	Aves: <i>Artemisiospiza belli canescens</i>	United States, Nevada, Clark County: Colorado River, 14 mi E Searchlig...	Collector(s): Seth B. Benson	female	1/10/1934
SDNHM Birds 14228	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	1/29/1931
SDNHM Birds 14250	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	1/31/1931
SDNHM Birds 14268	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	2/3/1931
SDNHM Birds 14299	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	2/7/1931
SDNHM Birds 14300	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	2/7/1931
SDNHM Birds 34349	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: Bard	L. M. Huey	female	12/1/1916
SDNHM Birds 34351	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: Bard	L. M. Huey	female	12/9/1916
SDNHM Birds 34352	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: Bard	L. M. Huey	female	12/9/1916
SDNHM Birds 34353	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: Bard	L. M. Huey	female	12/10/1916
SDNHM Birds 34354	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: Bard	L. M. Huey	female	12/10/1916
SDNHM Birds 34356	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. W Bard	M. Canfield	male	11/6/1928
SDNHM Birds 34357	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	10/1/1925
SDNHM Birds 34358	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. N Bard	M. Canfield	female	11/3/1924
SDNHM Birds 34361	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. N Bard	M. Canfield	female	11/11/1923
SDNHM Birds 34362	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. N Bard	M. Canfield	male	11/12/1923
SDNHM Birds 34365	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 3 mi. N Bard	M. Canfield	female	10/30/1924
SDNHM Birds 9066	Aves: <i>Amphispiza belli canescens</i>	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	11/6/1923

SDNHM Birds 9670	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	L. M. Huey	female	10/30/1924
SDNHM Birds 14229	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	female	1/29/1931
SDNHM Birds 14269	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	S. G. Harter	male	2/3/1931
SDNHM Birds 34350	Aves: Amphispiza belli canescens	United States, California, Imperial: Bard	L. M. Huey	male	12/9/1916
SDNHM Birds 34359	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	M. Canfield	female	11/3/1924
SDNHM Birds 34360	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	M. Canfield	female	11/10/1923
SDNHM Birds 34363	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	M. Canfield	female	10/27/1924
SDNHM Birds 34364	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	M. Canfield	female	10/27/1924
SDNHM Birds 8937	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	10/22/1923
SDNHM Birds 9101	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	male	11/11/1923
SDNHM Birds 9135	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	11/17/1923
SDNHM Birds 9182	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	12/20/1923
SDNHM Birds 9657	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	L. M. Huey	female	10/27/1924
SDNHM Birds 9658	Aves: Amphispiza belli canescens	United States, California, Imperial: 3 mi. N Bard	L. M. Huey	male	10/27/1924
SDNHM Birds 9681	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	male	11/3/1924
SDNHM Birds 9682	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	11/3/1924
SDNHM Birds 9683	Aves: Amphispiza belli canescens	United States, California, Imperial: 2 mi. N Bard	L. M. Huey	female	11/3/1924
SALTON SINK					
MVZ Bird specimens MVZ:Bird:106035	Aves: Artemisiospiza belli canescens	United States, California, Riverside County: Mecca	Collector(s): Allan C. Brooks Jr.	male	2/15/1913
MVZ Bird specimens MVZ:Bird:106038	Aves: Artemisiospiza belli canescens	United States, California, Riverside County: Mecca United States, California, Imperial: 9 mi. NNE Plaster City	Collector(s): Allan C. Brooks Jr.	female	2/4/1913
SDNHM Birds 44763	Aves: Amphispiza belli canescens Aves: Artemisiospiza belli canescens	U.S.A., California, Riverside: Thermal	P. Unitt	female	10/24/1986
UMMZ birds 169995	Aves: Artemisiospiza belli canescens	U.S.A., California, Riverside: Mecca	Jacot, Edouard C	female	1/11/1937
UMMZ birds 169996	Aves: Artemisiospiza belli canescens	U.S.A., California, Riverside: Mecca	Jacot, Edouard C	male	1/13/1937
UMMZ birds 169997	Aves: Artemisiospiza belli canescens	U.S.A., California, Riverside: Salton Sea, north end	Jacot, Edouard C	female	1/12/1937
LAGUNA SALADA AND SAN FELIPE					
MVZ Bird specimens MVZ:Bird:52423	Aves: Artemisiospiza belli canescens	Mexico, Baja California: Las Palmas Canyon, W side Laguna Salada, 15 m...	Collector(s): Chester C. Lamb	female	11/2/1927
MVZ Bird specimens MVZ:Bird:52424	Aves: Artemisiospiza belli canescens	Mexico, Baja California: Las Palmas Canyon, W side Laguna Salada, 15 m...	Collector(s): Chester C. Lamb	female	11/7/1927
MVZ Bird specimens MVZ:Bird:52425	Aves: Artemisiospiza belli canescens	Mexico, Baja California: Las Palmas Canyon, W side Laguna Salada, 15 m...	Collector(s): Chester C. Lamb	female	11/7/1927
MVZ Bird specimens MVZ:Bird:52426	Aves: Artemisiospiza belli	Mexico, Baja California: Las Palmas Canyon, W side	Collector(s): Chester	female	11/7/1927

