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WINTERING AREAS AND MIGRATION CHARACTERISTICS OF SWAINSON'S HAWKS THAT BREED IN THE CENTRAL VALLEY OF CALIFORNIA

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ABSTRACT.—We used satellite telemetry during 2011–2015 to identify and characterize wintering areas and migration patterns of Swainson's Hawks (*Buteo swainsoni*) that bred in California's Central Valley. Twenty tracked hawks wintered across 7500 km from western Mexico to central South America. Wintering areas in Mexico, Central America, and central South America were dominated by agriculture and in northern South America by shrub-scrub. All hawks followed similar migration routes, through the interior of California, Sonoran Desert, and western Mexico, with some continuing through Central America to South America. Compared to northerly wintering birds, birds wintering farther south spent more time in migration, flew greater distance per day during southward (but not northward) migration, spent less time in wintering areas, and arrived later at the breeding area. Central Valley birds substantially used stopover areas ($\bar{x} = 53$ d/individual) during southward migration but returned more directly from wintering to breeding areas ($\bar{x}=0.3$ stopover d/individual). Most stopovers occurred in western Mexico and the San Joaquin Valley, California. Land cover in stopover areas was dominated by agriculture and shrub-scrub. Use of varied wintering areas that have been altered from native habitat may indicate that migratory and wintering patterns have changed for this population. Advantages of using northern wintering areas may include less time spent in migration and earlier arrival in breeding areas. The diversity of wintering areas may provide resilience from effects of human activities compared to collective wintering in one area. Central Valley Swainson's Hawks' migration routes and wintering areas differ markedly from those of the rest of the species' North American population.

KEY WORDS: *Swainson's Hawk*; Buteo *swainsoni*; *Central Valley*; *conservation*; *migration*; *stopover habitat*; *wintering habitat*.

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ÁREAS DE INVERNADA Y CARACTERÍSTICAS DE LA MIGRACIÓN DE INDIVIDUOS DE *BUTEO SWAINSONI* QUE CRÍAN EN EL VALLE CENTRAL DE CALIFORNIA

RESUMEN.—Usamos telemetría satelital durante 2011–2015 para identificar y caracterizar las áreas de invernada y los patrones migratorios de individuos de *Buteo swainsoni* que crían en el Valle Central de California. Veinte individuos rastreados invernaron a lo largo de 7500 km, desde el oeste de México hasta el centro de Sudamérica. En México, Centroamérica y el centro de Sudamérica *B. swainsoni* invernó principalmente en áreas agrícolas, mientras que en el norte de Sudamérica lo hizo en áreas de matorral. Todos los individuos utilizaron rutas migratorias similares a través del interior de California, el Desierto de Sonora y el oeste de México, con algunos individuos continuando a través de Centroamérica y Sudamérica. A diferencia de las aves que invernaron al norte, aquellas que lo hicieron más al sur estuvieron más tiempo migrando, volaron distancias mayores cada día al migrar hacia el sur (pero no hacia el norte), pasaron menos tiempo en las áreas de invernada y arribaron más tarde al área de cría. Las aves del Valle Central usaron asiduamente las áreas de parada ($\bar{x}=53$ d/individuo) durante la migración hacia el sur, pero retornaron a sus áreas de cría en forma más directa ($\bar{x}=0.3$ paradas d/individuo). La mayoría de las paradas se dieron en el oeste de México y en el Valle de San Joaquín, California. La cobertura del suelo en las áreas de parada estuvo dominada por agricultura y matorrales. El uso de una variedad de áreas de invernada en ambientes naturales alterados puede indicar que los patrones migratorios y de invernada han cambiado para esta población. Las ventajas de invernar en las áreas ubicadas al norte incluirían un menor gasto de tiempo en migración y un arribo temprano a las áreas de cría. El uso de áreas de invernada diversas puede indicar resiliencia a los efectos de las actividades humanas, en comparación con una invernada colectiva en una sola área. La ruta migratoria y las áreas de invernada de *B. swainsoni* en el Valle Central varían considerablemente en relación al resto de su población norteamericana.

[Traducción del equipo editorial]

The Swainson's Hawk (*Buteo swainsoni*) breeding population in California's Central Valley (CV) is spatially disjunct from other populations that breed in open country in the rest of western and central North America (Hull et al. 2008, Bechard et al. 2010). Throughout their range, Swainson's Hawks primarily forage in open lands that support higher densities of suitable prey species (mainly rodents, but also large insects and birds) and low vegetation structure that provides suitable access to prey (Bechard 1982, Estep 1989, Woodbridge 1991, Babcock 1995, Bechard et al. 2010), particularly in agricultural areas (Swolgaard et al. 2008, Estep 2009, Estep and Dinsdale 2012). California's Central Valley population decreased substantially during the 20th century as a result of conversion of grassland and suitable agricultural foraging habitats to unsuitable crops and development, loss of tree nesting habitat, pesticide mortality in migration and wintering areas, and shooting (Bloom 1980, Battistone et al. 2016). The species was listed as Threatened under the State of California's Endangered Species Act in 1983. Most of the current California population is concentrated in the central portions of the CV (Anderson et al. 2005, Battistone et al. 2016). Swainson's Hawks that nest in the CV spend about six months of the year (mid-September to mid-March) in migration and wintering areas (Bechard et al. 2006, 2010).

