IRRUPTIVE MOVEMENTS OF THE BLACK-CHINNED SPARROW (Spizella atrogularis) in Response to Variations in Precipitation: Implications for Climate Change Resiliency

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Abstract.—The Black-chinned Sparrow (Spizella atrogularis) is a quintessential southwestern bird, its breeding range restricted to the southwestern U.S., central Mexico, and northernmost Baja California. This species stages sporadic breeding season incursions into northern California, however, and occasionally as far north as southern Oregon. These movements tend to be irruptive, with birds reported at several different locations during those years. We attempted to determine both the source population(s) and the factors influencing these northward irruptions. We tested whether these irruptions derived from birds normally breeding in southern California, and that years with below average precipitation in southern California drove some individuals to move north seeking better breeding conditions. We first looked for evidence of regional song dialects that could be used to identify the source of irruptive birds and found that all northern California breeders used song types of the subspecies *S. a. cana.* We found a significant negative correlation between the numbers of northern California Black-chinned Sparrows reported and southern California precipitation levels in the months prior to each breeding season. Our findings may have implications for the potential of this species to adapt to changing levels of precipitation by expanding its breeding range northward.

Key Words.--irruption; precipitation; song; song dialect; climate change.

INTRODUCTION

The primary range of the Black-chinned Sparrow (*Spizella atrogularis*; Fig. 1) includes most of the southwestern U.S. (southern California, Arizona, New Mexico, Texas, and southernmost Utah and Nevada) and much of central Mexico and Baja California (Tenney 1997). The species breeds sparsely in central California (San Luis Obispo County north to Monterey County and in the western foothills of the southern Sierra Nevada range) with intermittent breeding in the northern half of the state (e.g., Shuford 1993; Bolander and Parmeter 2000; Roberson 2002; Bousman 2007; Berner 2015). The nature of northern California breeding appears to be irruptive, with reports of birds both numerous and widespread during these years (Beedy and Pandolfino 2013; Rottenborn et al. 2013).

Four subspecies of *Spizella atrogularis* are currently recognized (Clements et al. 2021), *S. a. atrogularis* breeding in central Mexico, *S. a. evura* in northernmost Mexico and from western Texas to southeastern California, *S. a. cana* from Monterey County in California and the west-central Sierra Nevada foothills south to Baja California, and *S. a. caurina* breeding in the interior Coast Range of California from Contra Costa County south to eastern San Benito County. The winter range of *S. atrogularis* is almost entirely within Mexico, with the exception of small areas of southernmost Arizona, New Mexico, and westernmost Texas. The subspecies *S. a. cana* is believed to winter in Baja California Sud,

but the non-breeding ranges of each of the subspecies are uncertain (Tenney 1997). The status of *S. a. caurina* is controversial with some considering it synonymous with *S. a. cana* (Phillips et al. 1964; Patten et al. 2003; Pyle 2022). This subspecies was originally described based on just five specimens (Miller 1929) and subsequent physical measurements by others found broad (Van Rossum 1935) or complete (Tenney 1997) overlap with *S. a. cana*.



FIGURE 1. Irruptive Black-chinned Sparrow (*Spizella atrogularis*) in Amador County, California. (Photographed by Don Marsh).

The source of the intermittent breeders in northern California and the factors that may drive these irruptions have not been studied. Some have speculated that these extralimital breeders may include S. a. cana or S. a. caurina, or both (Miller 1929; Tenney 1997; Bousman 2007) and others suggested that drought conditions in the southern breeding range may be driving some birds to move north to find better conditions during those dry years (Beedy and Pandolfino 2013; Rottenborn et al. 2013). Although we found no studies bearing on these speculations or directly linking precipitation with breeding success for this species, this connection appears to be supported by a cascade of relationships, beginning with prey and habitat type. Spizella atrogularis depends largely on adult and larval insect prey during the breeding season and this species is strongly linked to post-fire Chaparral landscapes (Tenny 1997). A key characteristic of this type of habitat is a diverse and abundant herbaceous plant community in the aftermath of fire (Keeley et al. 1981; Quinn and Keeley 2006). The extent of herbaceous cover was significantly correlated with annual rainfall in San Diego County (Keeley et al. 1981), and the extent of herbaceous cover in post-fire chaparral was correlated with insect abundance (Force 1990). Indeed, Force (1990) asserted that flower-visiting insect abundance and diversity is higher in Chaparral than in any other California habitat. Thus, one might reasonably expect that drought years could produce fewer insects and negatively affect S. atrogularis breeding success.

