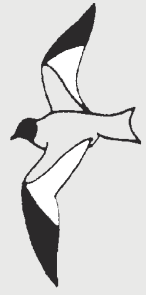


WESTERN BIRDS



Vol. 52, No. 4, 2021

Western Specialty:

Golden-crowned Sparrow



Photo by © Nancy Overholtz of Bishop, California:

Golden-crowned Sparrow (*Zonotrichia atricapilla*), near Nome, Alaska, 9 June 2019.

Edward R. Pandolfino and Lily A. Douglas studied variation in the song of the Golden-crowned Sparrow in its winter range, associating the variants with the dialects identified in the species' breeding range. They found that birds singing the dialect of northern and northwestern Alaska, as at Nome, have been recorded only in the northern part of the winter range, mainly around the Salish Sea. Birds singing the dialect characteristic of south-central Alaska have been recorded farther south, from near Portland, Oregon, to near Santa Barbara, California. Only six examples of variants characteristic of the Canadian portion of the breeding range have been recorded in winter, but all were within California. Thus movement of the Golden-crowned Sparrow seems to fit the pattern of chain migration.

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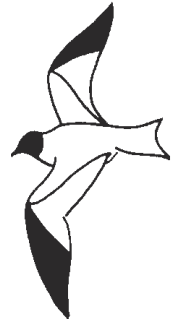
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Front cover photo by © Deborah J. House of Bishop, California: Bridgeport Reservoir, Mono County, California, 17 October 2018. Seventeen years of systematic surveys demonstrate the importance of Bridgeport Reservoir as a fall stopover for migrating waterfowl, especially dabbling ducks. Yet the trend in their numbers over this period has been a decline, paralleling the intensification of drought threatening the scattered wetlands of the Great Basin.

Back cover photos by © Ryan S. Terrill of Los Angeles, California: Western Tanager (*Piranga ludoviciana*) and Yellow-rumped Warbler (*Setophaga coronata*) as they pass in migration over Bear Divide, San Gabriel Mountains, Los Angeles County, California, on 5 May and 4 April 2021, respectively. Bear Divide is newly revealed as a point of concentration and unparalleled visibility of land birds as they head north in spring migration along the Pacific Flyway.

Western Birds solicits papers that are both useful to and understandable by amateur field ornithologists and also contribute significantly to scientific literature. Send manuscripts to Daniel D. Gibson, P. O. Box 155, Ester, AK 99725; avesalaska@gmail.com. For matters of style consult the Suggestions to Contributors to *Western Birds* (at <https://westernfieldornithologists.org/publications/journal>).

WESTERN BIRDS



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FALL WATERFOWL USE OF BRIDGEPORT RESERVOIR, MONO COUNTY, CALIFORNIA

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ABSTRACT: Aerial surveys from 2003 to 2019 documented the abundance of waterfowl at Bridgeport Reservoir in Mono County, California, from September through mid-November. Waterfowl totals at Bridgeport Reservoir averaged $33,106 \pm 4050$ (standard error) in the fall. Annual peak counts averaged $10,474 \pm 1349$, ranging from a low of 2583 in 2014 to the highest single-day count of 23,150 in 2005. Bridgeport Reservoir is a man-made water body in the intermountain West that waterfowl use primarily a mid-migration stopover site, with peak numbers occurring in September. The dominant waterfowl species, the Northern Shoveler (*Spatula clypeata*), Gadwall (*Mareca strepera*), Mallard (*Anas platyrhynchos*), Northern Pintail (*A. acuta*), and Green-winged Teal (*A. crecca*), showed both unimodal and bimodal migration chronologies. Regional drought, as indicated by the Palmer drought severity index, combined with a downward trend in waterfowl numbers explained 61.4% of annual variation in fall waterfowl totals. These data may allow future assessment of change in waterfowl abundance at Bridgeport Reservoir in the context of local or regional conditions, and as influenced by climate change.

Although developed for water storage to serve municipal, agricultural, or flood-control needs, reservoirs often also provide habitat for waterbirds. Designed to store water for agricultural irrigation, Bridgeport Reservoir is part of the Bridgeport Valley Important Bird Area designated by California Audubon (Cooper 2004). The reservoir lies within the intermountain West portion of the Pacific Flyway, a region where water and wetland resources carry a high value to wildlife, given their scariness on the landscape. Despite the potential importance of the Bridgeport area, there have been few avian studies of the reservoir proper. Published data on waterfowl use are lacking, and previous data from aerial surveys of waterfowl are limited to counts in October 1996 and September 1997 (J. R. Jehl, unpubl. data).

From 2003 to 2019, I conducted aerial waterfowl surveys from September through mid-November at Bridgeport Reservoir in conjunction with waterfowl surveys of two other Mono County lakes, Mono Lake and Crowley Reservoir. These surveys contributed to the Mono Basin Waterfowl Habitat Restoration Plan (LADWP 1996), with data from Bridgeport Reservoir serv-

ing as a basis for comparison with waterfowl numbers at Mono Lake, 29 km to the south-southeast in the same flyway. In this paper I describe the size, species composition, and migration phenology of fall waterfowl populations at Bridgeport Reservoir. I also investigated regional and local environmental factors influencing annual waterfowl abundance.

SURVEY AREA

Bridgeport Reservoir is located in Bridgeport Valley in northern Mono County, California, at an elevation of 1969 meters (Figure 1). The area has an arid continental climate (Zellmer 1977) with relatively cool, mild summers and cold, snowy winters (Sharpe et al. 2008). Annual precipitation averages 22.8 cm, mostly in the form of snow (Sharpe et al. 2008). By mid-September, average minimum temperatures drop below 0 °C (Western Regional Climate Center, <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca1075>). The reservoir's surface usually freezes over in winter, with ice typically developing by mid- to late November.

Bridgeport Reservoir was completed in 1923 to provide irrigation water to Smith and Mason valleys in Nevada (Sharpe et al. 2008) and currently also supports a recreational fishery, wildlife use, and other recreational activities including birding and hunting. The reservoir is owned and operated by the Walker River Irrigation District, based in Nevada, but the California State Water Resources Control Board controls storage and releases (Horton 1996).

The reservoir covers approximately 12.5 km² and is rather shallow (mean depth 4.6 m, maximum depth 13.3 m; Horne 2003). When at maximum storage, approximately half of the reservoir is less than 3 m deep (Horne 2003). Because of the shallow sloping topography of the southwestern portion of the valley, the reservoir's surface area varies greatly with the water level.

Bridgeport Reservoir is part of the hydrologically closed Walker River basin, which straddles the California/Nevada border. Several creeks originating from the east slope of the Sierra Nevada drain toward Bridgeport Reservoir. Creek water is diverted for upslope irrigation of rangeland, supporting the valley's primary land use of cattle grazing. The creeks directly tributary to the reservoir are the East Walker River, Robinson Creek, and Buckeye Creek (Figure 1). Downstream of Bridgeport Reservoir Dam, the East Walker River continues into Nevada, joining the West Walker River, and ultimately discharging into the terminal Walker Lake, Nevada. In Nevada, the Walker River system supports extensive agriculture.

Flood-irrigated pastures border the gently sloping southern and southwestern portion of Bridgeport Reservoir, while Great Basin scrub is dominant along the more steeply sloped north arm and east shore. In shallow areas and creek deltas, submergent aquatic vegetation is abundant, including broad beds of water smartweed (*Persicaria amphibia* var. *stipulacea*). Marsh, dense wetlands, and woody riparian vegetation are lacking in the immediate vicinity of the reservoir and Bridgeport Valley proper. The reservoir is eutrophic because of high nutrient loading and experiences summer blooms of colonial cyanobacteria that form a dense floating scum (Horne 2003).

FALL WATERFOWL USE OF BRIDGEPORT RESERVOIR, CALIFORNIA

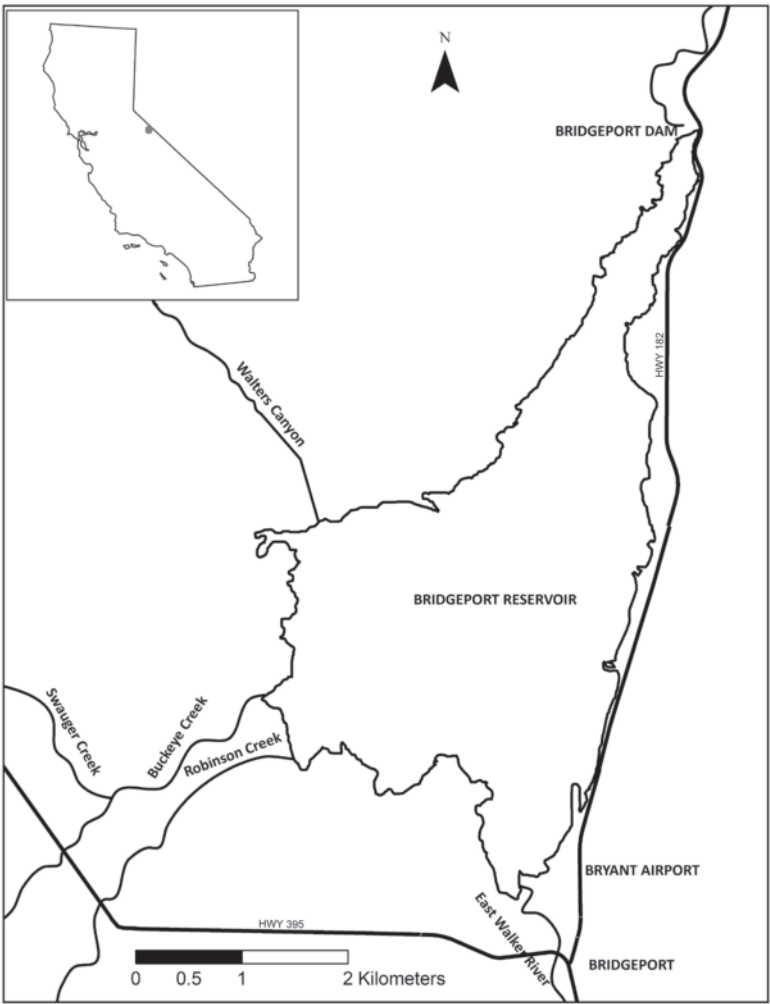


FIGURE 1. Location of Bridgeport Reservoir (inset), and tributary creeks.

METHODS

Waterfowl Surveys

I surveyed the waterfowl of Bridgeport Reservoir annually each fall from 2003 to 2019. Six surveys were completed at two-week intervals, starting the first week of September and ending in mid-November. A total of 102 surveys were completed over the 17-year study period.

Surveys were from a fixed-wing four-passenger airplane traveling at approximately 130 km/hr at a height of approximately 60 m above ground

level. Surveys took place in the morning, generally between 10:00 and 11:00 Pacific time, and were completed in approximately 20 minutes. The entire shoreline was circumnavigated twice, with an additional transect made over the open water of the southern end of the reservoir when birds were spread out into the bay and not well viewed during the shoreline flight.

During the flights, observers used a voice recorder to record waterfowl numbers and species composition and transcribed survey data later. Waterfowl were identified to species when possible, or to the lowest identifiable category, e.g., “unidentified teal.” Some closely related species difficult to identify reliably from an aircraft were combined into groups. The “Cinnamon Teal” (*Spatula cyanoptera*) may include some Blue-winged Teal (*S. discors*), a species seen in low numbers in Mono County (pers. obs.), and the “Lesser Scaup” (*Aythya affinis*) could include a few Greater Scaup (*A. marila*), a species also seen only infrequently in small numbers. Two observers were present on all flights, including one assistant besides myself. Consistency of observers has been high over the length of the study, as I was on all but one flight over the 17-year period, and there was little turnover in second observers.

DATA SUMMARY

Waterfowl Totals

The six survey periods were defined as early September (first week), mid-September, end September (includes the first week of October in some years), mid-October, end October, and mid-November. I generated totals for each survey period by summing all waterfowl (family Anatidae), including those not identified to species, then calculated total annual fall waterfowl abundance by summing the totals for the six survey periods. For each survey period, I calculated the mean, standard error, and low and high counts for the 2003–2019 study period. Descriptive statistics calculated for total fall waterfowl abundance for the duration of the study were annual mean and standard error and high and low totals for each year.

Species Composition

For each species, for the period 2003–2019, I calculated the mean by survey period, total annual mean, and standard error. In addition, I assessed community composition by grouping species into three broader categories: geese and swans, dabbling ducks, and diving ducks. The proportional abundance of each species group was calculated on the basis of totals over all surveys combined.

Migration Chronology

I assessed the intraseasonal pattern of waterfowl abundance at Bridgeport Reservoir by evaluating the mean and standard error of the totals for each survey period, 2003 to 2019, of the six most abundant ducks, the Green-winged Teal (*Anas crecca*), Gadwall (*Mareca strepera*), Mallard (*A. platyrhynchos*), Northern Pintail (*A. acuta*), Northern Shoveler (*Spatula clypeata*), and Ruddy Duck (*Oxyura jamaicensis*). I then calculated the proportion, with its standard error, of each species' total by survey period with respect to its yearly total. I

used the proportion of the yearly total rather than the actual survey total to standardize for variation from year to year. To interpolate species' abundance between surveys I used a cubic spline, a polynomial function that smooths curves and estimates the values of peaks that may have occurred between surveys (Gilmer et al. 2004).

Variables Influencing Waterfowl Totals

To analyze trends in annual totals with respect to year, local conditions (the reservoir's surface area), and regional conditions (drought severity), I used multiple linear regression analysis, $\log_{10}$ -transforming the numbers to fit the test's assumptions. The length of the shoreline and the availability of various depths of water vary with the reservoir's level, the exact nature of the relationships being influenced by the basin's topography. As a measure of this variation, I used the reservoir's surface area in September, estimated by linear regression with the reservoir's storage volume (km^3) the predictor variable and surface area (km^2) as the dependent variable. Data on the reservoir's storage volume were from the Department of Water Resources' California Data Exchange Center (<https://cdec.water.ca.gov/dynamicapp/QueryMonthly?s=BDP>). I selected the monthly value closest to the date of the satellite photo from which the volume was estimated each year. Based on imagery from the National Agriculture Imagery Program, values for surface area were obtained by mapping the shoreline in ArcGIS software by ESRI for the years 2005, 2009, 2010, 2012, 2014, 2016, 2018, and 2020 and with Google Earth's distance-measurement tool for 2006, 2013, and 2019, the years imagery was available through Google Earth. The resulting regression equation was highly predictive of the reservoir's surface area, given a particular storage volume ($r^2_{\text{adj}} = 0.976$, $p < 0.001$).

I estimated the reservoir's surface area in September of each year with the regression equation. I then included these predicted values in a multiple regression model to determine the effect of the reservoir's surface area on annual fall waterfowl totals at Bridgeport.

Regional conditions I assessed by means of the Palmer drought severity index (PDSI) for the western region (California and Nevada). The PDSI is a monthly index that incorporates both air temperature and precipitation data to evaluate the severity of hydrologic drought (Alley 1984, National Center for Atmospheric Research 2020). The combined effects of air temperature and precipitation influence evapotranspiration, which is the major factor controlling water balance in wetland habitats (Zhao and Liu 2016). Thus the PDSI may serve as a surrogate indicator of the extent or availability of wetlands in the region. The PDSI ranges from +10 (extremely wet) to -10 (extremely dry) (National Center for Atmospheric Research 2020). I averaged monthly PDSI values by water year (1 October through 30 September) for the water year immediately preceding each year's surveys.

I evaluated the model's performance by examining adjusted values of r^2 (r^2_{adj}), values of probability (p) for the model and individual variables, and the variance-inflation factor for variables.

RESULTS

Waterfowl Totals

From 2003 to 2019, the total number of waterfowl counted at Bridgeport Reservoir each fall (results of the six surveys summed) averaged $33,106 \pm 4050$ (SE; Table 1). Waterfowl concentrated primarily along the southwest shoreline from Walters Canyon to the East Walker River bay and offshore of the Buckeye Creek inlet (see Figure 1). Waterfowl abundance was highest in 2005 when 83,186 individuals were tallied over the six surveys. The fewest waterfowl were recorded in fall of 2014 when only 13,119 were tallied. The peak count for the year on a single survey averaged $10,474 \pm 1349$ and ranged from a low of 2583 in 2014 to the highest single-day count of 23,150 at the end of September in 2005.

Species Composition

Of the 23 species of waterfowl recorded at Bridgeport Reservoir in fall, geese and swans averaged 1280 per year, representing approximately 4% of all waterfowl (Table 2). The Snow Goose (*Anser caerulescens*) has been an infrequent, late-season migrant, seen in 5 of 17 years, with a peak count of 30 on 7 November 2017. The Greater White-fronted Goose (*A. albifrons*) has also been infrequent, seen between mid-September and the end of October in 3 of 17 years. The Cackling Goose (*Branta hutchinsii*) was detected only in 2016. The Canada Goose (*B. canadensis*) was the only species in this group recorded every year and averaged 1263 birds per year. The Tundra Swan (*Cygnus columbianus*) occurred as a late-season migrant in 12 of 17 years, with a high count of 85 on 14 November 2003.

Seven dabbling duck species (Table 2) averaged 29,789 annually and accounted for 90% of all waterfowl. The most abundant dabblers were the Northern Shoveler, Gadwall, Mallard, Northern Pintail and Green-winged Teal. The Northern Shoveler was the most abundant species overall, averaging 7741 ± 987 per year, constituting over 23% of all waterfowl. The Gadwall was almost equally abundant with 6369 ± 893 per year (19.2%). The yearly fall means for the Mallard, Northern Pintail, and Green-winged Teal were similar, each accounting for 10–12% of all waterfowl. The Cinnamon Teal was an early fall migrant, averaging 229 per year or approximately 1% of dabbling

TABLE 1 Abundance of Waterfowl at Bridgeport Reservoir, 2003–2019, All Species Pooled

Survey period	Mean	SE	High count	Low count
Early Sept	6763	899	12,160	2024
Mid-Sept	8754	1131	17,955	1962
End Sept	7078	1475	23,150	1633
Mid-Oct	4286	956	17,355	847
End Oct	3282	566	10,117	826
Mid-Nov	2943	462	6141	356
Peak count	10,475	1349	23,150	2583
Yearly total	33,106	4050	83,186	13,119

FALL WATERFOWL USE OF BRIDGEPORT RESERVOIR, CALIFORNIA

TABLE 2 Mean Number of Waterfowl by Survey Period, Total Annual Mean, and High Counts at Bridgeport Reservoir, 2003-2019

Species	Early Sep	Mid- Sep	End Sep	Mid- Oct	End Oct	Mid- Nov	Annual mean	SE ^a	Peak count
Geese and swans									
Snow Goose					<1	2	3	2	30
<i>Anser caerulescens</i>									
Greater White-fronted Goose <i>Anser albifrons</i>		1	<1		1		2	2	20
Cackling Goose					1		1	1	8
<i>Branta hutchinsii</i>									
Canada Goose	253	176	197	190	154	292	1263	198	940
<i>Branta canadensis</i>									
Tundra Swan					2	10	12	5	85
<i>Cygnus columbianus</i>									
Dabblers									
Cinnamon Teal	154	57	14				229	67	671
<i>Spatula cyanoptera</i>									
Northern Shoveler	2864	2560	1481	412	203	58	7741	987	8115
<i>Spatula clypeata</i>									
Gadwall	1483	2107	1606	434	362		6369	893	5700
<i>Mareca strepera</i>									
American Wigeon		15	22	9	8	9	66	25	220
<i>Mareca americana</i>									
Mallard	435	517	1102	816	782	538	4237	865	6605
<i>Anas platyrhynchos</i>									
Northern Pintail	154	759	993	1183	622	354	4173	699	6000
<i>Anas acuta</i>									
Green-winged Teal	562	614	768	473	523	658	3624	677	3600
<i>Anas crecca</i>									
Unidentified teal	757	1375	504	300	197	165	3352	823	5550
Divers									
Canvasback	<1			1	1	2	4	2	15
<i>Aythya valisineria</i>									
Redhead	4	12	19	11	19	7	72	20	155
<i>Aythya americana</i>									
Ring-necked Duck	3	1	7	16	4	77	109	75	1150
<i>Aythya collaris</i>									
Lesser Scaup			<1	12	14	17	44	11	137
<i>Aythya affinis</i>									
White-winged Scoter						<1	<1	<1	1
<i>Melanitta deglandi</i>									
Bufflehead	<1	1	5	16	64	105	194	50	810
<i>Bucephala albeola</i>									
Common Goldeneye				<1	<1	5	6	3	42
<i>Bucephala clangula</i>									
Hooded Merganser					1		1	1	10
<i>Lophodytes cucullatus</i>									
Common Merganser	21	16	17	11	12	15	93	16	93
<i>Mergus merganser</i>									
Red-breasted Merganser					<1		<1	<1	1
<i>Mergus serrator</i>									
Ruddy Duck	73	228	344	227	313	326	1513	231	1600
<i>Oxyura jamaicensis</i>									
Unidentified diving duck				2			2	2	30

^aStandard error.

ducks. The American Wigeon (*Mareca americana*) has averaged fewer than 100 birds per year, with a peak count of 220 in 2003.

Diving ducks were the most species-rich group, but although nine species were observed (Table 2), diving ducks as a whole accounted for only 6% of all waterfowl. Their species richness was low early in the season until most species arrived in mid-October. The Ruddy Duck was most abundant of the divers, averaging 1513 ± 230 per year. The Redhead (*Aythya americana*), Ring-necked Duck (*A. collaris*), Bufflehead (*Bucephala albeola*), and Common Merganser (*Mergus merganser*) also occurred regularly but each accounted for <1% of all waterfowl over the study period. The Bufflehead was the second most numerous diver, averaging 194 ± 50 annually. Although sometimes present early in the fall season, it was most consistently recorded in higher numbers after mid-October. The high of 810 Bufflehead was recorded on 13 November 2019. The Canvasback (*A. valisineria*), Lesser Scaup, and Common Goldeneye (*B. clangula*) were detected regularly after mid-October, with high counts of the Canvasback (15) recorded on 14 November 2003, of the Lesser Scaup (137) on 27 October 2017, and of the Common Goldeneye (42) on 14 November 2018. Species detected in only one year were the White-winged Scoter (*Melanitta deglandi*; 1), Hooded Merganser (*Lophodytes cucullatus*; 10), and Red-breasted Merganser (*Mergus serrator*; 1).