Movements of Swainson's Hawks that breed in western and central North America outside of the CV (hereafter "Great Basin–Great Plains" populations) migrate to spend the northern hemisphere winter (i.e., austral summer) in central Argentina (Houston 1990, Fuller et al. 1998, Kochert et al. 2011). This has led to the general characterization that all or nearly all Swainson's Hawks winter in southern South America (e.g., Newton 1979, Bechard et al. 2010, Dunn 2017). Some sources have noted wintering by the species in Brazil, Columbia, Central America, and along the Pacific slope of Mexico north of Narayit (Bechard et al. 2010, Clark and Schmitt 2017), in the southern US (Browning 1974), and central California (Herzog 1996). The CV Swainson's Hawk population has been characterized as migrating primarily through western Mexico and wintering exclusively in western Mexico (Woodbridge 2004), mostly in central Mexico (Beedy and Pandolfino 2013), in Mexico and South America (Hull et al. 2008), and from central California to South America (Wheeler 2003).

Data on rates and continuity of travel by Swainson's Hawks are also limited. Two Swainson's Hawks tracked twice per week with satellite transmitters moved nearly 10,500 km from Alberta to Argentina in 53 and 54 d ($\bar{x}$ = 194 and 198 km/d; Schmutz et al. 1996). Additional studies of 27 hawks from throughout the Great Basin–Great Plains breeding range reported an average migration distance of 10,139 km and direct-route travel rate of 188 km/d (Fuller et al. 1998, Bechard et al. 2006). Northward migration of the species occurs more rapidly than southward migration (Wheeler 2003, Kochert et al. 2011), but no information has been reported for the CV population.

Information on the movements of and the wintering areas used by CV Swainson's Hawks may be important for the species' conservation. For example, satellite telemetry tracking of Swainson's Hawks from the species' Great Basin–Great Plains range to wintering areas allowed detection of widespread incidental poisoning by the insecticide monocrotophos used on Argentinian agricultural lands (Woodbridge et al. 1995, Goldstein et al. 1997, 1999a). This discovery led to localized elimination of use of the pesticide and dramatic reduction in mortality in Argentina (Goldstein 1999b), but pesticides may continue to pose a risk to the species in Latin America (Bechard et al. 2010, Bravo et al. 2011).

Swainson's Hawks may also be affected during migration and in wintering areas by other forms of direct mortality (e.g., shooting; Bechard et al. 2010) or through changes in crop types or other land conditions that may affect roosting and foraging habitat as has been identified in breeding areas (Bechard 1982, Swolgaard et al. 2008, Estep and Dinsdale 2012). Therefore, identifying the locations of migratory stopover and wintering use areas is important for assessing population risk to factors that may affect mortality or reproductive rates.

We evaluated the migration patterns and land-use conditions in wintering and migratory stopover areas for the Swainson's Hawk population that breeds in the CV within northern Sacramento and adjacent Yolo and Sutter Counties (hereafter "CV Swainson's Hawks") as a companion to a study of movements and land use during the breeding season (Fleishman et al. 2016). Study objectives were to identify and characterize wintering areas; describe migration routes, rates, and duration; identify and characterize migratory stopover locations; and describe how different wintering areas may influence timing of movements.

STUDY AREA AND METHODS

Study Area. We studied Swainson's Hawks that nested within and adjacent to the Natomas Basin, a 375-km^2 area near the Sacramento River in Sacramento, Yolo, and Sutter Counties, California, USA (Fleishman et al. 2016, Fig. 1). This basin is within the central portion of the 47,000 km^2 CV, which supports the highest density of nesting hawks (Battistone et al. 2016). Nesting habitat consisted of riparian woodland, tree rows, and large, isolated, remnant trees, all located within a matrix of agricultural lands. Agricultural lands suitable for foraging include alfalfa, a variety of irrigated annual crops, and grasslands (Babcock 1995, Swolgaard et al. 2008, Estep 2009). Other land-cover types in the area that were not extensively used included orchards, water, and urban areas. See Fleishman et al. (2016) for more information on the breeding area.

Capture and Telemetry. We captured 12, 9, and 2 adult Swainson's Hawks during the nesting seasons in 2011, 2012, and 2013, respectively, using dho-gazas with a live Great Horned Owl (*Bubo virginianus*) as a lure (Bloom et al. 1992, Kochert et al. 2011) and standard handling techniques (Hull and Bloom 2001). Hawks were captured near nest sites during 19 April–26 July, the period when adults were most protective and thus susceptible to trapping. We determined sexes using measurements of weight, wing chord and foot pad, presence/absence of a brood patch, and nesting behavior (Hull and Bloom 2001, Sarasola and Negro 2004, Kochert and McKinley 2008, Pitzer et al. 2008). We trapped 16 males and 7 females. Due to mortality (one bird) and equipment failure (two birds), we acquired migration data on 16 males and 4 females.

We banded the hawks with standard USGS leg bands and colored/numbered leg bands. We fitted hawks with Solar 22-g ARGOS/GPS PTT–100 satellite transmitters (Microwave Telemetry, Columbia, MD, USA) using backpack-style harnesses with the transmitter positioned on the back of the bird and secured with Teflon ribbon. Transmitters were tested for locational accuracy before deployment and were found to match the manufacturer's reported ±18 m horizontal accuracy (Fleishman et al. 2016). Locations were transmitted 6 or 12 times daily between 0100 H and 2300 H PST during 15 March–14 October. During the nonbreeding season (15 October–14 March), transmitters recorded hawk locations twice daily at 0100 H and 1300 H PST. See Fleishman et al. (2016) for more details on

Figure 1. Natomas Basin breeding area, the Central Valley, California, USA, and wintering locations of 20 radio-tracked Swainson's Hawks that nested in the Natomas Basin during 2011–2015.

Table 1. Numbers of Swainson's Hawks that bred in the Central Valley, CA, USA, tracked each year by season.