We chose to address these questions by testing the predictions that members of the subspecies S. a. cana normally breeding in southern California were the source of these irruptions, and that below normal rainfall in southern California was a factor behind these irruptions. Because specimens of these northern extralimital breeders were not available, but recordings of songs of many of these individuals are archived, we chose to examine the songs of Spizella atrogularis subspecies to determine if song dialect could be used to identify the source population(s). Many bird species use distinct regional song dialects (Catchpole and Slater 2008). Dialects can be based on qualitative (distinctly different traces on a spectrogram) or quantitative (e.g., pitch, rates of singing, length of songs) characteristics of the songs (Kroodsma 2004; Catchpole and Slater 2008). Tenney (1997) suggested some differences between songs of birds in California (S. a. cana) and those in southern Nevada, Arizona, and Texas (S. a. evura) with California songs having generally fewer introductory and terminal notes than those of the eastern birds. Thus suggesting that song dialects may exist. This was based on a small number of samples (25 total), however. We tested our prediction that below normal rainfall in southern California was a factor in driving these northward movements by looking for correlation between the number of northern California breeders and southern California rainfall during the eight months prior to each breeding season.

Breeding Bird Survey data show significant declines in the abundance of the S. atrogularis since 1966, rangewide and within California (Sauer et al. 2020). This species is particularly sensitive to the effects of urbanization and habitat fragmentation (Bolger et al. 1997; Crooks et al. 2004), both of which are significant factors within the ranges both S. a. cana and caurina. In addition, this sparrow may face challenges as the climate changes. Most climate change models predict significant increases in temperature but equivocal projections for changes in precipitation for California during coming decades (Cayan et al. 2008; Ackerly et al. 2010; Feldman et al. 2021). Precipitation projections for southern California are particularly variable (Feldman et al. 2021) with some models predicting stable or slightly increasing precipitation and others significant decreases. As noted above, decreases in annual rainfall could lead to lower breeding success for Spizella atrogularis.

Irruption is an extreme example of facultative migration (i.e., migration that can occur some years, but not others; Newton 2012). To the extent that individuals of a species can make such movements in response to poor breeding conditions, facultative migration can have important conservation implications. Such extralimital breeding can be the precursor to expansion of the range of a species (Newton 2003). Expansions or shifts in breeding range can provide a basis for adapting to changes in climate or other conditions and such shifts have been documented for many bird species (e.g., Hitch and Leberg 2007; Tingley et al. 2009; Saracco et al. 2019).

METHODS

We used song recordings from the full range of Spizella atrogularis to look for evidence of distinct regional dialects by examining spectrograms with Raven Pro software (https://ravensoundsoftware. com/). We used all available recordings from the Mark Robbins/Macaulay Library (www.macaulaylibrary.org) and xeno-canto (www.xeno-canto.org) that were of sufficient quality to interpret and that included at least two examples of full song. We used recordings of 147 individuals made from April through July (Appendix 1). We assumed that multiple recordings from the same location and the same year to be of the same individual unless otherwise specified by the recordist. We identified 24 distinct song types (Appendix 2) and the six most common song types (Fig. 2) accounted for more than 83% of all songs recorded. Different song types were characterized based on the introductory notes and the first few notes of the following trill. Because individual S. atrogularis used two song types, usually alternated, the dialect assigned was based on the pair of song types used. In each case, the assignment of song types to a given recording was done in a blind manner. That is, the location of the recording was not known by the author



FIGURE 2. Examples of the six most common song types of the Black-chinned Sparrow (Spizella atrogularis).

when assigning the song type to avoid any possibility of unintentional bias.

To quantify precipitation prior to the breeding season (hereafter, pre-breeding precipitation), we used monthly precipitation data (https://www.ncdc.noaa. gov/cdo-web/) from the five counties that encompass the majority of the southern California breeding range of S. atrogularis (Santa Barbara, Ventura, Los Angeles, San Bernardino, and San Diego). We averaged total precipitation (cm) across these five counties during the eight months (August through March) prior to each breeding season. The southern California rainfall season in these California Chaparral habitats begins in late August (rare) with most precipitation from late fall through spring (Quinn and Keeley 2006). We chose to include the entire pre-breeding season rainfall period because the condition of the both the herbaceous (Keeley et al. 1981) and shrubby (Quinn and Keeley 2006) plant communities is influenced by annual rainfall.

To index the size of each annual irruption, we compiled reports of *S. atrogularis* in northern California from 1992 through 2021 from Monterey County north, including those within the published range of *S. a. caurina*, using eBird (https://ebird.org) and archives of North American Birds, both published (www.aba.org/ north-american-birds/) and unpublished (from Regional Editor records). We tallied occurrences from April through July and eliminated any duplicate reports from the same general location in the same year. We assumed eBird reports or reports from the North American Birds data from the same location in the same season were from a single individual unless the reporter specifically

noted the number of separate individuals observed. When multiple individuals were noted by more than one observer in one location, we used the highest total observed by any single observer on a single day in that location for the total number of birds. Because locations of eBird reports are based on where the user chose to start the checklist, we assumed eBird reports within 5 km of each other in the same season were of the same individual. Similarly, we indexed the size of the annual breeding population of *S. a. caurina* by tallying April through July reports of *S. atrogularis* within the range of *S. a. caurina* as approximated by Grinnell and Miller (1944) and Tenney (1997).

