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Population Trends of the Ferruginous Hawk (*Buteo regalis*) Wintering in California

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ABSTRACT.—The Ferruginous Hawk (*Buteo regalis*) is a raptor of conservation concern in much of its range. Population trend estimates from Breeding Bird Surveys and migration counts for this species are often contradictory and of low credibility. Therefore, we used Christmas Bird Count data to assess population trends for Ferruginous Hawks that winter in California, USA. Evidence suggests that the birds breeding in southeastern Washington and northeastern Oregon may represent a metapopulation that winters almost exclusively in California. Data for the 25-yr period from Count Year 98 (winter 1997–1998) to Count Year 122 (winter 2021–2022) from 22 California Christmas Bird Count circles in the core winter range of Ferruginous Hawks showed a significant positive trend. This positive trend contrasts with the continent-wide negative trends observed for most grassland/open country bird species and is surprising given ongoing declines of this species' preferred winter habitat in California during this same period. We discuss potential explanations that may account for these differences, including the possibility that the California-wintering Ferruginous Hawks include a large proportion of birds breeding outside of southeastern Washington and northeastern Oregon.

KEY WORDS: *Bird Conservation Region*; *California*; *Christmas Bird Count*; *population trends*; *winter*.

TENDENCIAS POBLACIONALES DE *BUTEO REGALIS* INVERNANDO EN CALIFORNIA

RESUMEN.—*Buteo regalis* es un ave rapaz de preocupación para la conservación en gran parte de su área de distribución. Los datos de tendencia poblacional obtenidos a partir de los Censos de Aves Reproductoras y de los conteos migratorios a menudo son contradictorios y tienen baja credibilidad. Por lo tanto, utilizamos datos provenientes del Conteo de Aves de Navidad para evaluar las tendencias poblacionales de los individuos de *B. regalis* que invernan en California, EEUU. Varias líneas de evidencia sugieren que las aves que crían en el sureste de Washington y el noreste de Oregón pueden representar una metapoblación que pasa el invierno casi exclusivamente en California. Los datos para un período de 25 años, desde el Año de Conteo 98 (invierno 1997–1998) hasta el Año de Conteo 122 (invierno 2021–2022), provenientes de 22 círculos del Conteo de Aves de Navidad de California ubicados en el núcleo del área de distribución invernal de *B. regalis,* mostraron una tendencia positiva significativa. Esta tendencia positiva contrasta con las tendencias negativas observadas a nivel continental para la mayoría de las especies de aves de pastizales y lugares abiertos, y resulta sorprendente dadas las disminuciones continuas del hábitat invernal preferido de esta especie en California durante el mismo período. Discutimos las posibles razones que pueden explicar estas diferencias, incluida la posibilidad de que los individuos de *B. regalis* que invernan en California incluyan una gran proporción de aves que se reproducen fuera del sureste de Washington y el noreste de Oregón.

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INTRODUCTION

Accurate information about population trends is critical to the conservation of any species. Bird species of low abundance or sparse distribution rarely provide robust trend data from Breeding Bird Surveys (BBS), as indicated by regional credibility measures in the dataset (Sauer et al. 2020). The Ferruginous Hawk (*Buteo regalis*), a raptor of western North American grassland/open country habitats, is one such species. Ferruginous Hawk trends based on range-wide and regional BBS data are of low credibility, and showed no statistically significant trends for the recent 1993–2019 period, but a significant positive range-wide trend over the longer 1966–2019 period (Sauer et al. 2020). Data from four of six migration monitoring sites in the western USA showed significant declines in Ferruginous Hawk numbers during the last decade of the 20th century (Hoffman and Smith 2003, Farmer et al. 2008). However, for broad-front migrants that do not concentrate along specific migration lines, such as the Ferruginous Hawk, migration counts are not a reliable source of trend data. Ng et al. (2017) cited several localized studies of population trends that showed widely variable results depending on location and timeframe. Thus, the available data leave the nature of current range-wide or regional population trends uncertain.

