

## ORIGINAL RESEARCH REPORT

Space Use by Swainson's Hawk (*Buteo swainsoni*)  
in the Natomas Basin, California

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We used satellite-based remote sensing to estimate home ranges for Swainson's Hawk, a species listed as threatened in California (USA), on its breeding grounds in the Natomas Basin (northern Central Valley, California) and to evaluate whether the species' space-use intensity (statistically derived density of telemetry locations) was associated with land cover, sex, reproductive success, or life stage of offspring. We differentiated seven classes of land cover—alfalfa, annually rotated irrigated crops, developed, grassland, orchard / vineyard, rice, and water. From 2011–2013, we fitted transmitters with global positioning systems to 23 adult Swainson's Hawks. We recorded a minimum of six locations per day per bird from spring through early autumn of each year. We used a fixed, bivariate-normal kernel estimator to calculate a utilization distribution at 30-m resolution for each life stage of each individual within each year. We used a linear mixed model to estimate the associations between intensity of space use and land cover, sex, and reproductive status. The majority of adult Swainson's Hawks traveled distances up to 8–10 km from the nest throughout the breeding season. Median seasonal home-range sizes in a given year ranged from 87–172 km<sup>2</sup>. The association between intensity of space use and grassland was 50–139% stronger, and the association between intensity of space use and alfalfa 23–59% stronger, than the associations between intensity of space use and any other land-cover type. Intensity of space use did not vary as a function of sex, reproductive status, or life stage. Given our results and additional knowledge of the species' ecology, we suggest that reproductive success and, in turn, population-level recruitment may be associated equally if not more closely with availability of nesting sites than with the current distribution of land cover.

**Keywords:** Central Valley; home range; land cover; land use; nesting success; utilization distribution

**Introduction**

Spatially extensive changes in land use and land cover affect the survival and reproduction of numerous species. Human activities reduce the probability of persistence of many native species, but generalists may adapt to or benefit from some forms of agricultural and suburban or exurban development [1, 2, 3]. Relations between population dynamics and different types of development vary geographically and among species. Identifying such relations can be highly relevant to regional land-use

planning and regulatory compliance, especially for species with legal protection.

Swainson's Hawk (*Buteo swainsoni*) is among the species most often invoked in assessments of the potential biological effects of contemporary land-use change in California's Central Valley. For example, conservation of Swainson's Hawk was emphasized in the Natomas Basin Habitat Conservation Plan [4] and is addressed in planning documents or administrative drafts for the Yuba–Sutter and Yolo County Habitat Conservation Plans [5, 6].

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Historical losses of the species' habitat in the state and decreases in its estimated abundance led to its listing as threatened under the California Endangered Species Act in 1983. Swainson's Hawks nest in riparian woodlands, oak woodlands, stands of trees along roads or edges of agricultural fields, and isolated trees [7]. They breed from southern Alberta, Saskatchewan, and Manitoba, Canada south through the Intermountain West and Great Plains of the United States and into northern Mexico. Isolated populations breed in interior valleys of British Columbia, Canada, California's Central Valley, and some valleys in the western Great Basin. The species winters from Mexico south through South America and occasionally in the southern United States [7, 8]. Some individuals also winter in the Sacramento–San Joaquin Delta in California [9].

The largest and densest populations of Swainson's Hawks in California are believed to occur in the Central Valley counties of Yolo, Solano, Sacramento, and San Joaquin [10, 11]. In Butte Valley (Siskiyou County, California), on the western edge of the Great Basin, annual apparent survival of adults varied from 0.85 to 0.9 over 30 years [12]. At least locally, food availability may be associated with temporal variation in brood size and nestling survival [13].

Throughout their range, Swainson's Hawks forage in native and non-native grasslands and in relatively open shrublands and woodlands [7]. In the Central Valley and other agricultural areas, Swainson's Hawks also forage in irrigated fields or pastures and in fields in which alfalfa, other hay crops, and some row crops and grains are grown [7, 14]. During the breeding season, Swainson's Hawks eat rodents, rabbits, birds, insects, and reptiles. Small mammals generally comprise the majority of the biomass consumed by adults during the breeding season and delivered to nestlings, although prey composition is spatially and temporally variable [15, 16]. During the non-breeding season, the species continues to feed opportunistically. When present, insects (especially grasshoppers) are a primary food source [7].

The extent to which Swainson's Hawks use different land-cover types and crops, and the extent to which use is associated with the distribution of the species or its reproductive success, varies considerably. For example, in northern Colorado, abundance of Swainson's Hawks during the breeding season was positively correlated with cover of tallgrass prairies and hay fields and not correlated with cover of pavement, buildings, and urban vegetation or with distance to prairie dog towns (a potential source of prey) [17]. The average distance between the nest site and agriculture (primarily irrigated alfalfa), and the average area of agriculture within a 500-m radius of the nest, were negatively related to adult survival in Butte Valley, California [12]. In southeastern Arizona, the density of Swainson's Hawks was higher in agricultural areas than in grasslands (similar to density patterns in the Central Valley) and desert scrub, but breeding success did not differ among those land-cover types [18].