The annual irruption index was related to pre-breeding precipitation using negative binomial regression to allow for overdispersion in the positive, integer-valued index (Ver Hoef and Boveng 2007). To fit negative binomial models in the R language for statistical computing (R Core Team 2021), we used function glm.nb from the MASS package (Venables and Ripley 2002). To further account for any excess zeros in the response variable, we used function zeroinfl from the pscl package (Jackman 2020). Within each regression framework, we compared a null (intercept-only) model of our annual irruption index with what we called a precipitation model that contained an intercept and an additive effect of prebreeding precipitation. Model support was evaluated using Akaike's Information Criterion (AIC) corrected for overdispersion and small sample size, QAICc, and we assumed that a difference in QAICc (Δ QAICc) of more than four units suggests strong support for the model with lower QAICc (Burnham and Anderson 2002).



FIGURE 3. Locations of recordings used and the song types from each recording. Filled circles indicate that the recording included only one song type and dotted lines indicate the approximate extent of the ranges of the subspecies based on Grinnell and Miller (1944) and Tenney (1997).

RESULTS

Songs and song dialects.—Songs of *Spizella atrogularis* in our sample followed the general form described by Pieplow (2019). Songs had variable numbers of musical, often high-pitched introductory notes, followed by an accelerating trill with notes becoming progressively less musical (progressing from slurred notes into a rapid unmusical trill). None of the individuals in our set showed more than two song types, and most birds alternated between their two types during a singing bout.

We found distinct regional song dialects for S. atrogularis recorded in the U.S. (Fig. 3). There were too few recordings (five) from central Mexico to assess dialects within the range of S. a. atrogularis. Nearly all birds (> 95%) recorded in the range of S. a. cana or caurina used song types 1 and 10. These two song types were also used exclusively by birds in the extralimital recordings west of the Sierra Nevada crest in California and were not found in any recording from the range of S. a. evura east of California. Among the five birds recorded in Inyo County, California, at the edge of the published range of S. a. evura (Grinnell and Miller 1944), four used song type 1 or 10, or both, and two used song type 8, with one individual using both 8 and 10. Within the range of S. a. evura, the dominant song types were distinct from those within the range S. a. cana or caurina. Song types used commonly in the western parts of the range of S.

a. evura (southeastern California, southernmost Nevada and Utah, and Arizona) differed from those in the eastern range (New Mexico and Texas). Song types 8 and 9 accounted for 61% of all song types in the west, and song types 14 and 15 comprised another 15%. Eastern *S. a. evura* birds used song types 5, 7, or 13 in 76% of recordings, and song type 9 accounted for another 18%.

Irruptions and precipitation.—We found a strong inverse relationship between the annual index of breeding season Black-chinned Sparrows in northern California (excluding those within the range of S. a. caurina) and pre-breeding precipitation in southern California (Fig. 4). The negative relationship between our irruption index and precipitation was well supported (QAICc of the precipitation model was 9.65 units lower than QAICc of the null model). In 10 of the 12 y in which a large number (> 14) of S. atrogularis was reported in northern California, southern California precipitation was below the 30-y average, ranging from 37% to 63% below average in those years. When we included only those reports within the published range of S. a. caurina (Fig. 5), the inverse relationship between our annual irruption index and pre-breeding precipitation was also well supported (QAICc of the precipitation model was 18.92 or 10.08 units lower than QAICc of the null model for negative binomial or zero-inflated negative binomial models, respectively; Table 1). The fitted value of the coefficient of pre-breeding precipitation was quite similar





FIGURE 4. Relationship between an index of irruption (number of extralimital breeders reported outside the range of *Spizella atrogularis caurina*) and southern California precipitation (cm) during the eight months prior to the breeding season, as determined through negative binomial regression (curve) and its 95% confidence interval (shaded region).

between the model based on all records of extralimital breeders (mean \pm standard error = -1.007 \pm 0.249) and the model based on only those breeders recorded within the range of *S. a. caurina* (-1.550 \pm 0.493).

DISCUSSION

Song dialects.—Tenney (1997) found some regional differences among the songs of *Spizella atrogularis*, with the length of the trill portion of songs significantly longer among birds in California (*S. a. cana* range) than birds in the range of *S. a. evura*, as well as differences in introductory and terminal notes. He also found some regional differences within *S. a. evura* in the highest pitch of notes in that trill, with the notes from birds in the eastern part of the range (New Mexico and Texas) reaching higher pitches than Arizona birds. Those results were based on small samples, however, and could have reflected clinal differences rather than distinct dialects. Thus, our work is the first demonstration of true song dialects in this species.

