NOCTURNAL FLIGHT CALLS DURING SPRING MIGRATION IN NORTHERN CALIFORNIA

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ABSTRACT: Monitoring of nocturnal flight calls to study bird migration is widely used in the eastern and central United States, but its application in the West has been limited. To assess the potential for such monitoring in northern California and to compare patterns of migration between sites in California's Central Valley and nearby locations in the Coast Ranges, we analyzed data on flight calls recorded in April and May 2022 by five automated units. We counted all recorded songbird calls and identified four common migratory western songbirds with distinctive flight calls as our focal species: the Swainson's Thrush (*Catharus ustulatus*), Wilson's Warbler (*Cardellina pusilla*), Yellow Warbler (*Setophaga petechia*), and Lazuli Bunting (*Passerina amoena*). We detected songbird calls at a higher rate at the sites in the Central Valley than at those in the Coast Ranges, found differences by site in the nightly frequency of calls from three of the four focal species, and noted more flight calls from migratory species other than songbirds at the Central Valley sites. BirdCast's radar estimates of nightly average birds in flight strongly predicted the number of songbird nocturnal flight calls we detected each night.

Every spring, birds migrate northward through California's Central Valley to reach summer breeding sites (Somveille et al. 2015, DeLuca et al. 2021). Birds migrate during the daytime (diurnally), at night (nocturnally), or in some combination of these two. Diurnal migration may be optimal if birds can use daytime atmospheric conditions for efficient flight (e.g., hawks soaring using rising air currents; Kerlinger 1989) or to intersperse foraging with migration (e.g., swifts and swallows catching prey from the air while migrating; Åkesson et al. 2012, Imlay et al. 2020). On the other hand, nocturnal migrants such as New World warblers and sparrows benefit from easier flight conditions with less air turbulence (Kerlinger and Moore 1989), may lose less water to evaporative cooling (Torre-Bueno 1978), and can reserve the daytime hours for foraging (Alerstam 2009). Nocturnal migrants navigate and orient by using a combination of magnetic, celestial, and twilight cues (Emlen and Emlen 1966, Moore 1980, Wiltschko et al. 2002, Cochran et al. 2004).

During flight, some species of nocturnal migrants give nocturnal flight calls, though individuals within a species vary in their rate of calling (Morris et al. 2016). Nocturnal flight calls are typically short calls that are consistent within a species but often differ from species to species. They are usually distinct from other call types such as alarm or contact calls (Farnsworth 2005). Nocturnal flight calls may help flocks of birds stay together and maintain accurate orientation while flying (Hamilton 1962, Simons 2004, Farnsworth 2005, Berdahl et al. 2018, Tegeler et al. 2018). They provide an opportunity for ornithologists to monitor nocturnal bird migration (Farnsworth 2005). Because many calls can be identified to species or a group of related species (Lanzone et al. 2009, Landsborough et al. 2019), nocturnal flight calls provide

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a way to note the movements of a diversity of species, potentially including rare species difficult to detect by day (Evans and Mellinger 1999).

Nevertheless, counts of nocturnal flight calls are not perfectly correlated with the number of birds migrating over a site. Environmental conditions such as ambient noise can reduce the calls' detectability (Larkin et al. 2002, Farnsworth and Russell 2007). Lighting may increase rates of calling (Gauthreaux and Belser 2006, Van Doren et al. 2017). Detectability is greater when winds blow in the migrants' target direction (Erni et al. 2002, Hüppop and Hilgerloh 2012, Smith et al. 2014) or when weather conditions such as precipitation or low visibility create poor conditions for migration (Graber and Cochran 1960). Temperature and humidity affect how sound travels, and higher atmospheric temperatures can increase the calls' detectability on more humid nights but lower it on less humid nights (Horton et al. 2015). The altitude of a calling bird also affects detection of a nocturnal flight call, as higher birds are farther away and so harder to detect (Horton et al. 2015). Furthermore, even within groups of related species, call rates vary by species and among individuals within a species (Morris et al. 2016).

Although nocturnal flight calls have been well studied east of the Rocky Mountains, there is less research in the American West (Lanzone et al. 2009, Burrell 2015, Evans 2021, Osterhaus et al. 2025). California's Central Valley is a key region for bird migration, as an estimated 65 million migratory landbirds travel through it annually each spring (DeLuca et al. 2021). Many of these migratory birds rely on food-rich stopover habitats such as riparian corridors (Cormier et al. 2013) and woodlands of the Valley Oak (*Quercus lobata*) (Greco and Airola 2018). Despite the importance of the Central Valley to migration, no studies using nocturnal flight calls to assess birds' nocturnal movements over this region have been published.