In response to a 1991 petition, the US Fish and Wildlife Service (USFWS) did not find listing the Ferruginous Hawk under the Endangered Species Act to be warranted (USFWS 1992), but it is considered a bird of conservation concern in some Bird Conservation Regions (BCRs; USFWS 2021) and is afforded protection under the Migratory Bird Treaty Act (USFWS 2020). The Ferruginous Hawk is listed as federally threatened throughout Canada, but has been recommended for downlisting to special concern. The species is considered threatened in the province of Manitoba and endangered in Alberta (Committee on the Status of Endangered Wildlife in Canada 2021). The species' conservation status in states of the USA varies from endangered in Washington (Hayes and Watson 2021), sensitive to sensitive-critical in ecoregions of Oregon (Oregon Department of Fish and Wildlife 2021), a species of concern in Colorado (Colorado Natural Heritage Program 2022) and Wyoming (Wyoming Natural Diversity Database 2023), to a level 1 conservation priority species in North Dakota (North Dakota Department of Game and Fish 2023). Of these, only the designations in Washington (Hayes and Watson 2021) and Alberta (Redman 2016) are supported by robust population trend data.

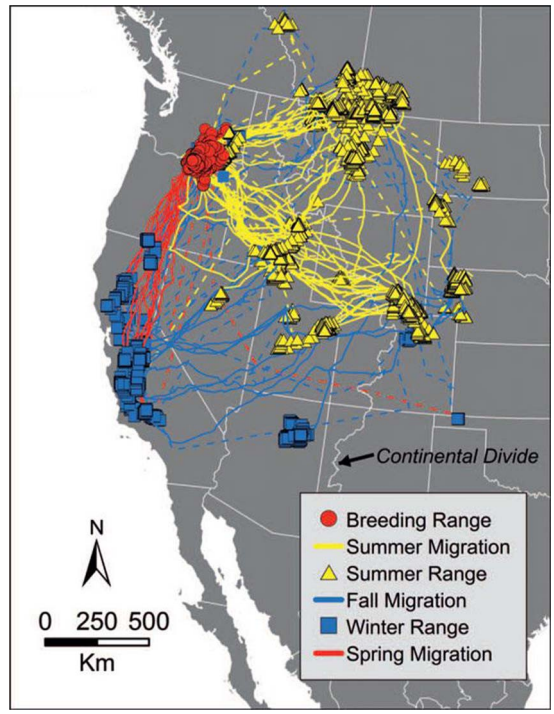

Figure 1. Year-round migration patterns of adult Ferruginous Hawks breeding in the Pacific Northwest, USA, and tracked for up to 6 yr ($n = 30$). Solid lines are tracks from birds outfitted with GPS transmitters; dotted lines are tracks from birds outfitted with ARGOS platform transmitter terminals (https://www.argos-system.org/products/transmitters/). Reprinted with permission from Watson et al. (2018).

Data from several sources suggest that Ferruginous Hawks breeding in southeastern Washington and northeastern Oregon may represent a distinct metapopulation that winters in California. Watson et al. (2018) used satellite telemetry to study the movements of adult Ferruginous Hawks from several regions within the species' breeding range. Most of these birds dispersed widely after breeding before settling on winter ranges. The hawks that bred in the southeastern Washington/northeastern Oregon region moved to the north and east soon after breeding, but nearly all eventually wintered in California (Fig. 1). All of the California wintering birds tracked by Watson et al. (2018) came from that Washington/Oregon breeding region. Within all studied populations, adult Ferruginous Hawks showed a high degree of fidelity to their winter and breeding ranges (Plumpton and Andersen 1997, Watson and Pierce 2003, Watson and Keren 2019) and immature birds generally wintered in the

same region as the adults from their natal areas (Watson 2003, Watson et al. 2019). Tracking studies of immature Ferruginous Hawks that wintered in California determined that those birds were hatched in the Washington/Oregon region and returned to that region by their second spring (Watson et al. 2019). Thus, all of these data support the supposition that the Ferruginous Hawks breeding in southeastern Washington and northeastern Oregon form a metapopulation showing strong regional migratory connectivity between their breeding area and California wintering ranges. However, the migration of Ferruginous Hawks breeding in some parts of the range (e.g., southeastern Oregon, Idaho, Nevada) has not been studied and their winter range remains uncertain.