Migration Chronology

From early September to mid-November, the total number of waterfowl observed at Bridgeport Reservoir rose and fell (Figure 2). Early-season (Sep-

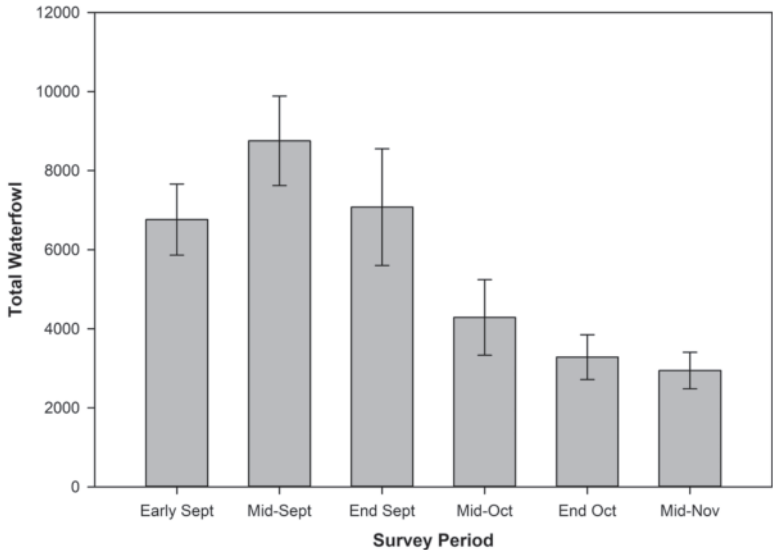


FIGURE 2. Mean total waterfowl ($\pm$ SE) per survey period, 2003–2019. Waterfowl use in early fall (early September to end September) is significantly higher than the late fall period of mid-October through mid-November.

tember) totals were significantly higher than later in the fall (October through mid-November). Seasonal totals were typically highest in mid-September, although some of the highest counts occurred in late September. The standard errors indicate that total waterfowl counts were most variable during the mid- and end of September periods. In two of the last six years, however, seasonal counts peaked in late fall. These late fall peaks were in mid-November 2014 and the end of October 2017.

Species Chronology

The Green-winged Teal's pattern of abundance was bimodal (Figure 3a). In any one year, approximately 60% of the seasonal population had been recorded by the end of September. The long-term average count through the month of September ranged from 562 to 768. Numbers decreased in October, followed by a second smaller peak in mid-November that averaged 658 birds.

The Gadwall showed a unimodal pattern of migration early in the season (Figure 3b). By mid-September, 60% of the yearly fall population was recorded. The long-term average seasonal peak of 2107 occurred in mid-September. Numbers dropped rapidly after mid-September, and from the end of October to mid-November, Gadwall averaged 433 or fewer.

The Mallard was a mid- to late-season migrant (Figure 3c), with populations building through September to a seasonal peak averaging 1102 in mid-September. A moderate but progressive decline in use was observed following the mid-September peak such that by mid-November, numbers averaged 537. The Mallard was one of the more abundant late-season species at Bridgeport.

The Northern Pintail's pattern of abundance was unimodal, and its numbers peaked in mid-season (Figure 3d). A significant proportion of the annual fall population had often arrived by mid-September, lingering through the end of October. Peak numbers occurred from the end of September through mid-October, with the highest average number of 1183 in mid-October.

The Northern Shoveler was the most abundant early-season migrant at Bridgeport (Figure 3e). Its migration chronology was somewhat similar to the Gadwall's with numbers peaking early in the season. Most of the annual fall population was recorded by mid-September, and the highest average count, of 2864, was in early September. Given that the high count generally occurred on the first survey, it is possible that in some years the annual peak preceded the first week of September. By mid-October, average numbers dropped to 412, and by mid-November, numbers averaged fewer than 100.

The Ruddy Duck had a bimodal pattern of abundance (Figure 3f). Total numbers were low in early September, then rose to a small peak averaging 344 and approximately 20% of the annual fall population at the end of September. A second and larger annual fall peak representing almost 30% of the annual fall population occurred at the end of October.

Variables Influencing Waterfowl Totals

The estimated extent of Bridgeport Reservoir averaged 5.3 km², ranging from a low of 2.5 km² in September 2014 to a high of 10.4 km² in September 2017. The extent of surface water was weakly related to waterfowl totals ($r^2_{adj} = 0.252$, $p = 0.051$), but because of multicollinearity with the PDSI and the model's resulting instability, I excluded this variable from the model.

FALL WATERFOWL USE OF BRIDGEPORT RESERVOIR, CALIFORNIA

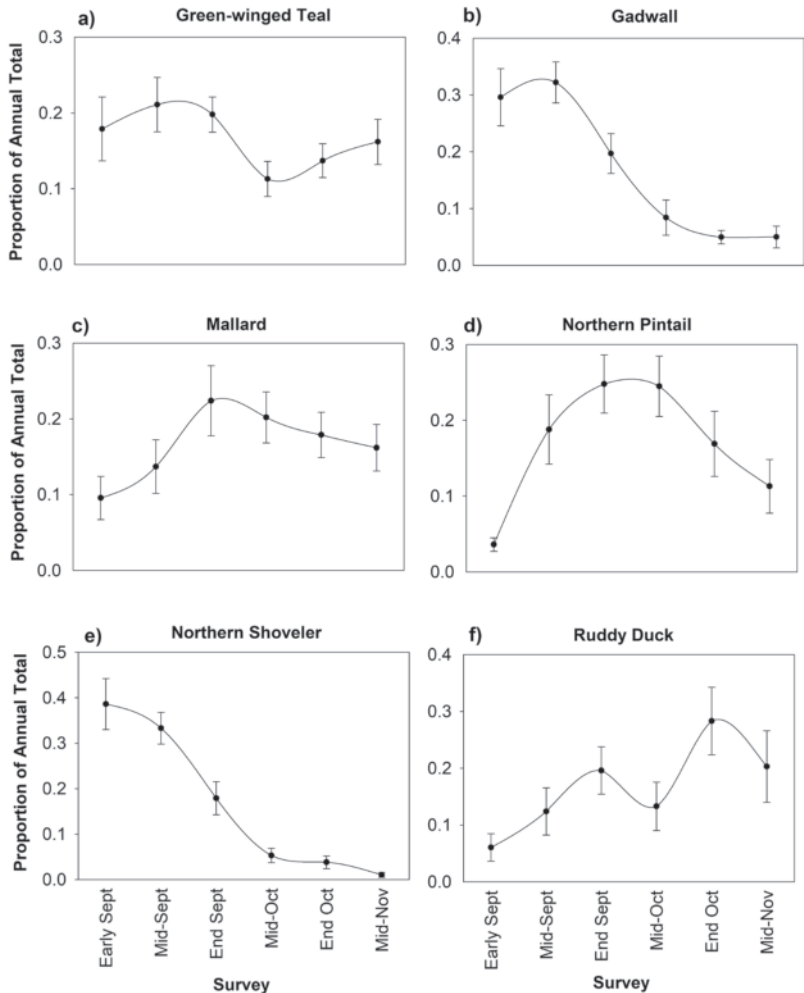


FIGURE 3. Migration phenology of the six most abundant species of dabbling ducks at Bridgeport Reservoir. Values represent the proportion of the species' annual fall totals present during each survey period.

The best-fit model encompassed the variables PDSI and year. These two variables combined explained 61.4% of the variability in annual waterfowl totals at Bridgeport Reservoir ($r^2_{\text{adj}} = 0.614$, $p < 0.001$).

Over the 17-year study period, the annual PDSI for California and Nevada ranged from -6.2 (extreme drought) to 2.9 (moist). The region experienced 7 years of severe to extreme drought ($\text{PDSI} \leq -3.0$), two of moderate drought ($\text{PDSI} -2.9$ to -2.0), six normal years ($\text{PDSI} -1.9$ to 1.9), and two moist years ($\text{PDSI} 2.0$ to 2.9).

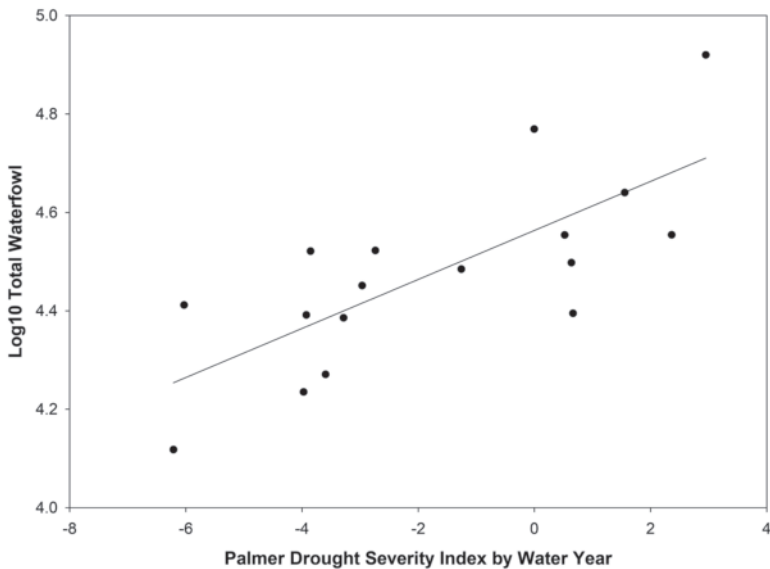


FIGURE 4. Relationship between total fall waterfowl numbers and the Palmer drought severity index.

The severity of drought, as indicated by PDSI in California and Nevada for the water year immediately prior to the survey year, influenced waterfowl totals strongly (Figure 4). This relationship was positive, indicating increased numbers as drought severity lessened and moisture conditions in the region improved, and decreased numbers during periods of drought.

Waterfowl totals were negatively correlated with year, indicating a trend of decline over the study period (Figure 5). There appears to be a cyclic pattern to annual waterfowl totals, however; since 2008, the peaks and troughs of total numbers have been lower than prior to 2008.

DISCUSSION

Bridgeport Reservoir is primarily a mid-migration stopover site for waterfowl in fall, as evidenced by high early-fall use through the month of September, followed by significantly lower numbers October through mid-November. Fall waterfowl use of Bridgeport Reservoir is unlike that at many other waterfowl sites in California in that use is highest in September. Lingering local breeders may contribute substantially to the fall numbers only in the case of the resident Canada Goose, which in some years can number several hundred in mid-summer. Otherwise, numbers of locally breeding ducks numbers appear to be insignificant compared to totals present in September (pers. obs.).

Fall waterfowl totals at Bridgeport Reservoir peak earlier than at many other sites in the intermountain West. At Lake Abert in eastern Oregon,

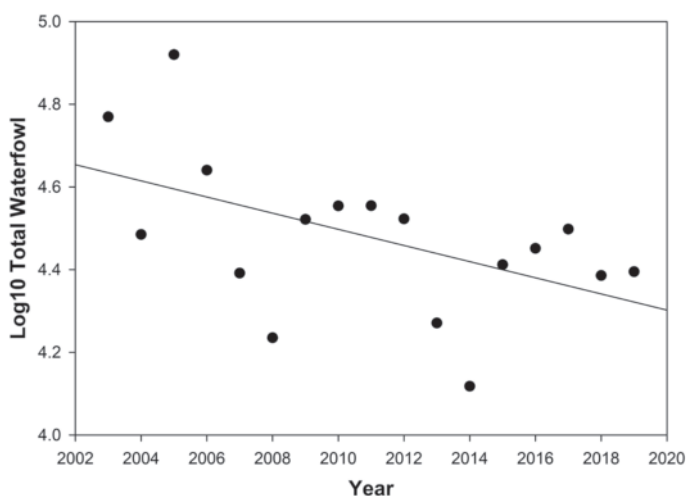


FIGURE 5. Trend in annual waterfowl totals, 2003–2019, $\log_{10}$ transformed.

Northern Shoveler numbers peak in mid- to late September, slightly later than observed at Bridgeport (East Cascade Audubon Society, <http://bit.ly/2s3Kwgt>). Total waterfowl numbers at Summer Lake, also in eastern Oregon, have been highest from late September through mid-October (Oregon Department of Fish and Wildlife 2020). Peak fall numbers of all ducks, as well as single-species counts for the Northern Shoveler, Gadwall, and Northern Pintail at Stillwater National Wildlife Refuge, Nevada, are in October (Bundy 2002). At Owens Lake in Inyo County, California, fall waterfowl numbers have been highest in October (Los Angeles Department of Water and Power, unpubl. data). Waterfowl use of Bridgeport in winter is much less than in early fall (pers. obs.). Although winter-hardy species such as the Mallard and Canada Goose overwinter on lakes and rivers of the intermountain West including Bridgeport Reservoir, waterfowl largely migrate out of the region with its harsh weather and freezing temperatures (Intermountain West Joint Venture 2013). The seasonal composition and abundance of waterfowl observed at Bridgeport Reservoir may reflect, in part, its location within the intermountain West and associated climate patterns including temperatures below freezing as early as September. This pattern of early fall departure may also indicate a depletion of high-energy foods sought by migrating waterfowl.

Waterfowl abundance at Bridgeport Reservoir is high relative to the size of the reservoir, and as compared to the other key waterfowl sites in Mono County—Crowley Reservoir and Mono Lake—where comparable aerial surveys were conducted over the same time period. Crowley Reservoir, which is almost twice as large as Bridgeport Reservoir at 34.2 km², has averaged 47,172

waterfowl annually over the same time period, or approximately 40% more waterfowl than at Bridgeport (unpubl. data). Waterfowl totals at Mono Lake, a saline lake covering 181 km², almost 10 times larger than Bridgeport, have averaged 24,731 (unpubl. data), or 25% less than at Bridgeport. Grant Lake Reservoir, also in Mono County and similar in size to Bridgeport Reservoir, supports few waterfowl (pers. obs., Lin and Jehl 1996).

Dabbling ducks are the most abundant waterfowl at Bridgeport Reservoir in fall, while geese, swans, and divers have constituted a small proportion of the overall numbers. Although Bridgeport Reservoir is potentially along a migration route for some portion of the western population of the Snow Goose, its use of Bridgeport has been low and sporadic. Likewise, Tundra Swan use was low and sporadic, although the western population is known to move from stopover locations in the intermountain West, including Great Salt Lake and Stillwater National Wildlife Refuge in Nevada to the north of Bridgeport, to wintering sites in California's Central Valley (Moermond and Spindler 1997), and wintering Tundra Swans are regular at Crowley Reservoir, approximately 80 km southeast of Bridgeport, arriving as early as the end of October. The majority of southbound Snow Geese and Tundra Swans wintering in the Central Valley cross west over the Sierra Nevada well to the north of Bridgeport Reservoir (F. Hall pers. comm.). Snow Geese also winter in the interior of California south of Bridgeport, including at Owens Lake (Inyo County), in Indian Wells Valley (Kern County), and in the Imperial Valley (Imperial County). The majority of waterfowl wintering in the Imperial Valley originate from central Canada and the northern Great Plains (Patten et al. 2003) and take a migratory path different from that taken by the majority of waterfowl wintering in cismontane areas of California (Bellrose 1980). Snow Geese wintering at Owens Lake and in Indian Wells Valley may originate from central Canada and the northern Great Plains as well. Thus Bridgeport Reservoir may lie outside the major migration routes Snow Geese and Tundra Swans follow, or the specific vegetation and food resources at Bridgeport may not make it attractive for a stopover.

At Bridgeport, the migration chronologies of the dominant species varied from primarily early in the season (e.g., Northern Shoveler and Gadwall) to mid-season (Northern Pintail) to mid-to-late season (Ruddy Duck and Mallard). In addition, both unimodal (Northern Shoveler, Gadwall, and Northern Pintail) and bimodal (Green-winged Teal, Mallard, and Ruddy Duck) seasonal patterns were observed. Bimodal patterns within a species may reflect different geographical source populations responsible for the early versus late pulse in numbers. The species for which bimodal patterns were observed are also typically among the most abundant species of waterfowl wintering in Mono County (pers. obs.). Early-season numbers of some species, particularly the Gadwall, presumably include small numbers of lingering local breeders.

Regional drought appears to influence waterfowl totals at Bridgeport strongly. Drought depresses waterfowl reproduction by reducing the availability of wetlands, but determining factors responsible for the effect of drought on waterfowl totals at any particular site in migration may be more complex. These factors may be influenced by the drought's severity and length at both local and regional scales, and the source population's reproductive dynamics.

With respect to migrating birds, drought has the potential to concentrate bird use in areas of suitable conditions, leading to a local increase in numbers, to decrease survival by eliminating resources along the migratory route, or to alter migration patterns, which could increase or decrease numbers. At Bridgeport Reservoir, the data do not suggest a concentration of use at this site in response to drought, as annual waterfowl use decreased as regional rainfall decreased. Drought may be influencing waterfowl use of Bridgeport Reservoir by altering migration patterns, depressing source populations, or affecting local conditions including food resources. Several studies have shown strong relationships between drought, breeding waterfowl populations, and habitat conditions (e.g., Sorenson et al. 1998, Krapu et al. 1983), thus providing a mechanism by which source populations are limited. Under the climate scenario predicted for the western U.S. of decreased precipitation, and increased temperatures reducing the effectiveness of precipitation, long-term drying is anticipated. Locally, dry periods are getting drier, and wet periods shorter (House and Honda 2018), resulting in less time for habitats and populations to recover from the consequences of dry periods. Periodic drying of wetlands can be beneficial in terms of increasing productivity, but long-term drought can lead to loss and reduction of the wetlands waterfowl use. In light of the response to regional drought, the declining trend in waterfowl numbers seen during this study could be due in part to recent changes in climate. Finally, although a relationship between reservoir level (which could influence the quantity or quality of the available habitat) and fall waterfowl numbers was not evident in this study, further investigation into the influence of reservoir level on habitat conditions may provide more insight.

Several factors are suspected to contribute to fall waterfowl abundance at Bridgeport Reservoir, including topography, available food resources, adjacent land use, and land-ownership patterns. The topography of the southern and southwestern shoreline of the reservoir results in ideal foraging conditions for dabbling ducks and geese. The gently sloping topography and the input of fresh water from the East Walker River and Robinson and Buckeye creeks combine to create extensive mudflats and shallow feeding areas along the southern and southwestern shoreline. Depending on the reservoir's level, in some years submergent and aquatic vegetation at Bridgeport is abundant, contributing to favorable foraging habitat (Fredrickson and Reid 1988). At reduced reservoir levels, the submergent vegetation, including smartweed, becomes exposed (pers. obs.), rendering seeds less available to foraging waterfowl. Similarly sized Grant Lake demonstrates how topography and surrounding land use can influence waterfowl use of a reservoir, as it is deeper, only has one perennial water source, is surrounded by upland vegetation, not irrigated pasture or meadow, and supports only small numbers of waterfowl.

Adjacent land use helps to sustain the abundance of fall waterfowl at Bridgeport Reservoir. Although cattle grazing can alter the physical structure of ecosystems, nutrient cycling, and species composition and cover (Fleischer 1994), this land use has helped to maintain open space surrounding Bridgeport Reservoir and has resulted in the persistence of meadows adjacent to it.

Fluctuating water levels at Bridgeport periodically inundate adjacent flood-irrigated pastures, and this process may be mimicking natural or man-

aged seasonally flooded wetlands (i.e., management through maintenance of moist soil) that can result in the production of key foods for waterfowl (Nelms 2007). The abundance of water smartweed along the southern shoreline of Bridgeport Reservoir in some years attests to the functioning of this area as a moist-soil wetland. The seeds of smartweeds are widely recognized for their value as waterfowl food (Martin and Uhler 1939, Fredrickson and Reid 1988), and smartweeds also support populations of diverse invertebrates (Nelms 2007), thus enhancing the abundance of waterfowl during fall migration at Bridgeport Reservoir.

In fall, migrating waterfowl accumulate energy reserves for long-distance flight and to withstand winter conditions that may include reduced food supply or severe weather (Davidson and Rothwell 1993). The accumulation of fat is of prime importance to waterfowl in fall. At this season, waterfowl increase their use of disturbance-free refuges (Madsen 1998, Evans and Day 2002). The southern and southwest portion of Bridgeport Reservoir's shore favored by waterfowl has limited human access not only because these areas are quite muddy but because adjacent private property limits access. Likewise, waterfowl hunting pressure is low, except for the opening day and weekend of hunting season (the third Saturday in October), and, because of difficult access and limited cover, most hunting in the valley is restricted to the creeks and ditches, as opposed to the reservoir (Tim Taylor, California Department of Fish and Wildlife, pers. comm). The combined forces of land ownership and land use keep disturbance low in the areas of Bridgeport Reservoir where waterfowl concentrate to feed and rest and may contribute to waterfowl use in the fall.

Knowledge of species' movement patterns is fundamental to habitat management and conservation planning. Chronologies of waterfowl migration have been described for broad geographic areas (e.g., Bellore 1980), but quantitative information is available only for localized areas (Baar et al. 2008).

Patterns of waterfowl migration have been observed to change over time (Lehikoinen and Jaatinen 2011, Reese and Weterings 2018), so the chronology data I present here may be useful for assessing waterfowl response to regional or local changes in conditions, including those induced by climate change.

A change in land use away from agricultural grazing lands to development is a potential threat to the nature and productivity of Bridgeport Valley. Most of the area immediately surrounding Bridgeport Reservoir and more than half of the total extent of Bridgeport Valley (19,341 hectares) are privately owned (Mono County Planning Department 2000). A small portion has been placed into conservation easements (<https://www.eslt.org/preserved-lands/bridgeport-valley/>). Land-use changes could alter water inputs to the reservoir, access, or the level of disturbance to wildlife including migratory waterfowl.

Changes to Bridgeport Reservoir and its habitat value for waterfowl could also occur as a result of the Walker Basin Restoration Program. The primary purpose of the Walker Basin Restoration Program is to restore and maintain Walker Lake in western Nevada, and to protect agricultural, environmental, and habitat interests in the Walker River basin (National Fish and Wildlife Foundation, <https://www.nfwf.org/programs/walker-basin-restoration-program>). Walker Lake is one of three desert terminal lakes in the United States

that supports a fishery, but a decrease in the lake's level and a subsequent increase in total dissolved solids have resulted in significant ecological changes (Collopy and Thomas 2010). To provide more inflow to Walker Lake, rights to surface water are being acquired from willing sellers in the watershed. Ciotti et al. (2014) cited reduced reservoir levels, reduced subsurface water flow, and a loss of flow in Robinson Creek as possible effects on Bridgeport Valley as a result of water transfers. A reduction in the level of Bridgeport Reservoir could degrade waterfowl habitat by reducing the extent of shallow flooded areas along the shoreline where the birds feed, and interrupting the connectivity of flooded pastureland to wetland habitats and open water.

Because of the general aridity of the intermountain West, the value of wetlands within the region is disproportionate to their extent (McKinstry et al. 2004), and areas with appropriate conditions tend to concentrate waterfowl, particularly during migration. Water resources and wetlands of the intermountain West have been profoundly altered, and those within Bridgeport Valley are no exception. Despite these alterations, Bridgeport Reservoir has been a locally important stopover site for migratory waterfowl in fall.