In this study we used automated recording units to explore the potential for detecting nocturnal flight calls in northern California's Central Valley and adjacent Coast Ranges, aiming to identify factors affecting the number of nightly calls detected and to assess the relationship between nightly call counts and nightly radar-based estimates of bird migration over the region provided by the Cornell Lab of Ornithology's BirdCast (https://dashboard.birdcast.info/region/US-CA-113). We hypothesized that the number of calls detected at sites in the Central Valley should exceed numbers in the Coast Ranges, and that we should find a positive relationship between nightly call counts and the radar-based estimates. Our work included classifying which nocturnal flight calls originated from songbirds, specifically focusing on the identification of a small set of common migrants with distinctive calls, and also, when possible, identifying calls of a range of species other than songbirds.

METHODS

Study Sites

We analyzed nocturnal data from five audio recorders positioned on an east–west transect between Lake Berryessa and Davis, California. The sites were at a similar latitude (approximately 38.5° N) but varied in their elevation and habitat (Table 1; habitat classified according to the California Wildlife Habitat Relationships System; Mayer and Laudenslayer 1988). The three

Central Valley sites were at elevations <30 m, while the two westernmost sites in the Coast Ranges were higher, 356 m at Quail Ridge Reserve and 113 m at Stebbins Cold Canyon Reserve. The recorders in the Coast Ranges and two of those in the Central Valley (at Russell Ranch and South Fork Preserve) were away from major sources of nighttime light. Because ambient light can increase the rate at which migrating birds call (Cochran and Graber 1958, Farnsworth 2005, Gauthreaux and Belser 2006, Van Doren et al. 2017, Welcker and Vilela 2018), we also placed a recorder within the city of Davis at a site with obvious nocturnal ambient light.

Monitoring Recorders

The automated recorders (Song Meter Micro; Wildlife Acoustics, Inc.) operated from 1 April through 31 May 2022. Recorders sampled at 44.1 kHz in a single 16-bit mono track, producing uncompressed files in the format .wav. To reduce the rate at which batteries needed to be replaced, recorders operated only every other calendar date. However, because each night spans the evening of one date and the morning of the next, this timing scheme sampled a portion of every night during the two-month interval, albeit not always the same portion. We use "night" to refer to the entire night, spanning two dates. The recordings from each night comprise either an evening (from 30 minutes after sunset until approximately midnight) or a morning (from midnight to 30 minutes before sunrise). For example, the recordings on 1 April included morning recordings from the night that began on 31 March

Table 1 Sites and Situations of Devices Recording Nocturnal Flight Calls between Lake Berryessa and Davis, California

Site name (shorthand)	Elevation (m)	Habitat type	County	Details of recorder location	Latitude, longitude
Quail Ridge Reserve (Quail Ridge)	356	Chamise–Redshank chaparral	Napa	Stake-mounted, on ridgeline, no nearby trees	38.4777, −122.1459
Stebbins Cold Canyon Reserve (Stebbins)	113	Blue Oak–Foothill Pine	Solano (< 650 meters away from both Napa and Yolo)	Stake-mounted, on slope above a gulch, few trees within 10 meters	38.5083, −122.0961
Russell Ranch (Russell)	29	Valley foothill riparian	Yolo	Stake-mounted, in field of annual grasses, few trees within 10 meters	38.5387, −121.8698
Davis	15	Urban	Yolo	Mounted on rooftop antenna, above height of nearby trees, 2 meters above reflective roof surface	38.55, −121.73[a]
South Fork Preserve (South Fork)	5	Valley foothill riparian	Yolo	Stake-mounted, adjacent to creek, several tall trees within 10 meters	38.5197, −121.6893

[a] Precision reduced to maintain homeowner's privacy.

and evening recordings from the night beginning 1 April. In total, we obtained 62 nights of recordings. At four sites we placed the recorders in stake-mounted buckets with a fine mesh cover to protect them from sun, wind, and debris, and to minimize sounds coming from directions other than the sky (Gayk and Mennill 2020). At the Davis site, the recorder was directly mounted to a rooftop antenna approximately 1.5 meters above the roof's surface.

Analyzing Spectrograms of Nocturnal Flight Calls

We counted all calls from songbirds and distinguished the easily identifiable calls of four species that occur in northern California commonly during some part of our spring sampling period (Fink et al. 2023): the Swainson's Thrush (*Catharus ustulatus*), Wilson's Warbler (*Cardellina pusilla*), Yellow Warbler (*Setophaga petechia*), and Lazuli Bunting (*Passerina amoena*) (Evans and O'Brien 2002). That source did not address the calls of the Lazuli Bunting but did include details on the similar calls of the Indigo (*P. cyanea*) and Painted (*P. ciris*) Buntings. Although some species' nocturnal flight calls may vary regionally, we verified the key identifying features of the calls of all four focal species with our own recordings of diurnal flight calls in the Coast Ranges near the Quail Ridge recording site.