Confirmation of song dialects is important not only because it is believed to confirm that song is learned rather than innate (Kroodsma 2004; Catchpole and Slater 2008), but also because such dialects can reveal early signs of speciation or sub-speciation (Marler and Tamura 1962;

FIGURE 5. Relationship between an index of breeding population size within the range of *Spizella atrogularis caurina* (number of breeders reported) and southern California precipitation (cm) during the eight months prior to the breeding season, as determined through a negative binomial regression (curve) and its 95% confidence interval (shaded region).

Nottebohm 1969; Baker 1975; Slabbekoorn and Smith 2002; Pandolfino and Pieplow 2015). Additionally, for birds that sing in winter or during migration, well-mapped dialects can be used to reveal migratory connectivity and strategy (DeWolfe and Baptista 1995; Pandolfino and Douglas 2021). There is evidence that *S. atrogularis*

TABLE 1. Akaike's Information Criterion (AIC) models corrected for overdispersion and small sample size (QAIC*c*) of Black-chinned Sparrow (*Spizella atrogularis*) irruption index across the extralimital range of the species (*y*), including a fixed effect of southern California precipitation (*precip*) or intercept only (1) and within the range of *S. a. caurina* (*y_s*), assuming negative binomial (NB) or zero-inflated negative binomial (ZINB) variation in the irruption index and including a fixed effect of southern California precipitation (*precip*) or intercept only (1). The symbol *k* = number of parameters.

Model	QAICc	$\Delta QAICc$	k	
Extralimital Range				
$y \sim precip$	70.43	0	3	
$y \sim 1$	80.08	9.65	2	
Within the Range				
NB, $y_s \sim precip$	84.19	0	3	
NB, $y_s \sim 1$	103.10	18.92	2	
ZINB, $y_s \sim precip$	166.18	81.99	4	
ZINB, $y_s \sim 1$	176.26	92.07	3	

sings in migration and winter (Unitt et al. 1995; Williams 1995), and we found one January song recording (https://xeno-canto.org/618609) from Central Mexico.

We found the songs of S. a. cana and evura distinct. No song types from the range of either subspecies were found in any of the recordings from the range of the other, with the exception of mixed song types in Inyo County, California. Thus, this area, originally mapped as within the range of S. a. evura (Grinnell and Miller 1944), may represent a contact zone between S. a. cana and evura. Indeed, one bird there used both song type 8, associated with S. a. evura, and song type 10, associated with S. a. cana. Such observations of mixed song types could be the result of individuals of one subspecies learning the song of another, or of intergradation between the subspecies. We also found differences between the songs in the western versus eastern ranges of S. a. evura. Combined with the findings of Tenney (1997) on differences in song pitch, our results suggest that S. a. evura may show regional variation worthy of more investigation.

We detected no difference in dialect used between the songs of birds in the *S. a. cana* versus *caurina* ranges, or among extralimital breeding birds in northern California. These birds used song types 1 and 10 almost exclusively. Song type 2 was found in two recordings in the range of *S. a. caurina* and one in the southern range of *S. a. cana*; however, this song type is very similar to song type 10 (see Appendix 2) and may be simply a variation on that song type. The extralimital recordings included those from birds that breed somewhat regularly (Bousman 2007) in the Santa Cruz Mountains along the border between Santa Clara and Santa Cruz counties. Unfortunately, there are no specimens of these birds available.

Northern California irruptions and Southern California precipitation.—Our finding of a strong negative relationship between southern California precipitation and the numbers of breeding season reports of *S. atrogularis* in California from Monterey County northward is consistent with an irruptive pattern driven by poor breeding conditions in the southern California breeding range. Most examples and most studies of irruptive migration are based on non-breeding season irruptions and are believed to be influenced by conditions in the usual winter range (Newton 2012). There are examples of breeding season irruptions, however, likely driven by birds seeking better breeding conditions (Shaw 1990; Whitaker et al. 1996; Lindström et al. 2005; Burbridge and Fuller 2007; Pedler and Lynch 2016).

Factors other than, or in addition to, precipitation in southern California may influence this irruptive behavior also. It is possible that unusually high over-winter survival during the preceding winter or high levels of breeding productivity in the breeding season of the year before the irruptions create an excess of breeders beyond the carrying capacity of the southern breeding range. We found no documented examples of either factor implicated in other breeding season irruptions, but movements of some fall/winter irruptive species such as the Pine Siskin (*Spinus pinus*) may be influenced by both breeding and non-breeding range conditions (Strong et al. 2015).

We also found a strong negative relationship between our index of irruption and pre-breeding season southern California precipitation when including only birds reported within the published range of *S. a. caurina*, suggesting that birds breeding in that range are also influenced by breeding season conditions in southern California. This finding, coupled with the use of song dialects identical to those of *S. a. cana*, lends support to recommendations for synonymizing these two taxa (Phillips et al. 1964; Patten et al. 2003; Pyle 2022). Indeed, based on our findings and the significant overlap of morphological measurements, *S. a. caurina* does not meet the requirements for valid subspecies status suggested by Patten and Unitt (2002) and Patten (2015).