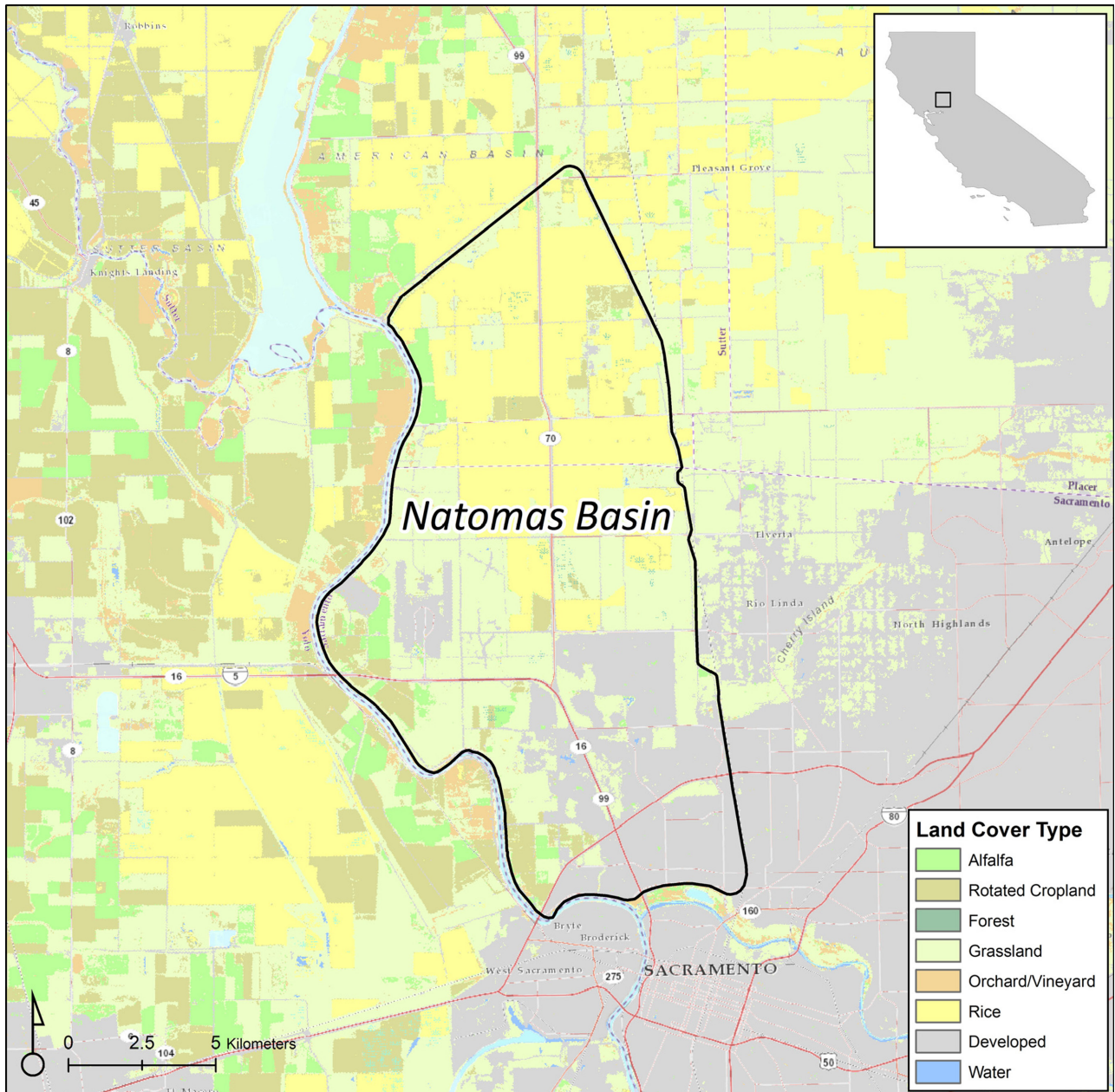
From 1973–2000, agriculture consistently covered about 72% of the Central Valley [19]. Although the total

area of agriculture has changed little, row crops, hay, and grains have been replaced locally by orchards and vineyards, and some regional droughts resulted in widespread fallowing. Additionally, increases in California's human population are leading to gradual increases in the developed area of the Central Valley. Swainson's Hawks nesting in the Natomas Basin (Sacramento and Sutter Counties, California; roughly at the lower end of the northern third of the Central Valley; **Figure 1**) have been monitored annually by J.E. since 2001 to comply with the Natomas Basin Habitat Conservation Plan, which was adopted in 1997 and revised in 2003 [4]. Habitat Conservation Plans are required prior to issuance of a federal permit to non-federal parties for incidental take of species that are listed under the U.S. Endangered Species Act or that may become listed during the permit period. Forty-three to 65 nesting territories were reported as active each year, and the number of pairs nesting in the Natomas Basin from 2001–2013 was stable, if not gradually increasing [20]. The mean number of young fledged per active nesting territory per year during this period was 1.00 (SD 0.33, range 0.26–1.55) (J.E. unpublished data).

We capitalized on the increasing feasibility of satellite-based remote sensing to objectively track space use (the locations where animals are present) of Swainson's Hawks. Past inferences about habitat use or environmental attributes associated with presence of Swainson's Hawks during the breeding season or the winter [9] largely were based on visual surveys [9, 14, 21], point counts [17], or the locations of nests [22]. Use of radio telemetry to assess space or habitat use by Swainson's Hawks has been relatively uncommon but see [23, 24, 25] and, to the best of our knowledge, global positioning systems (GPS) have not been used previously. Space use is most informative when it can be related to a measure of survival or reproduction. With the goal of informing ongoing and future land-use planning in the Natomas Basin, we estimated home ranges for Swainson's Hawks that are present in or adjacent to the basin during the breeding season and evaluated whether space-use intensity (statistically derived density of telemetry locations) was associated with land cover, sex, reproductive success, or life stage of offspring.