Period	Months	Number of Hawks Tracked per Year[a]					
		2011	2012	2013	2014	2015	Total
Southward migration	July–Dec	10	8	5	6		29
Wintering	Nov–Mar[b]	9	8	6	6		29
Northward migration	Feb–May		8	8	9	5	30

[a] Includes records with telemetry data that were transmitted continuously over the period. Additional data from periods with fragmentary records due to equipment failures were used in calculating departure and arrival dates, and stopover periods.
[b] Records shown during year in which wintering period began.

transmitter schedules. We used the daily hawk locations at 1300 H PST for all analysis of migration and wintering use.

Transmission periods for individual hawks ranged from 1 to 45 mo, which provided data for the number of birds by activity period and year (Table 1). We assigned location records for each bird to seasonal periods (southward migration, wintering, northward migration) based on the observed pattern and timing of movements as described below.

Fourteen (70%) of the captured birds transmitted data on trips between breeding and wintering areas in >1 year. We incorporated all available data (including data from single individuals in multiple years) into characterizations of migratory movements, stopovers, and use of wintering areas. We report two samples sizes (number of records, which includes multiple records of the same individuals from different years, and number of unique individuals). To avoid bias from multiple records of individuals, we averaged values for dates, timing, and distances across years for each individual and used those values to calculate averages for the tracked hawk group. We used the number of individual birds as the sample size for statistical analysis. Many of the sample sizes for comparisons of dates of birds wintering in different regions (e.g., departure and arrival dates, duration of travel) were too small for statistical comparison. In such cases, we present averages for birds that used different wintering areas and compare these averages without formal statistical tests, and we note potential differences or trends based on the magnitudes of differences.

Characterization of Wintering Areas. Contrary to Kochert et al. (2011), we use the traditional North American-centric term *wintering area,* rather than *areas used in the austral summer,* to indicate the area used by hawks during the winter (November–March) in the northern hemisphere, because hawks we studied wintered in both the northern and southern hemisphere.

Based on the distribution of wintering birds, we designated four large geographic areas as wintering regions, including western Mexico, Central America, northern South America, and central South America. We defined wintering areas as the areas used after directional southward migratory movements ceased (see Migratory Movements below). We characterized land-use conditions within wintering areas by identifying land-cover type at each transmitted daily point location, defined in general terms as: agriculture, grassland, shrub-scrub, forest (including deciduous and evergreen forest and mixed woodland), and other (including areas considered low suitability as habitat: barren, wetland, mangrove, and urban). Land uses were determined from the ArcGIS World Land Cover 30m BaseVue 2013 (Esri 2017).

Migratory Movements. We characterized the start of southward and northward migration as the period from the date on which continued consistent directional movements >100 km began until birds reached wintering or breeding areas, respectively, following Kochert et al. (2011). In all cases, migratory movements could be clearly differentiated from movements associated with breeding, post-breeding wandering, and wintering. We used Student's *t*-tests (SPSS Version 24) to compare the timing of breeding-area departure and arrival on wintering grounds for successful and unsuccessful breeders (one-tailed test of the hypothesis that unsuccessful birds left breeding areas earlier). We compared departure and arrival timing between males and females using a two-tailed independent samples *t*-test. Data were tested for normality using SPSS. We assumed an $\alpha = 0.05$ for all statistical tests.

We characterized migration distances and calculated movement rates in several ways. *Migration distance* was calculated as the distance along the migratory pathway of each bird to and from breeding and wintering areas (i.e., did not include backtracking movements and movements within stopover areas; see below). The *seasonal movement rate* (km/d) was the total migratory movement distance divided by the number of days from start to completion of migratory movements. The *migration speed* (km/d) was the distance traveled on days when migration movements occurred (i.e., excluding wintering days, stopovers, and other days when movements were <5 km/d). Throughout, we present data as mean ± SD.

Breeding Success and Arrival Time. We annually determined nest success of each pair that included a tracked bird, where successful birds were those that fledged at least one young. We compared mean arrival date at the breeding areas of birds from pairs that were subsequently successful and unsuccessful (using Student's *t*-test; SPSS Version 24), to determine if earlier arrival to the breeding area was associated with nesting success.

Characterization of Stopover Areas. Stopover areas consisted of locations where hawks temporarily paused during migration and presumably made use of an area along the route. We defined stopover sites as areas where individuals did not proceed along the main travel route for at least 4 d. We assumed a 4-d stopover indicated birds were foraging, rather than just resting or waiting out bad weather conditions.

We identified stopover concentration areas using the ArcGIS Kernel Density algorithm (Silverman 1986) to develop a point density raster (unweighted). The outcome was a continuous surface of point density (points/10,000 km^2, or approximately one square degree of latitude/longitude in the study area). We applied the point density raster to the ArcGIS Contour tool (Esri, 2017) to create point density isolines at 10-unit increments. Through visual examination, we selected the isoline representing 60 points/10,000 km^2 to represent stopover areas. Land cover at stopover areas was characterized based on the land-cover types at daily point locations in each stopover area, using the same land-cover designations and sources described for wintering areas.

RESULTS

Wintering Area Locations, Use, and Characteristics. The 20 CV nesting birds tracked to wintering areas used widely separated locations, including western Mexico (states of Sinaloa, Narayit, and Jalisco; $n = 5$), Central America including Guatemala (Escuinta) and Nicaragua (Chinandega, Managua, Leon, and Boaco; $n = 3$), Northern South America including Venezuela (Meta and Vichada) and Colombia (Guarico, Portuguesa, Zulia, and Apure); $n = 8$), and Central South America including southern Bolivia (Santa Cruz) and northernmost Argentina (Salta); $n = 4$; Fig. 1). Locales that included >10% of wintering locations included Sinaloa, Mexico; Meta, Columbia; and Salta, Argentina.