We assessed population trends for this possible metapopulation using data from Christmas Bird Counts (CBC) in California. Although CBC data are not collected using a standardized protocol, these data have been used widely to reveal winter abundance trends of many species in California (e.g., Vandenbosch 2000, Pandolfino and Handel 2018) and across North America (e.g., Butcher et al. 1990, 2005, Sauer et al. 2003, Meehan et al. 2019). The large areas covered by each CBC circle (45,769 ha) and the generally large number of observers participating in each count (often 10 or more parties of 2–4 observers per party for each count) produce many more observations than are collected from BBS routes. For raptors with relatively high rates of first-year mortality (e.g., 55–66% for the Ferruginous Hawk; Woffinden and Murphy 1989, Schmutz et al. 2008), population dynamics can be strongly influenced by overwinter survival that is a function of wintering habitat condition (Watson and Pierce 2003). Thus, it is particularly important to understand population trends and changing habitat conditions for wintering Ferruginous Hawks, especially when these wintering populations are linked to at least one breeding region where declines have been confirmed. To assess habitat conditions, we examined changes in grassland/pasture habitat in the CBC circles and in the five California BCRs (Babcock et al. 1998) between 2001 and 2019.

METHODS

We used data on Ferruginous Hawk abundance from California CBC circles (National Audubon Society 2020) from Count Year 98 (winter 1997–1998; hereafter 1998) through Count Year 122 (winter 2021–2022; hereafter 2022). We used data from 22 CBC circles in the core winter range of the species (i.e., those that averaged >5 Ferruginous Hawks/yr and at least 0.3 Ferruginous Hawks/10 party hr; Fig. 2). To reduce potential biases in estimates of trends over time, we restricted our attention to circles within which counts were conducted during at least 19 of the 25 yr in the analysis period, including at least 7 of the first 12 yr and 7 of the last 12 yr.

We estimated trends in Ferruginous Hawk CBC abundance following Meehan et al. (2022) and similar analyses of trends in BBS data (Link and Sauer 2002, Link et al. 2006, Sauer and Link 2011, Soykan et al. 2016). Specifically, we divided the focal region (i.e., California) into a number of strata (i) and estimated a stratified index of annual population abundance ($N[i, t]$) using a hierarchical model to account for stratum-level effects on both the population and observation processes (such as survey effort) that generate $N[i, t]$. Stratum-level trends were then defined as interval-specific measures of change in $N[i, t]$. After adjusting each $N[i, t]$ for the area and occupancy of its stratum, composite trends at broader spatial scales were calculated using annual values of $N[i, t]$ summed over i strata in the focal region.

For the current analysis, we stratified California by BCRs (CA BCR), resulting in five CA BCR strata within the State, each containing 1–12 count circles. We assigned circles that overlapped more than one BCR to the BCR that predominated in that circle. We modeled the yearly counts in each circle as an overdispersed Poisson random variable using a log-linear Bayesian hierarchical model. We assumed the log of the expected count varied additively with stratum, circle, and year, as well as a potentially saturating effect of survey effort (total daytime field-hours summed across observers in each circle and year) and a temporal trend indexed to the base year (1998; Soykan et al. 2016). Distributional assumptions and diffuse prior distributions were as described in Link et al. (2006). We derived annual $N[i, t]$ values for each CA BCR from fitted estimates of year and stratum effects, adjusted by stratum-specific area and the proportion of circles in which Ferruginous Hawks were detected. We derived annual $N[t]$ values for California by summing $N[i, t]$ across the five CA BCRs. Finally, we derived trends in each CA BCR and across California as the geometric mean rate of change in $N[i, t]$ and $N[t]$, respectively, from 1998–2022.

We estimated the posterior distribution of each model parameter using Markov chain Monte Carlo methods implemented in JAGS (version 4.3.1, Plummer 2003). We called JAGS remotely from the R platform for statistical computing (version 4.2.2, R Core Team 2022) using the package *runjags* (Denwood 2016).