Conservation implications.—Spizella atrogularis faces a spectrum of challenges, particularly in its core Southern California breeding range. This species is highly susceptible to conversion or fragmentation of habitat (Bolger et al. 1997; Crooks et al. 2004), both of which are continuing threats in this area (EcoAdapt. 2017; Climate change vulnerability assessment for the Southern California Climate Adaptation Project. http://ecoadapt.org/data/documents/ Available from EcoAdapt_SoCalVASynthesis_Chaparral_FINAL2017. pdf [Accessed 15 July 2022]). Even in more remote locations, drought in southern California has limited the recovery of the Chaparral habitats of the species from the many recent wildfires (Storey et al. 2020). In addition, projected climate change may reduce the quality of the remaining habitat and increase the frequency and intensity of those fires (EcoAdapt 2017, op. cit.).

To persist in the face of declining habitat quality, a species must either adapt to the new conditions or move to areas that offer better options. One or both of these strategies have been observed to be in process among a huge array of organisms (Parmesan and Yohe 2003; Inouye 2022), including plants (Parmesan and Yohe 2003; Corlett and Westcott 2013), insects (Parmesan and Yohe 2003; Forrest 2016; Howe et al. 2022), mammals (Parmesan and Yohe 2003; Inouye 2022), and birds (e.g., Thomas and Lennon 1999; Hitch and Leberg 2007; Tingley et al. 2009; Saracco et al. 2019; Curley et al. 2020) in response to climate change. Many have adjusted migratory or breeding phenology (Forrest 2016; Inouye 2022) or shifted their wintering and/or breeding ranges (Thomas and Lennon 1999; Parmesan and Yohe 2003; Hitch and Leberg 2007). Most birds have shifted ranges poleward, north in the northern hemisphere and south in the southern hemisphere (Thomas and Lennon 1999; Hitch and Leberg 2007). In general, these range shifts have closely tracked the climatic ideal of the species (Tingley et al. 2009; Saracco et al. 2019; Curley et al. 2020), although many are still facing climate mismatches that may pose a threat (Viana and Chase 2022). Most of these range shifts have been ascribed to changing climate; however, Newton (2003) stressed that direct human impacts on habitat could also be a factor in some or most of these examples.

While shifts and expansions of the ranges of species are well-documented, the mechanisms by which they occur remain largely unknown. Both irruptions (sporadic, but regular, movements beyond the typical range) and vagrancy (occasional or rare out-of-range movements) have been proposed as possible precursors to range expansions or shifts (Grinnell 1922; Patten and Marantz 1996; Newton 2003). Confirming this with birds or mammals would require extensive longterm studies, though the expansion of the Cattle Egret (Bubulcus ibis) into the western hemisphere (Newton 2003; Telfair 2020) provides an intriguing example. Perhaps the only well-documented case of irruptions leading to range expansion involves the Western Balsam Beetle (Dryocoetes confusus) expansion into western Canada (Howe et al. 2022).

The ability of the *S. atrogularis* to stage these irruptions into northern California may offer the species a means to mitigate the effects of climate change and human development in their southern California range. Although the entire state is expected to see increasing temperatures and variable precipitation in the coming decades, the northern California locations used by this sparrow (which include coastal Monterey, Marin, and Santa Clara counties and the foothills of the Sierra Nevada and the Coast Ranges) are projected to remain cooler and wetter than southern California (Cayan et al. 2008). They are also generally further from urbanized areas and likely to see less development impact than most of the southern California Chaparral areas.

It remains to be seen whether these irruptions lead to an actual range expansion. As noted by Newton (2003), such an expansion requires that a number of conditions are met, including: (1) movements of sufficient numbers of irruptive individuals to permit pairs to meet; (2) the ability to breed successfully in the expanded range; and (3) a lack of excessive competition in the new range. If conditions in southern California deteriorate, the first requirement may be met; however, the other requirements suggest the need for further study of the birds occupying these irruptive locations.

Conclusions.—Our results demonstrated distinct regional dialects among the subspecies of the *S. atrogularis*. Nearly every bird recorded in California used identical song dialects, including individuals recorded in the published range of *S. a. cana* and *caurina*, and the northern California irruptive birds. Our finding that these northern irruptions correlated well with years

of drought in the southern California range suggests that some individuals may be migrating further north in those years, seeking better breeding conditions. Continued monitoring will be needed to determine if these irruptions lead to a northward expansion of the breeding range of this species.