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AGE AND SEX INFLUENCE NATAL AND BREEDING DISPERSAL OF PURPLE MARTINS

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ABSTRACT: Dispersal patterns deepen our understanding of population dynamics. Dispersal by all age and sex classes enhances a species' ability to respond to environmental changes, such as in habitat availability, artificial nest sites, and climate. The migration dynamics of the eastern subspecies of the Purple Martin (*Progne subis subis*) are well known, but we know less about its patterns of annual dispersal. We compared the frequency, distance, and direction of dispersal by each age/sex cohort of martins in central Alberta, at the northwestern limit of their breeding range. We used two datasets: (1) adult martins banded in central Alberta as nestlings and encountered during the summers of 2017 and 2018, and (2) records of encounters of banded martins in Canada from 1935 to 2016 from the Canadian Wildlife Service's Bird Banding Office. In Alberta, 36% of birds dispersed from natal sites (by an average distance of 24 km), most commonly to the northeast. Across Canada, 29% of birds dispersed (by an average distance of 183 km), most commonly to the east and northeast. In Alberta, martins at least two years old dispersed less frequently than yearlings since some older martins returned to their natal site after first breeding elsewhere. Dispersal distances of after-second-year martins, which represent natal plus breeding dispersal, were greater than those of second-year birds, which represent natal dispersal alone. Thus some martins continue to disperse after their second year and do not maintain complete fidelity to a breeding site, which is different from our current understanding.

Dispersal refers to the distance and direction an organism moves from where it originated to where it breeds in subsequent years (MacDonald 2003). Dispersal behavior shapes the geographical distribution, population structure, and population dynamics of any species (Walters 2000). There are two major categories of dispersal from one year to the next. Natal dispersal is defined as movement from the site where a bird fledges to where it first breeds, while breeding dispersal is any change in subsequent locations of breeding (Greenwood and Harvey 1982, Colbert et al. 2001). Species in which site fidelity or philopatry are strong return to their place of fledging to breed each year following their seasonal migration (Förschler et al. 2010), so their distances of natal dispersal are low. Dispersal is different from post-fledging wandering by young, in which fledglings or juveniles move from site to site before their first migration (Miller et al. 2001). Dispersal also differs from migration, the regular seasonal movement of animals between their breeding and nonbreeding ranges, in that dispersal does not include the migration route (Winkler et al. 2016). In this paper, we examine the frequency, distance,

and direction of dispersal of the eastern subspecies of the Purple Martin (*Progne subis subis*) in central Alberta and across Canada.

Walters (2000) called for more research on dispersal to help in understanding and modeling population dynamics and structure. Dispersal can vary by sex and age. This variation can be important in analysis of apparent survival rates that are based on capture–mark–recapture studies which, in birds, are typically done by banding individuals and searching for them in subsequent years. If dispersal rates and distances vary by age and sex, apparent survival rates calculated from recaptures or resightings will be skewed (Stutchbury et al. 2009). In addition, a good understanding of dispersal may help in conservation of wildlife populations affected by climate change and human development. For example, dispersal patterns can indicate future range expansions or contractions. Similarly, dispersal among subpopulations can help maintain a metapopulation (Esler 2000), but net dispersal from a subpopulation could contribute to the decline of that subpopulation. Moreover, understanding dispersal patterns can provide insights into the evolution and adaptations of migrants (Rappole 2013). Drivers of dispersal differ both between and within species (Greenwood and Harvey 1982). Ultimately, dispersal is an important life-history characteristic that affects species' persistence and evolution (Colbert et al. 2001).

In many though not all species, younger birds disperse more often than older birds (Greenwood and Harvey 1982). Moreover, Rappole (2013) noted that adults of many species force dispersal of younger birds soon after the young birds arrive at breeding sites. Greenwood and Harvey (1982) showed that among a wide variety of birds, although not some waterfowl, females tend to disperse more than males (Alison 1977). Rappole (2013) suggested that return rates for females are lower than for males because of lower female survivorship and greater female dispersal combined.

The Purple Martin, North America's largest swallow, is a colonial aerial insectivore. Primitively, martins nested primarily in tree cavities, though, over time, they became habituated to nesting in human-made structures (Tautin et al. 2009). Today, the eastern subspecies relies heavily on the provision and maintenance of suitable nest boxes (Brown and Tarof 2013). This article is concerned with dispersal in the eastern subspecies only.

Previous studies have found that rates of Purple Martin dispersal are low (Morton and Patterson 1983, Stutchbury et al. 2009, Zelt et al. 2012). The limited dispersal could restrict the species' ability to respond to habitat and climate changes. In a long-term study of a small area in Pennsylvania, the martin's natal fidelity was 84% for females and 87% for males; breeding fidelity was 91% for females and 94% for males (Stutchbury et al. 2009).

Past studies also showed distances of martins' dispersal from both their birth sites and the sites of their successful clutches to be short. Among the few studies, the most common dispersal distances were less than 50 km; distances of 80 km or farther were unusual, and of >300 km were rare (Hill 2003, Ray and Schoenhals 2011). The frequency distribution of dispersal distances is skewed, with many shorter dispersals and few longer dispersals. Hill (2003) reported dispersal distances averaging 13.6 km (range 7–607 km) and that 96% of banded martins bred within 60 km of where they hatched at sites in Pennsylvania, Ohio, and Illinois. In Texas, 86% of banded martins encountered were within 80 km of their natal colony, with the longest dis-

persal distance being 422 km, by a martin of unknown sex and age (Ray and Schoenhals 2011). Other reports of long-distance dispersal are 928 km for a male of unknown age from its original nest to a breeding colony (Houston and Houston 2011), 2060 km for a male of unknown age from its natal site to a nesting site five years later (Chambers 2011), and 2635 km for a bird of unknown sex and age from its natal site to a nesting colony. The longer dispersal distances in band-encounter studies are due, in part, to the larger study area (Greenwood and Harvey 1982).

Results from studies of dispersal directions are mixed, including southward and eastward for martins in Alberta (Finlay 1975) and no trend in Pennsylvania and Ohio (Hill 2003). Ray and Schoenhals (2011) speculated that the availability of nest boxes, particularly in less occupied directions, can aid martins' range expansion, giving them more opportunities to colonize new sites.

Comparisons can be made with studies of other species' dispersal. Dispersal rates range from 50% for adult small passerines to 10% for long-lived species like gulls (Rappole 2013). For the well-studied Tree Swallow (*Tachycineta bicolor*), Hosner and Winkler (2007) found that the percentage of individuals that dispersed less than 13.6 km varied from about 90% in New York to about 50% from band recoveries across the USA. In Saskatchewan, 20% of breeding Tree Swallows studied by Shutler and Clark (2003) had been banded locally as nestlings; thus 80% of breeders had dispersed from elsewhere. In New York, Winkler et al. (2004) found that older female Tree Swallows were less likely to disperse than younger females. More generally, females disperse more frequently than do males in the Barn Swallow (*Hirundo rustica*; Schaub and von Hirschheydt 2009) and Tree Swallow (Shutler and Clark 2003). Female Tree Swallows are more likely to disperse if their nests fail than if they succeed (Hosner and Winkler (2007). With respect to breeding dispersal, Winkler et al. (2004) found that 14% of female Tree Swallows, but only 4% of males, moved between successive breeding sites. In contrast, among Barn Swallows in Spain and Denmark, females are less likely to disperse than are males (Balbontin et al. 2009).

In our study we investigated how Purple Martin dispersal, specifically its frequency, distance, and direction, varies by age/sex cohort in central Alberta and across Canada. We predicted that second-year male martins should disperse farther and more frequently than other age/sex classes because older males arrive and establish nesting territories earlier than do younger males and all females (Brown and Tarof 2013). From the high degree of site fidelity found in previous studies, we predicted that natal dispersal should account for any dispersal patterns of all age/sex classes. Since there is little information on directional preferences for dispersal, we hypothesized that birds should disperse in all directions to promote stability in subpopulations. An alternate hypothesis is that martins should disperse north with warming temperatures brought on by climate change.

METHODS

We used a multi-scale sampling strategy (after Hosner and Winkler 2007) to compare data from a local area with national data. While we expected dispersal distances based on the cross-Canada data to be larger than those

based on the Alberta data, we wanted to determine whether the two scales' patterns for frequency, short/long distances, and directions were consistent.

Our local 10,000-km² study area in central Alberta extended from the Ellis Bird Farm (52.390° N, 113.611° W) 130 km north to Islet Lake (53.452° N, 112.825° W) and from Daysland (52.865° N, 112.261° W) 80 km west to Wetaskiwin (52.969° N, 113.366° W). We selected eight sites that had a history of housing martin colonies and were the focus of previous banding of nestlings, plus three sites without banding. Banding efforts at or near the former sites increased the likelihood that we could encounter banded birds in later years. For two seasons in early July of 2017 and 2018, our team of four to six people visited each site to search for banded martins.

During the nesting season we captured banded martins in one of two ways. With the first method, we observed all four sides of the square martin houses simultaneously; two observers watched from opposite sides from a distance of 10–15 m for about 30 minutes. We used telescopes and binoculars to identify banded birds entering and exiting compartments and recorded the compartment number, suspected sex, and age of the bird by its plumage. After the target birds had left the house, we lowered it to equip compartments with traps. These traps consisted of a piece of white plastic puck board with two holes drilled into opposite corners, screwed above the existing entrance hole. A washer on either side of the puck board ensured that the puck board would effectively seal the entrance hole after a firm tug of an attached monofilament line tied to the second hole. We strung the line, weighted with a hexagonal nut, through a fencing staple hammered into the wooden compartment to help prevent it from entangling or scaring birds. Once we returned the house to its position at the top of the pole, catchers sat 5–20 m away to wait for the target bird to enter the compartment. At any one time we set up one to four compartment traps. Once the target bird safely entered the compartment, an observer pulled on the fishing line to close the trap door. We lowered the house, carefully removed the bird from the compartment, and transferred it to a cotton bag. For each bird, we recorded its age as second year (SY) or after second year (ASY), sex (visual comparisons with sources such as Stokes et al. 1997), and band number. We tried to capture all banded birds so that the sample was representative of the age/sex cohorts in each colony. After taking other measurements (e.g., weight, wing, tail, and tarsus length), we released the bird.

With the second method, we mass-trapped martins at the Ellis Bird Farm. On the morning of trap day, we attached a white, wooden trap door above the entrance hole of each compartment of each martin house (10 houses with 8–12 compartments per house) with a loose-fitting screw. For each trap, we strung a monofilament line from the top corner of this door down the pole to a central location at the bottom of the pole. We added tension on each line to raise the trap door above the entrance hole. After dusk, at 23:00, when we were confident that most or all of the adult martins were in their compartments to roost for the night, we simultaneously cut the monofilament lines at all of the nesting poles, releasing the trap doors to fall and cover the entrance holes. We banded each captured bird and recorded its age, sex, and band number before returning it to its original compartment. Before local sunrise at 05:00, we removed trap doors so the birds could exit.

Under both methods, we also recorded the location, house number, compartment number, date, and time of capture. Overall, we captured 161 previously banded birds. The Patuxent Wildlife Research Center's Bird Banding Laboratory provided information about the bird's original banding, including band number, location, and sex. We compared this information with similar details on the bird at the time of recapture.

We also obtained Canadian records of past encounters (1935–2016) with banded martins from the Canadian Wildlife Service's Bird Banding Office. We included only encounters from May to July in years subsequent to the year of banding, i.e., those representing dispersal. We did not include records from our central Alberta study in this analysis of Canada-wide dispersal. Staff at the Ellis Bird Farm also provided records of encounters that were not part of Canada's Bird Banding Office database. We defined an encounter as handling of a live banded bird, recovery of a banded bird found dead, or reading and reporting a band number on a live bird that was not handled (Gustafson et al. 1997). We had no control over the proportion of birds in each age/sex cohort.

For analysis of datasets, we recorded the age of each bird (SY or ASY) by comparing its year of banding to its year of encounter. We recorded its sex as male, female, or unknown, as identified in the original banding records or through visual assessment. From both datasets, we identified a dispersal when the banding location was different from the encounter location. We calculated dispersal distance and direction from the coordinates provided by the banding office, measuring distances (in km) in Google Earth. For dispersal direction, we used the eight cardinal and intercardinal compass directions (N, NE, E, SE, S, SW, W, NW). To account for post-fledging wandering, we excluded any cases of fledglings banded and encountered in the same year.

In the central Alberta dataset, we excluded any cases where the bird's sex was unknown, leaving 153 records for further analyses (25 SY males, 27 SY females, 52 ASY males, and 49 ASY females). Using SPSS 25.0 (IBM, Armonk, NY), we conducted a one-way ANOVA test to look for differences of dispersal distance in relation to age/sex cohorts. Post hoc Tukey's honestly significant difference (HSD) was used to identify differences among age/sex cohorts. We used chi-squared tests to evaluate differences in frequencies and direction of dispersal by age/sex cohort.

In the cross-Canada dataset, after excluding records of birds banded and encountered west of the Rocky Mountains in British Columbia, we ended up with a total of 397 records. The majority of these records were incomplete, as 90% lacked a verified sex, thus reducing our dataset to 38 records with known sex (2 SY males, 1 SY female, 10 ASY males, and 25 ASY females). The higher rate of unknown sex was probably due to the birds' deteriorated condition—most encounters in this sample were of martins found dead—and the lack of general public knowledge of plumages. Because the sample size was small, we used a Mann–Whitney nonparametric test to evaluate differences between age/sex cohorts in dispersal distance. We used this test rather than a Kruskal–Wallis nonparametric test because essentially only two cohorts, ASY males and ASY females, were represented in the cross-Canada dataset. Again we used chi-squared tests to assess differences in frequencies and direction of dispersal by age/sex cohort.

In both datasets, we based descriptive tests of average distance and

NATAL AND BREEDING DISPERSAL OF PURPLE MARTINS

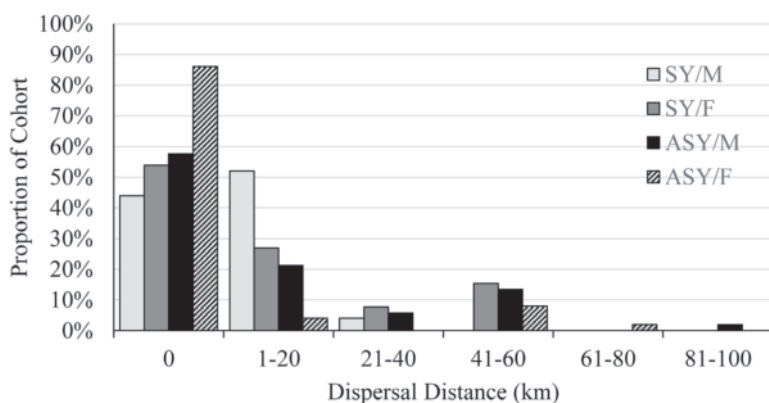


FIGURE 1. Proportion of encounters of banded Purple Martins of each age/sex cohort by distance of dispersal (km) from their natal colonies in central Alberta ($n = 153$).

direction of dispersal exclusively on dispersing birds. We set the significance thresholds at $P < 0.05$. We report the statistical details only for tests yielding differences that were significant.

RESULTS

Within our central Alberta dataset ($n = 153$), 33% of the encountered martins were one-year-old birds and 67% were older; the mean age was 2.0 years (range 1–8); 50% were male and 50% were female. Overall, 36% of the birds dispersed from the sites where they were banded originally. Among these dispersers ($n = 55$), the mean dispersal distance was 23.7 km (range 4–82 km; Figure 1) and the most common dispersal direction was northeast (51%; Figure 2). For each sex, we can describe the characteristics of natal dispersal

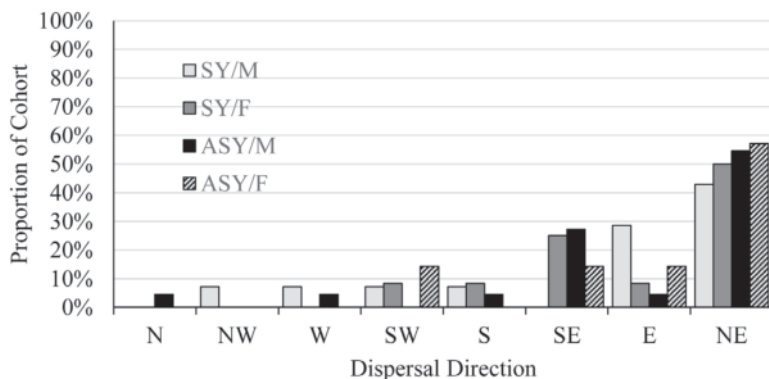


FIGURE 2. Proportion of encounters of banded Purple Martins of each age/sex cohort by direction of dispersal from colonies in central Alberta ($n = 55$).

NATAL AND BREEDING DISPERSAL OF PURPLE MARTINS

TABLE 1 Numbers of Encounters of Banded Purple Martins with Respect to Dispersal and Age/Sex Cohort^a

Dispersal and age	Central Alberta dataset		Cross-Canada dataset	
	Male	Female	Male	Female
Dispersed				
SY	14 (09.0)	12 (09.7)	0 (0.6)	0 (00.3)
ASY	22 (18.7)	7 (17.6)	6 (2.9)	5 (07.2)
At natal colony (no dispersal)				
SY	11 (16.0)	15 (17.3)	2 (1.4)	1 (00.7)
ASY	30 (33.3)	42 (31.4)	4 (7.1)	20 (17.8)

^aValues in brackets indicate values expected from a chi-squared crosstabs test.

for SY birds, but because of the limited sample size we can describe only the characteristics of natal and breeding dispersal combined for ASY birds.

Of the dispersing martins ($n = 55$), 47% were SY with males ($n = 14$) and females ($n = 12$) represented similarly. Older martins constituted 53% of the sample; ASY males ($n = 22$) outnumbering females ($n = 7$). Frequencies of dispersal of the age/sex cohorts differed significantly ($\chi^2 = 16.112$, $df = 3$, $P = 0.001$, Table 1). Of the birds recaptured where banded ($n = 98$), SY birds (26%) were less frequent than ASY birds (74%), and males (42%) were less frequent than females (58%; Table 1).

The average distance of natal dispersal for SY birds (sexes combined) was 16.8 km (range 4–56 km), whereas for ASY birds (sexes combined) it was 29.9 km (range 5–82 km). For both age cohorts, females' average dispersal distance was greater than males' (Table 2). The bird that dispersed farthest was an ASY male displaced 82 km to the northeast.

Dispersal distance of age/sex cohorts differed significantly (one-way ANOVA, $P = 0.006$, $F = 4.699$, $df = 3$). Post hoc Tukey's HSD test revealed that the significance was between the means of SY males and ASY females. We found no significance between age/sex cohorts in direction of dispersal (Figure 2).

In our cross-Canada dataset ($n = 38$), 8% of the banded birds encountered were SY and 92% were ASY; regarding sex, 32% were male, 26% were female, and 42% were of unknown sex. All dispersing martins ($n = 11$) in this sample

TABLE 2 Averages and Ranges of Distances of Dispersal (km) from Natal Sites of Purple Martins by Age/Sex Cohort

Age	Central Alberta dataset ($n = 55$)		Cross-Canada dataset ($n = 11$)	
	Male	Female	Male	Female
SY	10.1 (4–23) ^a	24.6 (4–56) ^{a, b}	0 (0)	0 (0)
ASY	26.7 (5–82) ^{a, b}	39.8 (8–69) ^b	145.2 (11–544)	228.7 (3–1023)

^{a, b}Cases with different letters indicate differences significant according to Tukey's HSD post hoc test.

NATAL AND BREEDING DISPERSAL OF PURPLE MARTINS

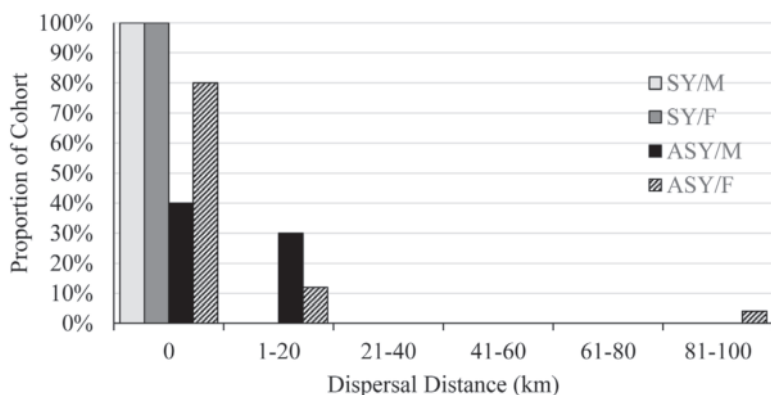


FIGURE 3. Proportion of encounters of banded Purple Martins of each age/sex cohort by distance of dispersal (km) from colonies in the cross-Canada dataset ($n = 38$).

were ASY; of these, 6 were males and 5 were females (Table 1). Of the 35 ASY birds, 11 individuals (31%) dispersed and 23 (69%) did not disperse. Of the nondispersing birds ($n = 27$), many more were ASY (89%) than SY (11%) and females (78%) predominated over males (22%; Table 1). The average dispersal distance for ASY birds (males and females combined) was 183.1 km ($n = 11$, range 3–1023 km, Figure 3). Of the ASY birds, females had the greater average dispersal distance and dispersal range (Table 2). The most common directions of dispersal were east and northeast (Figure 4). Of all encounters, the bird that dispersed the farthest was an ASY female displaced 1023 km to the southeast. Because of the incompleteness of the cross-Canada dataset and small sample sizes, we did not use statistics to compare the age/sex categories in relation to distance and direction of dispersal.

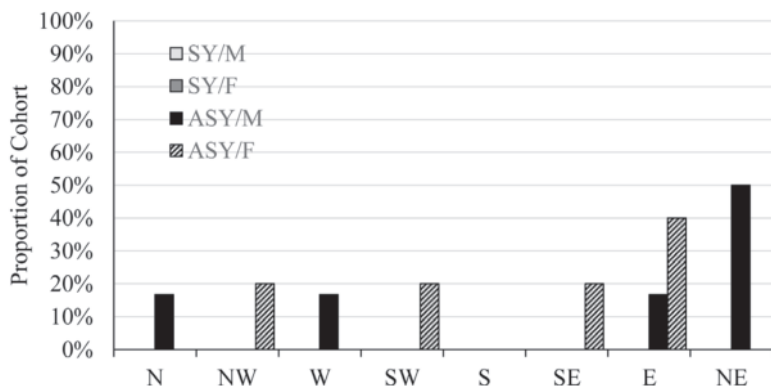


FIGURE 4. Proportion of encounters of banded Purple Martins of each age/sex cohort by direction of dispersal from colonies in the cross-Canada dataset ($n = 11$).