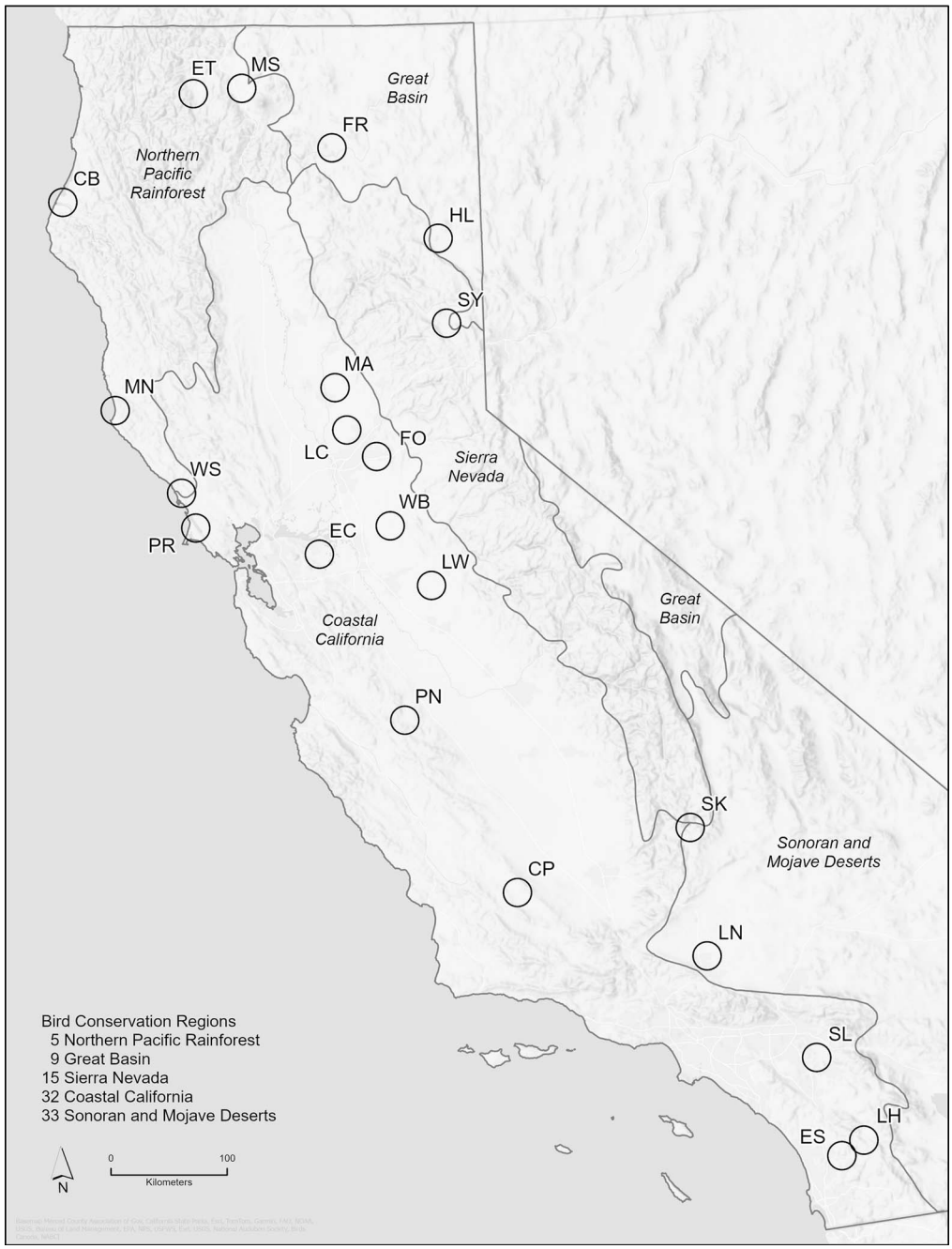

Figure 2. Locations of the Christmas Bird Count (CBC) circles used for this study and the Bird Conservation Regions (BCRs) within California. The 24-km diameter CBC circles are shown to scale. CBC circle names are (north to south): MS = Mount Shasta; ET = Etna; FR = Fall River Mills; CB = Centerville Beach-King Salmon; HL = Honey Lake; SY = Sierra Valley; MA = Marysville; MN = Manchester; LC = Lincoln; FO = Folsom; WS = West Sonoma; PR = Point Reyes Peninsula; WB = Wallace-Bellota; EC = East Contra Costa; LW = La Grange-Waterford; PN = Panoche Valley; SK = South Fork Valley; CP = Carrizo Plain; LN = Lancaster; SL = San Jacinto; LH = Lake Henshaw; ES = Escondido. BCR boundaries in California are delineated with gray lines; identification numbers are shown on the lower left.

Table 1. Estimated trends in Christmas Bird Count population indices from winter 1997/98 through winter 2021/22 for 22 count circles encompassing the core winter range of Ferruginous Hawks in California, and stratified to represent the within-state portions of five Bird Conservation Regions (BCRs).