All 11 birds tracked to wintering areas in >1 year returned annually to the same wintering regions, including six birds tracked for two winters, three birds for three winters, and two birds for four winters. The amount of time spent on wintering areas was inversely related to distance between breeding and wintering areas, with those wintering in western Mexico spending an average of 8 d more on the wintering area than those wintering in Central America and 26–30 d more than those wintering in South America (Fig. 2).

Land-cover types used in wintering areas were predominantly agriculture and grassland, but with differences among regions (Fig. 3). Wintering areas used in western Mexico and Central America were strongly dominated (>80%) by agricultural lands. Wintering areas in central South America supported a mixture of agricultural and shrub-scrub lands, whereas most (>80%) of the areas used in northern South America supported grassland and shrub-scrub, which were created through clearing of native forest (Etter et al. 2006).

Migration Routes. Southward migration proceeded along a southeasterly route through the San Joaquin Valley, across the Mojave Desert, through the Imperial Valley and Sonoran Desert, and along coastal western Mexico (Fig. 4). Migrants that continued south proceeded through the central Mexican highlands, to or through Central America, and then either east to Columbia and Venezuela or south across the Amazon Basin to interior Bolivia and northern Argentina. The southward and northward migration routes were similar with several exceptions. The southward route through southern California, Arizona, and Sonora was more dispersed and extended farther to the east than the northward route. The northward route was more dispersed through southern and central Mexico, with some birds initially following the eastern track used by the Great Basin–Great Plains breeding population before crossing back to the Pacific side (Fig. 4).

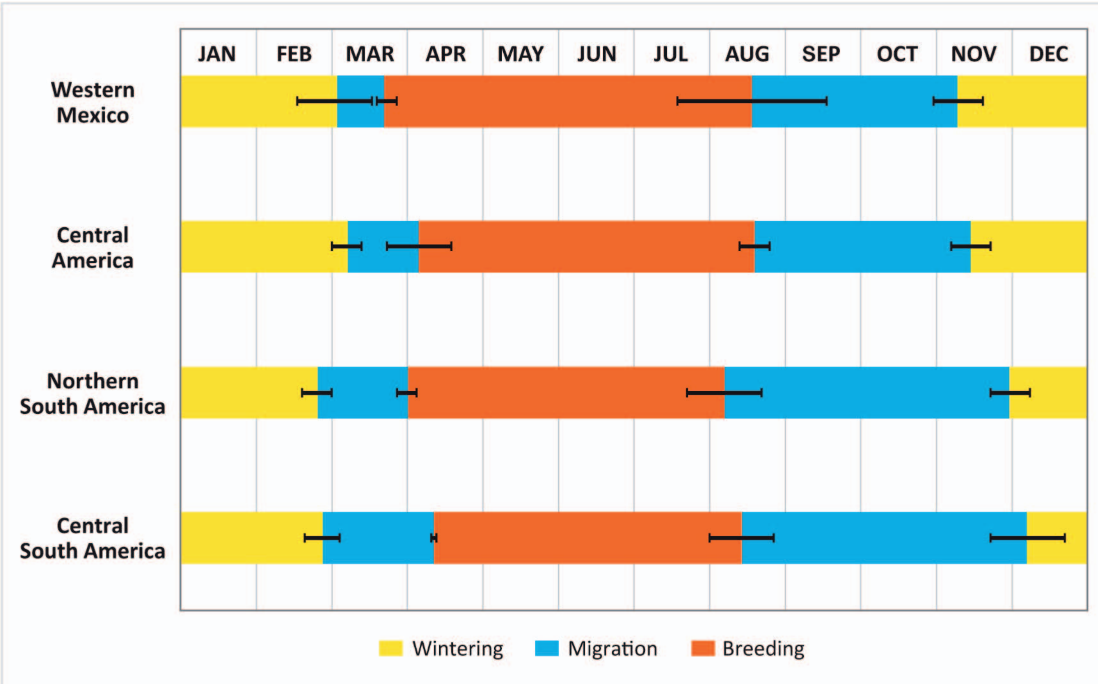

Figure 2. Time of departure and arrival, and average durations of migration, wintering, and breeding periods of Swainson's Hawks that bred in the Central Valley, California, USA, and wintered in the different regions shown. Bars show standard deviations of average dates.

Breeding and Wintering Area Departure and Arrival. Swainson's Hawks initiated southbound migration from the Natomas Basin breeding area over a broad period of 119 d from 15 June to 12 October ($\bar{x}$ = 14 August; Fig. 2). Hawks arrived on their wintering areas over a 71-d period between 5 November and 15 January ($\bar{x}$ = 25 November). Although sample sizes were small, wintering location did not appear to affect departure timing from breeding areas (Fig. 2).

Swainson's Hawks that nested unsuccessfully departed on southward migration an average of 20 d earlier ($\bar{x}$ = 29 July ± 29 d, n = 13 trips, 14 individuals) than successful breeders ($\bar{x}$ = 18 August ± 10 d, n = 19, 29; t = –2.666; df = 2,9; P = 0.020). Unsuccessful breeders also arrived at wintering areas an average of 21 d earlier ($\bar{x}$ = 7 November ± 35 d, n = 9, 15) than successful breeders ($\bar{x}$ = 28 November ± 12 d, n = 15, 21; t = –1.74; P = 0.054).

The few tracked female hawks departed an average of 9 d earlier ($\bar{x}$ = 6 August ± 20 d, n = 4, 10) than males ($\bar{x}$ = 15 August ± 9 d, n = 17, 32), but this difference was not statistically significant (t = –1.075; df = 19; P = 0.299). On average, females also arrived on wintering areas 6 d earlier (19 November ± 11 d, n = 4, 10) than males (November 25 ± 12 d, n = 14, 22), but this difference also was not significant (t = 0.776; df = 16; P = 0.808).