DISCUSSION

Overall, the rates of dispersal of the Purple Martin in our samples (36% for central Alberta and 29% for all of Canada east of the Rocky Mountains) were in the mid-range of the rates reported for the Tree Swallow (Hosner and Winkler 2007, Shutler and Clark (2003) and in Rappole's (2013) review. Dispersal patterns vary considerably among and within bird species (Sutherland et al. 2000, Rappole 2013). Some studies of martins have not distinguished natal and breeding dispersal. All ages combined, 36% of the martins in our Alberta study area dispersed from their natal site where they were banded. This is slightly more than the 24% reported in a subsample of martins in west Texas, based on breeding within a 30-mile and 50-mile radius of their natal site (Ray and Schoenhals 2001).

Differences in rates of dispersal of each age and sex class in our Alberta study indicate that fidelity has a pattern more complex than previously described for this species. Our results gave only weak support for our prediction that SY male martins should disperse at frequencies greater than other age/sex classes; the frequency of dispersal of SY males, SY females, and ASY males was greater than that of ASY females.

In agreement with our prediction that natal dispersal should account for any patterns of dispersal by age/sex class, 50% of SY martins of both sexes in our study dispersed from their natal colony, but only 29% of ASY martins had dispersed from their natal colony in their second or subsequent breeding season. Provided that conditions in the Alberta study were similar from year to year, these numbers indicate that about 20% of martins return to their natal colony in their second season after spending their first season elsewhere. This difference is most pronounced in females, of which only 14% of those older than one year are not at their natal colony. For male ASY martins, 40% continued to nest away from their natal colony. Some of those martins that dispersed as yearlings continue to disperse, since the distances of dispersal of ASY martins are greater than those of SY martins. In summary, 50% of martins dispersed in their first year, but in year two and subsequently, the sum of natal and breeding dispersal is less than natal dispersal alone. Thus some martins return to their natal site in their second and subsequent breeding seasons.

This pattern of fidelity could be explained by the age/sex-specific timing of the martins' return to nest sites. The sequence of the return to breeding colonies is that martins >3 years old arrive first and those 1 year old arrive last, with males arriving before females (Morton and Derrickson 1990, Tarof et al. 2011). Therefore, SY martins are less likely to find suitable nest sites available and are forced to disperse to vacant sites elsewhere, as has been shown in other species (Greenwood and Harvey 1982). However, we found that 20–35% of martins return to their natal sites in later years and secure nest sites at their natal colony, which they were not able to do as yearlings. The pattern was not included in the analysis of the martin's annual survival by Stutchbury et al. (2009) but will affect estimates of survival.

In both our central Alberta and Canada-wide datasets, encounters of ASY martins exceed those of SY martins. This pattern is not surprising since the category SY represents only a one-year cohort while ASY includes the

remaining annual cohorts. The central Alberta dataset had an even balance of encounters between the sexes, while the Canada-wide dataset had more encounters of females than of males. While the Alberta data were from live-trapped martins, the Canada-wide data were mostly from martins found dead by the public, presumably at nesting sites. Hill (2003) and Stutchbury et al. (2009) found that because of the high energy expenditures and stresses of laying eggs, female martins tend to have shorter life spans. In particular, SY females have an apparent probability of survival lower than that of SY males (Stutchbury et al. 2009), which could lead to more females found dead in the Canada-wide sample at breeding sites. The difference in recovery rates between our Alberta sample and the Canada-wide encounters implies that females are more likely than males to die during the breeding season.

We found that male Purple Martins (both age cohorts combined) were more likely to disperse than were females, as have other studies (Hill 2003, Ray and Schoenhals 2011). Hill (2003) reported that female martins tend to prefer experienced males, which can result in SY males not mating at their natal sites and choosing to disperse. A possible explanation for fewer females dispersing than males is the “martin hog theory,” the concept that some large colonies attract more SY females than they produce (Morton and Stutchbury 1997, Hill 2003). This pattern reduces the dispersal of SY females to unoccupied sites and is an example of conspecific cueing. Conspecific cueing is an individual assessing habitat quality by the presence of other individuals (Nordell and Valone 2017). The pattern of male martins dispersing more than females (Hill 2003, Ray and Schoenhals 2011) may result from competition for mates. If females are the limiting factor (by choosing to stay close by in hopes of attracting an older male), then younger males would need to disperse to find available breeding females.

Contrary to our prediction that SY male martins should disperse farther than other age/sex classes, we found that the mean distance of dispersal of ASY females was greater than that of SY males, as in the Tree Swallow (Winkler et al. 2005).

Of course, the distances of dispersal we recorded varied with the size of the study area. Our cross-Canada dataset included encounters from all of southern Canada east of the Rocky Mountains, but our Alberta dataset limited the maximum distance to 148 km, the longest diagonal in our rectangular study area. Estimates of dispersal distances will affect analysis of annual survival, such as that of Stutchbury et al. (2009), the radius of whose study area was only 50 km. In the Tree Swallow, Shutler and Clark (2003) found that breeding dispersal of females averaged farther than that of males, but distance of natal dispersal did not vary by sex. Hosner and Winkler (2007) reported that one-year-old Tree Swallows dispersed farther than older adults, but distances of natal dispersal did not differ by sex.

Contrary to our initial prediction that martins should disperse in all directions equally, the dominant directions in both datasets were east and northeast. Our alternate hypothesis that martins should disperse north with warming temperatures was partially supported. Ray and Schoenhals (2011) suggested that the martin's dispersal can be directed to previously unoccupied areas by providing nesting structures. This strategy could support martins

dispersing northward into new habitats that become available through climate change and are suitable with regard to other requirements such as food.

Some limitations of our study should be considered. First, as in any study of dispersal, our local central Alberta study area was limited in extent. We were not able to encounter banded birds outside of the study area, and we were not able to measure mortality in successive seasons (Greenwood and Harvey 1982). Second, given the privacy concerns of some bird banders (who did not report exact locations of banding to us), some banding locations are expressed only as the coordinates of the center of blocks measuring 10 minutes on a side (<https://www.pwrc.usgs.gov/BBL/MANUAL/loc.cfm>); thus in central Alberta the exact location can vary by 5 km (<https://stevemorse.org/nearest/distance.php>). Third, since the effort at banding across our study area varied from year to year, rates of subsequent encounters likely varied as well. Last, we did not record data on other variables that can influence sex-biased dispersal, such as colony size, social behavior, density (Shutler and Clark 2003, Förschler et al. 2010, Steifetten and Dale 2012), plumage color, body size (Sutherland et al. 2000), ectoparasite load (Brown and Brown 1992, Saino et al. 2014), feeding guild (Sutherland et al. 2000), and breeding success (Greenwood and Harvey 1982, Shutler and Clark 2003, Winkler et al. 2004, Schaub and von Hirschheydt 2009).

In the future, researchers can use new technologies, such as the Motus Wildlife Tracking System (<https://motus.org>), geolocators, and geotags, to examine patterns of dispersal throughout the breeding season before and after migration, rather than at only two points in time. For example, a dense array of Motus stations could allow an investigation of pre-breeding movements between colonies of martins of all ages and sexes (i.e., scouting of future nest sites). Future research could also investigate other factors affecting patterns of dispersal, including juvenile survivorship (Miller et al. 2001, Tarof et al. 2011), arrival times after migration (Nordell and Valone 2017), breeding success (Shutler and Clark 2003, Winkler et al. 2004), and post-fledging wandering (Morton and Patterson 1983, Miller et al. 2001, Hill 2003, Stutchbury et al. 2009). Last, future research should investigate the benefits and costs of dispersal (e.g., reproductive success and lifespan) over the lifetimes of individual martins (Balbontin et al. 2009, Schaub and von Hirschheydt 2009). Such investigations are relevant to many other species that could be affected by climate change and have a largely “eastern” distribution, but with ranges extending into the West.

CONCLUSIONS

The continued dispersal of martins ≥ 2 years old should facilitate range expansion as needed because of climate change or other factors. Since nesting success is typically higher for these older birds, in general and in martins in particular (Stutchbury et al. 2009), we should expect that their chance of dispersing successfully and establishing new colonies is greater. Future estimates of annual survival should include the frequency of birds returning to breed in their natal colony at an age of ≥ 2 years, and studies of dispersal should encompass larger areas to account for dispersal over longer distances.

The frequency and distances of martin dispersal we recorded are greater

than those reported in other studies of eastern populations of the species. Why? Dispersal is likely tied to the degree of stability in the breeding habitats. Prior to European contact, martins nested in natural cavities in trees and cliffs as well as in gourds provided by Indigenous Peoples (Bent 1942, Taverner 1945). While the cliff sites should have offered stability from year to year, the tree sites are in large, typically dead trees that remain standing for a limited time. Thus martins should be adapted to seek new nest sites when needed.

External factors could be key to the Purple Martin's future. First, with climate change forcing temperature patterns northward, we should expect range expansions in a similar direction. Patterns of dispersal can be an indication of range expansions (Duckworth and Badyaev 2007). We found most dispersals toward the northeast and east, with north being consistent with climate change in Alberta and Canada (Romero-Lankao et al. 2014). Changing prey availability in response to climate change is a concern for martin conservation since martins do not adjust their migration schedule in response to increased temperatures (Fraser et al. 2013).

Second, landlords (people who manage martin nest boxes) play a critical role in the success of martin colonies. If human-made nest boxes are a limiting factor, then the direction, proximity, and management of these nest boxes might influence dispersal patterns and subsequent range expansion or recolonization. Nest boxes provided to the northeast and east within 80 km of existing colonies at the edge of the species' breeding range may aid in changing the direction of dispersal over time. Landlords' efforts to manage martin colonies can affect nest-box occupancy (Anderson and Hvenegaard 2021) and the number of birds that survive to disperse in later years (Raleigh et al. 2019). Such conservation efforts are important because according to the results of the Breeding Bird Survey, 1996–2019, Purple Martin numbers are declining across North America (<https://www.mbr-pwrc.usgs.gov/>) and the eastern population relies almost completely on human-provided nest boxes.

Third, the declines in aerial insectivores in general, and the Purple Martin in particular, are concentrated in the northeastern part of their ranges (Nebel et al. 2010). Our results suggest that these declines are not directly affected by dispersal but by other factors (Spiller and Dettmers 2019). However, since all age classes of the Purple Martin disperse, the species retains the capability of adapting to changing environments and new opportunities for nesting. It is important to continue to monitor patterns of dispersal in bird populations to account for changes in movement ecology and provide better scientific support for conservation programs.

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USING SONG DIALECTS TO ASSESS THE MIGRATION STRATEGY OF THE GOLDEN- CROWNED SPARROW

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ABSTRACT: Most techniques used to study migration of wild birds require capture for banding or for attachment and/or recovery of tags or transmitters. We took advantage of the fact that the Golden-crowned Sparrow (*Zonotrichia atricapilla*) sings in winter, combined with published data on the distribution of its distinct song dialects in the breeding range, to assess its migration strategy and migratory connectivity by means of these dialects. Using recordings of the Golden-crowned Sparrow's song across much of its winter range, we categorized these birds by song type to identify their likely origin in some subset of the breeding range. This method allows examination of migration without the need to capture birds. Our results fit best with a pattern of chain migration, with the northernmost breeders wintering in the northernmost part of the winter range, and the southerly breeders wintering farther south. The results suggest strong migratory connectivity between segments of the breeding and winter ranges, though our small sample size makes it difficult to draw firm conclusions on connectivity.

The patterns of migration of long-distance migrants have been traditionally characterized as one of two types—chain migration or leapfrog migration (Berthold 2001, Newton 2008). Chain migration is characterized by the most northerly breeding populations of a species wintering in the most northerly portions of the winter range and the more southerly breeders wintering to the south. In leapfrog migration, the most northerly breeders winter farthest south, leaping over the southern breeders, which winter farther north. While chain migration seems the more straightforward and efficient strategy, leapfrog migration has been confirmed among many species. Swarth (1920), using specimens, is credited as the first to document leapfrog migration of various subspecies within the Sooty (*unalaschcensis*) subspecies group of the Fox Sparrow (*Passerella iliaca*). Since then, leapfrog migration has been demonstrated in many different taxa including numerous species of shorebirds (Salomonsen 1955, Boland 1990, Drent and Piersma 1990, Alves et al. 2012, Duijns et al. 2012), Bulwer's Petrel (*Bulweria bulwerii*; Ramos et al. 2015), Golden Eagle (*Aquila chrysaetos*; Nelson et al. 2015), American Kestrel (*Falco sparverius*; Hobson et al. 2009), Western Yellow Wagtail (*Motacilla flava*; Bell 1996), Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*; Lisovski et al. 2019), and Wilson's Warbler (*Cardellina pusilla*; Kelly et al. 2002). Bredis et al. (2020) examined the migration strategies of 23 transequatorial migrants of the Old World and found leapfrog migration the dominant strategy.

More recent data from techniques such as tagging birds with geolocators have demonstrated that migration is much more variable and nuanced than previously appreciated (McKinnon et al. 2013). For example, many species, especially among those breeding in western North America, undergo a molt

migration (Pyle et al. 2009, 2018) in which they move first from the breeding area to an intermediate location to complete molt before continuing to their winter range. Reverse migration (Nilsson and Sjöberg 2016), involving movement in counter-intuitive directions, also occurs frequently. In some species, post-breeding migration is a prolonged affair, with some individuals spending more time in transit than on the winter grounds (Wolfe and Johnson 2015). Satellite tracking of Ferruginous Hawks (*Buteo regalis*) revealed that some populations made enormous post-breeding movements, in some cases resulting in migrations three to four times longer than the distance between breeding and wintering locations (Watson et al. 2018).

Hypotheses to account for the seemingly counterintuitive nature of leapfrog migration fall into three main categories. The “competition hypothesis” (Salomonsen 1955, Pienkowski et al. 1985, Holmgren and Lundberg 1993) proposes that more southerly breeders of some species may simply out-compete the northern breeders on the wintering grounds by virtue of their physical or behavioral attributes or because of their prior occupancy of those areas, forcing the northern breeders to migrate farther to find available winter habitats. The other two hypotheses both assume that winter conditions in the more southerly section of the winter range are superior by virtue of milder winters, and that conditions in the northern breeding range permit those breeders to take advantage of those more favorable southern winter conditions. The “spring predictability hypothesis” (Alerstam and Högstedt 1980) suggests that the more predictable timing of conditions ideal for breeding in the far north allows those breeders to make a more direct, continuous migration north in the spring than the southerly breeders that may be forced to interrupt their spring migration if conditions in their breeding range are not ideal. The “time-allocation hypothesis” (Greenberg 1980) is based on the breeding season being much shorter in the north, forcing those breeders to spend more time on the winter grounds. Spending a longer period in their winter range leads them to benefit from the use of more productive southerly wintering areas. All three hypotheses have their proponents, and the observation of Boland (1990:284) holds true today, “at present, there is no consensus as to why leapfrog migration occurs.”

As we understand the migration strategies used by more species, we may come closer to understanding what drives the adoption of one strategy over the other. In particular, knowing the migration strategies of closely related species that share similar breeding and winter ranges should help to focus on the key factors that determine which strategy is best for which species. Two sparrow taxa, the Gambel's White-crowned Sparrow and the Sooty Fox Sparrow, migrate in the leapfrog pattern and broadly overlap in range, both breeding in Alaska and western Canada and wintering from southwestern Canada south into northern Mexico (Dunn and Alderfer 2017). Another sparrow, the Golden-crowned (*Z. atricapilla*), also occupies similar ranges and is a congener of the White-crowned Sparrow. Gambel's White-crowned Sparrows and Golden-crowned Sparrows also overlap broadly in winter habitat and often winter in mixed flocks. Therefore, we decided to investigate the the Golden-crowned Sparrow's migration strategy, to determine if that species also migrates in the leapfrog pattern or in some variation on that strategy.

We approached this question by taking advantage of Shizuka et al. (2016)

having mapped the song dialects in the Golden-crowned Sparrow's breeding range in detail, plus its tendency to sing through the winter (Kelly 1968). Thus, assuming that wintering Golden-crowned Sparrows sing the same song they sing in their breeding range, we should be able to map the winter ranges of the dialects identified by Shizuka et al. (2016) and assess the extent to which birds breeding in specific subsets of the breeding range winter in specific subsets of the winter range, the concept termed "migratory connectivity." Furthermore, provided that connectivity between breeding and winter locations is strong, the high degree of winter site fidelity of the Golden-crowned Sparrow (Mewaldt and Farnier 1957, Seavy et al. 2012, Cormier et al. 2016) should increase the likelihood that wintering birds' song types can be mapped into discrete geographic regions. Understanding migratory connectivity is important if conservation efforts for a migratory species are to be focused on the appropriate area.

METHODS

We used winter song recordings from our own collections, as well as from the Macaulay Library (www.macaulaylibrary.org) and Xeno-canto (www.xeno-canto.org). We only used recordings made from November through February to avoid recordings from birds still in migration. This criterion limited the number of suitable recordings available because, while this species sings frequently in October and March, the frequency of song decreases markedly in winter (Kelly 1968, pers. obs.). Table 1 lists the 38 recordings that met our criteria.

To assign winter songs to the song types identified by Shizuka et al. (2016), we examined spectrograms to assess specific elements or combinations of elements that characterize each song type. Shizuka et al. (2016) found that 90% of all breeding individuals they recorded sang one of five song types. Therefore, we assigned winter songs to one of those five song types. Songs that could not be clearly assigned to one of those five types we designated as "other."

Characteristics Defining Song Types

Typical examples of each of the four major song types we found in our samples are shown in Figure 1. Note that we did not encounter any examples of song type 4 in our set of winter recordings.

Song type 1: All Golden-crowned Sparrow songs start with a descending whistle, but only song type 1 starts with two descending whistles. The second whistle is followed by one or more short whistles at the same pitch as the end of the second descending whistle.

Song type 2: This song type is characterized by two whistles following the descending whistle, the first of which is on the same pitch as the end of the descending whistle, and the second at a lower pitch.

Song type 3: In this song type the descending whistle is followed by a whistle at a pitch lower than the end of the descending whistle, then another whistle at a pitch intermediate between the end of the descending whistle and the first whistle, and then a short trill at the same pitch as the last whistle.

Song type 4: This includes three short whistles all at the same pitch as the end of the descending whistle, followed by a trill at a lower pitch.

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TABLE 1 Recordings of Wintering Golden-crowned Sparrows

Catalog number ^a	Song type	Date	Latitude	Longitude	Recordist
ml281908681	1	21 Nov	49.242	-123.112	Neill Vanhinsberg
ml80124441	1	25 Dec	48.667	-122.325	Shane Sater
ml188444351	1	17 Nov	48.641	-123.448	Jody Wells
xc41864	1	26 Dec	48.578	-122.540	Taylor Brooks
ml212346641	1	28 Feb	48.498	-123.395	Carl Hughes
ml199981081	1	17 Jan	48.498	-123.395	Carl Hughes
ml141633631	1	19 Feb	48.491	-123.394	Daniel Donneck
xc159804	other	12 Nov	48.386	-123.514	Ian Cruickshank
xc153785	1	9 Nov	48.361	-123.542	Ian Cruickshank
ml127786091	2	23 Nov	45.617	-123.162	Oliver Burton
xc481149-52	2	14 Dec	45.565	-122.698	Thomas Magarian
ml173424721	1	21 Nov	43.396	-123.345	Joseph Mooney
ml40873151	3	22 Nov	39.387	-122.050	Ed Pandolfino
ml283141541	3	24 Nov	39.148	-123.174	Bryan McIntosh
xc662998	2	1 Nov	38.936	-121.332	Ed Pandolfino
xc662999	2	1 Nov	38.884	-121.194	Ed Pandolfino
xc663000	5	6 Dec	38.850	-121.208	Ed Pandolfino
xc65301-03	2	4 Nov	38.570	-121.762	Steve Hampton
xc347901	2	25 Dec	38.569	-121.371	Jim Holmes
ml43500411	2	25 Dec	38.566	-121.381	James Holmes
ml281114321	2	5 Nov	38.464	-122.708	Teresa & Miles Tuffli
ml307879351	2	2 Nov	38.445	-122.816	Bob Hasenick
ml223909621	2	1 Dec	38.430	-122.657	Will Anderson
ml284068211	2	23 Nov	38.247	-122.906	Connor Cochrane
ml218240101	2	7 Nov	38.043	-122.799	Teresa & Miles Tuffli
xc600009	2	2 Nov	37.912	-122.707	Ed Pandolfino
ml310971881	2	16 Feb	37.867	-122.310	Teale Fristoe
ml288643601	2	23 Nov	37.827	-121.203	Steven Hunter
ml293752871	2	18 Dec	37.539	-121.825	Derek Heins
ml193012701	2	13 Dec	37.327	-122.082	V. Langdon-Lassagne
ml192706281	2	11 Dec	37.236	-121.881	Garrett Lau
ml285955441	2	29 Nov	37.170	-121.736	Michelle Thurber
ml300227011	5	20 Jan	36.425	-121.233	Paul Fenwick
xc645157	2	14 Feb	35.555	-121.094	Thomas Graves
ml279251891	5	11 Nov	34.928	-119.908	Anonymous
ml212116621	other	26 Feb	34.818	-119.709	Anonymous
ml133972091	2	8 Jan	34.432	-119.555	John Callender
xc395966	5	13 Dec	34.195	-118.120	Lance Benner

^aml, Macaulay Library; xc, Xeno-canto.

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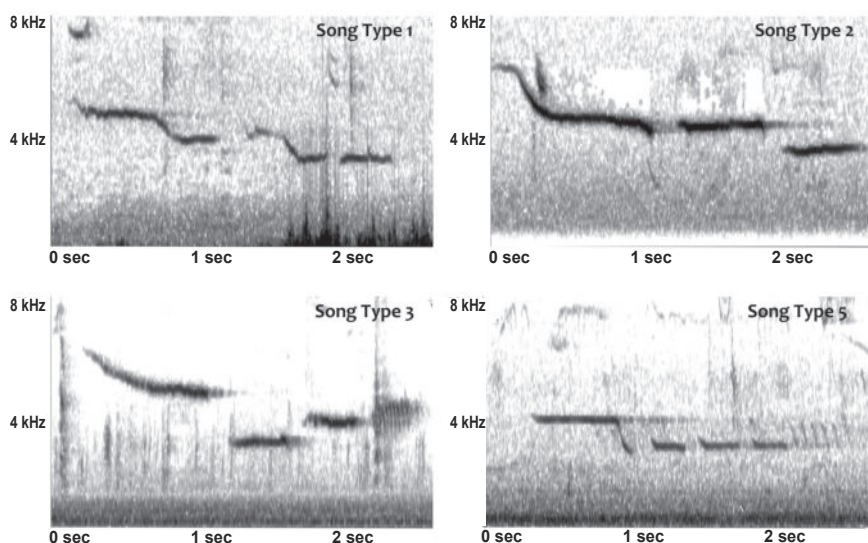


FIGURE 1. Examples of the four Golden-crowned Sparrow song types (as per Shizuka et al. 2016) in our collection of winter songs. Song type 1 (ml188444351) recorded 17 November in British Columbia by Jody Wells; song type 2 (xc481151) recorded 14 December in Multnomah County, Oregon, by Thomas Magarin; song type 3 (ml40873151) recorded 22 November in Tehama County, California, by Ed Pandolfino; song type 5 (xc663000) recorded 6 December in Placer County, California, by Ed Pandolfino.