Stratum	Mean[1]	SD	Lower 95% CRI[2]	Upper 95% CRI[2]
Statewide	**1.012**	**0.005**	**1.001**	**1.022**
BCR 5 Northern Pacific Rainforest	**1.044**	**0.010**	**1.024**	**1.062**
BCR 9 Great Basin	0.997	0.020	0.957	1.034
BCR 15 Sierra Nevada	0.981	0.049	0.883	1.077
BCR 32 Coastal California	1.006	0.006	0.995	1.017
BCR 33 Sonoran and Mojave Deserts	1.015	0.014	0.988	1.042

[1] Bold highlighting indicates a significant trend.
[2] Bayesian credible interval.

Because California-wintering Ferruginous Hawks are almost exclusively associated with grassland habitats (Pandolfino et al. 2011), we used the National Land Cover Database (Dewitz and US Geological Survey 2021) to determine the extent of conversion of grassland/pasture land cover to cultivated crops or development for each of the five CA BCRs and each of the 22 CBC circles used between the years 2001 and 2019. We then used linear regression to compare these conversion values to the observed abundance trends.

RESULTS

Ferruginous Hawk winter abundance in the 22 CBC circles increased significantly from 1998–2022 (Table 1; Fig. 3f). At the BCR level, circles in BCR 5 showed a significant positive trend (Fig. 3a), circles in two other BCRs showed nonsignificant positive trends (Fig. 3d, 3e), and none of the five BCRs showed a significant negative trend.

Appropriate land cover to support wintering Ferruginous Hawks decreased during 2001–2019, falling 8.6% across the 22 CBC circles and 4.3% across the five BCRs. Twenty of 22 CBC circles and all five BCRs showed a net loss of suitable habitat; however, no linear relationship between grassland habitat loss and Ferruginous Hawk abundance trends was evident ($P = 0.78$).

DISCUSSION

Our finding of an apparent positive population trend among Ferruginous Hawks wintering in California was unexpected given: (1) the general decline of grassland/open country birds in North America (Droege and Sauer 1993, Knopf 1994, Farmer et al. 2008, Rosenberg et al. 2019, North American Bird Conservation Initiative 2022) and the Central Valley of California (Pandolfino and Handel 2018); (2) widespread conversion of such grassland/open country habitats in California to unsuitable cropland and developed land cover types (Cameron et al. 2014, Hammond et al. 2022, Pandolfino and Douglas 2022); and (3) significant declines in Ferruginous Hawks breeding in Washington (Hayes and Watson 2021).

One possible explanation for the discrepancy is that the increasing numbers of Ferruginous Hawks tallied on these counts were an artifact caused by the overall decrease in appropriate habitat in California. The increasing counts could reflect greater concentration of hawks in remaining suitable habitat or increases in observer time spent in those habitats. Indeed, the types of land cover to which suitable grassland/open habitats have been converted in California (i.e., orchards, vineyards, and development; Cameron et al. 2014) tend to get relatively little coverage by CBC participants (E. Pandolfino unpubl. data). However, the widespread general declines of grassland/open country birds documented by Pandolfino and Handel (2018) and Pandolfino and Douglas (2022) in many of these same CBC circles suggest that is not a significant factor for Ferruginous Hawks using these habitats. If an artifact of either birds concentrating in remaining habitat or disproportionate observer effort within that habitat were present, one might expect to have seen similar patterns in counts of other species using these same habitats. However, none of the grassland/open country species that showed significant decreases in the aforementioned studies uses the same prey base as Ferruginous Hawks. Therefore, unknown trends in the density of Ferruginous Hawk prey across the CBC circles and CA BCRs also could have influenced the observed patterns, with the potential for increased prey populations to offset the effects of reduced habitat area.