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ED PANDOLFINO received his Ph.D. from Washington State University, Pullman, and has served as president of Western Field Ornithologists, vice-president of the San Francisco Bay Bird Observatory, and on the board of the Institute for Bird Populations. He co-authored Birds of the Sierra Nevada: Their Natural History, Status, and Distribution (University of California Press 2013) and is lead author of Sacramento Breeding Birds: A Tale of Two Atlases and Three Decades of Change (Central Valley Bird Club 2021). Much of his past research covered status, distribution, and conservation of western birds, with particular emphasis on the Central Valley of California. Many of his recent publications involve bird vocalizations and their application to studies of taxonomy, migration, and breeding phenology. (Photographed by Kathleen Lynch).



LILY DOUGLAS is the Assistant Coordinator for the Central Valley Joint Venture at the U.S. Fish and Wildlife Service, Sacramento, California, and is on the board of the Central Valley Bird Club. She earned a B.S. in Biological Sciences from California State University, Sacramento, and has worked on conservation issues related to the Golden Eagle (*Aquila chrysaetos*), Greater Sage-Grouse (*Centrocercus urophasianus*), Owen's Pupfish (*Cyprinodon radiosus*), and Townsend's Big-eared Bat (*Corynorhinus townsendii*), among other species. Lily is coauthor of Sacramento Breeding Birds: A Tale of Two Atlases and Three Decades of Change (Central Valley Bird Club 2021) and recent publications covering song dialects of Goldencrowned Sparrows (*Zonotrichia atricapilla*), Ruby-crowned Kinglets (*Corthylio calendula*), and avian breeding phenology. (Photographed by Lily Douglas).



CHRIS RAY is a Research Ecologist with the Institute for Bird Populations, Petaluma, California. She completed a Ph.D. at the University of California-Davis and has been a Research Associate with the University of Colorado-Boulder since 2002. Chris has studied population biology in a variety of plant and animal systems with a number of research teams and has a special interest in the population dynamics of species responding to habitat fragmentation and climate change. Her most recent publications for IBP address data requirements needed to estimate avian survival rates, landbird population trends in the Sierra Nevada, and song characteristics in Cassin's Vireos (*Vireo cassinii*) and Plumbeous Vireos (*Vireo plumbeus*). (Photographed by Mike Gilpin).

APPENDICES

APPENDIX 1. Metadata for all recordings used for our analyses. The asterisk (*) indicates catalog numbers that are preceded by "xc" are from xeno-canto, all others from Macaulay Library.

Catalog No *	State	Latitude	Longitude	Date	Recordist
15209	Oavaaa	18.00	07.24	02 June 1061	
20222	Arizona	21.02	-97.24	18 April 1997	Cliver H. Hewitt
10621	Toxos	31.92	-109.20	10 April 1987	Gaoffray A. Kallar
40031	Texas	21.07	-104.82	09 May 1960	Cooffroy A. Keller
43002	California	31.97	-104.81	25 April 1980	Geoffrey A. Keller
56879	California	33.01	-116.83	09 May 1991	Geoffrey A. Keller
64226	Arizona	31.93	-109.37	10 May 1979	William W. H. Gunn
147801	Texas	31.98	-104.75	13 May 2008	Benjamin Clock
147804	Texas	31.99	-104.76	13 May 2008	Benjamin Clock
215898	Durango	23.97	-104.61	26 June 1991	Steve N. G. Howell
224467	California	39.65	-120.30	19 June 2000	Gregory Budney
27237461	California	33.64	-117.39	17 April 2016	Julie Szabo
30050001	New Mexico	32.72	-105.34	10 June 2016	Bob Nieman
30616601	Arizona	31.72	-110.77	26 June 2016	David Stejskal
30862081	Arizona	31.75	-110.80	03 July 2016	Laurens Halsey
32309861	Texas	31.91	-104.85	27 July 2016	Jay McGowan
56033941	California	37.97	-122.63	28 April 2017	Mark Forney
57014421	New Mexico	32.34	-106.59	06 May 2017	Wyatt Egelhoff
57934581	California	33.64	-117.39	13 May 2017	Julie Szabo
58300691	California	33.65	-117.40	16 May 2017	Greg Cross
60738361	California	37.88	-121.91	10 June 2017	Steve Lombardi
60762621	New Mexico	32.37	-106.56	10 June 2017	Bill Tollefson
60934901	California	34.86	-119.24	30 May 2016	Ed Thomas
61315251	California	32.96	-116.58	17 June 2017	Eve Martin
77282271	Utah	37.10	-113.82	12 May 2013	Kenny Frisch
96838851	California	36.93	-118.32	27 April 2018	Rosie Howard
97023421	New Mexico	34.60	-106.48	28 April 2018	Nancy Hetrick
98281091	New Mexico	35.28	-106.48	05 May 2018	Spencer Follett
99699371	California	32.96	-116.58	11 May 2018	Eve Martin
101411471	California	37.10	-121.85	21 May 2018	Rvan Phillips
103556271	California	33.68	-117.50	06 June 2018	Brad Dawson
103789261	Utah	37.13	-113.82	03 June 2018	Kenny Frisch
103885601	California	34.22	-117.71	09 June 2018	Lance Benner
105077381	California	37.72	-118 61	20 June 2018	Rosie Howard
107220181	California	37.85	-121.93	05 May 1976	Darrell Peterson
129975381	California	37.89	-122.23	09 June 2012	Ken Schneider
152114651	New Mexico	35.09	-106.43	19 April 2012	David Buckley
152135651	Arizona	33.92	-111 44	15 April 2019	John Biorkman
152545651	New Mexico	35.12	-106.48	21 April 2019	TI Hathcock
154726381	Litah	37.21	-113 64	25 April 2019	Matt Cabill
156786071	California	36.51	-117.37	04 May 2019	Chris Howard
157745001	California	37.72	-117.57	10 June 2019	Loshua Staay
161797001	California	37.72	-118.01	19 June 2018	Glopp Kinopid
162502421	Arizona	34.33	-120.04	01 June 2019	Suson Droum
162105721	California	24.02	-112.33	01 June 2019	John Collondor
103103/31	California	34.33	-120.04	07 June 2019	John Canender
103343491	California	54.55 20.51	-120.00	09 June 2019	George Unapman
103800411		39.51	-122.94	02 June 2019	Bryan McIntosh
100015291	New Mexico	35.14	-106.48	11 June 2019	Liam Wolff
10/002/91	lexas	29.25	-103.31	27 April 2019	Max Wilson
181069/41	Arizona	31.40	-110.27	23 April 2015	Brian Henderson
226058201	Arizona	32.61	-110.73	21 April 2020	Tim DeJonghe
227687331	California	32.69	-116.91	26 April 2020	Paul Marvin