Song type 5: This song type is very similar to type 4, except that the ending trill is at the same pitch as the three short whistles.

Distribution of the Song Types in the Breeding Range

Shizuka et al. (2016) found song type 1 only at the extreme northern edge of this species' breeding range, on the Seward Peninsula and in the Brooks Range of northern Alaska. Song type 2 was found along the Gulf of Alaska, while song type 3 was widespread through the eastern and southern parts of the breeding range, from southwestern Yukon Territory south through most of coastal and inland British Columbia. Song type 4 was the rarest of the five major song types identified by Shizuka et al. (2016), recorded principally in inland northern British Columbia. Most recordings of song type 5 were from coastal central British Columbia, with a few from inland northern British Columbia.

RESULTS

The distribution of winter song types we analyzed did not conform to the Golden-crowned Sparrow migrating in a leapfrog pattern (Figure 2). Song type 1 recordings were found only at or near the northern limit of the winter range. Song type 2 was the variation most frequently encountered in

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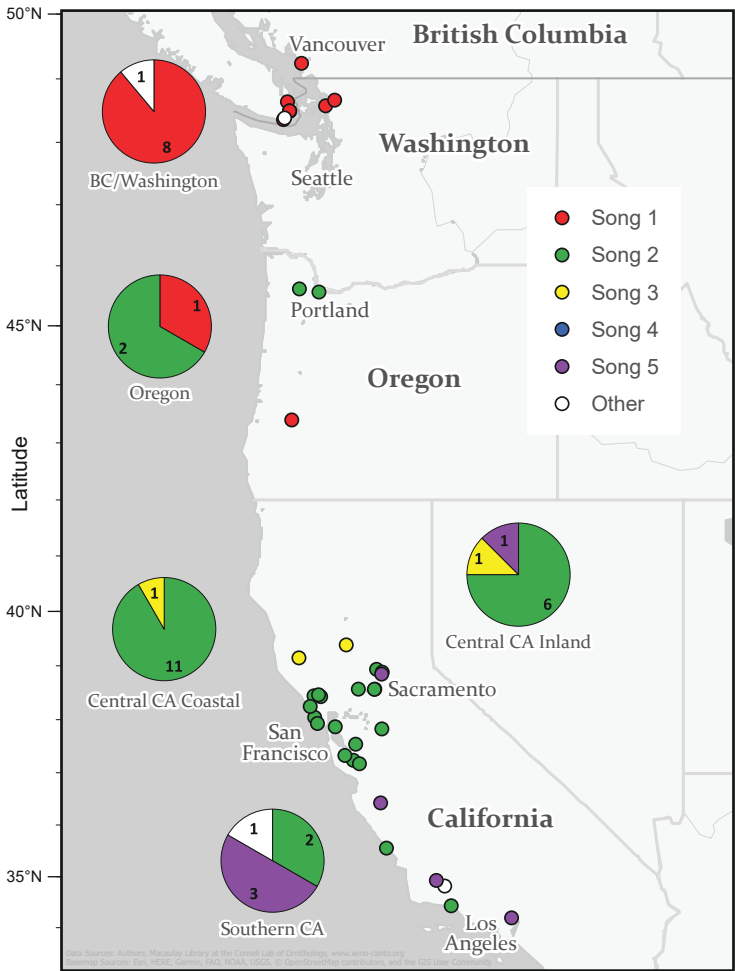


FIGURE 2. Locations and distribution of various song types (based on Shizuka et al. 2016) of the Golden-crowned Sparrow recorded in winter.

winter, with examples from northern Oregon to southern California. Nearly all the songs recorded in the San Francisco Bay area and central California were of type 2. We identified only two recordings as song type 3, both from north-central California. Of the four recordings of song type 5, three were from southern California.

These winter song recordings show a pattern generally consistent with chain migration. The song type of the most northerly breeders (type 1) was found only in the northern part of the winter range, while song type 5, which Shizuka et al. (2016) found mainly in the southern portions of the breeding range, occurred only in the southern parts of the winter range. We obtained

no recordings of song type 4. The preponderance of song type 2 in our sample is likely a reflection of those Gulf of Alaska breeders being common in central California in winter, combined with the high concentration of birders and birding effort in the greater San Francisco Bay area, plus the Golden-crowned Sparrow's relatively high abundance in those same areas.

The two song types we encountered most frequently (1 and 2), showed some geographic clustering. Eight of the nine winter recordings of song type 1 were from extreme southwestern British Columbia or northwestern Washington, and 17 of the 21 examples of song type 2 were from central California, between latitudes 37.2° and 38.9° N.

DISCUSSION

Despite the small sample size, our results appear to rule out leapfrog migration as a general strategy for the Golden-crowned Sparrow. The two song types Shizuka et al. (2016) found most geographically concentrated within the breeding range (1 and 2) both showed a winter pattern best associated with chain migration. That is, song type 1 (birds breeding in northern and northwestern Alaska) was encountered mainly in the northernmost part of the winter range, whereas song type 2 (birds breeding around the Gulf of Alaska) was concentrated in the central part of the winter range.

Our findings are consistent with data from geolocator-tagged birds (Seavy et al 2012, Cormier et al. 2016). These authors tagged wintering Golden-crowned Sparrows near Bolinas north of San Francisco (Marin County) and in inland central California (Placer County). Because those two locations are at similar latitudes, the results of their work do not shed light on this species' migration strategy, though they do allow us to test the consistency of our findings with these independent data. We obtained winter song recordings from the same general locations of those authors' study. Birds from north of San Francisco sang songs of type 2, and the geolocator data showed those birds breeding around the Gulf of Alaska (Seavy et al. 2012), where that song type is expected. Birds we recorded in inland central California sang songs of types 2, 3, or 5. Geolocator data from Cormier et al. (2016) showed most of their birds that wintered in inland central California were breeding in southern Yukon or northern inland British Columbia, where song types 3, 4, and 5 are expected. However, one of those tagged birds bred near the Gulf of Alaska, where song type 2 predominates. The fact that we did not encounter more examples of song type 3 in inland central California may be due to the sampling by Cormier et al. (2016) being highly localized. These authors tagged birds at a single location in the Sierra Nevada foothills near the eastern edge of the species' winter range. This could also reflect that at this scale song types do not allow reliable assessment of location of breeding. Many more samples of winter song are needed to clarify the winter ranges of each dialect population at a finer scale.

Seavy et al. (2012) and Cormier et al. (2016) found a strong degree of migratory connectivity between breeding and wintering locations for the birds at their two sampling locations. Our results appear generally consistent with their observations, at least for birds singing songs of types 1 and 2, in that we found the preponderance of recordings of those birds in relatively

discrete winter locations. We did not find enough examples of the other song types to draw any conclusions about migratory connectivity for those dialect populations.

It is particularly interesting that Lisovski et al. (2019) found that the Gambel's White-crowned Sparrow, a close relative of the Golden-crowned Sparrow and a taxon that shares overlapping breeding and winter ranges and similar habitat preferences, migrates in the leapfrog pattern. However, their data are not conclusive. They used a combination of banding, stable-isotope, and geolocator data and found that only the stable-isotope data suggested leapfrog migration. The banding data were compromised by having only three individuals with clear breeding date recoveries. All four of their geolocator-tagged birds wintered at a single site in central California. Of those four, two bred in southwestern Alaska and the other two in northeastern Alaska. Data from more birds of this taxon tagged from a wider range of latitudes could confirm their use of leapfrog migration. This would offer an intriguing basis for speculation about why these taxa use different migration strategies.

The evidence for leapfrog migration in the Sooty Fox Sparrow subspecies is more compelling (Swarth 1920, Bell 1997), though geolocator data from a small sample of birds representing a subset of such sparrows did not corroborate it (Fraser et al. 2018). The winter ranges of this segment of the Fox Sparrow and the Golden-crowned Sparrow are nearly identical. However, the breeding ranges differ substantially. The Sooty Fox Sparrows breed along the coasts of southern Alaska and British Columbia, all areas of relatively wet, mild climate. The Golden-crowned Sparrow's breeding range extends well north and east of this and encompasses a much wider range of climate and habitat types (Norment et al. 1998). Its winter behavior and habitat preferences are also different, with the Fox Sparrow tending to be solitary in winter and found in shady areas with dense understory (Weckstein et al. 2002). Golden-crowned Sparrows are gregarious in winter and use a variety of more open, brushy habitats (Norment et al. 1998, pers. obs.). Bell (1997) concluded that leapfrog migration in these Fox Sparrow subspecies could be explained by ideal winter conditions occurring later in the season in California, causing the early-breeding southern populations to truncate their southward migration but allowing the later-breeding northern birds to continue south to the most favorable locations. It seems that those same reasons should drive the Golden-crowned Sparrow to adopt a similar leapfrog migration, but our results are not consistent with that. Perhaps the contrasting winter habitat preference of the Golden-crowned Sparrow is responsible for the difference in migration strategy. In any case, a direct comparison with the Gambel's White-crowned Sparrow, should that species be confirmed as a leapfrog migrant, would provide a much better basis for assessing factors resulting in a different type of migration strategy.

Our use of winter song dialects to assess migration strategy offers some advantages over other methods. It does not require the capture or recapture of birds and can benefit from the rapidly increasing number of recordings being archived. It does require that the breeding-season dialects be discernable, documented, and well-mapped, and that the species sings in winter. Indeed, DeWolfe and Baptista (1995) used this method to investigate migration of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*). They found that

wintering flocks were composed of birds singing various dialects, and this subspecies did not appear to demonstrate leapfrog migration.

DeWolfe et al. (1974) and Nelson (1998) both examined variation in songs of the Gambel's White-crowned Sparrow at a few locations and found little evidence of regional dialects. Subsequently, Chilton et al. (2002) reviewed songs of this sparrow over a much broader range and did find distinct regional dialects. There are numerous recordings of Gambel's White-crowned Sparrow song throughout its winter range. Therefore, application of this song-dialect approach to the Gambel's White-crowned Sparrow, if it confirms leapfrog migration in this subspecies, may yield important clues about the basis for selection of different migration strategies by these two *Zonotrichia* sparrows.

Wider implementation of this approach, of song dialects as a tool to study bird migration on a broader scale and for more species, is dependent on access to more recordings, from all seasons. With more and more access to recording devices (even a smart phone can work well), the potential for community science to make important contributions grows. Archives such as the Macaulay Library (www.macaulaylibrary.org), which maintains all recordings uploaded to www.eBird.org, and Xeno-canto (www.xeno-canto.org), make it easy to upload and access recordings. We encourage everyone to record and upload recordings of bird vocalizations as often as possible.

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A NOVEL LOCALITY FOR THE OBSERVATION OF THOUSANDS OF PASSERINE BIRDS DURING SPRING MIGRATION IN LOS ANGELES COUNTY, CALIFORNIA

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ABSTRACT: Avian migration is a spectacular phenomenon, representing the annual movements of billions of birds globally. Because the greatest diversity and numbers of birds migrate at night, opportunities to observe active migration are rare. At a number of localities in North America, however, observers can quantify movements of many typically nocturnal migrants during daylight where they continue after dawn. Such locations have provided much information about species-specific phenology, status, and orientation during migration. Localities where morning flights of land birds can be observed are unevenly distributed, however, and are little reported along the Pacific coast. Here we describe a novel location for the observation of spectacular morning flights of nocturnal migrants during spring migration at Bear Divide, in the western San Gabriel Mountains, Los Angeles County, California. In two years of informal surveys at the site, we have recorded at least one morning with an estimated ~13,500 individual birds passing. Our preliminary analyses suggest that the peak of a species' migration at Bear Divide is correlated with the latitude of a species' breeding, being later in the spring as that latitude increases. Our data from Bear Divide provide an independent perspective on migration as quantified by local radar. Further work at this locality may help inform our knowledge of migration phenology and population trends.

Morning flight is the phenomenon of migrating birds, generally nocturnal migrants, continuing migration into daylight hours. Morning flight has been hypothesized to involve mainly correction for displacement when birds find themselves flying over water (Gauthreaux 1978, Wiedner et al. 1992, Yaukey 2010, Archibald et al. 2017) or a continuation of nocturnal flight (Bingman 1980) when birds do not encounter a locality suitable for stopover before dawn. When birds are displaced by wind, they often use the morning hours to reorient their migration (Horton et al. 2016). Reorientation of nocturnal migrants during the early morning may occur as the mainland becomes vis-

ible or through orientation with the rising sun (Moore 1986). Morning flights are fairly well known in the eastern United States, especially at locations like Cape May, New Jersey, Taddousac Dunes, Quebec, and Lake Pontchartrain, Louisiana. Less well known are sites of visible morning flight in the western United States. One such location is Butterbrecht Spring in eastern Kern County, California, where large numbers of migrating birds can be observed in morning flight in the spring. This flight is inland and not due to reorientation over water; rather, it is thought that these birds are “funneled” by a canyon oriented northwest–southeast and a lack of arboreal habitat in which to forage (Heindel 1991).

Observations of morning flight can illuminate what we know about avian migration (Van Doren et al. 2015). Studies of morning flight have provided vital information on the timing of passage (Heindel 1991, Sokolov et al. 1998, Archibald et al. 2017), status of species (Heindel 1991), orientation (Gauthreaux 1978, Bingman 1980, Archibald et al. 2017), and the interactions of weather and climate with avian migration (Pyle et al. 1993, Hüppop and Hüppop 2003, Swanson and Palmer 2009). Because of the dearth of reported localities of visible morning flight along the Pacific Flyway, much remains to be learned about migration of land birds in this region. For example, the large-scale movements of a few western birds, including the Phainopepla (*Phainopepla nitens*; Baldassarre et al. 2019), Black Swift (*Cypseloides niger*; Beason et al. 2012), and Wilson’s Warbler (*Cardellina pusilla*; Ruegg et al. 2014), have been clarified only recently by spatial tracking and genomic methods. Field observations of birds in migration can supplement these methods to provide a more complete view into avian movements. In addition to field observation, recent advances in the processing of radar data (Sheldon et al. 2013, Van Doren and Horton 2018, Lin et al. 2019) allow for detailed observations of migration incidental to monitoring of weather by radar (La Sorte et al. 2015, Farnsworth et al. 2016).

On 11 May 2016, Maxwell observed hundreds of migrant land birds moving through a small saddle in the western San Gabriel Mountains in Los Angeles County, California. This location is just west of the Bear Divide Vista picnic area and is often called simply “Bear Divide.” Hilly chaparral, with some nearby conifers, characterizes this area, and montane species such as the Mountain Quail (*Oreortyx pictus*) are common, as are birds breeding in chaparral such as the Wrentit (*Chamaea fasciata*), Rufous-crowned Sparrow (*Aimophila ruficeps*), and California Thrasher (*Toxostoma redivivum*). Bear Divide is a low pass, at 514 m above sea level. It is very narrow, with the surrounding hills quickly rising above 820 m (Figure 1). This topography appears to funnel birds that are flying north through this narrow gap, where they often fly within 1–2 m of the ground as they move over the pass.

After the initial discovery of visible morning flight at this site, we, in collaboration with other observers, informally surveyed the morning movement of birds there during spring 2019 and 2020.

METHODS

Observation began on most mornings 10–15 minutes before sunrise. In general, one to five observers were present, although on a few days we

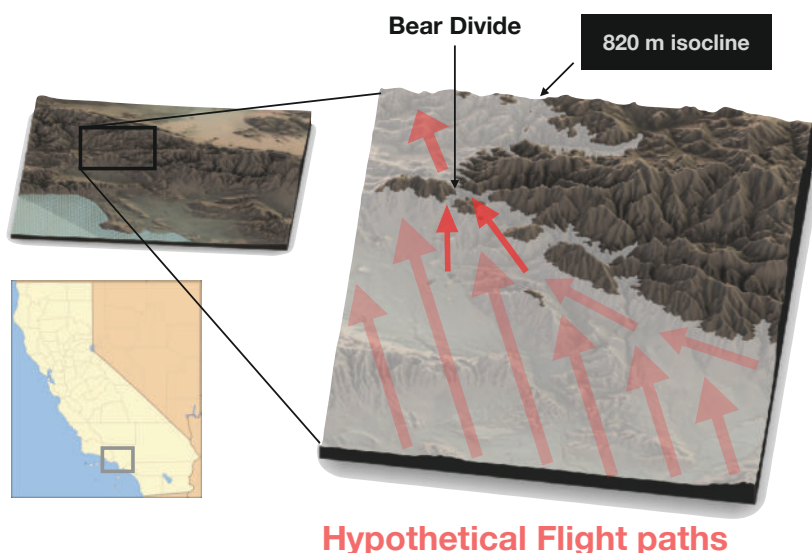


FIGURE 1. Bear Divide, in the western San Gabriel Mountains. Birds that are flying north or northwest over the Los Angeles basin encounter the San Gabriel Mountains and must either cross or attempt to go around them. If these birds follow the base of the mountains, Bear Divide is the first low (<820 m) pass they encounter. The broad, low base of the two canyons that feed into Bear Divide, combined with the narrow and steep topography at Bear Divide, may contribute to the large numbers of migrating birds that can be observed at the site.

assembled a larger group, especially in 2020. In all, 15,871 observer-hours were logged over 27 days between 27 March and 25 May. Effort was concentrated mostly on counting birds at the western saddle, but on occasions we observed at the picnic area, near the fire station, and along adjacent trails and fire breaks. In general, observation was completed between 08:30 and 10:00 Pacific Standard Time, depending on conditions. Most observation took place on days of favorable weather, and little to no observation was carried out on days when visibility was limited by fog or low clouds. We used current weather predictions, along with maps of forecast and live migration from <https://birdcast.info> (Van Doren and Horton 2018, Dokter et al. 2019), a product of the Cornell Lab of Ornithology, Colorado State University, and University of Massachusetts, Amherst, that, among other research efforts, applies data from weather-surveillance radar to predict and characterize bird migration in the contiguous United States.

The enormous number of birds moving through the study area at times proved challenging to count and identify. On slower days, we attempted to count and identify as many individuals as possible. On the more active days, we made intermittent 1- or 5-minute point counts of all birds, with one observer attempting to count every individual bird moving through the divide during the period but without attempting to identify the birds. On these

days, we began a new point count either at 30-minute intervals or whenever magnitude of the movement seemed to change. We then extrapolated these numbers through the beginning of the next count period. For identification, we attempted to track species composition, including nonspecific identifications such as “passerine sp.,” warbler sp.,” or “hummingbird sp.” by relative abundance, and then extrapolated all of these categories to the total by multiplying our estimated percent abundance by the count total. Observers identified species in the field or from photographs.

We used the birds’ dates of passage at Bear Divide to test the hypothesis that species breeding at higher latitudes migrate through Bear Divide later in the spring by using a hierarchical linear regression in a Bayesian context. We modeled individual records of migrating birds, representing the ordinal day of passage for individual i as a Gaussian random variable with mean μ_i and standard deviation σ_i . We further defined the expected date of passage for each individual as $\mu_i = \beta_{0,j} + \beta_1 \times \text{lat}_i$, where $\beta_{0,j}$ is a random intercept for each species j drawn from a hierarchical normal distribution, β_1 is a slope, and lat_i represents the latitude (in degrees) of breeding of individual i of species j . Since the exact latitude of breeding for each individual was unknown, yet the breeding range of each species is well documented, we treated lat_i as a random variable drawn from a uniform distribution bounded by the 95% quantile of latitudes of breeding for each species j . To define this range of latitudes, we extracted records for July from the full database at <https://www.ebird.org>. We then filtered out subspecies unlikely to occur, including resident Mexican subspecies of Vaux’s Swift (*Chaetura vauxi*), eastern subspecies of Wilson’s, Nashville (*Leothlypis ruficapilla*), and Orange-crowned (*L. celata*) Warblers, and eastern populations of the Chipping Sparrow (*Spizella passerina*) and Yellow Warbler (*Setophaga petechia*). Although the Myrtle Warbler (*S. coronata coronata*) undoubtedly occurs at Bear Divide, the vast majority of Yellow-rumped Warblers appear to be Audubon’s (*S. c. auduboni*), so we excluded the breeding range of *S. c. coronata* from the analysis of breeding ranges. To ensure that fitted relationships of β_1 were not overly sensitive to eBird’s filtering, we repeated the analysis but recalculated 95% quantiles while retaining all eBird records for each species for July.

We fit our model to the data with JAGS (Plummer 2003) using the statistical programming language R, version 3.5.3 (R Core Team 2019) and the package “R2jags” (Su and Yajima 2014). We used vague priors (i.e., normal with $\mu = 0$, $\tau = 0.001$). We ran three chains of 10,000 iterations thinned by 10 with a burn-in of 5000, yielding a posterior sample of 3000 across all chains. We checked convergence visually with traceplots and confirmed it with a Gelman–Rubin statistic < 1.1 (Gelman 2004). To assess the model’s fit, we calculated the marginal R^2 of the fixed effects, following Nakagawa and Schielzeth (2013).

We also used our data set to compare observed migration at Bear Divide with bird migration recorded at nearby weather stations. For detailed methods for analyzing radar data, see Dokter et al. (2011, 2019). Briefly, the National Oceanic and Atmospheric Administration (NOAA) and Amazon Web Services Cloud provide and host, respectively, the archive of the Next Generation Weather Radar (NEXRAD; Ansari et al. 2018). The NEXRAD network contains 143 WSR-88D stations recording weather data by radar in

the contiguous United States, and this sensor network incidentally records data on bird migration as well as data describing meteorological phenomena (Horton et al. 2016, Van Doren and Horton 2018, Dokter et al. 2019). We used established methods (Dokter et al. 2011) to extract vertical profiles of the density, speed, and direction of nocturnally migrating birds, using the rain-segmentation model MistNet to remove meteorological scattering (Lin et al. 2019). We calculated profiles for three radar stations, KSOX in the Santa Ana Mountains 97 km southeast of Bear Divide, KEYZ at Edwards Air Force Base 81 km northeast of Bear Divide, and KVTX in Los Angeles County, 48 km west-northwest of Bear Divide. We examined the predictive value of each, then compared the total individuals estimated in each morning's flight to the cumulative migration traffic per night (in numbers per kilometer) and migration traffic rate (in numbers per kilometer per hour), integrated over the altitude column from ~923 to 4000 m above sea level. Because KSOX provided the most predictive data, we restricted further analyses to data from that station only. Note that coverage below 923 m at KSOX is below the actual radar antenna—the station is 923 m above sea level. We used a linear regression to examine the relationships between total cumulative migration traffic per night and the total number of birds we estimated during morning flight at Bear Divide. Because the count data included outliers with large numbers of birds on a few days, we also ran a linear regression with log-normalized count data.