Despite initial plans to use automated-detection software, we found no methods suitable for our data. Software for automated detection of flight calls can analyze audio recordings, producing a list with the start time of every potential call in a recording. We tested several software applications: Tseep (Evans 2005a), Thrush (Evans 2005b), BirdVoxDetect version 0.6.0 (Lostanlen et al. 2019) run with Vesper version 0.4.14 (Mills 2023), and the band-limited energy and entropy detectors in Raven Pro version 1.6.4 (K. Lisa Yang Center for Conservation Bioacoustics 2024). Nevertheless, despite our intensive effort, the specificity and sensitivity of all of these methods were low in comparison to a human listener's counts and identifications of the calls.

Therefore, we instead processed recordings manually, using the open-source software application Audacity version 3.1.3 (Audacity Team 2021) to view spectrograms. We produced the spectrograms with Audacity's fast-Fourier-transform tool with a Blackman window of size 512 and a zero padding factor of 4, and we viewed the spectrograms on a linear frequency scale from 0 to 10,000 Hz. Spectrograms offer a way to represent raw audio data graphically with time on the *x* axis and the strength of an audio signal at each frequency on the *y* axis. We counted the numbers of calls of each of the four focal species in each recording and pooled the counts of all other songbirds. The flight call of each of the four focal species is distinctive in its combination of duration, frequency, and degree of modulation (rapid shifts in frequency giving the spectrogram a "wavy" look). Figure 1 illustrates typical examples of the nocturnal flight calls of each focal species. We categorized a sound as a call made by other other songbirds if we could positively identify the nonfocal species (e.g., the distinctive call of the Savannah Sparrow, *Passerculus sandwichensis*) or if the call's pattern was typical of the majority of known songbird flight calls in the United States: a duration <250 milliseconds and a spectrogram pattern with one or two unmodulated bands or a single modulated note. These criteria helped us eliminate any sounds from insects, frogs, night-singing local birds, and mechanical noises. We tallied calls of

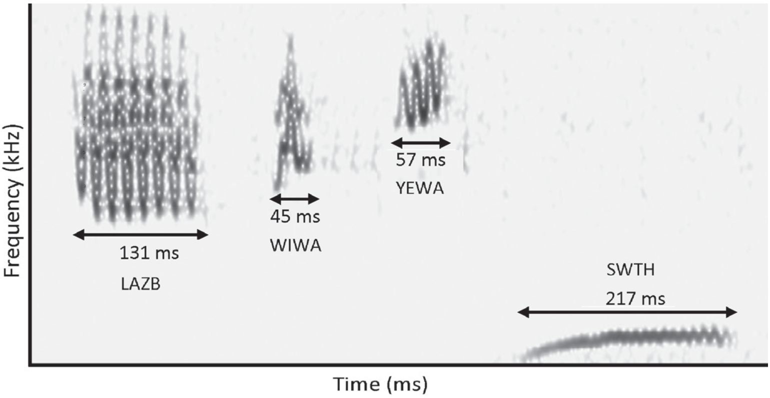

Figure 1. Example spectrograms of the flight calls of the four focal species: Lazuli Bunting (LAZB), Wilson's Warbler (WIWA), Yellow Warbler (YEWA), and Swainson's Thrush (SWTH). Each species' call has a distinctive duration (labeled in milliseconds), range of frequencies, and degree of modulation. The spectrograms for the Lazuli Bunting, Wilson's Warbler, and Yellow Warbler are based on diurnal flight calls we recorded in May 2023. Furrow recorded the Swainson's Thrush call nocturnally in May 2021.

non-songbirds such as shorebirds and waterfowl separately; their calls tended to be longer in duration and were generally identifiable to species.

Tescher and Furrow established inter-rater reliability by analyzing the same recordings independently, then reconciling any differences until we consistently identified the same species and counts of flight calls within a recording. During this process we shared our list of the starting time and identification of every call we detected in a recording. For each difference (either because a call was detected by only one of us or because our identifications did not match) we then compared the call with reference spectrograms and audio clips until we reached consensus on a positive identification or concluded that the sound was ambiguous and not countable. This process continued with new recordings until we matched in our detection and identification of 99% of the calls detected in a night's recording; we worked for several weeks and analyzed a total of 35 hours of recordings to reach this level of reliability. Tescher and Furrow then each analyzed separate sites. We initially analyzed only half the recordings at each site. After noting the low number of calls at some sites, we expanded the analysis to include every recording at three sites: Stebbins Cold Canyon, Russell Ranch, and Davis. Aguilar, Böttcher, Chen, Morris, Velisaris, and Yang analyzed these additional nights, flagging all potential nocturnal flight calls. Furrow then manually confirmed all identifications to get the final counts.

Data Analysis

To compare nightly call counts by site, we totaled the number of individual songbird calls recorded at each site on each night. We defined an "active night" at a site as a night in which at least one songbird call was detected; we calculated the proportion of active nights at each site and calculated the mean nightly number of nocturnal flight calls on the basis of the site's active nights only. We also totaled counts of calls of birds other than songbirds, all of which were waterbirds, but did no further data processing of those calls.