## Materials and Methods

We differentiated seven classes of land cover—alfalfa, annually rotated irrigated crops, developed, grassland, orchard / vineyard, rice, and water—within a 2000-km<sup>2</sup> area that encompassed the Natomas Basin and a 16-km buffer around the perimeter of the basin (Supporting Information). We selected these land-cover classes on the basis of the assumption that they were the most likely to be associated with space use by Swainson's Hawks (J.E. and R.L.A. unpublished data). Alfalfa was dominated by alfalfa and clover. Annually rotated irrigated crops primarily included row crops, field crops, and grains. Developed included all intensities of development (including roads), open space in developed areas (e.g., parks and golf courses), and barren areas. Grassland included non-alfalfa hay crops, grass-covered areas used as pasture, fallowed



**Figure 1:** The Natomas Basin (Sacramento and Sutter Counties, California) and its location within California (inset).

cropland, non-native annual grasses, and a small proportion of native annual and perennial grasses. About 5% of orchard / vineyard was non-agricultural trees and shrubs; about 90% was orchard. Detailed definitions of each class are in Supporting Information. We used the National Agricultural Statistics Service's Cropland Data Layer (<http://nassgeodata.gmu.edu/CropScape/>) for 2012 to determine the locations and extents of each land-cover class. Alfalfa covered 9% of the analysis area, annually rotated irrigated crops 21%, grassland 26%, orchard / vineyard 11%, rice 14%, developed 18%, and water 1%. Field evaluation (described fully in Supporting Information) indicated that classification accuracy was  $\geq 84\%$  and that within these classes, land cover changed little from 2011 through 2013.

We selected Swainson's Hawks to be fitted with satellite transmitters from pairs on nesting territories in the

Natomas Basin or within a 3-km buffer around the Natomas Basin. In this manuscript, we define a nesting territory as the area around the nest that is defended by an adult; this is a narrower definition than that of Steenhof and Newton [26]. We searched for nesting Swainson's Hawks by driving all accessible roads within the Natomas Basin, including both sides of the peripheral watercourses (Sacramento River, Natomas Cross Canal, and Steelhead Creek). Where no roads provided access to trees large enough to be used by Swainson's Hawks for nesting [27, 28], we conducted surveys on foot. We searched for Swainson's Hawks in potential nest trees with binoculars or a spotting scope.

We trapped Swainson's Hawks with the dho-gaza method [29, 30, 31]. We tethered a potential predator, a live Great Horned Owl (*Bubo virginianus*), behind a 2 m  $\times$  6 m, four-shelf mist net (210 denier / 2 ply, 100 mm mesh)

(Avinet, Inc., Freeville, New York). To elicit defensive behavior by the adult Swainson's Hawks, we arranged the trap near active nests with young. We targeted nests that were accessible by foot and that had enough open, unobstructed area nearby that a Swainson's Hawk could dive safely on the owl. The locations in which we arranged the trap also allowed us to protect the owl from contact with the hawk and had sufficient shade in which to process the captured hawk. We trapped adults at nests in which the young were 10 days of age or older to minimize the probability of adults abandoning the nest or of juveniles being unable to thermoregulate on their own. We made trapping attempts between 0500 and 1300 on a given day. Given the limited number of nests, we did not stratify nests by environmental covariates or attempt to trap a certain proportion of either sex.

From July 2011 through April 2013, we fitted transmitters with GPS (22-gram solar-powered Argos / GPS PTT 100, Microwave Telemetry, Columbia, Maryland) to 23 adult Swainson's Hawks. In 2011, we captured 12 Swainson's Hawks. In 2012, we fitted transmitters to nine Swainson's Hawks. In April 2013, we fitted transmitters to two Swainson's Hawks before nesting began. We used Teflon ribbon to attach the transmitters as backpack mounts. Processing time for each Swainson's Hawk was one to two hours and included taking measurements, fitting the backpack-transmitter to the hawk, and placing a band (Bird Banding Laboratory, Pautuxent, Maryland) on its leg. The weight of a transmitter was equivalent to 3% or less of the average body weight of an adult Swainson's Hawk [32]. All transmitters had motion-based mortality sensors.

Six of the transmitters were programmed to record six locations per day at fixed times (one every other hour from 0900 to 1900, the period during which Swainson's Hawks typically are most active) from 16 March through 10 October. Coordinates were transmitted via satellite. These six transmitters also included very high frequency (VHF) transmitters with signals that were broadcast continuously from 0900 through 2100 each day from 16 March through 15 September (data not reported or analyzed here). The 15 remaining transmitters, two of which were fitted to different birds during different years, were programmed to record 12 locations per day at fixed times (one per hour from 0900 to 2000) from 16 March through 10 October. Coordinates were transmitted via satellite. All transmitters were programmed to record two locations per day from 11 October through 15 March; data on overwintering locations will be reported elsewhere. The manufacturer estimated that the GPS sensors had a horizontal accuracy of  $\pm 18$  m. Except in the situations noted below, the analyses reported here were based on the six or 12 locations per day.