RESULTS

During the springs of 2019 and 2020, we recorded ~44,900 birds passing through Bear Divide. Peak passage occurred in late April (Figure 2), but substantial migration lasted at least from mid-March to late May. In general, migration was concentrated within the first 2–3 hours of the morning. Species composition clearly changed over the course of the spring (Figure 3). Appendix 1 lists details by species. We stress here that these results are preliminary, as effort was neither consistent nor standardized.

Species that breed at higher latitudes migrated through Bear Divide at later dates. On average, for every 1° of latitude of breeding range, a bird passed through 0.57 days later (95% credible interval: 0.54–0.60). The general sign and magnitude of this relationship still held (95% credible interval: 0.16–0.25) even without exclusionary filtering of June–July occurrence records for subspecies and subsets of species that clearly do not migrate through this portion of southern California. For the former model, the effect of latitude of breeding alone explained half of the variance in passage date (posterior mean of Nakagawa's marginal $R^2 = 0.50$).

We found a significant but barely predictive correlation between dawn flight counts at Bear Divide and movement observed at the KSOX radar, as interpreted by cumulative migration traffic per night, over the air column from 2000 to 3000 m above ground level ($p < 0.001$, adjusted $R^2 = 0.066$) (Figures 4 and 5). Fits to the data by hour were similar, being closest from about 22:00 to 02:00 Pacific Standard Time (Figure 6). Much of the stochasticity not explained by the linear model arose from nights (mornings?) with large movements of birds at Bear Divide that were not evident on the radar. This

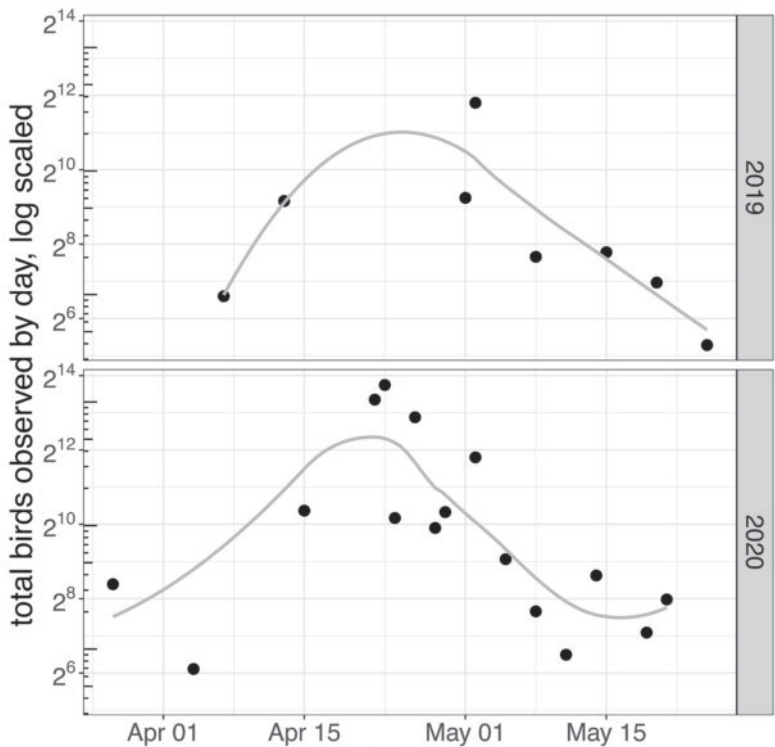


FIGURE 2. Total number of birds observed by day at Bear Divide during spring migration 2019 and 2020. In addition, we also counted in 2016 on 11, 17, and 19 May.

may be due to migrant birds accumulating in the Los Angeles basin to the northwest of the radar station in the Santa Ana Mountains, between the radar site and Bear Divide itself. When the count data were log-normalized, the correlation decreased somewhat (adjusted $R^2 = 0.02$), though the relationship remained significant ($p < 0.01$).

DISCUSSION

The magnitude of visible migration at Bear Divide makes it unique along the Pacific coastal flyway, so far as is known. The local topography seems to funnel migrating land birds through a narrow pass, where they often fly low. This site has already provided opportunity for both public engagement and scientific study of spring migration in coastal California. In general, the largest passage of birds occurs from mid-April to early May, though visits from March to June have been productive. Species composition varies substantially through the spring. Some groups of birds or species, such as raptors, thrushes, and flycatchers, seem to be underrepresented at Bear Divide in comparison to other sites in California where migration has been observed. However, some

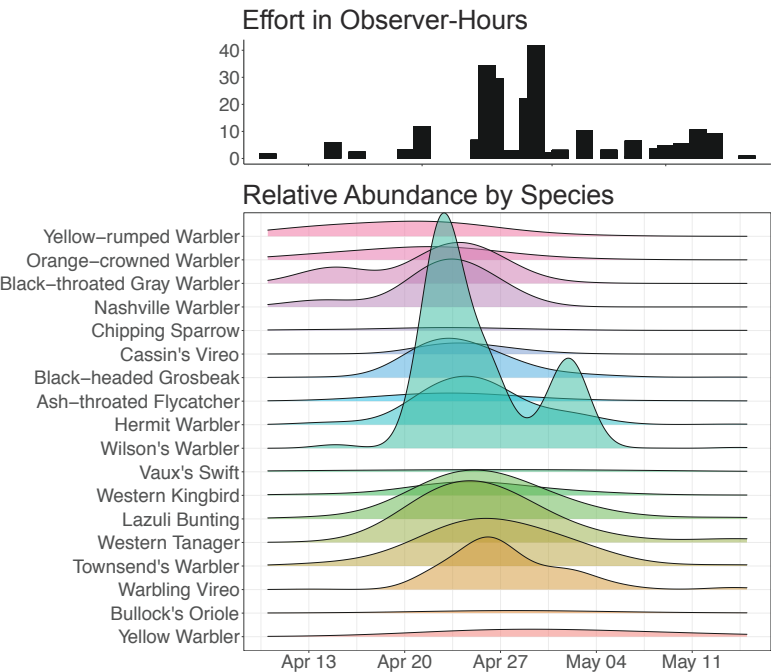


FIGURE 3. Timing of observation effort and relative seasonal abundance of the 18 most common migrant land birds at Bear Divide, ordered by mean date of peak passage.

individual days have seen notable passages of both thrushes and flycatchers; further study may reveal that these families use Bear Divide more than we have observed. The weather associated with passage of migrant birds may vary by location and season, but the most important predictors for the magnitude of spring migration are air temperature, surface pressure, and meridional wind (Van Doren and Horton 2018). We have also noticed that wind from the north can improve visibility of birds, as it appears to cause birds to fly closer to the ground and thus closer to observers. This behavior may reduce the amount of time birds spend flying into headwinds as they cross Bear Divide.

We found some, but rather little, predictive value in the raw radar data for forecasting the magnitude of visible migration at Bear Divide. This is likely due to the movement of birds at Bear Divide being largely dependent on local weather. Low clouds or fog in the Los Angeles basin or San Gabriel Mountains may cause birds to not move through Bear Divide, even if conditions were favorable for migration elsewhere the previous night. Much more research is needed into the relationship between radar detection and point estimates, particularly the likely complicated relationship between weather and buildup of migrants over multiple days. For example, the days of greatest movement at Bear Divide followed several days of apparently bad weather

A CONCENTRATION POINT OF SPRING MIGRATION NEAR LOS ANGELES

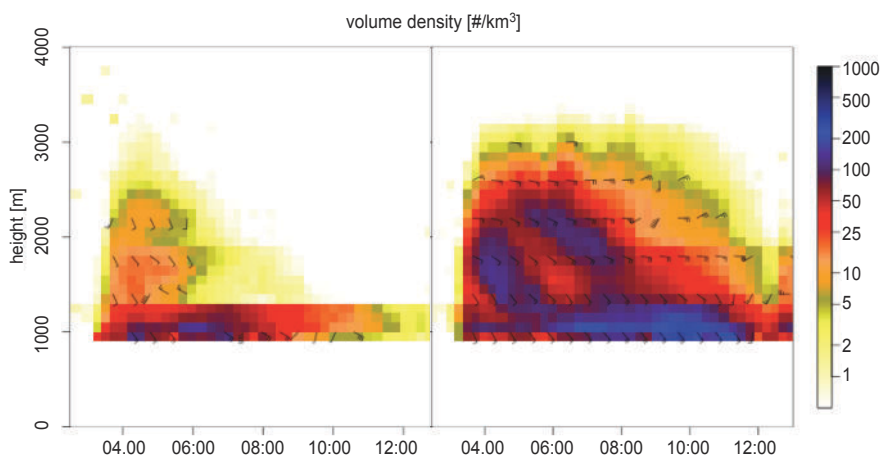


FIGURE 4. Volume density of migrating birds (number per cubic kilometer) detected by radar at the KSOX weather radar station in the Santa Ana Mountains, Orange County, California, expressed by height above the ground on the y axis and time of night on the x axis. Yellow colors indicate lighter migration traffic, purple colors heavier traffic. Times are in Greenwich Mean Time, so 4:00 is 21:00 Pacific Standard Time and 12:00 is 05:00 Pacific Standard Time. (A) 5 May 2019, the night before ~2000 birds were observed at Bear Divide. (B) 22 April 2019, the night before ~13,500 birds were observed at Bear Divide. Much heavier migration traffic is observed throughout the atmosphere, through the night and early morning hours.

for migration with few birds. Such weather may cause birds to accumulate in the Los Angeles basin, then all move at once when the weather becomes favorable. This effect would cause large movements of birds at Bear Divide without associated peaks in radar data at more distant sites.

Each species' seasonal status at Bear Divide is idiosyncratic, with a unique median passage date and degree of temporal clustering. We found that some of this difference in seasonality is explained by latitude of breeding range, with species that breed farther north migrating later in the spring. This parallels results found within Wilson's Warbler (Ruegg et al. 2014), in which populations breeding farther north migrate in spring at later dates. This result is in contrast to Hagan et al. (1991), who found the winter range, and not the breeding range, predicts timing of spring migration. We did not compare species by winter range because the coverage of the winter ranges of many of these species in eBird is very heterogeneous, and in the tropics such data can be strongly biased toward sites popular for ecotourism. Other sources of data on winter ranges, such as specimen collections, are at least as patchy.

The rather limited time we have spent at Bear Divide has already yielded important data. Because this site is so productive, with more systematic effort it could provide profound insight into the migration of land birds along the Pacific Flyway. We encourage other observers to undertake similar surveys of passing land birds at any site of visible dawn flight.

A CONCENTRATION POINT OF SPRING MIGRATION NEAR LOS ANGELES

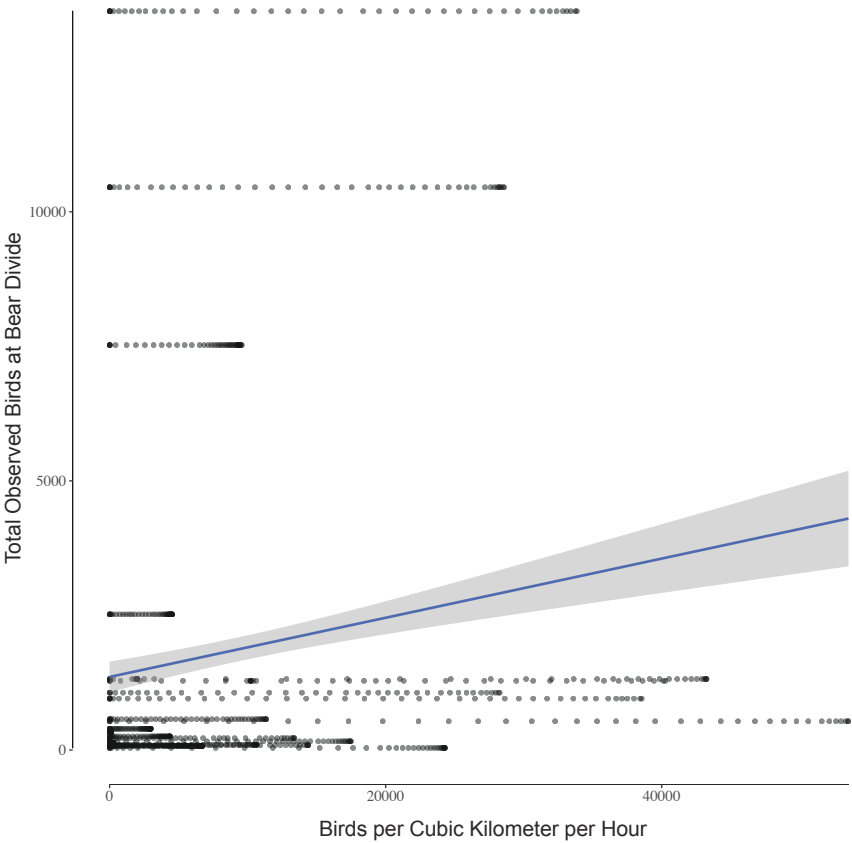


FIGURE 5. The relationship between total migration traffic detected by radar at the KSOX weather radar station in the Santa Ana Mountains, summed over each night, and total number of migrant birds counted in a morning at Bear Divide. Each point represents one night of migration, with migration traffic the previous night represented on the *x* axis, and total birds observed at Bear Divide the next morning on the *y* axis; the blue line represents correlation by linear regression; gray shading represents the 95% confidence interval. A weak (adjusted $R^2=0.066$) but significant ($p<0.001$) relationship indicates that radar traffic does predict movement somewhat at Bear Divide, but that we still have much to learn about where these birds are coming from and when they are moving toward Bear Divide.

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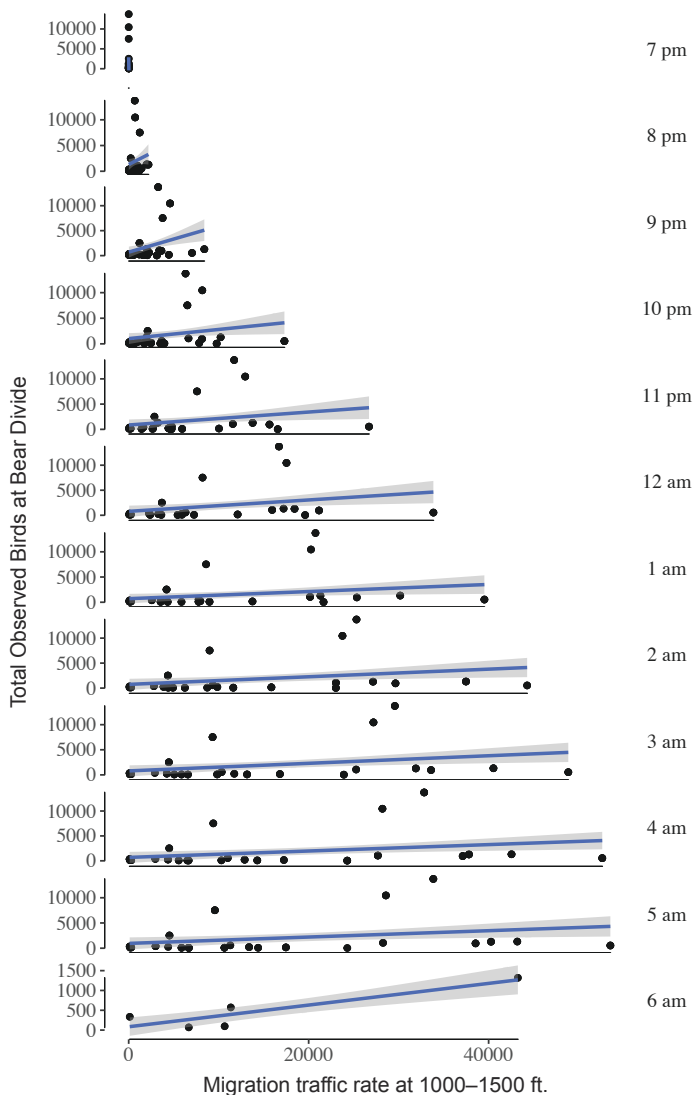


FIGURE 6. Relationships between hourly migration traffic (birds per cubic kilometer per hour) detected by radar at the KSOX weather radar station in the Santa Ana Mountains (x axes) and total number of birds counted in a morning at Bear Divide (y axes). Each point represents the total number of birds seen at Bear Divide the morning after the radar observation on the Y axis, and the migration traffic rate by hour, if detected that hour, on the x axis; blue lines represent correlation by linear regression; gray shading represents 95% confidence intervals. Migration traffic was recorded in the 06:00 hour on only 5 days, so the number of points per graph varies, aside from points being overprinted. Positive relationships indicate a predictive capability of the radar for that hour for bird movement observed at Bear Divide, and these correlations were most significant for the early morning hours.

White, a regular and enthusiastic volunteer and counter at Bear Divide, who tragically lost his life recently. We will always remember his enthusiasm, kind heart, and daily delivery of doughnuts.

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Appendix 1 Birds Recorded at Bear Divide, San Gabriel Mountains, Spring Migration, 2016–2020

Canada Goose (*Branta canadensis*), total 17, 13 Apr–2 May; high count 7, 2 May 2020.
Mountain Quail (*Oreortyx pictus*), total 66, 27 Mar–25 May; high count 5, 15 May 2019.

California Quail (*Callipepla californica*), total 56, 27 Mar–21 May; high count 5, 11 May 2016.

Band-tailed Pigeon (*Patagioenas fasciata*), total 128, 27 Mar–21 May; high count 10, 20 May 2019. It is unclear whether this species is a passage migrant or whether the individuals observed moving through the divide are making only local movements through the San Gabriel Mountains. Many observations of this species at Bear Divide are of birds flying south, implying local movement rather than migration.

Eurasian Collared-Dove (*Streptopelia decaocto*), total 5, 13 Apr–1 May; high count 3, 1 May 2019.

Mourning Dove (*Zenaida macroura*), total 78, 27 Mar–25 May; high count 7, 2 May 2019. As with the Band-tailed Pigeon, the extent to which these individuals represent local movements or migration is unclear.

Vaux's Swift (*Chaetura vauxi*), total 202, 13 Apr–2 May; high count 68, 2 May 2019. This species appears to be a major component of nonpasserine flight at Bear Divide in mid- to late April. Flights larger than the recorded high count seem likely.

Chimney Swift (*Chaetura pelagica*)/Vaux's Swift, 1, 2 May 2019.

White-throated Swift (*Aeronautes saxatalis*), total 73, 15 Apr–21 May; high count 13, 15 May 2019.

Black-chinned Hummingbird (*Archilochus alexandri*), total 26, 13 Apr–20 May; high count 13, 13 Apr 19. Many hummingbirds passing Bear Divide are not identifiable, but adult males of this species may be distinguished in flight by the distinctive sound made by their wings (Feo and Clunk 2010). Individuals later in the spring may be local breeders (Garrett and Dunn 1981).

Anna's Hummingbird (*Calypte anna*), total 39, 13 Apr–25 May; high count 21, 26 Apr 2020. Like those of other hummingbirds and local residents, this species' identification in flight and categorization of status are problematic.

Costa's Hummingbird (*Calypte costae*), total 43, 13 Apr–25 May; high count 5, 2 May 2019. A common breeder at Bear Divide, this species may also occur as a migrant.

Rufous Hummingbird (*Selasphorus rufus*), total 36, 27 Mar–15 May; high count 17, 13 Apr 2019. Many *Selasphorus* hummingbirds pass through Bear Divide unidentified. Because Allen's Hummingbird (*S. sasin*) is very rare on the north slope of the San Gabriel Mountains (Clark 2017) and we have not confirmed it at Bear Divide, the vast majority of *Selasphorus* hummingbirds at this site are likely to be Rufous.

Rufous/Allen's Hummingbird, total 15, 22 Apr–19 May; high count 4, 5 May 2020.

Unidentified hummingbird, total 81, 7 Apr–19 May; high count 40, 24 Apr 2020.

Western Sandpiper (*Calidris mauri*), 11, 23 Apr 2020.

Turkey Vulture (*Cathartes aura*), total 14, 23 Apr–25 May; high count 4, 25 May 2019. The extent to which these birds are migrants or local residents is unclear.

Sharp-shinned Hawk (*Accipiter striatus*), 1, 27 Mar 2020. Raptors in general seem to be sparse at Bear Divide, possibly because our effort has been slight in the afternoon when more raptors are likely to be aloft. More work is needed to ascertain whether raptors use this area for migration.

Cooper's Hawk (*Accipiter cooperii*), total 2, 24 Apr, 2 May.

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- Swainson's Hawk (*Buteo swainsoni*), 1, 27 Mar 2020.
- Red-tailed Hawk (*Buteo jamaicensis*), 21, 4 Apr–21 May; high count 2, 1 May 2019 and 2 May 2020.
- Lewis's Woodpecker (*Melanerpes lewis*), total 2, 29 Apr 2020. One bird moving through Bear Divide appeared to be a passage migrant.
- Acorn Woodpecker (*Melanerpes formicivorus*), total 47, 7 Apr–21 May; high count 9, 1 May 2019. These birds may be a mix of local residents and passage migrants. On some mornings, we have observed numbers of Acorn Woodpeckers flying north with other migrating birds.
- Downy Woodpecker (*Dryobates pubescens*), total 2, 22 and 26 Apr. Although the species is considered to be resident throughout its southern California range (Garrett and Dunn 1981), both Downy Woodpeckers that we observed appeared to be moving through the pass; we did not detect this species as a local resident on any other days.
- Nuttall's Woodpecker (*Dryobates nuttallii*), total 2, 1 and 17 May.
- Hairy Woodpecker (*Dryobates villosus*), total 4, 28 Apr–20 May; high count 1.
- Northern Flicker (*Colaptes auratus*), total 9, 7 Apr–21 May, high count 1.
- Unidentified woodpecker, total 3, 15–29 Apr, high count 1.
- American Kestrel (*Falco sparverius*), 1, 2 May 2020.
- Olive-sided Flycatcher (*Contopus cooperi*), total 12, 22 Apr–19 May; high count 2, 22 Apr 2020. Uncommon passage migrant.
- Western Wood-Pewee (*Contopus sordidulus*), total 30, 22 Apr–25 May; high count 5, 2 May 2020. Fairly common passage migrant.
- Willow Flycatcher (*Empidonax traillii*), 1, 21 May 2020. Fairly common but late migrant in the region, and the dearth of records at Bear Divide may simply be a function of reduced observer effort in late May and early June.
- Hammond's Flycatcher (*Empidonax hammondi*), total 11, 13–24 Apr; high count 5, 23 Apr 2020. In general, *Empidonax* flycatchers appear to be underrepresented at Bear Divide by comparison to localities nearby, especially desert migrant traps. Possibly they tend to move through vegetation rather than higher up and thus are missed by observers looking for birds in flight.
- Gray Flycatcher (*Empidonax wrightii*), total 12, 13–29 Apr; high count 4, 23 Apr 2020.
- Dusky Flycatcher (*Empidonax oberholseri*), 1, 23 Apr 2020.
- Hammond's/Dusky Flycatcher, total 2, 24 Apr, 2 May.
- Pacific-slope Flycatcher (*Empidonax difficilis*), total 30, 7 Apr–19 May; high count 10, 23 Apr 2020. The most common *Empidonax* flycatcher at Bear Divide was also the most vocal of the genus during our observations.
- Empidonax* sp., total 19, 22 Apr–14 May; high count 8, 23 Apr 2020.
- Black Phoebe (*Sayornis nigricans*), total 6, 7 Apr–8 May; high count 2, 8 May 2020.
- Say's Phoebe (*Sayornis saya*), total 2, 13 Apr, 5 May.
- Ash-throated Flycatcher (*Myiarchus cinerascens*), total 380, 7 Apr–25 May; high count 270, 23 Apr 2020. A common migrant in mid to late April, this species may move through Bear Divide later in the morning than other birds. On the day of the high count for this species, the majority passed through later in the morning, from about 07:30 to 08:15.
- Cassin's Kingbird (*Tyrannus vociferans*), total 39, 27 Mar–25 May; high count 8, 27 Mar 2020. At least one pair appears to be resident at the fire station, but flights of this species in late March appear to be regular migratory movements. This species is mostly resident in coastal southern California, so which breeding populations these birds represent is an open question.
- Western Kingbird (*Tyrannus verticalis*), total 586, 27 Mar–21 May; high count 203, 23 Apr 2020. Common migrant at dawn and through the morning.
- Cassin's Vireo (*Vireo cassinii*), total 296, 13 Apr–2 May; high count 135, 23 Apr 2020. Fairly common mid- to late April.