Both members of the one mated pair that were tracked in the same year left the breeding area on the same day (22 August 2011). The pair wintered in different regions, the female in northern South America (Colombia and Venezuela) and the male in Central America (Guatemala), and returned to the breeding area within 3 d of each other (5 and 8 April 2012).

Swainson's hawks that bred in the CV and wintered in western Mexico spent fewer days in fall migration and arrived earlier at wintering areas than those wintering farther south (Fig. 2). Average fall migration duration for birds wintering in Mexico was 17 d shorter than for birds wintering in Central America and 21–28 d shorter than for birds wintering in northern and central South America. The average arrival date for birds wintering in Mexico was 5 d earlier than for birds wintering in

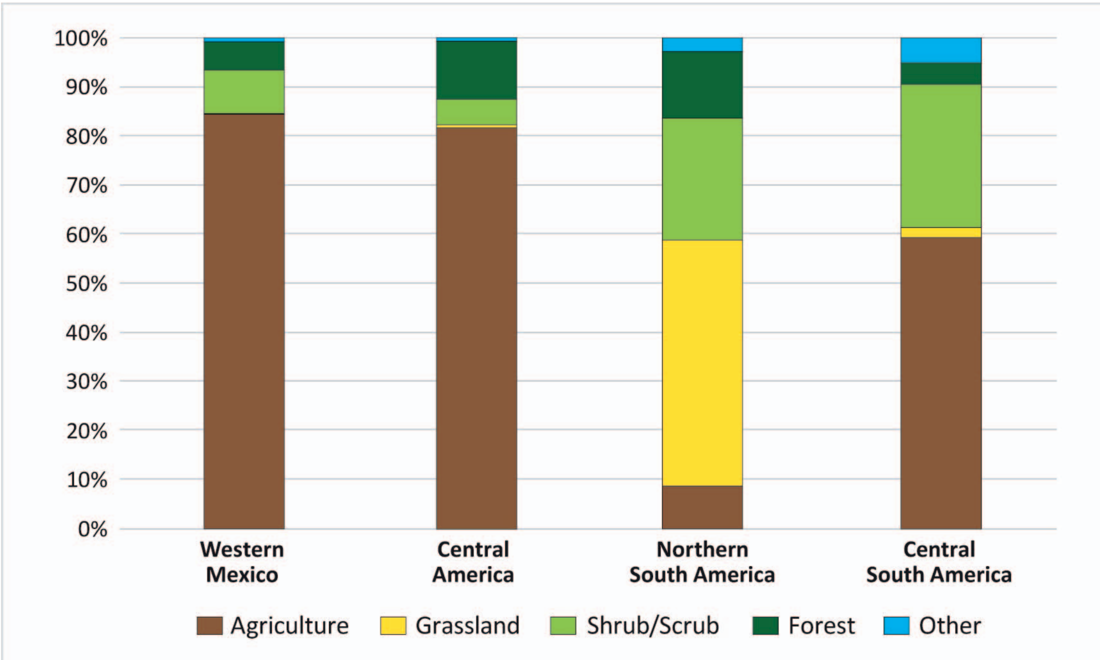

Figure 3. Land-cover types (% of locations) in four wintering areas used by Swainson's Hawks that bred in the Central Valley, California, USA ($n = 2527$ locations).

Central America and 21–28 d earlier than for birds wintering in northern and central South America (Fig. 2).

Swainson's Hawks departed their wintering areas over a 36-d period of from 1 February to 8 March ($\bar{x}$= 25 February; n = 18, 33). Hawks arrived at their breeding areas over a 48-d period between 13 March and 5 May ($\bar{x}$ = 30 March ± 10 d; Fig. 2). Average starting dates for northward migration of hawks were later for northern wintering hawks than for those wintering farther south, with birds in western Mexico departing an average of 4–23 d later than those from other wintering sites (Fig. 2). Despite starting northward migration later than other populations, the average date of arrival on breeding areas of birds wintering in western Mexico was 9–20 d earlier than those of birds wintering farther south (Fig. 2). On average, females arrived on breeding areas 5 d earlier (March 25 ± 4 d, n=4, 8) than males (March 30 ± 13 d, n = 13, 20), but this difference was not significant (t = 0.734; df = 15; P = 0.474).

Breeding Success and Arrival Time. Birds that subsequently bred successfully (n = 12, 15) arrived 27 March (± 11 d), which was 4 d earlier than the average for unsuccessful breeders (t = –1.121; df = 17; P = 0.025).

Migration Travel Distance and Rates. Average distances traveled between the CV breeding areas and different wintering areas varied by nearly 7500 km, from an average of nearly 2500 km for birds wintering in western Mexico to nearly 10,000 km for birds wintering in central South America (Table 2). The seasonal movement rates (i.e., km/d from departure to arrival) of hawks during southward migration averaged only 36% of the rate of northward migration (72 vs. 202 km/d), as a result of greater time spent in stopovers during southward migration (Table 2).

The average migration speed of hawks (i.e., movement rate on days when actively migrating) was 25% slower during southward migration than during northward migration (161 vs. 214 km/d; Table 2). The average southward migration speed of birds wintering in western Mexico was lower than for birds using other wintering areas, but migration speeds among hawks wintering in Central and South America were similar. Average migration speeds of individuals from different wintering areas were similar during northbound migration (Table 2).

Figure 4. Southward and northward migration routes of Swainson's Hawks that bred in the Central Valley, California, USA.

Migratory Stopover Use and Characteristics. CV Swainson's Hawks spent a substantial amount of time in migratory stopovers during southward migration. All 20 tracked hawks used at least one stopover during southward migration, averaging 2.6 ± 1.2 stops/trip for an average of 53 ± 27 stopover d/trip during southward migration (Table 3). No differences in the numbers of stopovers or days spent in stopover during fall migration were evident among birds that wintered in different locations (Table 3). Northbound hawks traveled much more directly from

Table 2. Average migration distance, seasonal movement rates, and daily migration speeds of Swainson's Hawks that bred in the Central Valley of California, USA, and wintered in four different areas.