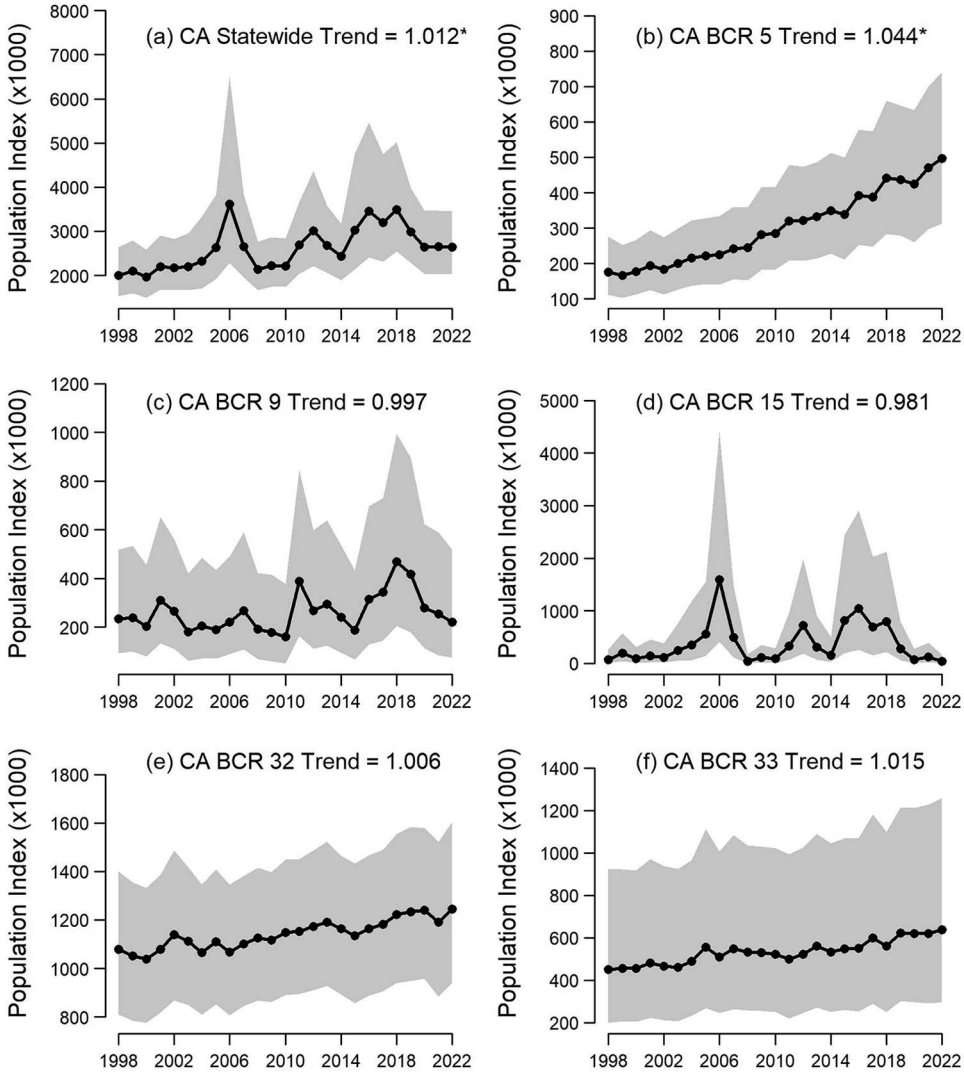

Figure 3. Annual indices of Ferruginous Hawk abundance (dots = means, shaded regions = 95% credible intervals) across the state of California (a) and in each California Bird Conservation Region (CA BCR) (b–f). The 95% credible interval on our estimate of geometric mean annual trend was greater than 1 in two cases, indicated by asterisks in panels (a) and (b), suggesting significant positive trends in data aggregated at the state level and in CA BCR 5 (Table 1).

Watson et al. (2018, 2019) determined that all Ferruginous Hawks they tracked that wintered in California came from Washington or Oregon, with those birds undertaking broad loop migrations before settling to winter in California. It is probable that Ferruginous Hawks wintering in California also include birds from breeding ranges not studied by those authors. Breeding Ferruginous Hawks are also common in southeastern Oregon, southern Idaho, and northern Nevada, and some of those birds may undertake similar loop migrations that end with wintering in California. If a large proportion of the California-wintering Ferruginous Hawks breed in those areas, and if those breeders are increasing, that could explain our finding of increasing winter abundance in California. In addition, Watson (2020) noted that a single individual that bred in Alberta, Canada, wintered in southern California. While this

Table 2. Population trend results for selected species of raptors based on Breeding Bird Survey data from Washington and Oregon for 1993–2019 (adapted from Sauer et al. 2020).

	Washington	Oregon
Northern Harrier (*Circus hudsonius*)	negative*	positive
Red-tailed Hawk (*Buteo jamaicensis*)	negative*	positive
Swainson's Hawk (*Buteo swainsoni*)	positive	positive*
Ferruginous Hawk (*Buteo regalis*)	negative	positive
Golden Eagle (*Aquila chrysaetos*)	positive	negative
American Kestrel (*Falco sparverius*)	negative	negative
Prairie Falcon (*Falco mexicanus*)	positive	positive*

* Significant trend.

is likely a rare occurrence based on Watson et al. (2018), it supports the likelihood that Ferruginous Hawks wintering in California include birds from other breeding areas beyond southeastern Washington and northeastern Oregon.