We visually monitored all nesting territories from which Swainson's Hawks were captured until the hawks migrated. Visits were spaced about a week apart, although neither the number of days on which surveys were conducted nor the interval between surveys was standardized. During each visit, we recorded whether the territory was occupied by a pair of Swainson's Hawks (regardless

of nesting success), whether the nest was active (eggs or young were present), and, where relevant, the number of young fledged [23]. We defined a successful nest as one in which at least one young fledged [26] and a failed nest as one in which no young fledged.

We used a fixed, bivariate-normal kernel estimator to calculate a utilization distribution (UD [33]) at 30-m resolution for each life stage (see below) of each individual within each year. The bivariate normal is a statistical distribution of values of pairs of related, normally distributed variables (e.g., in two-dimensional space, an x-coordinate and a y-coordinate [34]). A kernel is a point or polygon around which one estimates the density of other points, lines, or polygons, including natural or human-created environmental features. This method places a circular kernel over each cell in a regular lattice, and produces a weighted count, or density estimate, of the telemetry locations that fall within the kernel; the weights decrease as the distance from the center of the kernel increases [34]. The bandwidth selector,  $h$ , defines the radius of the kernel and therefore the level of overall smoothing. A UD permits one to make a probabilistic estimate of the intensity of space use for each individual at a given location [35]. Thus, the intensity of space use represents the density of telemetry locations as derived from the UDs. We estimated UDs with the  $cv/h$  bandwidth selector, which limited both identification of areas of high space-use intensity where Swainson's Hawks were not recorded (i.e., oversmoothing) [36] and fragmentation of the home range [37]. The  $cv/h$  also helps minimize potential lack of independence among locations or biases in acquisition of locations [36]. We defined the home range represented by each UD as the area within its 99% isocline (the area bounded by 99% of its volume).

We excluded some data for a subset of Swainson's Hawks in one or more years because the animal died or its transmitter temporarily or permanently stopped functioning. We also excluded points from individuals for which life stages were not defined, either because the bird did not nest or because nest-observation data were insufficient. We further excluded data when the number of locations recorded for a given individual for a given life stage was fewer than 30.

Where data were sufficient or applicable, we calculated UDs for each of four life stages within each year, two of which are associated with development of offspring: arrival – day of arrival in the Natomas Basin through day before first observation at the nest, prehatching – day of first observation at nest through day before first observation of hatched young, nestling – day of first observation of hatched young through day before first observation of fledging, and premigration – day of first observation of fledging through day before seasonal departure from the Natomas Basin. We determined seasonal departure on the basis of GPS locations and directional movements away from the Natomas Basin.

We used a linear mixed model to estimate the associations between intensity of space use and land cover, sex, and reproductive status for each year. We restricted our

models to points that fell within the 99% isoclines of the corresponding UD. Our data indicated that late in the breeding season, Swainson's Hawks sometimes fly distances that are quite long relative to typical daily movements earlier in the breeding season. The 99% isocline excluded many of the points corresponding to these long-distance movements. We used orchard / vineyard, the only land-cover class over which all Swainson's Hawks in our sample were recorded in all three years, as the reference land-cover class. Female was the reference class for sex. We differentiated three classes of reproductive status: nested and at least one young fledged, nested but no young fledged, and did not nest, with did not nest as the reference class.

We included a random intercept in our models, with levels defined by individual, life stage, and year, to account for variation in space-use intensity among individuals and over time. Additionally, to account for the fact that many points were near nests, we manually defined for each individual, within each year and life stage, a distance from the nest (i.e., a radius) beyond which there was little evidence of concentrated use of space. We recorded whether each telemetry location was within or beyond this radius (referenced as the *nest zone threshold*), and included the binary (within or beyond) variable as a random-effect level. To account for potential reduction in space-use intensity as distance from the nest increased, our final model also included a random slope effect, with the same two levels of the nest zone threshold, for distance from the nest site.

We used spatial covariance functions to explore the modeling of spatial autocorrelation among model residuals [38]. We did not include a covariance model in the final model due to overestimation of function parameters, which apparently were related to concentration of use around the nest. Accordingly, we used the Huber-White sandwich estimator [39] to calculate standard errors in the presence of any remaining subject-level heterogeneity. We used Akaike's Information Criterion (AIC) to assess whether the support for our global model was substantially different (e.g., a difference  $\geq 4$  AIC) than that for a null model. We used a paired *t*-test ( $\alpha = 0.05$ ) to test, for each variable, whether there was a statistically significant difference in the strength of associations between occupancy and a given class (of land cover, sex, reproductive status, life stage, or year) versus the reference class of that variable. We derived all estimates with SAS PROC MIXED (v9.3; SAS Institute, Inc., Cary, North Carolina).

## Results

In 2011, six of the Swainson's Hawks that we tracked fledged young and four nested but did not fledge young. In 2012, 14 of the Swainson's Hawks fledged young, two nested but did not fledge young, and one did not nest. In 2013, four of the Swainson's Hawks fledged young, nine nested but did not fledge young, and one did not nest.

We included in our analyses a total of 3,374 locations from six Swainson's Hawks (five males) in 2011, 10,917 locations from 15 Swainson's Hawks (12 males) in 2012, and 4,880 locations from 4 Swainson's Hawks (all male)

in 2013 (**Table 1**). The analyses included data for 3 males that were tracked in all three years, 2 males tracked in two of three years, and 8 males and 4 females tracked in one year.