	canescens	Laguna Salada, 15 m...	C. Lamb, J. E. Green		
MVZ Bird specimens MVZ:Bird:52427	Aves: Artemisiospiza belli canescens	Mexico, Baja California: Las Palmas Canyon, W side Laguna Salada, 15 m...	Collector(s): J. E. Green	female	11/8/1927
SDNHM Birds 14168	Aves: Amphispiza belli canescens	Mexico: San Felipe	S. G. Harter	male	1/18/1931
CARRIZO CREEK					
SDNHM Birds 34366	Aves: Amphispiza belli canescens	United States, California, Imperial: Carrizo Creek	L. M. Huey	female	1/6/1918
SDNHM Birds 34367	Aves: Amphispiza belli canescens	United States, California, Imperial: Carrizo Creek	L. M. Huey	female	1/6/1918
SDNHM Birds 34368	Aves: Amphispiza belli canescens	United States, California, Imperial: Carrizo Creek	M. Canfield	female	1/8/1918
SDNHM Birds 34369	Aves: Amphispiza belli canescens	United States, California, Imperial: Carrizo Creek	L. M. Huey	female	1/8/1918
BORREGO SPRINGS					
SDNHM Birds 43509	Aves: Amphispiza belli canescens	United States, California, San Diego: 3.4 mi. SE Borrego Springs	P. Unitt	female	12/2/1984
SDNHM Birds 49401	Aves: Amphispiza belli canescens	United States, California, San Diego: Borrego Sink, 5.3 mi. SE Borrego...	P. Unitt	female	10/22/1995
LITTLE SAN BERNARDINO MOUNTAINS					
MVZ Bird specimens MVZ:Bird:94328	Aves: Artemisiospiza belli canescens	United States, California, Riverside County: 2 mi SE Cottonwood Spring...	Collector(s): Alden H. Miller	female	10/22/1945

Appendix 2. Bell's Sparrows collected during the winter season (Oct–Feb) within or near the breeding range and housed at the San Diego Natural History Museum (SDNHM), the Museum of Vertebrate Zoology (MVZ), and the University of Michigan Museum of Zoology (UMMZ). (Records compiled at VertNet <http://portal.vertnet.org/search?q=artemisiospiza+belli+canescens>).

Specimen	Taxon	Location	Collector	Sex	Date
MIDWAY VALLEY, BUENA VISTA VALLEY, MCKITTRICK VALLEY, ELK HILLS, TEMBLOR RANGE					
MVZ Bird specimens MVZ:Bird:60095	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: 2 mi E McKittrick	Collector(s): Joseph Grinnell	female	2/23/1932
MVZ Bird specimens MVZ:Bird:60097	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: 2 mi E McKittrick	Collector(s): Joseph Grinnell	male	2/23/1932
MVZ Bird specimens MVZ:Bird:92768	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: Taft	Collector(s): Rollo H. Beck	male	12/25/1934
MVZ Bird specimens MVZ:Bird:121871	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: Taft	Collector(s): Rollo H. Beck	male	12/25/1935
SDNHM Birds 28378	Aves: <i>Amphispiza belli canescens</i>	United States, California, Kern: Tupman	S. G. Jewett	female	11/12/1939
SDNHM Birds 28379	Aves: <i>Amphispiza belli canescens</i>	United States, California, Kern: Tupman	S. G. Jewett	male	11/12/1939
UMMZ birds 169992	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	U.S.A., California, Kern: Taft	Beck, Rollo H	female	12/24/1935
UMMZ birds 169993	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	U.S.A., California, Kern: Taft	Beck, Rollo H	female	12/24/1935
PANAMINT MOUNTAINS					
MVZ Bird specimens MVZ:Bird:28409	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Inyo County: 5 mi N Jackass Spring, Panamin...	Collector(s): Joseph Grinnell, Joseph S. Dixon	female	10/2/1917
VICTORVILLE					
MVZ Bird specimens MVZ:Bird:35764	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, San Bernardino County: Victorville	Collector(s): Joseph Grinnell	male	12/23/1904
MVZ Bird specimens MVZ:Bird:35765	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, San Bernardino County: Victorville	Collector(s): Joseph Grinnell	male	12/25/1904
MVZ Bird specimens MVZ:Bird:35766	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, San Bernardino County: Victorville	Collector(s): Joseph Grinnell	male	12/3/1904
MVZ Bird specimens MVZ:Bird:35767	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, San Bernardino County: Victorville	Collector(s): Joseph Grinnell	male	12/31/1904
ARGUS RANGE					
MVZ Bird specimens MVZ:Bird:65772	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Inyo County: Junction Ranch, Argus Mts.	Collector(s): Joseph Grinnell	female	10/17/1934
WALKER BASIN					
MVZ Bird specimens MVZ:Bird:63981	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: Rankin Ranch, Walker Basin	Collector(s): Raymond M. Gilmore	male	11/14/1938
MVZ Bird specimens MVZ:Bird:63982	Aves: <i>Artemisiospiza belli</i> <i>canescens</i>	United States, California, Kern County: Rankin Ranch, Walker Basin	Collector(s): Raymond M. Gilmore	male	11/18/1933