Catalog No.*	State	Latitude	Longitude	Date	Recordist
228180741	California	33.87	-117.69	26 April 2020	brendan galvin
229785731	California	32.64	-116.10	25 April 2020	Justyn Stahl
231183491	California	36.51	-117.37	04 May 2020	Chris Howard
231448321	California	34.86	-119.24	03 May 2020	Ed Thomas
233243501	Arizona	34.50	-112.46	08 May 2020	Janine McCabe
234456381	California	32.91	-116.46	10 May 2020	Hans Petermann
234585541	California	37.10	-121.85	14 May 2020	Jason Vassallo
235452091	California	34.48	-119.25	16 May 2020	Rick Ridgeway
235642271	California	34.42	-118.27	16 May 2020	Naresh Satyan
237407481	California	34.36	-118.35	21 May 2020	Naresh Satyan
237578451	New Mexico	35.22	-106.49	25 May 1983	Arch McCallum
239160261	California	37.10	-121.85	27 May 2020	Garrett Lau
240202501	California	34.93	-119.91	31 May 2020	Anonymous
240360221	California	37.44	-122.40	01 June 2020	Malia DeFelice
240645541	Texas	31.99	-104.77	02 June 2010	Arch McCallum
241301801	California	37.85	-122.20	05 June 2020	Teale Fristoe
242862691	California	32.60	-116.84	12 June 2020	Paul Marvin
243982011	New Mexico	35.29	-106.44	17 June 2020	Spencer Follett
244853031	California	34.27	-116.73	20 June 2020	George Chapman
245381141	Texcoco	19.50	-98.85	24 June 2020	Anuar López
246758061	Baja California	31.81	-116.57	09 May 2020	Antonio Maldonado
264866981	Texas	29.25	-103.31	18 May 2009	Andrew Spencer
313549581	California	37.97	-122.63	06 May 2017	Connor Cochrane
325706481	Texcoco	19.50	-98.82	12 April 2021	Anuar López
326627911	California	34.10	-117.12	15 April 2021	Mikael Romich
326905781	California	35.42	-120.76	16 April 2021	Jay Carroll
331684751	California	34.21	-118.31	29 April 2021	Andrew Birch
332557321	California	37.19	-121.55	01 May 2021	Mike Ambrose
332616521	California	34.54	-120.05	30 April 2021	John Callender
332990401	California	34.36	-118.40	01 May 2021	Becky Kitto
333953001	California	36.93	-118.32	04 May 2021	Nancy Overholtz
334094421	California	34.22	-117.75	01 May 2021	Naresh Satyan
335206671	California	38.70	-122.76	06 May 2021	Bob Hasenick
338630551	California	33.65	-117.45	12 May 2021	Ron Overholtz
339240351	California	37.10	-121.85	16 May 2021	Carter Gasiorowski
341374131	California	34.21	-118.31	22 May 2021	Andrew Birch
342372351	California	37.10	-121.85	25 May 2021	Cindy Cummings
342505511	Texas	29.25	-103.31	04 May 2021	Jason Vassallo
342565251	Utah	37.37	-113.35	23 May 2021	V. Schneggenburger
343417871	California	37.10	-121.85	29 May 2021	Emilie D
343858501	California	34.02	-117.00	29 May 2021	Gary McLarty
344726951	New Mexico	35.37	-106.17	02 June 2021	Chris Chappell
344811351	Arizona	34.33	-110.29	02 June 2021	Eric Hough
345174711	New Mexico	35.88	-106.23	04 June 2021	T. Jay Adams
346406511	California	37.10	-121.85	24 May 2021	Bill Pelletier
346845751	California	36.45	-121.92	10 June 2021	Bill Hubick
348140831	California	32.97	-116.60	15 June 2021	Gary Leavens
349166831	California	37.85	-121.93	25 May 2021	Teale Fristoe
350307531	Arizona	33.92	-111.41	17 April 2021	Damon Haan
351036271	New Mexico	35.14	-106.48	28 June 2021	Aidan Place
355789081	Nevada	36.27	-115.58	20 July 2021	Jan Hansen
362300631	Arizona	34.36	-110.43	07 July 2021	Eric Hough
362301701	Arizona	34.32	-110.29	20 July 2021	Eric Hough
421840981	California	34.34	-117.98	21 May 2021	Diana Dovle
421844781	California	33.70	-116.65	27 May 2021	Diana Doyle