In all years, the vast majority of adult Swainson's Hawks traveled distances up to 8–10 km from the nest throughout the breeding season. Nest zone thresholds (**Figure 2**) for individuals that fledged young generally ranged from about 1000 to 4000 m, and did not appear appreciably different during different life stages (**Table 1**). The upper bound of nest zone thresholds for individuals that did not produce offspring or whose offspring did not fledge was greater, to about 7500 m. Data were insufficient to analyze statistically whether nest zone thresholds varied as a function of year, sex, life stage, and reproductive success.

Home-range sizes varied among individuals, years, and life stages (**Table 1**). Median seasonal home-range sizes, calculated on the basis of points within the 99% isocline, were 109 km<sup>2</sup> (range 10–336) in 2011, 172 km<sup>2</sup> (range 43–1427) in 2012, and 87 km<sup>2</sup> (range 77–341) in 2013. Home ranges generally were smallest when adult Swainson's Hawks were caring for young. Median home-range sizes during the arrival stage were 25 km<sup>2</sup> (range 2–12860, or 2–47 excluding one individual's anomalously large home range) in 2012 and 323 km<sup>2</sup> (one individual) in 2013 (**Table 1**). During the pre-hatching stage, median home-range sizes were 33 km<sup>2</sup> (range 4–202) in 2012 and 110 km<sup>2</sup> (range 41–226) in 2013. Median home-range sizes during the nestling stage were 80 km<sup>2</sup> (range 4–137), 69 km<sup>2</sup> (range 6–350), and 30 km<sup>2</sup> (range 5–174) in 2011, 2012, and 2013, respectively. Home ranges of pre-migratory Swainson's Hawks were 95 km<sup>2</sup> (range 8–357) in 2011, 201 km<sup>2</sup> (range 6–604) in 2012, and 88 km<sup>2</sup> (range 4–400) in 2013, respectively.

The global model (presented here) had an AIC value 411.3 lower than the null model. Across the three years, intensity of space use was more strongly associated with five of the land-cover classes—grassland, alfalfa, developed, water, and rice—than with the reference class, orchard / vineyard (**Table 2, Figure 3**). The association between intensity of space use and grassland was 50–139% stronger than the positive associations between intensity of space use and any other land-cover type. The association between intensity of space use and alfalfa was 23–59% stronger than the association between space use and water, developed, or rice (**Table 2**). Strengths of association between intensity of space use and either water or developed were relatively similar. Intensity of space use did not vary as a function of sex, reproductive status, or life stage.

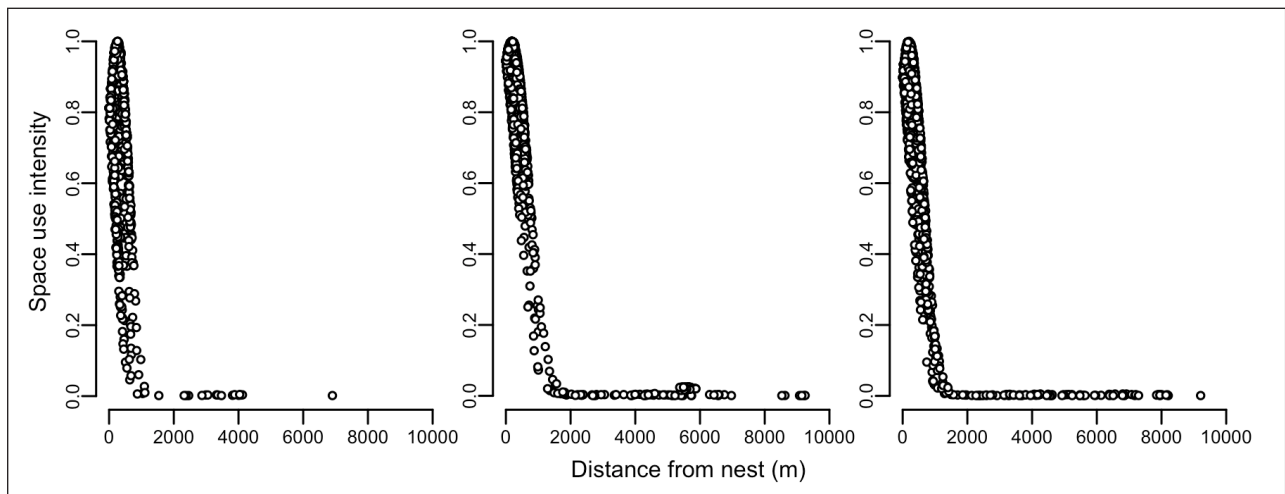
## Discussion

Although there was considerable annual variation in reproductive success of the Swainson's Hawks we tracked, intensity of space use did not vary as a function of reproductive status. Our nest zone thresholds generally were consistent with previous estimates from elsewhere in California. For example, in Butte Valley from 1984 through 1994, nesting Swainson's Hawks moved  $2.2 \pm 0.23$  km (mean  $\pm$  SE), with a range from 0.97–6.3 km [40]. In the