For a comparison among sites that controlled for extraneous variables potentially influencing calls' detectability, we used generalized linear modeling. We modeled the average total nightly counts of nocturnal flight calls (summed across the four focal species plus other songbirds) by using site as our focal predictor variable and time of night (evening vs. morning), radar-based estimate of nightly average number of birds in flight, and migrants' average altitude (Van Doren and Horton 2018, https://dashboard.birdcast.info/region/US-CA-113), average temperature, and average wind profit (the favorability of the wind direction and speed) as covariates.

BirdCast's estimates of the average number of birds in flight per night allowed us to assess the relationship between our counts of nocturnal flight calls and the overall quantity of birds passing overhead, while migrants' estimated altitude provided an important control related to the probability of a call being loud enough to be detected by the recorders and positively identified during processing. BirdCast uses data from weather radar to generate real-time estimates of the number, altitude, and direction of nocturnal migrants, and the tool also reports a nightly summary of the average number of birds in flight. We considered analyzing the altitude and average number of birds in flight over both Yolo and Napa counties, because the majority of Yolo County's area is on the Central Valley floor while a greater proportion of Napa County's area includes the Coast Ranges. However, the estimates of number of birds in flight across Yolo and Napa correlated almost perfectly ($r = 0.99$), so we elected to use only the Yolo County estimates as a covariate in the regression. To correct for a strong right skew in the raw counts, we log-transformed the values for birds in flight with the natural logarithm. We also used only the Yolo County estimates of birds' average altitude at midnight because the Yolo and Napa values were highly correlated ($r = 0.97$) and the mean altitudes (1075 m in Yolo, 1102 m in Napa) did not differ significantly (Wilcoxon test; $p = 0.164$). BirdCast reports altitude estimates by 10-minute intervals throughout the night, but we used only a single measurement (midnight, or the average of 23:55 and 00:05 Pacific Daylight Time if the midnight altitude was not reported) as a coarse measure of whether birds were generally flying higher or lower that night. We compared these measurements with the estimated altitude at 03:00 PDT each night and found a high correlation ($r = 0.87$); this provided a check that birds' tendency to fly at higher or lower altitudes was consistent within a night.

We calculated atmospheric variables (temperature and wind profit) on the basis of data from a single National Weather Service Automated Surface Observing System (ASOS) site: Vacaville Nut Tree Airport. For all of our recording sites, this was the closest ASOS site for which data during our study period were complete, with observations of air temperature and wind speed and direction every 15 minutes. For each night we calculated the mean air temperature and wind profit averaged across all observations within the night's recording period. Wind profit combines wind direction and speed in comparison to a target direction and migratory speed of 12 meters/second, quantifying the degree and speed to which wind is drifting birds with respect to that target direction (Erni et al. 2002). A moderate wind in the general direction a bird intends to fly produces a positive wind profit, while winds that are perpendicular or in the opposite direction of the target produce negative wind profit. On the basis of BirdCast observations of migration direction in Yolo County we used a target direction of due north and calculated an average wind profit for each night by first calculating the wind profit for each 15-minute ASOS measurement within the night's recording period, then taking the mean. We did not include cloud-ceiling measurements in our model because variation across the study period was limited (85% of nights had no measurable cloud cover). Similarly, we did not include dew-point measurements because on all nights except one the average measurement was less than 13° C, which is commonly considered the upper threshold for "dry" atmospheric conditions (National Weather Service, https://www.weather.gov/arx/why_dewpoint_vs_humidity).

All numerical covariates were centered to a mean of 0 and scaled to a standard deviation of 1. We initially considered a Poisson regression model, but overdispersion of the data was statistically significant, with greater than expected variation relative to the mean rates of nightly counts ($p < 0.001$ from the function "check_overdispersion" in the R package "performance"; Gelman and Hill 2006, Lüdecke et al. 2021). We instead fit a negative binomial model to correct for this overdispersion (Zuur et al. 2009). This model no longer suffered from overdispersion ($p = 0.376$), and it did a good job of explaining variation in the nightly flight-call counts (McFadden's pseudo-$R^2 = 0.207$; McFadden 1979). Negative binomial regression fits a linear combination of the predictors to the natural logarithm of the outcome variable (nightly call counts). We report the raw coefficients and convert them back to the original count scale when appropriate to clarify the magnitudes of effects. After fitting the model, we also made pairwise comparisons of the estimated marginal mean counts per site, using the function "emmeans" in the R package "emmeans," with Tukey's method of adjusted p-values to control for multiple comparisons (Searle et al. 1980, Lenth 2025). To statistically test for the overall differences among sites, we used a likelihood-ratio test comparing a negative binomial model with and without "site" as a predictor.

For species-specific comparisons among sites we used chi-squared tests of independence, testing the null hypothesis that the proportion of nights with at least one detection of a flight call was identical at all sites. The regression framework detailed in the previous paragraphs could not be applied at the species level because total counts of calls of the focal species at specific sites were often very low. We used simulated probabilities for the chi-squared tests via the function "chisq.test" in R to avoid inaccurate values for infrequently detected species.