Wintering Area	Average Migration Distance in km (± SD)	Average Seasonal Movement Rate (km/d)[a]		Average Migration Speed (km/d)[b]		n^c
		Southward	Northward	Southward	Northward	
Western Mexico	2551 (± 488)	40	165	119	204	6, 6
Central America	5266 (± 470)	60	217	181	230	5, 5
Northern South America	7129 (± 583)	75	217	151	217	11, 13
Central South America	9998 (± 1041)	102	191	201	212	7, 4
Total average	**6392 (± 2567)**	**72**	**202**	**161**	**214**	**31, 26**

[a] Migration distance/total days from departure to arrival
[b] Migration distance/days during which migratory movements occurred (i.e., excluding stopover days)
[c] Trips: southward, northward

Table 3. Characteristics of stopover use during southward and northward migration of Swainson's Hawks that bred in the Central Valley, California, USA.

	SOUTHWARD MIGRATION				NORTHWARD MIGRATION			
WINTERING AREA	MEAN NO. STOPOVERS/ TRIP (RANGE)	MEAN TOTAL STOPOVER DURATION (d/TRIP) (RANGE)	NO. BIRDS	NO. TRIPS	MEAN NO. STOPOVERS/ TRIP (RANGE)	MEAN TOTAL STOPOVER DURATION (d/TRIP) (RANGE)	NO. BIRDS	NO. TRIPS
Western Mexico	2.3 (2–3)	52 (20–77)	5	6	0.7 (0–2)	10 (0–25)	5	6
Central America	3.0 (2–4)	62 (49–92)	3	5	0.0	0	3	5
Northern South America	3.1 (1–6)	55 (11–112)	6	11	0.1 (0–1)	0 (0–9)	7	13
Central South America	1.9 (1–4)	45 (21–95)	2	7	0.5 (0–1)	5 (0–14)	2	4
Averages	2.6	53			0.25	3		
Totals			16	30			17	28

wintering to breeding areas. Only seven (35%) of the tracked hawks stopped over during 28 northward migration trips (0.25 stopovers/trip), and overall, hawks spent an average of only 3 d in stopover per trip.

Central Valley Swainson's Hawks used certain areas along the southbound migration route as stopover habitats (Fig. 5). Nearly all (94%) of 1968 stopover locations occurred in eight regions (Table 4). The large Santa Cruz Valley–western Sonora–

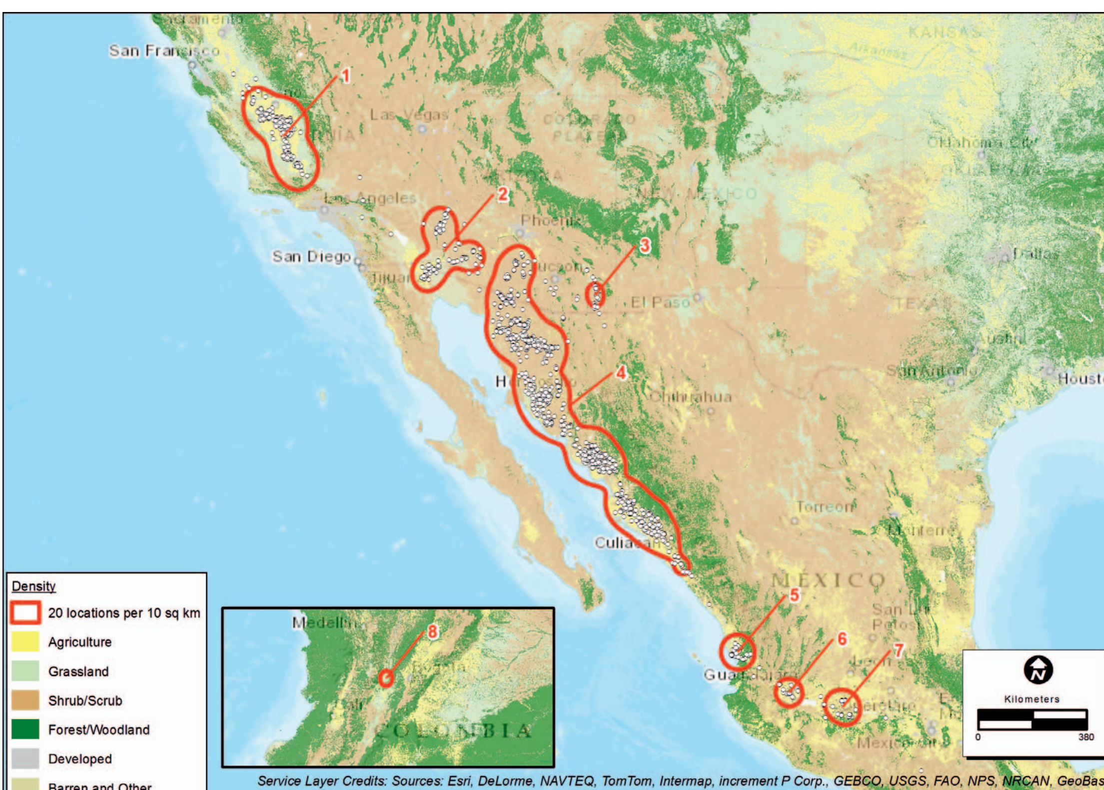

Figure 5. Eight areas of concentrated stopover (>20 locations/10 km^2) used during migration by Swainson's Hawks that bred in the Central Valley, California, USA. See Table 5 for description of locations, frequency of use, and land-cover types.