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Catalog No.*	State	Latitude	Longitude	Date	Recordist
xc125082	California	34.19	-116.90	03 June 2001	Richard Webster
xc125085	California	34.19	-116.90	03 June 2001	Richard Webster
xc125088	California	34.26	-116.71	22 May 2001	Richard Webster
xc125089	California	34.19	-116.90	03 June 2001	Richard Webster
xc125726	California	34.25	-116.75	05 May 2006	Richard Webster
xc135973	California	36.29	-121.56	01 June 2013	Brian Sullivan
xc136118	Arizona	31.91	-109.14	04 July 1990	Dan Lane
xc153422	California	32.80	-166.48	12 April 2012	Paul Marvin
xc153436	Texas	29.27	-103.30	07 April 2012	Paul Marvin
xc153437	Texas	31.88	-104.87	16 June 2011	Paul Marvin
xc179725	Arizona	33.99	-111.44	26 May 2014	Tim Marquardt
xc181407	California	34.30	-118.01	07 June 2014	Lance Benner
xc246100	Arizona	35.09	-113.89	24 May 2015	Bobby Wilcox
xc247517	Arizona	35.09	-113.89	24 May 2015	Jarrod Swackhamer
xc314118	California	37.10	-121.84	28 April 2016	Alex Rinkert
xc325723	Arizona	31.72	-110.77	04 July 2016	Nick Komar
xc34034	Texas	31.91	-104.88	10 May 2009	Andrew Spencer
xc34134	Texas	31.91	-104.88	15 May 2009	Andrew Spencer
xc34135	Texas	31.91	-104.88	15 May 2009	Andrew Spencer
xc34571	Texas	29.25	-103.31	18 May 2009	Andrew Spencer
xc366792	California	38.14	-122.59	28 April 2017	Derek Lecy
xc368284	California	37.97	-122.63	16 May 2017	Jim Holmes
xc408008	California	32.75	-116.45	15 May 2015	Frank Lambert
xc418264	Nevada	36.42	-115.76	08 May 2018	Bobby Wilcox
xc418279	Nevada	36.39	-115.74	10 May 2018	Bobby Wilcox
xc428178	California	34.22	-117.71	08 June 2018	Lance Benner
xc444605	California	38.50	-120.29	28 May 2014	Ed Pandolfino
xc475295	Nevada	35.96	-115.56	11 May 2019	Bobby Wilcox
xc483157	Arizona	33.92	-111.42	16 April 2018	Keith Corliss
xc551165	California	34.46	-117.82	26 April 2020	Lance Benner
xc553310	Arizona	35.09	-113.89	01 May 2020	Bobby Wilcox
xc5803	California	37.88	-121.91	07 May 1977	Darrell Peterson
xc611125	Arizona	33.06	-109.44	29 May 2020	Richard Webster
xc6143	Guanajato	20.92	-100.75	04 June 2006	Manuel Grosselet
xc618609	Cuidad	19.32	-98.97	30 January 2021	Manuel Grosselet
xc639459	California	33.14	-116.85	08 April 2021	Paul Marvin
xc645514	California	36.94	-118.30	04 May 2021	Ron Overholtz
xc647005	California	34.22	-117.71	10 May 2021	Ethan Van Arnam
xc648850	California	33.67	-117.46	12 May 2021	Ron Overholtz
xc655752	California	39.13	-120.66	10 June 2021	Ed Pandolfino
xc76071	Colorado	39.03	-108.63	17 April 2011	Nathan Pieplow

APPENDIX 2. Examples of all 24 Black-chinned Sparrow (*Spizella atrogularis*) song types we identified from our review all recordings.