RESULTS

Sites varied in the number of flight calls detected per night (Figure 2A, Table 2) and in the percentage of active nights (Figure 2B, Table 2). The Davis site had the highest percentage of active nights (95.2%) and the highest mean rate of detections of songbird flight calls during the site's active nights (36.3 calls/night). The sites in the Coast Ranges had fewer active nights (55.9% of recording nights at Quail Ridge, 27.9% at Stebbins Cold Canyon) and fewer calls during their active nights (mean of number of calls per active night 6.7 at Quail Ridge, 3.8 at Stebbins Cold Canyon). These differences in the total nightly count of songbird calls were statistically significant (Table 3; $p < 0.001$).

The negative binomial model allowed us to test the overall differences in call counts by site and the relative importance of other covariates. Statistically significant covariates in the model included the number (log-transformed) of birds in flight according to BirdCast (more birds in flight correlated with more call detections; $p < 0.001$), time of night (morning recordings yield $e^{1.902} = 6.7$ times more calls per night than evening recordings; $p < 0.001$), and wind profit (each standard deviation increase in wind profit yields $e^{0.231} = 1.3$ times

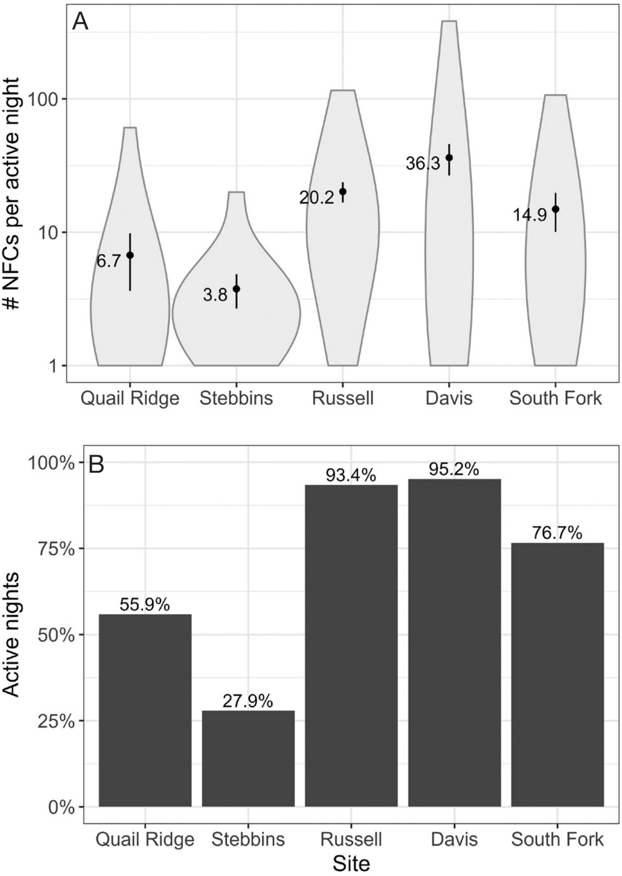

FIGURE 2. (A) Violin plot of the total number of nocturnal flight calls (NFCs) of songbirds recorded each night at each site. The point and number indicate the mean and the bars show standard error above and below the mean. The *y* axis is logarithmically scaled. (B) Percentage of nights with any flight calls recorded (active nights) at each site.

Table 2 Counts of Nocturnal Flight Calls by Species and Site[a]

Site	Lazuli Bunting	Wilson's Warbler	Yellow Warbler	Swainson's Thrush	Other songbirds	Total	Number of nights analyzed
Quail Ridge	1 (1)	2 (2)	4 (3)	58 (4)	63 (17)	128 (19)	34
Stebbins	0 (0)	0 (0)	1 (1)	14 (4)	49 (13)	64 (17)	61
Russell	8 (6)	50 (17)	88 (21)	61 (13)	944 (55)	1151 (57)	61
Davis	15 (6)	21 (11)	105 (22)	518 (16)	1481 (53)	2140 (59)	62
South Fork	4 (3)	4 (3)	23 (7)	51 (5)	261 (22)	343 (23)	30

[a] Number of nights with at least one detection in parentheses.

more call detections; $p = 0.0375$). Wind profit varied minimally from night to night; measurements ranged only between −6.9 and +4.4 meters/second, with 90% of nights having wind profit higher than −4 meters/second. Among the numerical covariates, the number of birds in flight according to BirdCast showed the strongest relationship, with each standard deviation increase in the natural logarithm of that measure yielding $e^{0.546} = 1.7$ times more calls per night. On a linear scale, Figure 3 shows the expected differences in flight-call counts by site, while illustrating the relationship between counts and BirdCast's estimates of birds in flight. We did not find a statistically significant relationship between our nightly counts of flight calls and migrants' altitude estimated by BirdCast ($p = 0.9735$) or average nightly temperature ($p = 0.504$).