It is also possible that, although the Washington breeding population is in decline, the Ferruginous Hawks breeding in Oregon are not. BBS data may provide some support for this supposition (Table 2). BBS data for the Ferruginous Hawk and six other diurnal raptors that use similar habitats showed negative trends in Washington for four species, with the trends significant for two species. In contrast, Oregon data showed five of the same seven species increasing, with two of those trends significant. These data raise the possibility that raptors using grassland/open country habitats in Oregon may be doing better than those in southeastern Washington and may be, in part, the source for the increasing numbers of Ferruginous Hawks wintering in California.

Another possible reason for the apparent discrepancy between breeding-season and winter trends for this population could be the age subset being monitored. CBC datasets do not include age ratios; however, data collected during the winter raptor surveys in California's Central Valley (Pandolfino et al. 2011) included information on the ages of birds observed. These data showed winter adult:juvenile ratios of 6:1 overall, and as high as 9:1 during December when most CBCs are conducted. If those ratios apply to the data we analyzed, the population we assessed consisted primarily of adults. Although adults tend to dominate in populations of long-lived raptors with low rates of immature survival (e.g., Sergio et al. 2011), the predominance of adults indicated by the above ratios appears high. It is possible that the age ratios have changed over time and that the population assessed by Pandolfino et al. (2011) from 2007–2010 was not representative of earlier or current ratios.

In any case, the increasing winter abundance despite a decrease in appropriate winter habitat is of interest. This suggests that these California habitats offered sufficient prey density and availability to support larger numbers of hawks and adequate overwinter survival to maintain a growing winter population in the state. It is possible that other wintering areas have lost even more prime habitat than California, driving some birds to winter here. Perhaps the preference of the Ferruginous Hawk for somewhat larger prey, such as black-tailed jackrabbits (*Lepus californicus*) and California ground squirrels (*Otospermophilus beecheyi*), compared to most of the raptors that share these winter habitats in California allows this species to make better use of decreasing habitat. Black-tailed jackrabbits are particularly abundant in these California open habitats (Caro et al. 2000, Simes et al. 2015). Of the diurnal raptors that share these winter habitats, only the Red-tailed Hawk (*Buteo jamaicensis*) and Golden Eagle (*Aquila chrysaetos*) regularly take such large prey (Preston and Beane 2009, Katzner et al. 2020). Plumpton and Andersen (1997) observed kleptoparasitism of wintering Ferruginous Hawks by Golden Eagles in Colorado. However, Golden Eagles are uncommon to rare in lowland grassland/open country areas of California (Pandolfino et al. 2011) and are unlikely to have a significant effect on Ferruginous Hawks. The Red-tailed Hawk is common to abundant throughout California in winter in a variety of habitats (Pandolfino et al. 2011). Although we are aware of no observations of this species successfully kleptoparasitzing the larger Ferruginous Hawk, competition for prey with this more numerous species may be a factor. Therefore, it is possible that these California habitats may support an adequate abundance of prey particularly suitable for the Ferruginous Hawk to permit their numbers to grow despite the net decrease in habitat. An increase in density of appropriate prey in remaining habitat could have contributed to the increased numbers of Ferruginous

Hawks. In the absence of historical data on prey abundance in these areas, quantitative and qualitative assessment of the prey taken by Ferruginous Hawks, as well as current density of such prey and overwinter survival of California-wintering birds could help to shed light on this hypothesis. Additionally, it is possible that Ferruginous Hawks have expanded into other habitats (e.g., croplands that are not actively farmed in winter) or have broadened their prey base to include smaller rodents, for example.

Watson et al. (2018) studied movements of Ferruginous Hawks from five different parts of the breeding range and demonstrated that birds from each region showed some degree of regional migratory connectivity between breeding and winter ranges within regional breeding populations. Therefore, this same approach of assessing population trends conducted in other parts of the winter range could shed more light on the overall population status of this species. In addition, telemetry studies of birds breeding in other parts of the range could clarify the source(s) of increasing numbers of Ferruginous Hawks wintering in California.

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