Table 4. Use levels of concentrated stopover areas and of major land-cover types used during migration by Swainson's Hawks that bred in the Central Valley, California, USA. Location numbers are as shown in Figure 5.

	Stopover Use			Use by Land-cover Type (%)				
Location	No. Birds	Total Use-days	Use-days (%)	Agriculture	Shrub-scrub	Grassland	Forest	Other
1. San Joaquin Valley, CA, USA	10	349	17	73	0	21	0	5
2. Lower Colorado and Gila Rivers, CA and AZ, USA	5	112	6	57	17	15	0	11
3. Wilcox Playa, AZ, USA	1	15	1	27	73	0	0	0
4. Santa Cruz Valley, AZ, USA, and western Sonora and Sinaloa, Mexico	19	1290	65	43	43	2	11	1
5. Coastal Nayarit, Mexico	3	41	2	51	2	0	46	0
6. West of Lake Chapala, Jalisco, Mexico	3	27	1	67	26	0	4	4
7. East of Lake Chapala, Jalisco and Michoacan, Mexico	1	39	2	74	5	0	21	0
8. Near Bogota, Cundinamarca, Colombia	1	10	1	50	0	40	10	0
Outside concentration areas	12	114	6	35	29	9	23	4
All Stopovers				50	31	7	10	2

Sinaloa stopover area, encompassing the Sonoran Desert and agricultural lands in coastal northwestern Mexico, was by far the most extensively used stopover, used for stopover by 95% of birds and for 65% of all stopover use-days (Table 4). This stopover area (Fig. 5) extended far to the north of the western Mexico wintering area (Fig. 1), and four of the five hawks that wintered in western Mexico stopped over at least once north of the wintering area before arriving on the wintering grounds. The overlap between the western Sonora and Sinaloa stopover and the western Mexico wintering area indicates that hawks were using the western Mexico wintering area for both purposes. The San Joaquin Valley, California, was also extensively used for stopover (50% of birds and 17% of total use-days). The only other stopover used by ≥25% of southward migrants and 5% of stopover locations was the lower Colorado and Gila River valleys (Table 4, Fig. 5).

Land-cover types used during stopover were similar to those used in wintering areas. Land-cover types at 1968 stopover locations were dominated by agriculture (50%) and shrub/scrub (32%), with lesser amounts of deciduous and evergreen forest and grassland, and negligible amounts of other types (Table 4).

DISCUSSION

Wintering Areas. The wide range of wintering areas used by Swainson's Hawks that bred within 30 km of each other in the Natomas Basin region of the CV is the most striking outcome of the study. Our findings more definitively characterize the wintering areas of the CV population, which had been variously described previously (Woodbridge 2004, Wheeler 2003, Hull et al. 2008). The 7500-km north-to-south expanse of the CV Swainson's Hawks' wintering areas differed markedly from the pattern of the larger Great Basin–Great Plains breeding populations, which wintered within a 740,000-km^2 area in Argentina and Uruguay (Kochert et al. 2011) that is entirely separate from wintering areas of CV hawks.

Factors influencing the CV Swainson's Hawks' wintering patterns we observed are unknown. Although typically associated with open grassland, the species has adapted to environments with a high proportion of agriculture in its breeding ranges in both the Great Plains–Great Basin (Goldstein et al. 2000, Canavelli et al. 2003, Bechard et al. 2010) and CV (Estep 1989, Babcock 1995, Swolgaard et al. 2008). The Great Basin–Great Plains-breeding Swainson's Hawks also selected agricultural lands on their austral summer range in Argentina (Goldstein et al. 2000, Canavelli et al. 2003). The CV population's association with agricultural lands on its wintering grounds demonstrates that similar adaptation to agriculture has occurred there. In all wintering areas, CV Swainson's Hawks used agricultural and pasture lands that were converted from desert or wooded habitats in the last century (Reynolds 1970, Etter et al. 2006). Perhaps CV Swainson's Hawks are gradually adapting to this conversion of native vegetation by wintering in increasing numbers in agricultural and pasture lands north of former wintering areas that formerly were not suitable. A similar change in migratory pattern to winter north of historical wintering areas in response to changes in agricultural land use has been documented for Snow Geese (*Chen caerulescens*) in central North America (Davis et al. 1989, Alisauskas 1998) and for wintering waterfowl in the CV (Fleskes et al. 2018).

Because migration is generally considered a period of stress and risk for individuals (Houston 1990, Hedenström 2008), Swainson's Hawks that winter in more northerly areas could experience enhanced survival by being exposed to less risk of unfavorable weather, prey shortages, persecution, or other sources of mortality or stress. Therefore, if northern wintering habitat is sufficient to maintain individuals' fitness, there should be advantages to remaining north rather than making a longer journey south. For example, Swainson's Hawks that winter in western Mexico migrate only about 5000 km round-trip, or 25% of the 20,000 km travelled annually by CV birds that winter in central South America.

Greater nesting success for Swainson's Hawks that arrived earlier to the breeding area may reflect several benefits. Based on 10 yr of observations of 32 color-banded Swainson's Hawk nesting pairs in and adjacent to our study areas, J. Estep (unpubl. data) determined that most pairs remain mated for an average of 4 yr and return to traditional nesting territories. Therefore, earlier return to breeding areas may be less likely to result in benefits in selecting superior mates or territories than in some other raptor species (Poole 1989), except for young birds that are acquiring a mate for the first time or adults that have lost a mate.