When the model's covariates were controlled for, the predicted nightly counts varied widely from site to site. Table 4 reports these estimated marginal nightly mean counts; Davis had the highest predicted count (16.681 calls per night), while Stebbins Cold Canyon Reserve had the lowest (0.625 calls per night). The estimated means do not exactly match the numbers depicted in Figure 2A because the modeled values control for the covariates and summarize all nights of recording, both active nights and nights with no flight calls detected. Most pairs of sites differed significantly in nightly call counts at the $\alpha = 0.05$ level (Table 4), except for Quail Ridge versus South Fork Preserve and Russell Ranch versus Davis.

Comparing sites for differences in the nightly probability of detection of the four focal species, we found statistically significant variation by site for

Table 3 Summary of Negative Binomial Regression Predicting the Natural Logarithm of Nightly Counts of Songbird Flight Calls

Predictor	Estimate	Standard error	p
Site	—	—	<0.001
Time of night:morning	1.902	0.209	<0.001
ln(birds in flight)	0.546	0.114	<0.001
Altitude	−0.003	0.101	0.9735
Wind profit	0.231	0.111	0.0375
Temperature	0.081	0.122	0.504
θ (dispersion parameter)	0.835	—	—
			McFadden's pseudo-R^2 = 0.207

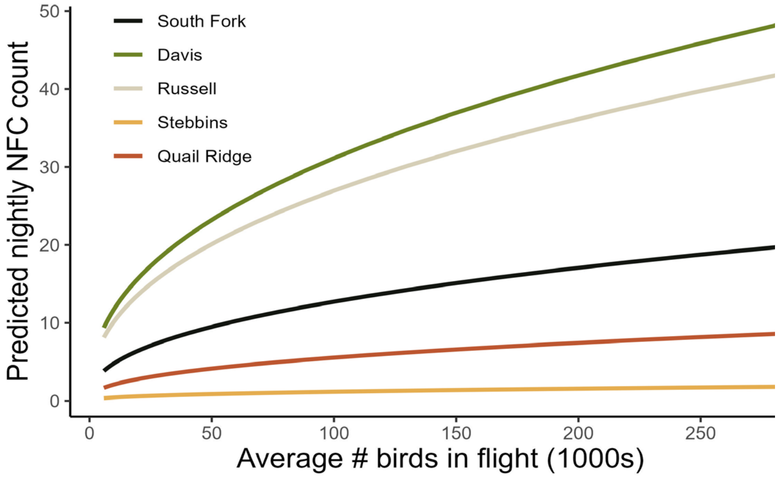

Figure 3. Nightly counts of flight calls at each site as predicted from the fitted negative binomial model as a function of the radar-estimated average number of birds in flight (BirdCast), averaged across morning and evening recordings and based on mean values for all other numerical predictors.

Wilson's Warbler ($p < 0.001$), the Yellow Warbler ($p < 0.001$), and Swainson's Thrush ($p = 0.047$). The differences among sites appear to be driven largely by the nightly frequency of detection being greater at Russell Ranch and Davis than at the two sites in the Coast Ranges and at the South Fork Preserve (Table 2). We did not observe statistically significant variation in detection among sites for the Lazuli Bunting ($p = 0.091$).

In addition to songbirds' nocturnal flight calls, we also detected flight calls of other birds on more nights at the sites in the Central Valley than at those in the Coast Ranges (Table 5). All these other birds were waterbirds. In the Coast Ranges, we detected only three species or species groups of waterbirds: the Western/Clark's Grebe (*Aechmophorus* spp.), Marbled Godwit (*Limosa fedoa*), and Willet (*Tringa semipalmata*). We also detected Willet flocks at two Central Valley sites (Russell Ranch and Davis). Other waterbirds detected at Central

Table 4 Estimated Marginal Means of the Nightly Counts of Flight Calls for Each Site and Pairwise Comparisons among Sites[a]

		Ratio of nightly count compared to:			
Site	Estimate	Stebbins	Russell	Davis	South Fork
Quail Ridge	2.974	4.76 (<0.001)	0.206 (<0.001)	0.178 (<0.001)	0.436 **(0.086)**
Stebbins	0.625	—	0.043 (<0.001)	0.038 (<0.001)	0.092 (<0.001)
Russell	14.452	—	—	0.867 **(0.964)**	2.119 (0.049)
Davis	16.681	—	—	—	2.445 (0.010)
South Fork	6.822	—	—	—	—

[a] Values of p in parentheses; values >0.05 in **bold**.

Valley sites included the Greater White-fronted Goose (*Anser albifrons*), American Wigeon (*Mareca americana*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Common Gallinule (*Gallinula galeata*), Spotted Sandpiper (*Actitis macularius*), Dunlin (*Calidris alpina*), Least Sandpiper (*C. minutilla*), and Western Sandpiper (*C. mauri*). We detected no other calls that clearly originated from birds but were not identifiable to a species or species group.