Identification number	Sex	Year	Number of young fledged	Life stage	Nest zone threshold (m)	Area of home range (km <sup>2</sup> ), 99% isocline	Area of home range (km <sup>2</sup> ), 95% isocline
105921	male	2011	1	annual	1750	250	130
				nestling	1500	40	20
				premigration	1500	291	155
105922	male	2011	1	annual	1750	78	35
				premigration	1750	78	35
105922	male	2012	2	annual	1000	156	71
				arrival	1000	47	17
				prehatching	1000	133	60
				nestling	1000	138	69
				premigration	1000	163	94
105922	male	2013	1	annual	1200	341	208
				prehatching	1250	226	133
				nestling	1250	174	109
				premigration	1000	400	245
105923	male	2012	1	annual	2500	204	69
				prehatching	2000	202	70
				nestling	2000	63	30
105925	female	2012	1	annual	1500	43	20
				premigration	1500	43	20
105926	male	2012	2	annual	2000	249	122
				premigration	2000	249	122
105927	male	2012	2	annual	4000	1428	498
				arrival	4000	12,860	7842
				prehatching	3000	11	3
				nestling	3500	69	31
				premigration	3000	267	153
105928	male	2011	2	annual	2500	57	20
				premigration	2500	57	20
105928	male	2012	2	annual	2000	58	10
				arrival	1500	2	1
				prehatching	1750	44	17
				nestling	1750	6	2
				premigration	1750	37	15
105928	male	2013	1	annual	4000	89	15
				prehatching	3000	142	33
				nestling	4000	5	2
				premigration	4000	88	30
105930	male	2011	2	annual	1000	10	2
				nestling	1000	4	2
				premigration	1000	8	2
105930	male	2012	2	annual	1500	172	47
				prehatching	1100	4	2
				nestling	1500	32	10

Identification number	Sex	Year	Number of young fledged	Life stage	Nest zone threshold (m)	Area of home range (km <sup>2</sup> ), 99% isocline	Area of home range (km <sup>2</sup> ), 95% isocline
105930	male	2013	1	premigration	1500	491	237
				annual	1100	84	21
				arrival	900	323	171
				prehatching	1200	41	10
				nestling	1300	30	10
105931	female	2012	0	premigration	1250	4	2
				annual	1700	81	38
				premigration	1700	81	38
105933B	male	2012	1	annual	2000	69	26
				premigration	2100	70	26
105935	female	2011	1	annual	2200	336	177
				nestling	1500	137	69
				premigration	2000	357	196
105936	male	2011	1	annual	2200	141	63
				nestling	1500	121	71
				premigration	2100	112	56
105936	male	2012	1	annual	2000	65	15
				arrival	2000	3	2
				prehatching	2000	21	8
				nestling	1750	15	7
				premigration	1750	105	39
117526	male	2012	1	annual	2000	228	123
				nestling	2000	350	211
				premigration	2500	240	127
117527	male	2012	1	annual	6000	571	288
				nestling	7500	209	134
				premigration	4000	604	305
117527	male	2013	1	annual		78	46
117528	male	2012	2	annual	2000	88	27
				nestling	2000	200	115
				premigration	2000	6	3
117529	female	2012	1	annual	2500	313	162
				premigration	2500	313	162
117530	male	2012	2	annual	2200	610	338
				premigration	2200	399	231

**Table 1:** Swainson's Hawks tracked with satellite telemetry in 2011, 2012, and 2013, associated demographic attributes, and nest zone thresholds for individuals that nested or reproduced. Data were insufficient to calculate nest zone thresholds for all life stages for all individuals. There was no indication of concentrated use of space around the nest for individual 117527 in 2013. Arrival – day of arrival in the Natomas Basin through day before first observation at the nest, prehatching – day of first observation at nest through day before first observation of hatched young, nestling – day of first observation of hatched young through day before first observation of fledging, premigration – day of first observation of fledging through day before seasonal departure from the Natomas Basin. Nest zone thresholds are fairly discrete clusters of points beyond which there was little to no evidence of concentrated use of space. Area of home range defined on the basis of the 99% or 95% isocline.



**Figure 2:** Space-use intensity as a function of distance from the nest for an illustrative male Swainson’s Hawk (identification number 105930) throughout the 2011, 2012, and 2013 breeding seasons. Data included 1060 locations for 2011, 1651 for 2012, and 1604 for 2013. We defined the nest-zone thresholds as 1000 m for 2011, 1500 m for 2012, and 1100 m for 2013.

Variable	Estimate	SE	t-value	p-value
Land cover				
Alfalfa	0.63	0.20	3.21	0.00
Annually rotated irrigated crops	0.37	0.19	1.98	0.05
Grassland	0.81	0.17	4.82	0.00
Rice	0.42	0.21	2.02	0.04
Developed	0.44	0.19	2.26	0.02
Water	0.26	0.10	2.62	0.01
Sex				
Male	-0.07	1.78	-0.04	0.97
Reproduction				
Nested, without young	0.31	4.01	0.08	0.94
Life Stage				
Arrival	1.95	1.47	1.33	0.19
Offspring are pre-hatching	0.08	1.39	0.05	0.96
Offspring are nestlings	0.10	1.12	0.09	0.93
Year				
2011	-0.12	1.57	-0.08	0.94
2012	0.06	1.17	0.05	0.96