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Warbling Vireo (*Vireo gilvus*), total 1492, 7 Apr–21 May; high count 608, 26 Apr 2020.

Very common, some days one of the more common species.

Vireo sp., total 139, 23–29 Apr; high count 135, 23 Apr 2020.

Steller's Jay (*Cyanocitta stelleri*), total 4, 26 Apr–2 May; high count 2, 26 Apr 2020.

California Scrub-Jay (*Aphelocoma californica*), total 78, 27 Mar–21 May; high count 6, 7 Apr 2019.

American Crow (*Corvus brachyrhynchos*), total 4, 1–20 May; high count 2, 20 May 2019.

Common Raven (*Corvus corax*), total 90, 27 Mar–25 May; high count 13, 1 May 2019.

Mountain Chickadee (*Poecile gambeli*), 1, 24 Apr 2020.

Oak Titmouse (*Baeolophus inornatus*), total 6, 7 Apr–17 May; high count 3, 7 Apr 2019.

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), total 14, 15 Apr–19 May; high count 4, 22 Apr 2020. In general, swallow movements at Bear Divide appear limited to small numbers, possibly because our observations focused on the early morning and did not cover the full day.

Tree Swallow (*Tachycineta bicolor*), total 10, 27 Mar 2020.

Violet-green Swallow (*Tachycineta thalassina*), total 24, 15 Apr–20 May; high count 6, 2 May 2019.

Barn Swallow (*Hirundo rustica*), total 22, 15 Apr–19 May; high count 5, 22 Apr 2020.

Cliff Swallow (*Petrochelidon pyrrhonota*), total 16, 15 Apr–2 May; high count 8, 22 Apr 2020.

Bushtit (*Psaltiriparus minimus*), total 5, 27 Mar–21 May; high count 2, 27 Mar 2020.

Wrentit (*Chamaea fasciata*), total 61, 27 Mar–25 May; high count 5, 17 May 2016.

Ruby-crowned Kinglet (*Corthylio calendula*), total 7, 7 Apr–2 May; high count 2, 7 Apr 2019.

Red-breasted Nuthatch (*Sitta canadensis*), total 4, 24 Apr–2 May; high count 1.

White-breasted Nuthatch (*Sitta carolinensis*), total 6, 2–19 May; high count 4, 19 May 2016.

Blue-gray Gnatcatcher (*Poliophtila caerulea*), total 20, 13 Apr–20 May; high count 3, 29 Apr 2020.

Rock Wren (*Salpinctes obsoletus*), total 6, 23 Apr–20 May; high count 1.

Canyon Wren (*Catherpes mexicanus*), total 3, 7 Apr–19 May; high count 1.

House Wren (*Troglodytes aedon*), total 16, 27 Mar–19 May; high count 4, 7 Apr 2019.

Bewick's Wren (*Thryomanes bewickii*), total 12, 27 Mar–19 May; high count 2, 27 Mar 2020.

European Starling (*Sturnus vulgaris*), total 19, 15 Apr–21 May; high count 3, 23 Apr 2020.

California Thrasher (*Toxostoma redivivum*), total 31, 27 Mar–25 May; high count 4, 17 May 2016.

Northern Mockingbird (*Mimus polyglottos*), total 6, 22 Apr–5 May; high count 1.

Western Bluebird (*Sialia mexicana*), total 47, 27 Mar–21 May; high count 6, 27 Mar 2020.

Townsend's Solitaire (*Myadestes townsendi*), total 5, 27 Mar–29 Apr; high count 2, 23 Apr 2020. It is unclear whether these individuals were local birds moving short distances or true migrants moving longer distances.

Swainson's Thrush (*Catharus ustulatus*), total 52, 26 Apr–21 May; high count 24, 2 May 2020. *Catharus* thrushes seem less numerous than expected at Bear Divide, though this may be due to their more nocturnal migratory habits. Recording of night flight calls at this location would provide more insight into the abundance of thrushes in this area as spring migrants.

Hermit Thrush (*Catharus guttatus*), total 12, 15–26 Apr; high count 8, 23 Apr 2020.

Catharus sp., total 9, 28–29 Apr; high count 7, 28 Apr 2020.

American Robin (*Turdus migratorius*), total 4, 27 Mar–24 Apr; high count 2, 24 Apr 2020.

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- Cedar Waxwing (*Bombycilla cedrorum*), total 207, 27 Mar–21 May; high count 45, 11 May 2016.
- Phainopepla (*Phainopepla nitens*), 165, 22 Apr–21 May; high count 40, 11 May 2016. A regular migrant, especially in May. This species has been shown to make regular long-distance movements throughout western North America (Baldassarre et al. 2019), and our observations corroborate this result. These individuals may be moving between desert and woodland breeding areas.
- American Pipit (*Anthus rubescens*), 1, 23 Apr 2020.
- House Finch (*Haemorhous mexicanus*), total 158, 27 Mar–21 May; high count 20, 26 Apr 2020.
- Purple Finch (*Haemorhous purpureus*), total 20, 27 Mar–23 Apr; high count 18, 27 Mar 2020.
- Pine Siskin (*Spinus pinus*), total 6, 22 Apr–19 May; high count 2, 17 May 2016.
- Lesser Goldfinch (*Spinus psaltria*), total 231, 27 Mar–25 May; high count 25, 21 May 2020. Fairly common migrant, but at least some likely represent local movements.
- Lawrence's Goldfinch (*Spinus lawrencei*), total 487, 27 Mar–21 May; high count 75, 26 Apr 2020. Abundant migrant, but the extent to which individuals are moving locally or in migration is not understood.
- American Goldfinch (*Spinus tristis*), total 14, 22–23 Apr; high count 10, 22 Apr 2020.
- Chipping Sparrow (*Spizella passerina*), total 146, 7 Apr–15 May; high count 60, 22 Apr 2020.
- Brewer's Sparrow (*Spizella breweri*), 1, 24 Apr 2020.
- Black-chinned Sparrow (*Spizella atrogularis*), total 49, 4 Apr–25 May; high count 4, 8 May 2019.
- Lark Sparrow (*Chondestes grammacus*), total 59, 27 Mar–21 May; high count 6, 7 Apr 2019.
- Fox Sparrow (*Passerella iliaca*), total 3, 4–23 Apr; high count 1.
- Dark-eyed Junco (*Junco hyemalis*), total 9, 27 Mar–19 May; high count 3, 19 May 2016.
- White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), total 4, 7–13 Apr; high count 2, 7 Apr 2019.
- White-crowned Sparrow (subspecies uncertain), total 40, 27 Mar–29 Apr; high count 10, 22 Apr 2020.
- Golden-crowned Sparrow (*Zonotrichia atricapilla*), total 8, 7 Apr–1 May; high count 3, 13 Apr 2019.
- Lincoln's Sparrow (*Melospiza lincolni*), total 10, 7–23 Apr; high count 8, 23 Apr 2020.
- California Towhee (*Melospiza crissalis*), total 76, 27 Mar–21 May; high count 10, 17 May 2016.
- Rufous-crowned Sparrow (*Aimophila ruficeps*), total 23, 22 Apr–21 May; high count 6, 14 May 2020.
- Green-tailed Towhee (*Pipilo chlorurus*), 1, 23 Apr 2020.
- Spotted Towhee (*Pipilo maculatus*), total 55, 27 Mar–25 May; high count 6, 27 Mar 2020.
- Yellow-breasted Chat (*Icteria virens*), 1, 22 Apr 2020.
- Hooded Oriole (*Icterus cucullatus*), total 76, 13 Apr–21 May; high count 15, 26 Apr 2020. Uncommon migrant.
- Bullock's Oriole (*Icterus bullockii*), total 159, 13 Apr–21 May; high count 30, 26 Apr 2020. Breeds near Bear Divide but also a common migrant, especially in late April.
- Red-winged Blackbird (*Agelaius phoeniceus*), total 13, 27 Mar–2 May; high count 6, 1 May 2019.
- Brewer's Blackbird (*Euphagus cyanocephalus*), 2, 24 Apr 2020.
- Brown-headed Cowbird (*Molothrus ater*), total 5, 23–26 Apr; high count 2, 23 Apr 2020.
- Unidentified blackbird, total 3, 15–22 Apr; high count 2, 15 Apr 2020.
- Orange-crowned Warbler (*Leiothlypis celata*), total 641, 13 Apr–11 May; high count 200, 22 Apr 2020. Common migrant, mainly mid- to late April.

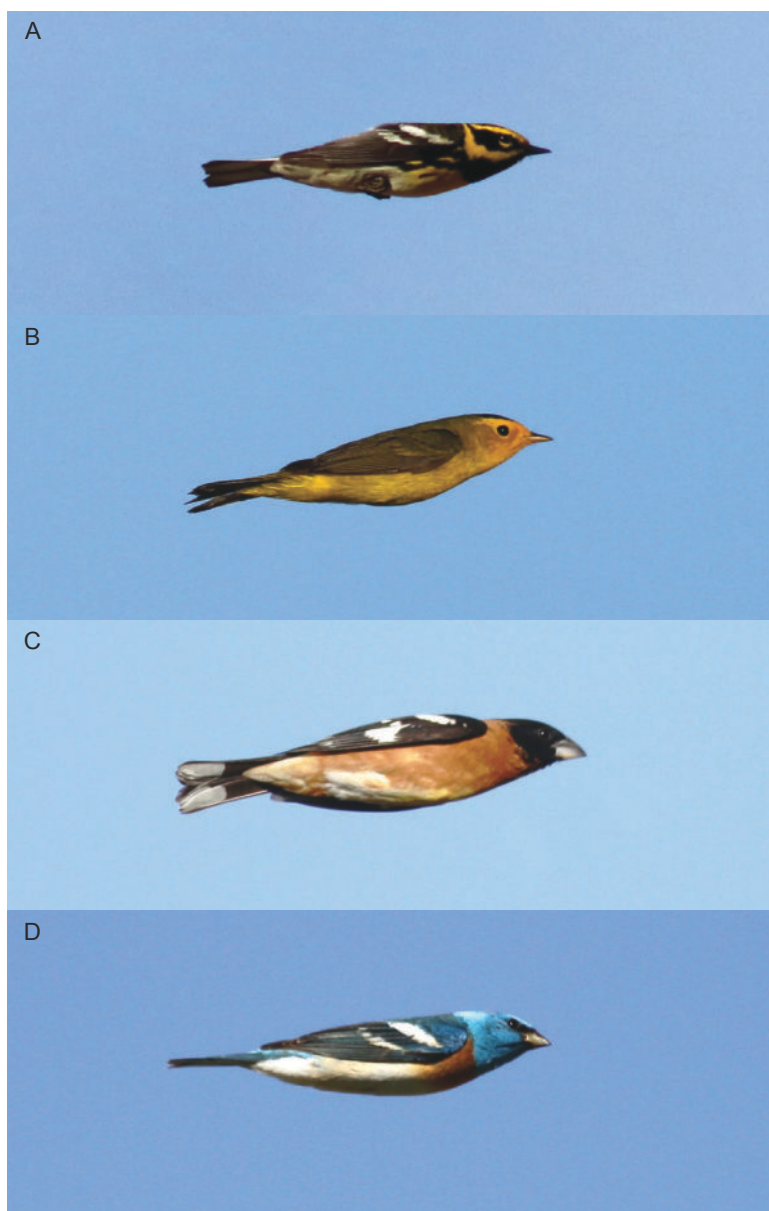


FIGURE 7. Four of the most numerous spring migrants passing over Bear Divide: (A) Townsend's Warbler (*Setophaga townsendi*), 2 May 2019; (B) Wilson's Warbler (*Cardellina pusilla*), 12 May 2021; (C) Black-headed Grosbeak (*Pheucticus melanocephalus*), 19 May 2021; (D) Lazuli Bunting (*Passerina amoena*), 29 April 2020.

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- Nashville Warbler (*Leiothlypis ruficapilla*), total 1352, 4 Apr–2 May; high count 400, 22 Apr 2020. Abundant migrant mid- to late April.
- MacGillivray's Warbler (*Geothlypis tolmiei*), total 11, 13 Apr–5 May; high count 2, 13 Apr 2019. Most individuals of this species were observed in vegetation, not flying over the divide like other warblers. Its skulking habits suggest that many stay under cover at Bear Divide and go undetected.
- Common Yellowthroat (*Geothlypis trichas*), total 3, 13 Apr–2 May; high count 1.
- Yellow Warbler (*Setophaga petechia*), total 715, 13 Apr–25 May; high count 230, 26 Apr 2020. This species appears to be relatively scarce at dawn flight locations along the immediate coast (Paul Lehman pers. comm.) and more common inland at sites like Butterbrecht Spring (Heindel 1991). The relative abundance of the Yellow Warbler at Bear Divide, especially in early May, hints at the site being connected to inland, rather than coastal, migratory movements.
- Yellow-rumped Warbler (*Setophaga coronata auduboni*), total 237, 27 Mar–2 May; high count 141, 13 Apr 2019. Common migrant late March and early April, uncommon through early May.
- Yellow-rumped Warbler (subspecies uncertain), total 787, 27 Mar–2 May; high count 300, 22 Apr 2020.
- Black-throated Gray Warbler (*Setophaga nigrescens*), total 1380, 4 Apr–11 May; high count 380, 26 Apr 2020. Fairly common migrant in April and early May; peak passage occurs slightly before that of Townsend's Warbler.
- Townsend's Warbler (*Setophaga townsendi*); Figure 7, 2087, 13 Apr–21 May; high count 760, 26 Apr 2020. Despite wintering locally, this species is a rather late migrant, with the main peak well after that of the Black-throated Gray Warbler, consistent with Townsend's more northerly breeding range.
- Hermit Warbler (*Setophaga occidentalis*), total 1570, 13 Apr–21 May; high count 608, 26 Apr 2020. Fairly common migrant in April and early May.
- Townsend's × Hermit Warbler (hybrid), total 2, 22 Apr, 5 May. Two individuals with clearly intermediate characters were well photographed, suggesting that this hybrid may be more common within the large numbers of poorly seen warblers moving across the divide.
- Wilson's Warbler (*Cardellina pusilla*); Figure 7, total 4954, 27 Mar–21 May; high count 1920, 23 Apr 2020. The most abundant migrant at Bear Divide, both in total numbers and on most individual days from mid-April to mid-March. Ruegg et al. (2014) found that in the West, southerly breeding populations move through migratory sites earlier in the spring, followed later by more northerly breeding populations.
- Unidentified warbler, total 14,272, 4 Apr–25 May; high count 7436, 23 Apr 2020.
- Summer Tanager (*Piranga rubra*), 1, 20 May 2019. A rare local breeder (*P. r. cooperi*) that also occurs regularly as a migrant to California at this time (*P. r. rubra*); we do not know from which population this individual originated.
- Western Tanager (*Piranga ludoviciana*), total 3004, 13 Apr–21 May; high count 800, 22 Apr 2020. Abundant migrant at the divide through much of the period of spring movement.
- Black-headed Grosbeak (*Pheucticus melanocephalus*), total 1259, 7 Apr–25 May; high count 500, 22 Apr 2020. Common migrant.
- Blue Grosbeak (*Passerina caerulea*); Figure 7, total 5, 26 Apr–5 May; high count 1. Rare.
- Lazuli Bunting (*Passerina amoena*), total 1998, 7 Apr–25 May; high count 608, 26 Apr 2020. Common migrant.
- Unidentified passerine, total 3927, 4 Apr–14 May; high count 1487, 23 Apr 2020.

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BURROWING OWLS PRODUCE SECOND BROOD IN MOUNTAIN VIEW, CALIFORNIA

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Western Burrowing Owls (*Athene cunicularia hypugaea*) are capable of laying up to 12 eggs in a single clutch (Haug et al. 1993). If the first nest attempted in a season fails, the female often lays a replacement clutch (Thomsen 1971, Wedgewood 1976). But rearing of a second brood after the fledging of a first brood (double brooding) is uncommon in this species (Millsap and Bear 1990, Gervais and Rosenberg 1999). In 2020, after 23 years of continuous monitoring of Burrowing Owls nesting around the southern periphery of San Francisco Bay at Shoreline Regional Wildlife Area in Mountain View, Santa Clara County, California, we confirmed double brooding for the first time. The Burrowing Owls were being supplementally fed with mice to assess whether such feeding during the breeding season increases their reproductive success; this experiment may have resulted in the double brood. However, this instance of double brooding occurred three years after supplemental feeding commenced.

Shoreline Regional Wildlife Area is a closed landfill, posing management issues for a species such as the Burrowing Owl because the decomposition of the trash causes the ground to subside. The subsequent repairs of the cap of clay sealing the landfill destroy California Ground Squirrel (*Otospermophilus beecheyi*) burrows that are critical for the owls' survival (Haug et al. 1993). To mitigate for the continuing loss of squirrel burrows, we install artificial burrows consisting of an irrigation valve box for the nest chamber and a 6-foot-long flexible drainage pipe to simulate the burrow tunnel. These artificial burrows have proven very successful. During the 2020 breeding season, six of the eight breeding pairs at Shoreline successfully nested in artificial burrows.

The pair of Burrowing Owls that double brooded in 2020 used two different nests. Every breeding season, we have observed some pairs at our study sites abandon a nest after 28–30 days of an unsuccessful attempt, then move to a new nest burrow, renest, and successfully produce nestlings. From our field observations of nesting materials and decoration at the burrow entrance, food delivery by the male to the female, and the female remaining underground for several weeks, we presumed the female in these failed first nests was incubating eggs.

In 2017, we started a supplemental-feeding study in which we fed Burrowing Owl pairs at two of our four study sites, to allow for comparison of the success of supplementally fed pairs and unfed pairs. The sites other than Shoreline Regional Wildlife Area are the Ames Research Center at Moffett Field, the San Jose–Santa Clara regional wastewater facility in Alviso, and the Warm Springs Unit of Don Edwards San Francisco Bay National Wildlife Refuge, all around the south end of San Francisco Bay (Table 1). The Burrowing Owl pairs were fed with fourteen dead mice, over two feedings per week, for the duration of the breeding season, April to August of each year. On the basis of the initial success of the supplemental-feeding study (100% nest success and largest number of chicks fledged since 2004) and the Burrowing Owl's continuing decline in the region, we decided to supplementally

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TABLE 1 Numbers of Burrowing Owls Monitored around South San Francisco Bay

Site	Study period	Total number of adults	Total number of breeding females/pairs	Minimum number of breeding females/pairs in a year	Maximum number of breeding females/pairs in a year
NASA Ames Research Center at Moffett Field	1998–2020 (23 seasons)	679	323	2 (2020)	30 (1999)
San Jose–Santa Clara Regional Wastewater Facility bufferlands in Alviso	2015–2020 (6 seasons)	122	57	3 (2020)	17 (2017)
Don Edwards San Francisco Bay National Wildlife Refuge, Warm Springs Unit	2015–2020 (6 seasons)	36	15	0 (2020)	4 (2016 & 2017)
Shoreline Regional Wildlife Area in Mountain View	1998–2020 (23 seasons)	250	125	1 (2019)	12 (2000)
Total		1087	520		

feed all breeding Burrowing Owls in 2019. Results include the largest brood in over 22 years at one site and a 100% nest-success rate at another site, which we had never observed prior to the supplemental-feeding study. Therefore, it is possible that supplemental feeding stimulated this double brooding.

Since 2012, we have banded each captured owl with a U.S. Geological Survey band on the right leg and pop-riveted an Acraft colored band bearing a unique alphanumeric code on the left leg, allowing us to distinguish resident, migratory, and supplemented/relocated owls. We surveyed the colony at Shoreline Regional Wildlife Area weekly, year round, collecting data on pair formation, longevity, breeding success, and patterns of movement within the colony and to additional sites in Santa Clara County and adjacent counties. At least monthly, we used binoculars, spotting scopes, or a long-lens camera to identify individuals by resighting the color and code on their Acraft bands. Motion-activated cameras, banding, and trapping with one-way-door bubble traps or bow nets during the breeding season allowed for identification of banded owls and recording of biometric data.

The successful pair that double brooded had been banded previously, allowing us to assess their breeding success over several years. The life history of this pair, female 5C (red-over-blue) and male 7R (red-over-blue), is as follows. In June 2014, we banded 7R as a fledgling at Shoreline from a brood of two young. From 2015 to 2018, remaining at Shoreline, he paired up with a different female each breeding season. In 2015 and 2017, no young were produced. In 2016, male 7R formed an incestuous relationship with his mother 6U (red-over-blue) and produced four young. From 2018 to 2020, male 7R paired up with female 5C and successfully produced young for three consecutive seasons. In June 2018, we banded female 5C as an adult at Shoreline. The pair fledged six young in 2018 and six young in 2019, both years nesting in a complex of artificial burrows (#245).

In 2020, 7R and 5C paired up for the third consecutive season, this time using a different artificial burrow complex (#246), 68 meters from #245, first raising three young. Young were first observed on 18 May outside the entrance of #246, where a motion-activated camera photographed three fledglings on 19 May (Figure 1). On

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FIGURE 1. Female 5C with her three nestlings (14–22 days old) at nest #246 on 19 May 2020.

26 May, we observed both adults at burrow location #245 where they had nested during 2019. By 27 May, the adults had moved their young to burrow #245. On 28 May, we banded two of the three fledglings from nest #246 at location #245.