DISCUSSION

Our results demonstrate the potential for consistent detection of songbirds' nocturnal flight calls during spring migration in northern California, particularly within the Central Valley. The counts' being higher at the Central Valley sites than in the Coast Ranges supports our initial hypothesis and aligns with prior evidence that California's Central Valley is a key migration corridor during spring migration (DeLuca et al. 2021). In addition, the strong positive relationship between BirdCast's estimated average nightly number of birds in flight and the number of songbird flight calls counted nightly suggests that nights with high levels of estimated migration may be the most productive, depending on one's objectives.

Although these counts were calculated by human review of every recording, an automated process would better allow for large-scale monitoring. When using recordings made with directional microphones and low background noise, Furrow has had success with Tseep, Thrush, and BirdVox-Detect, so we suspect that our limited success with automated detection software stemmed in part from the specific setup of our microphones. These nondirectional microphones were positioned relatively close to the ground, with a poor ratio of the amplitude of the target sounds (nocturnal flight calls) to the amplitude of background noise such as wind, frogs, night-singing local birds, and anthropogenic sounds. However, Osterhaus et al. (2025), having recorded flight calls with same recorder type as ours (Song Meter

Table 5 Number of Nights with Identification of a Flight Call of a Bird Other Than a Songbird

	Site					
	Quail Ridge	Stebbins	Russell	Davis	South Fork	Total
Greater White-fronted Goose	—	—	—	5	1	6
American Wigeon	—	—	1	—	—	1
Western/Clark's Grebe	2	—	—	—	—	2
Virginia Rail	—	—	—	—	1	1
Sora	—	—	—	1	1	2
Common Gallinule	—	—	1	1	—	2
Marbled Godwit	—	1	—	—	—	1
Spotted Sandpiper	—	—	1	1	—	2
Willet	—	1	1	1	—	3
Dunlin	—	—	—	1	—	1
Least Sandpiper	—	—	1	—	—	1
Western Sandpiper	—	—	1	—	—	1

Micro), reported recent success with an automated process for detecting and analyzing them with a newer software application, Nighthawk (Van Doren et al. 2024). Unfortunately, this software was not widely available when we undertook our analysis.

The relatively weak relationships we found between nightly call counts and weather and altitude measurements may reflect the consistency of the weather in northern California's Central Valley during our study period. Although average wind profit had a weak positive relationship with nightly call counts, on no night was it below –7 meters/second, the cutoff Erni et al. (2002) proposed for a consistently strong negative effect on the nightly number of birds migrating. We were surprised by the lack of a significant relationship between BirdCast's estimated altitude at midnight and the nightly count of flight calls. Altitude may be conflated with other variables affecting call rates or the number of birds in flight, so a study mapping the exact timing of each detected call with the estimated altitude of migrating birds at that moment could offer more insights.

Several environmental factors confounded the comparison of the sites in the Central Valley with those in the Coast Ranges. The Davis site had both the most nighttime ambient light and the most nocturnal flight calls. Light influences the rate at which birds call; environmental light brings migratory birds lower to the ground (Gauthreaux and Belser 2006), increasing the rate of detections of nocturnal flight calls (Farnsworth 2005, Van Doren et al. 2017, Welcker and Vilela 2018). The setup of the recorder at Davis also differed (mounted to a rooftop antenna), so we compared the Davis results with a partial dataset from another ground-level stake-mounted recorder installed at another home in Davis and it yielded comparably high call counts. The rate of detections at Russell Ranch, west of Davis, was similarly impressive. This site was along a wooded creek and not near any urban center, but several nearby homes implied the potential for some nighttime light. Of the three Central Valley sites the South Fork Preserve had both the lowest density of nearby human homes and the lowest call count, though the count was still statistically significantly higher there than at Stebbins Cold Canyon Reserve in the Coast Ranges.

Another possibly confounding factor is the difference in topography between the Coast Ranges and Central Valley. For example, over mountainous regions birds may fly at higher altitudes to avoid turbulence caused by updrafts on windy evenings, thus reducing their detectability. However, the vast majority of nocturnal flight calls we detected were after midnight (during "morning" recordings), and BirdCast's estimates of migratory birds' altitude at midnight over Napa and Yolo counties did not differ significantly. These coarse measurements may still conceal variation in flight altitude both within and across species; for example, smaller species may be more affected by updrafts on windy nights. A future study that more directly incorporates turbulence data and the precise timing of species-specific calls during the night could reveal more about potential effects of topography.