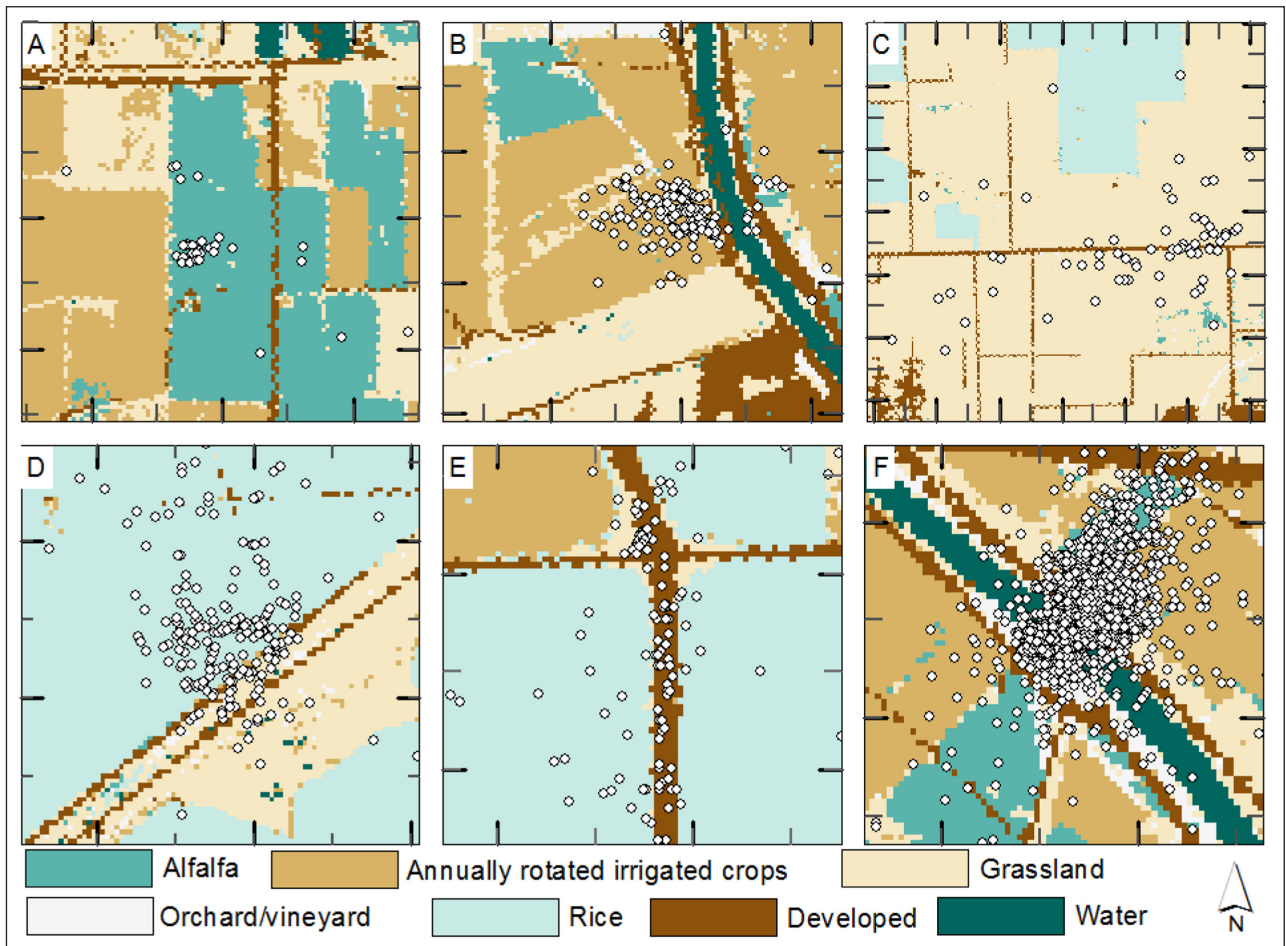
**Table 2:** Space use intensity for Swainson’s Hawks that were tracked from 2011 through 2013. Estimates are the values of regression coefficients for each effect. SE, standard error.

Sacramento Valley, the longest recorded distance from the nest that a Swainson’s Hawk foraged was 22.5 km [25]. The distance traveled from the nest may be negatively correlated with probability of nestling survival [12]. Our observations of Swainson’s Hawks within their nesting territories suggested that among individuals, there was substantial variation in the mean distance from the nest that was associated with different behaviors (e.g., flying,

circling, feeding) (R.L.A. unpublished data). These differences among individuals appeared to be considerably greater than any differences in behavior as a function of distances from nests.

Our estimates of home-range size during the breeding season were as much as two times larger than previous estimates in the same general geographic area that were based on radio telemetry and minimum convex polygons [23, 25].





**Figure 3:** Examples of high relative intensity of space use by Swainson's Hawks over alfalfa (a), annually rotated irrigated crops (b), grassland (c), rice (d), developed areas (e), and water (f). Each small, white dot is one location record. Each panel includes data from a different Swainson's Hawk during one or more life stages. Large and small ticks on the axes indicate distances of 1000 m and 500 m, respectively.

Estep [23] recorded a median home-range size of 20 km<sup>2</sup> for 12 Swainson's Hawks (range 3–87), and Babcock estimated a median home-range size of 39 km<sup>2</sup> (range 7–77) for 4 Swainson's Hawks. There are at least three reasons why our estimates may have been larger. First, we recorded movements over a 10-hour period each day regardless of the birds' locations, whereas Estep [23] recorded movements of birds that could be observed visually over a 4-hour period and Babcock [25] recorded movements of birds that could be observed visually on  $\geq 2$  days per week. Estimates that are strictly visual may underestimate home-range size, especially during life stages in which movement distances are relatively long and birds cannot readily be followed by the human eye. Second, home ranges estimated with minimum convex polygons are not directly comparable to those estimated with UD [41]. Third, Babcock [25] based home-range estimates on the 95% contour rather than the 99% contour. Use of the 99% contour or isocline allowed us to maximize our sample size for inferences about land-cover associations while excluding late-season movements that were quite long relative to typical daily movements earlier in the breeding season. For consistency, we used the same isocline to estimate home-range size. However, median

seasonal home-range sizes that were based on the 95% isocline were considerably smaller than those based on the 99% isocline: 49 km<sup>2</sup> (range 2–177) in 2011, 69 km<sup>2</sup> (range 10–498) in 2012, and 34 km<sup>2</sup> (range 15–208) in 2013 (Table 1).