Swainson's Hawks also frequently compete for their traditional nest sites and for nesting territories with other raptors that begin nesting earlier, including Great Horned Owls (*Bubo virginianus*), White-tailed Kites (*Elanus leucurus*), and especially Red-tailed Hawks (*Buteo jamaicensis*; J. Estep unpubl. data). Returning earlier to nesting territories, when other species are busy incubating rather than tending young, may help Swainson's Hawks successfully defend their nest sites or establish alternative nest sites nearby.

Use of agricultural lands in wintering areas poses certain higher risks to CV Swainson's Hawks than less intensively managed native habitats, including potential for exposure to agricultural pesticides, changes in agricultural practices, and human persecution (Bloom 1980, Goldstein et al. 1999a, 1999b, Battistone et al. 2016). The large variation in locations where CV Swainson's Hawks winter, however, may buffer some potential ill effects to the population, in that adverse actions in any one wintering area presumably would affect only a small proportion of the population.

Migration Routes, Timing, Duration, and Rates. Our results indicate that, although all breeding CV birds depart the breeding area at generally the same time, the more northerly wintering birds spend less time in migration and more time in wintering areas. Hawks wintering in northern areas also depart wintering areas later and arrive on breeding areas substantially earlier than birds that winter farther south.

In addition to wintering in separate locations, migration routes of the CV population differ from those of the Great Basin–Great Plains North American Swainson's Hawk population (Kochert et al. 2011). Swainson's Hawks that breed in the Great Basin and Great Plains concentrate in migration along the Gulf of Mexico coast, while CV birds migrate along the Pacific coast. Thereafter, routes of birds migrating through Central and South America are similar. The only known overlap of routes of Great Basin–Great Plains and CV birds was of a Great Basin bird from the Modoc Plateau in northeastern California that migrated like a CV bird, through the CV and along the west coast of Mexico (Kochert et al. 2011).

Duration of CV hawk southward migration averaged longer ($\bar{x} = 99$ d/individual) than for Great Basin–Great Plains North American hawks ($\bar{x}=66$ d/

individual; Kochert et al. 2011), despite a shorter migration distance, apparently because CV hawks spent more time in stopover areas than Great Basin–Great Plains birds. Great Basin–Great Plains and CV birds both spent less time in stopover during northward migration than during southward migration.

The Role of Stopover Habitat. Use of stopover habitat has been previously recognized for the Great Basin–Great Plains Swainson's Hawk population (Kochert et al. 2011). Our results more precisely document the use of stopover habitat by the CV Swainson's Hawk population. The extensive use of stopover habitat ($\bar{x}$ = 53 d/individual) during southward migration approaches the duration of time spent on wintering areas ($\bar{x}$ = 90 d) and demonstrates the importance of this habitat component to the population. The extensive use of stopover habitat by CV Swainson's Hawks blurs the distinction between migratory and wintering distributions in this species. It may be more accurate to characterize the CV Swainson's Hawk movement pattern as a series of rotating stopovers of which the southernmost one (i.e., that on the "wintering" area) is only moderately longer than others.

The Great Basin–Great Plains Swainson's Hawk population also made extensive use of stopover habitat, but most stopovers occurred at more northern latitudes than those used by CV birds (Kochert et al. 2011). The single Great Basin bird from northeastern California that followed the same migratory route as the CV birds also stopped over in the San Joaquin Valley. Our results add to those of other recent studies on the importance of stopover habitat to other long-distance migrant raptors (Martell et al. 2001, 2014) and other bird species (Wikelski et al. 2003, Warnock 2010, Wright et al. 2018)

Conservation Implications. The identification of areas of concentrated migratory, stopover, and wintering use provides a framework in future land-use decisions for maintaining all annual habitat components necessary to sustain the CV population. Currently, substantial effort and resources are expended protecting the species within its CV breeding range (Battistone et al. 2016), but we are unaware of any purposeful conservation actions taken on lands within migration and wintering areas. Notably, because of their highly disturbed nature, agricultural lands used by CV Swainson's Hawks for wintering and stopover may be unlikely to receive conservation attention for other reasons.

The diversity of wintering and migratory areas used by CV hawks poses challenges and benefits for conservation. Dispersal of these key habitat components across multiple countries complicates efforts to enact comprehensive conservation measures. Conversely, as noted, the dispersion of migratory and wintering use areas provides resiliency from localized land-use decisions, such as pesticide use, detrimental crop conversions, or other factors that may occur only within one or a few countries.

The use of more northern wintering areas by the CV Swainson's Hawks compared to Great Basin–Great Plains birds (including hawks nesting in northeastern California) could be beneficial to the CV Swainson's Hawk population for several reasons. It could reduce higher mortality risk that may be associated with long migration routes (Newton 2006, Klaassen et al. 2013) allowing earlier arrival, which has been shown in other birds to increase probability of territory and mate acquisition, fecundity, and reproductive success (Møller and Gregersen 1994, Smith and Moore 2005, Dunn et al. 2011, Bejarano and Jahn 2018). If use of northern wintering areas becomes more prevalent, however, it could also diminish the current inherent protections from detrimental human influences (i.e., persecution, pesticides, habitat change) associated with dispersion of wintering birds across multiple geographic areas and national borders.

Our study more completely documents the differences in wintering areas used by CV Swainson's Hawks and the Great Basin–Great Plains North American population, which was cited by Hull et al. (2008) as a factor that may be causing the long-term differentiation of these allopatric populations. Although genetic differentiation apparently has not yet proceeded to the level that would confer separate subspecies designations, these distinctions may support the recognition of the CV Swainson's Hawk population as a distinct population segment, as defined under the Federal Endangered Species Act (FESA; US Department of Interior and Department of Commerce 1996). Given its continued listing under the California Endangered Species Act, the clearer documentation of separation of the CV Swainson's Hawk population from those individuals in the rest of the species' range may warrant more detailed status assessment for listing consideration under FESA.

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