Although our nightly counts of flight calls were generally higher within the valley, the exact patterns of detection varied by species. In particular, Swainson's Thrush calls constituted a high proportion of all calls detected at both Quail Ridge and Stebbins Cold Canyon, while the valley sites had proportionally more Wilson's Warblers and Yellow Warblers. While Swainson's

Thrush as a species breeds across a transcontinental swath of boreal forest, the principal subspecies migrating through California in spring, the russet-backed *Catharus u. ustulatus*, breeds along the Pacific coast from northwestern California north to southeastern Alaska (Delmore et al. 2012, Cormier et al. 2013, Humple et al. 2020). In comparison, one of the two subspecies of the Yellow Warbler migrating commonly through California, *Setophaga p. morcomi*, also breeds widely in inland parts of northern California (Heath 2008). This disproportionate concentration of Swainson's Thrush in the Coast Ranges could reflect a greater concentration along a narrower path toward coastal breeding locations in northern California or the Pacific Northwest.

Confoundingly, despite the breeding range of Wilson's Warbler also extending far to the north along the Pacific coast, we rarely detected that species in the Coast Ranges. This could reflect the historical importance of Central Valley wetlands as insect-rich stopover habitat during spring, as well as challenges with the definitive identification of Wilson's Warbler's flight call (which, when weak, can have a pattern that is difficult to visually discern in a spectrogram). Populations of Wilson's Warbler breeding in different geographic regions may also differ in their spring migration routes (Paxton et al. 2007), but monitoring of nocturnal flight calls is unlikely to offer additional insights here unless the calls of Wilson's Warblers from different breeding populations differ consistently.

Even though the Lazuli Bunting breeds abundantly near our sites in the Coast Ranges, we detected relatively few of its flight calls at any site. This could reflect relatively low numbers of migrants, a lower baseline rate of nighttime calling, or limitations in our ability to detect these calls. The extremely fine modulation of this species' flight call may have resulted in our overlooking quiet calls as snippets of white noise; using a spectrogram window with a finer temporal resolution might improve our detection of these calls during visual inspection of spectrograms. In contrast, calls of the Yellow Warbler and Swainson's Thrush could often be identified unambiguously even when very faint; the detectability and identifiability of faint Wilson's Warbler's calls were seemingly intermediate.

Willets and Other Waterbirds

Our study shows promise for detecting movements in northern California of shorebirds such as the locally uncommon Willet. Some Western Willets (subspecies *Tringa semipalmata inornata*) winter along the California coast at sites less than 80 km from our recorders. Western Willets breed as close as the Great Basin (Haig et al. 2002) as well as in northern parts of the Great Plains (Lowther et al. 2001). To reach their breeding grounds, some individuals wintering on the California coast may cross the Central Valley, but these birds are only rarely detected in spring (Fink et al. 2023). Nevertheless, we recorded the Willet at three sites across three different nights. All of these detections appeared to be of flocks rather than of single individuals, consistent with observations of the Eastern Willet (*T. s. semipalmata*) migrating in small flocks (Tomkins 1965). The Willet's low rate of diurnal detection could reflect a nonstop migration. Some other large shorebirds make far longer nonstop migrations, capped by the Bar-tailed Godwit (*Limosa lapponica baueri*), which flies from Alaska to New Zealand without stopping (e.g., Battley et al.

2012). The Western Willet may be more easily detected in migration by its nocturnal flight calls than by any diurnal efforts.

Our results also support the use of nocturnal flight calls to detect the movements of secretive birds like rails. We detected the Virginia Rail, Sora, and Common Gallinule. Although rails tend to be hard to detect diurnally in their dense marsh habitats (Winkler et al. 2020), migratory rail species are readily detected as nocturnal migrants (e.g., Evans and Mellinger 1999, Wilson 2022). Nocturnal recording may be an effective strategy to identify the timing and routes of rail migration, including species of conservation concern such as the Yellow (*Coturnicops noveboracensis*) and Black (*Laterallus jamaicensis*) Rails (Evans and Mellinger 1999). However, the relationship between rates of nocturnal flight calling and the actual number of migrating birds is confounded by calling behavior and a variety of environmental variables, so sporadic rail detections reveal limited information about the magnitude of such movements.

Although the Central Valley is important for wintering waterfowl (e.g., Gilmer et al. 1982), our study took place too late in spring to detect much waterfowl migration. For example, peak northbound migration of the Northern Pintail (*Anas acuta*), which winters abundantly in the Central Valley, is in February and March (Miller et al. 2011). Nevertheless, we noted calls of two species of waterfowl, the American Wigeon and Greater White-fronted Goose, the goose on six different nights and at two sites. A study monitoring nocturnal flight calls in the Central Valley from January through March should detect a greater number and diversity of ducks and geese.

CONCLUSION

In this study we detected thousands of nocturnal flight calls by songbirds during spring migration in northern California, demonstrating the potential for monitoring of these calls in this region. Nightly counts of calls were generally higher at sites in the Central Valley than at those in the Coast Ranges, and we also detected multiple calls of waterfowl, shorebirds, and rails. The high counts from a site within the city of Davis suggests that monitoring may be particularly productive at urban sites. Future efforts to expand this monitoring could focus on automating the call-detection process and targeting detection of species that pass overhead nonstop, such as the Willet.

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