Although our remotely sensed location data did not provide information on an animal's behavior at a particular location, we believe that our use of satellite telemetry data and our analytical focus on space-use intensity offer a more objective basis for assessing land-cover associations of Swainson's Hawks than do use-availability assessments [24]. Use-availability assessments compare attributes of locations at which one or more individuals were present to a random sample of locations from the area assumed to be available to those individuals or to the estimated proportion of different land-cover types. The results and inferences from use-availability models can be biased by errors in definition of the size and configuration of the available area [42]. Integration of a use-availability assessment with a UD-based model of space-use intensity would require us to identify nest-site cutoffs on the basis of the data and then to exclude points near the nests from analyses of UD. It also would be necessary to assign greater weight to points far from the nest than to

points close to the nest, and potentially to make assumptions about resource use on the basis of distances from the nest or land-cover types. The biological rationale for selecting a given weighting algorithm is not apparent, and we do not have a strong biological basis for assuming that use of space within the nest zone is less meaningful than use of space further away. We did not omit data near the nest because Swainson's Hawks frequently use that space and because our telemetry data did not allow us to make assumptions about differences in behavior at different distances from the nest. In other words, space use may affect fitness and population viability regardless of proximity to the nest.

Our results are consistent with others' suggestions that Swainson's Hawks are generalists that have adapted to agriculture and development [7]. The manner in which we aggregated finely resolved land-use and land-cover types into a smaller number of land-cover classes (Supporting Information) may explain many of the positive associations we identified between a given land-cover class and space use. For example, as noted above, the most intensively used land-cover class, grasslands, included land uses from fallowing of crops to livestock grazing. Similarly, the developed land-cover class included roads in agricultural areas, along which Swainson's Hawks often perch on power lines or telephone poles (e.g., **Figure 3**). Additionally, Swainson's Hawks may attempt to nest in relatively old suburban neighborhoods in which planted or retained trees are relatively tall and foraging habitat is within a few km [28]. The resolution of our data does not allow us to assess whether intensity of development is associated with intensity of space use. The positive association between intensity of space use and water likely reflects that the nests of most of the birds we tracked were near watercourses. Because rice is grown near many of the nests of the Swainson's Hawks we tracked, some locations over rice fields probably were inevitable.

Data on the locations at which Swainson's Hawks are obtaining food has potential to provide information about relations among space use, resource use, and reproduction. Raw measures of space use could be correlated with food captured. However, there are two reasons why raw measures of space use may not reflect habitat with the greatest food availability or the greatest proportion of food captures. First, birds are not always foraging. There are few reliable data on activity budgets of Swainson's Hawks, especially during the nesting period but see [43]. Second, birds may not spend most of their time in the highest-quality habitat. For example, it is possible that in high-quality habitat, birds catch prey quickly and then leave to take the prey back to the nest, whereas in low-quality habitat, it takes more time to find food. It also is possible that a successful forager can obtain its food requirements for the day relatively quickly and then spend time soaring or perching. If any of these scenarios apply to Swainson's Hawks, raw measures of space use could produce misleading inferences.

Because our data do not allow us to draw inference to behavior, it is unclear whether space-use associations

reflect use of resources within different land-cover types. For example, we cannot determine whether a Swainson's Hawk that was recorded over grassland was foraging, feeding, or engaged in a different behavior. The assumption that Swainson's Hawks spend the most time in locations with the greatest food availability could be tested by identifying an association between telemetry data and a direct measure of the prey base or food capture. It remains unknown whether food availability is a limiting resource in the Natomas Basin or elsewhere in the species' range. Bechard [43] suggested that vegetation type was more strongly associated than prey abundance with foraging locations of Swainson's Hawks in southeastern Washington.

Visual observations of Swainson's Hawks in alfalfa fields and other hay crops and observed attempts to capture prey [24] have led to inferences that most foraging occurs in those land-cover types, especially when harvest or mowing exposes rodents [9, 17, 24]. For example, investigators conducted road surveys in the Central Valley in which Swainson's Hawks were considered to be foraging if they were observed coursing, circling, kiting, or hovering  $\leq 100$  m above a field [14]. These observations were compared to the proportion of different land-cover types within the area surveyed, with the inference that Swainson's Hawks foraged in vineyards less than expected, and in dryland grain or irrigated alfalfa, ryegrass, or clover more than expected, although apparent use of different crops varied throughout the breeding season [14]. Swolgaard et al. [14] also suggested that plant height, density, and cover may affect the location or intensity of foraging by Swainson's Hawks.

Because Swainson's Hawks are listed as threatened in California, they will continue to be a focus of regional conservation plans regardless of their biological status. Given that Swainson's Hawks are highly territorial, we suggest that mating and reproductive success and, in turn, population-level recruitment may be associated equally if not more closely with availability of nesting sites [13] than with the current distribution of land-cover types.

### Competing Interests

The authors declare that they have no competing interests.

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## Supporting Information

Details of the Natomas Basin land-cover mapping and accuracy assessment is available at <http://dx.doi.org/10.1525/collabra.35.smo>

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