On 3 June, we observed nest decoration, nesting material, and one adult at artificial burrow complex #243, a distance of 55 meters from location #245. Then, on 23 July, both banded adults and a single nestling were observed at nest #243; the motion-activated camera photographed one young approximately 14 days old there on 24 July (Figure 2). On 3 August, we banded a 24-day-old fledgling. On 17



FIGURE 2. Second brood observed on 24 July 2020 with male 7R and unbanded nestling at nest #243.



FIGURE 3. Fledgling 2P from second brood (nest #243) identified at nest #246 on 17 August 2020.

August, we observed that male 7R and the banded fledgling, approximately 38 days old, had relocated a distance of 116 meters and returned to nest #246 (Figure 3). That only one young fledged in the second brood compared to three young in the first brood is a difference consistent with other studies of double brooding that have found the second brood tends to be smaller. Catlin and Rosenberg (2007) found a trend of decreasing clutch size with successive renesting attempts of Burrowing Owls in California.

Dietary limitations can impair the Burrowing Owl's reproductive success (Wellcome et al. 2013, Haley and Rosenberg 2013). On the basis of pellet analysis and remains of prey collected at burrows, including those at Shoreline Regional Wildlife Area, Trulio and Higgins (2012) found that 98% of the diet of Burrowing Owls in the south San Francisco Bay area consisted of invertebrates, the Dermaptera being the order of insects most frequently recorded, representing 48.6% of all prey items by total number.

A diet low in rodents can depress the Burrowing Owl's reproductive success (Haley 2002, York et al. 2002, Rosenberg and Haley 2004). This situation, plus the Burrowing Owl usually catching only one prey item at a time, may be reducing the owls' reproductive success at Shoreline. Hence the purpose of the supplemental feeding study is to increase productivity. Preliminary results of the continuing supplemental-feeding study have been positive, with fed pairs producing twice as many young as unfed pairs. Haley (2002) also reported an increase in productivity of supplementally fed Burrowing Owls, and Wellicome (1992) reported supplementally fed females to lay more eggs and hatch more young than did those not supplementally fed.

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CHARACTERISTICS OF NESTS OF BELDING'S SAVANNAH SPARROW AT ESTERO PUNTA BANDA, MÉXICO

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Belding's Sparrow (*Passerculus sandwichensis beldingi*) is one of the 17 currently recognized subspecies of the Savannah Sparrow (Wheelwright and Rising 2008). It can be found in saltmarshes from Point Conception, California, to the estuary of Arroyo El Rosario, Baja California (Van Denburgh 1924, Zembal et al. 1988, Wheelwright and Rising 2008) and since 1974 has been designated as endangered by the California Department of Fish and Wildlife. Bradley (1994) suggested that this subspecies is largely isolated, with a low capability for dispersal, and Powell and Collier (1998) found no movement in or out of a marsh on San Diego Bay isolated by only 0.5 km from the next nearest marsh.

Here we describe the nests and habitat of Belding's Sparrow at Estero Punta Banda, Ramsar site no. 1604 (31° 44' N, 116° 37' W), in Baja California, México. This is a wetland with 300 ha of salt marshes on the Pacific coast, 13 km south of Ensenada.

From May to July of 2017, 2018, and 2019, Moreno-Higareda monitored Belding's Sparrow nests at Estero Punta Banda from 06:30 to 10:30 every third day during the reproductive season for a total of 120 hours/year over 30 days/year, covering 13 of 72 ha (18%) of the marsh available for nesting. Although around San Diego Belding's Sparrow begins nesting as early as 15 March (Unitt 2004, egg collections in the Western Foundation of Vertebrate Zoology, Camarillo, California), we found no evidence of nests before May; neither did we observe young of the year during our first observations. Our search efforts follow the dates reported by Zembal et al. (1988) and local nesting dates obtained from casual observations since 2014.

All nests found were on mounds above high tide levels, helping guide our searches. During this study we found 36 nests: three in 2017, 14 in 2018, and 19 in 2019. Overall, five nests were lost to high tides. Massey (1979) and Powell and Collier (1998) reported that these birds prefer to nest in middle and high marshes, building their nests in vegetation whose base may be flooded at high tide. The availability of high marsh that is currently rarely if ever flooded could prove critical to Belding's Sparrow in the future as sea levels are on the rise worldwide. At present we have no detailed maps of the highest points around Estero Punta Banda that could become the only suitable nesting habitat.

In Estero Punta Banda, where the most dominant and conspicuous plants are the pickleweeds *Salicornia pacifica* and *S. bigelovii* and the cordgrass *Spartina foliosa* (Delgadillo et al. 1992), nests were also built near saltwort (*Batis maritima*), Western Marsh Rosemary (*Limonium californicum*), Marsh Jaumea (*Jaumea carnosa*), Estuary Seablite (*Suaeda esteroa*), and Salt Marsh Bird's Beak (*Chloropyron maritimum maritimum*). No nests were recorded near or in a plant foreign to the salt marsh. Most invasive plants are above the higher marsh, and their cover in the marsh area is <

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3%. Notably, Belding's Sparrows used the same nesting sites from year to year, at the same spot. Whether the same pairs reoccupy nesting sites or the sites are determined and limited by their availability above the level of the high tide are questions to be answered in the future. On the San Benito Islands, Salinas-Ortiz et al. (2015) found nests of Savannah Sparrows of subspecies *sanctorum* reoccupied for a second time during the same reproductive season.

All nests found at Estero Punta Banda were consistently wineglass-shaped and built with dry material from the native grasses, desert saltgrass (*Distichlis spicata*) and California cordgrass (*Spartina foliosa*). Nests have a thick exterior layer attached to the various supporting plants. The nests' inner lining was of thinner material, forming a small disc at the bottom. Marbled Godwit (*Limosa fedoa*) feathers lined one nest, and other species' feathers were found in other nests (Figure 1). Salinas-Ortiz et al. (2015) reported gull feathers in the nests in the San Benito Islands; both subspecies used materials readily available locally. We found no human-made material in the nests at Estero Punta Banda (e.g., no synthetic fibers). All nests were placed between 5 and 18 cm from the ground. The mean exterior diameter was close to 7 cm, similar to that of Savannah Sparrow nests reported by Dixon (1972) for the Bay of Fundy, New Brunswick. Salinas-Ortiz et al. (2015) reported a mean internal diameter of 6.48 cm for three nests of *P. s. sanctorum* archived at the Universidad Autónoma de Baja California, Ensenada.

The nest characteristics are shared with subspecies *alaudinus*, found north of Point Conception to Humboldt Bay (Wheelwright and Rising 2008) and with sub-



FIGURE 1. Sequence of construction of a Belding's Sparrow nest at Estero Punta Banda. (1) Small disk used as the base for the whole nest. Over this, a wineglass-shaped nest is interwoven with nearby vegetation, and (2) lined with feathers, here Marbled Godwit (*Limosa fedoa*), but other species' feathers have been observed. (3) The eggs are laid in the shadow of dwarf saltwort (*Salicornia bigelovii*), and the nest is woven with blades of desert saltgrass (*Distichlis spicata*) and California cordgrass (*Spartina foliosa*). This nest had a diameter of 9 cm and was 20 cm above the ground.

Photos by Hiram Moreno-Higareda

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species *rostratus* from the Colorado River delta. This last subspecies uses Palmer's grass (*Distichlis palmeri*), abundant in the area, but its nests lack an inner lining (Bancroft 1927). Dixon (1972) mentioned that Savannah Sparrow nests in the Bay of Fundy contained "a few feathers."

At Estero Punta Banda, the Belding's Sparrow lays one to four eggs; the mean clutch size is 3.06 ± 0.05 [s.d.] eggs. The incubation period is 13 days; chicks stay in the nest 7–11 days. Only females incubate, regulating nest temperature (Davis et al. 1984); chick care in this subspecies is biparental.

Publications on nesting habits for the subspecies in California are abundant: Bradley (1973), Massey (1979), Zembal et al. (1988), Powell (1993), and Powell and Collier (1998), but we found no published literature for Baja California, México.

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FIRST RECORD OF THE LONG-TAILED DUCK FOR COAHUILA, MEXICO

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The Long-tailed Duck (*Clangula hyemalis*) is a distinctive sea duck that breeds on high arctic coasts and tundra of both the eastern and western hemispheres. In North America, it winters south along the Pacific coast to California and along the Atlantic coast to northern Florida. In the interior of the continent, it winters regularly in large numbers on the Great Lakes (AOU 1998, Robertson and Savard 2002). The species occurs in migration or winter in all states of the continental U.S., including south to the Gulf of Mexico from Florida to Texas, and across the interior of the border states of Texas, New Mexico, Arizona, and California, where rare but annual in occurrence (AOU 1998, <https://eBird.org>).

The Long-tailed Duck was historically known in Mexico only from coastal areas in the northwest, primarily in the Gulf of California, where first reported in 1926 (Huey 1927). In the gulf it was historically rare, but records extend south to Sinaloa and Jalisco (Howell and Webb 1995); Mexico's first and still only specimen (an unsexed juvenile, number 4777 deposited in Humboldt State University Museum, Arcata, California) was collected on 27 December 1979, 15 km southwest of Guamúchil, Sinaloa (Kramer 1982). Russell and Monson (1998) and Erickson et al. (2001) added four additional records for the states of Sonora and Baja California through the 1990s, and Erickson et al. (2013) added a record from Bahía de los Angeles, Baja California, in 2006. Over the past two decades, however, reports have increased considerably in that region; since 2000, there have been at least 14 records along both coasts of the Baja California Peninsula south to Loreto, where photographed 24–28 December 2017 (<https://eBird.org/checklist/S41326540>), representing the first well-supported record for Baja California Sur. Furthermore, seven records in eBird since the 1990s in coastal Sonora south to Bahía Santa Rosa, Isla Tiburón (Rojas-Soto et al. 2002) include observations of groups of up to six birds (at Golfo Santa Clara; <https://eBird.org/checklist/S82628948>).

During field work in northern Coahuila on 23 November 2013, we photographed a winter-plumaged female Long-tailed Duck (Figure 1). The site (28° 05' 02.3" N, 101° 37' 45.9" W, elevation 505 m) was a small pluvial lake (45 m long and 13 m wide) located along state highway 20, 25 km north-northwest of the town of Melchor Múzquiz. The duck was initially seen feeding close to shore, but as we approached it swam out to the center of the puddle. Other waterbirds there were two Greater Scaup (*Aythya marila*) and a Pied-billed Grebe (*Podilymbus podiceps*). The previous records of the Long-tailed Duck nearest our sighting are of single individuals

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FIGURE 1. Long-tailed Duck 25 km north-northwest of Melchor Múzquiz, Coahuila, México, 23 November 2013

Photos by Hugo González-Páez

photographed in the Rio Grande valley at Laredo, Texas, 17 December 2016 (<https://ebird.org/checklist/S33057392>) and in the trans-Pecos region of Texas at Marathon 7 December 2013 (<https://ebird.org/checklist/S15883753>). Also, according to the records taken from eBird, from 1972 to 9 August 2021, there were 11,260 observations of the species between the USA and Mexico; all of those between latitudes of 26° and 31° N represent occurrences during fall migration and winter. Mexico and Texas together account for 2633 sightings; of these, 567 are from Mexico and the border counties of Texas. Therefore, we consider that our record does not represent a vagrant or accidental; more field studies are required in order to define the regularity of this species in Mexico.

To the best of our knowledge, this constitutes the first record of the Long-tailed Duck for the state of Coahuila. In addition, it appears to be the first record for anywhere in interior Mexico and the easternmost record for the country and the first located in the Atlantic drainage.

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FIRST DOCUMENTED BREEDING OF THE BLACK-HEADED GROSBEAK IN ALASKA

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The Black-headed Grosbeak (*Pheucticus melanocephalus*) breeds regularly across much of western North America from Oaxaca north to southern British Columbia and from the Pacific coast to central Nebraska (Ortega and Hill 2010). The northern limit of the species' range has expanded steadily in British Columbia since the 1940s (Campbell et al. 2001, Martell 2015). Here we report the first documented instance of the Black-headed Grosbeak breeding in Alaska.

During a six-day trip exploring the lower reaches of the Stikine River and its tributaries, we discovered two adult male Black-headed Grosbeaks and a lone fledgling on 28 June 2020 (Figure 1). All sightings occurred within 8 km of the international border. We detected the first adult male 1.2 km west of the Alaska–British Columbia border along the banks of the Kikahe River in a woodland dominated by alder (*Alnus* sp.) and willow (*Salix* sp.) with widely spaced mature Sitka spruce (*Picea sitchensis*). We found the second adult male 3.6 km from this location on the north side of the Stikine River in a dense *Alnus*–*Salix* thicket with dispersed mature spruce along Guerin Slough. Farther downriver we found a fledgling 1.5 m above the bank and 5 m above the river in a dense thicket of *Alnus*, *Salix*, and salmonberry (*Rubus spectabilis*) overhanging the Ketili River (56.6783° N, 131.9565° W; Figure 2). The fledgling remained motionless while giving an incessant “*phoe-oo*” call, which is characteristic of juveniles from just before fledging to independence (Ortega and Hill 2010; Figure 3). We watched the bird for 30 min waiting for a food delivery, but no deliveries were observed. The flight feathers of both the wing and tail were still growing, indicating that the bird was not yet capable of sustained flight and that the nest was likely nearby. While distinguishing the juvenile Black-headed from the juvenile Rose-breasted Grosbeak (*P. ludovicianus*) can be difficult, the rufous-orange breast, faint to no streaking on the central breast feathers, and very fine streaking along the flanks point to the Black-headed.

The first sighting of a Black-headed Grosbeak in Alaska was at Middleton Island in late September 1981 (Gibson 1982), followed by a singing male along the Stikine River on 30 June 1996 (Tobish 1996). Since 1996, the species has been a rare visitant to southeast Alaska with records annual since 2001 (Tobish 2003, 2011, <https://eBird.org>). The Black-headed Grosbeak is listed as rare (annual or possibly annual in small numbers) in the 27th edition of the Checklist of Alaska Birds (Gibson et al. 2021). Along the Stikine River, Black-headed Grosbeaks were recorded by the North American Breeding Bird Survey (Pardieck et al. 2020) in 4 of 15 years dating back to 1998. The only Alaska specimen (Univ. Alaska Museum) was collected in September 1996 at Petersburg (Gibson and Kessel 1997), 40 km northwest of the mouth of the Stikine. Extralimital records in summer extend as far north as Anchorage, in fall as far west and north as Kodiak Island, Shageluk, and St. Lawrence Island (Tobish 2002, 2006, 2017).

While the Black-headed Grosbeak's range has expanded northward and the species now occurs more regularly in Alaska, it had not been recorded breeding in the state. A similar pattern of range expansion without subsequent breeding records also occurred in coastal British Columbia (Campbell et al. 2001). Prior to our discovery,

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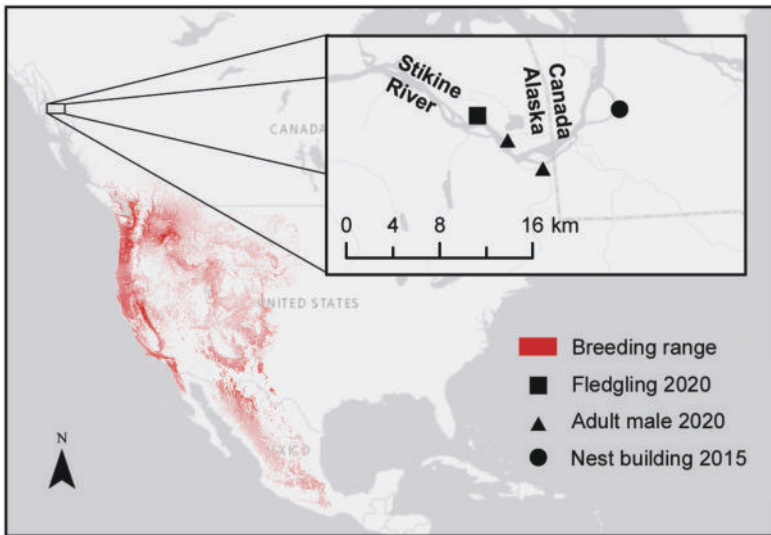


FIGURE 1. Locations of sightings of adult and fledgling Black-headed Grosbeaks along the Stikine River in 2020 and of adult carrying nest material in 2015, in context of the species' breeding range (Fink et al. 2020).



FIGURE 2. Fledgling Black-headed Grosbeak (*Pheucticus melanocephalus*) along the Stikine River in southeast Alaska on 28 June 2020. This photograph represents the first documentation of breeding of the Black-headed Grosbeak in Alaska.

Photo by Zachary Pohlen

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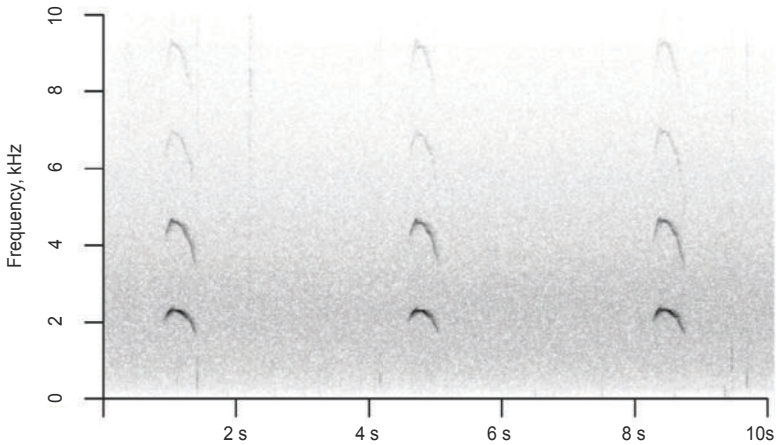


FIGURE 3. Spectrogram of calls of the Black-headed Grosbeak fledgling along the Stikine River in southeast Alaska on 28 June 2020 (macaulaylibrary.org/asset/248168031).

nest building had been observed ~12 km away in adjacent British Columbia, where a female was seen carrying the hair of a moose (*Alces alces*) in 2015 (B. Sampson, <https://ebird.org/checklist/S23777545>).

This first record of the Black-headed Grosbeak breeding in Alaska provides a marker for this species' possible continued range expansion in the state. Occurrences north of the species' normal breeding range have been recorded increasingly since the late 1940s in British Columbia and since 1980s in Alaska. These, along with our observation, parallel northward range expansions experienced by other species due to climate change (Parmesan and Yohe 2003). The major rivers of southeast Alaska were likely sites for a first breeding attempt. For many species, these rivers, of which the Stikine is the largest, act as routes of unencumbered dispersal between interior Canada and coastal Alaska (Johnson et al. 2008). It is also possible that increased ornithological coverage in these large remote river systems could yield more first breeding records for Alaska of other inland breeding species.

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BOOK REVIEW

Birdpedia: A Brief Compendium of Avian Lore, by Christopher W. Leahy. 2021. Princeton University Press, Princeton, NJ. 272 pp.; hardbound with black and white sketches. \$16.95. ISBN978-0-691-20966-1.

Having spent parts of my life in the worlds of academic biochemistry, the medical device business, and ornithology, I know only too well how much those who dwell in these fields love to use jargon. In some cases, the jargon provides a more succinct way to describe an observation (it is easier to say that the Common Nighthawk is largely crepuscular than to say it is most active in the twilight of evening and early morning). On the other hand, if you saw a Bald Eagle steal a fish from an Osprey, you are just showing off if you insist, in polite conversation, on saying that the eagle kleptoparasitized the Osprey. Use of such terms can create a barrier to those just getting interested in birds and ornithology. Leahy's earlier tomes, *The Birdwatcher's Companion* (1982) and *The Birdwatcher's Companion to North American Birdlife* (2004), provided a source for those of all levels of interest to translate our ornithological jargon into plain English. These books also provided a fairly exhaustive treatment of many aspects of the field, including the history and personalities that shaped ornithology in North America. In many ways, one can consider *Birdpedia* a "sampler" from those larger books. Indeed, in his preface Leahy refers to this book as a "teaser," with the intent to turn a "nagging curiosity into a compelling fascination ... with the natural world." In this sense, the target reader is likely someone who birds and is becoming more interested in understanding the world of birds more broadly and deeply.

This is not to say that even one relatively steeped in ornithology might not learn some new things from this book. Did you know that most hawks and owls tend to be left-handed (or, rather, "left-footed")? However, *Birdpedia* is likely to be of more value to someone listening to birders refer to "caching," or "brood parasitism," and wanting to understand these terms. And yes, the book defines crepuscular and kleptoparasitism, though the latter is buried under the term "piracy" in this alphabetically arranged format (an index would have been a very useful addition). *Birdpedia* goes beyond defining terms and explains many aspects of avian behavior, elegantly summarizing the most recent findings in many areas of ethology. In spite of the condensed form of this book, Leahy gives outstanding and surprisingly thorough reviews of aspects of bird navigation and evolution.

I enjoyed his short bios of important names in ornithological history, including some often overlooked contributors such as Florence Merriam Bailey. And I was very pleased to see that Leahy and I are in full agreement that Alexander Wilson is "even more deserving than Audubon of the title of Father of American Ornithology."

While understanding that the book's intent is to give one just a taste, I still often found myself perplexed by what was included and what was omitted. For example, Leahy defines contour feathers, down, filoplumes, and vibrissae, but nowhere could I find definitions of even more commonly used terms for plumage such as primaries, secondaries, tertials, or rectrices.

All in all, while it isn't for everyone, I recommend *Birdpedia* for those who are finding themselves with a growing interest in, and curiosity about, ornithology. I think that may describe many WFO members, or those who might find themselves on the gift lists of WFO members.

Edward R. Pandolfino

THANKS TO *WESTERN BIRDS*' REVIEWERS AND ASSOCIATE EDITORS

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Philip Unitt

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Photo by © Glen Hvenegaard of Camrose, Alberta, Canada:

Purple Martin (*Progne subis*), Camrose, Alberta, Canada, 17 June 2012—during the annual Camrose Purple Martin Festival, where nature enthusiasts learn about wildlife conservation and becoming an effective martin landlord.

As they report in this issue of *Western Birds*, Carolyn A. Cook, Glen T. Hvenegaard, Geoffrey L. Holroyd, Hardy Pletz, and Myrna Pearman investigated the dispersal of the Purple Martin in central Alberta and across Canada east of the Rocky Mountains more generally, on the basis of recapture of 153 birds of known sex banded in central Alberta and 38 recoveries of banded birds of known sex elsewhere in Canada. At the age of one year, half of the birds returned to their natal colony, half relocated elsewhere.

But among older birds, especially females, the proportion returning to the natal colony was higher. Distances of dispersal of martins at least two years old were greater than those of yearlings, implying that among the older martins that do not return to their natal colony, site fidelity to the new colony is incomplete.

