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FULL RESEARCH ARTICLE

Conservation of threatened San Joaquin antelope squirrels: distribution surveys, habitat suitability, and conservation recommendations

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The San Joaquin antelope squirrel (*Ammospermophilus nelsoni*: SJAS) is listed as Threatened pursuant to the California Endangered Species Act due to profound habitat loss throughout its range in the San Joaquin Desert in California. Habitat loss is still occurring and critical needs for SJAS include identifying occupied sites, quantifying optimal habitat conditions, and conserving habitat. Our objectives were to (1) conduct surveys to identify sites where SJAS were present, (2) assess habitat attributes on all survey sites, (3) generate a GIS-based model of SJAS habitat suitability, (4) use the model to determine the quantity and quality of remaining habitat, and (5) use these results to develop conservation recommendations. SJAS were detected on 160 of the 326 sites we surveyed using automated camera stations. Sites with SJAS typically were in arid upland shrub scrub communities where desert saltbush (*Atriplex polycarpa*) or jointfir (*Ephedra californica*) were the dominant shrubs, although shrubs need not be present for SJAS to be present. Sites with SJAS usually had relatively sparse ground cover with >10% bare ground and Arabian grass (*Schismus arabicus*) was the dominant grass. SJAS were more likely to occur on sites where kangaroo rats (*Dipodomys spp.*) were present and burrow abundance was greater, but SJAS were less likely to be present on sites with California ground squirrels (*Otospermophilus beecheyi*). Based on our habitat suitability model, an estimated 5,931 km^2 of high or moderately high quality habitat and 4,753 km^2 of lower quality habitat remain. To conserve SJAS, we recommend (1) conducting additional SJAS surveys on sites not surveyed but with suitable habitat, (2) conserving unprotected lands with suitable habitat, (3) managing

vegetation on occupied sites if necessary, (4) restoring disturbed lands to increase suitability for SJAS, and (5) conducting translocations of SJAS to unoccupied sites with suitable habitat.

Key words: *Ammospermophilus nelsoni*, conservation, distribution, habitat suitability, San Joaquin antelope squirrel, San Joaquin Valley, threatened

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The San Joaquin antelope squirrel (*Ammospermophilus nelsoni*: SJAS) is a small ground squirrel endemic to the San Joaquin Desert in central California (USFWS 1998; Germano et al. 2011). This species once was widely distributed in arid shrubland and grassland habitats in the western and southern portions of the San Joaquin Valley from western Merced County south to Kern County and also in the Carrizo Plain and Cuyama Valley (Fig. 1). Much of the habitat in this region has been converted to agricultural, urban, and industrial uses. Due to this profound habitat loss, the SJAS was state listed as Threatened by the California Fish and Game Commission in 1980 (USFWS 1998).

Adult SJAS weigh 130–170 g (USFWS 1998) and are considerably smaller than the ubiquitous and more familiar California ground squirrel (*Otospermophilus beecheyi*). Typical of ground squirrels, SJAS are diurnal and omnivorous (Best et al. 1990). They consume a variety of seeds, green vegetation, and a diversity of invertebrates (Hawbecker

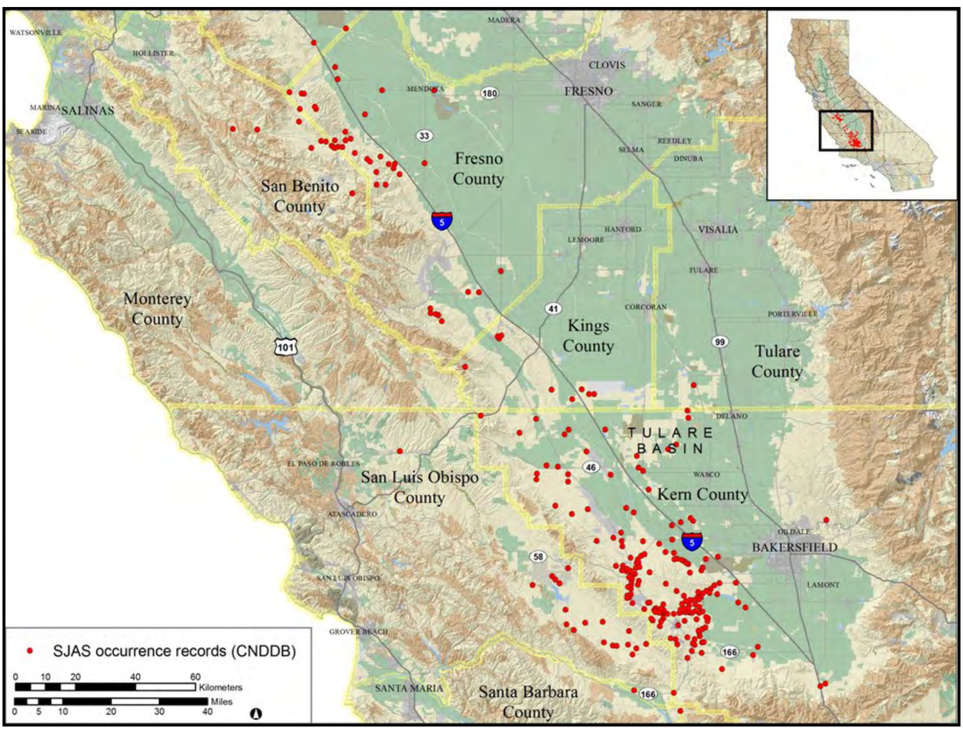

Figure 1. California Natural Diversity Data Base occurrence records for the San Joaquin antelope squirrel (SJAS) in central California, USA.

1947; Harris 2019). Although they can excavate their own burrows, they readily use those of other species, particularly kangaroo rats (*Dipodomys spp.*; Hawbecker 1975; Harris and Stearns 1991). SJAS live in small familial colonies and home ranges are approximately 4 ha in size (Best et al. 1990). Reproduction occurs during late winter and early spring, and young (usually 6–11) are born between March and April (Best et al. 1990). Most SJAS live less than 1 year (Hawbecker 1975).

Kelly et al. (2005) estimated that by 2000, the area of grasslands and shrublands, the two types of habitat in which SJAS are primarily found, had been reduced by 65.1% and 63.7%, respectively, relative to pre-European settlement in the San Joaquin Valley. Habitat loss, fragmentation, and degradation are still occurring, and this continuing loss threatens to isolate and extirpate remaining populations. The distribution of SJAS has not been assessed since the 1980s. Also, optimal habitat conditions for this species are not well known. Additionally, the effects of competitors such as California ground squirrels are poorly understood (Harris and Stearns 1991; USFWS 1998).

We conducted surveys for SJAS at selected sites throughout their historic range. At each survey location, we quantified a suite of ecological attributes and correlated these with the presence of SJAS. This information was used to define preferred habitat conditions for SJAS and to prepare a habitat suitability model for the species. Finally, based on our results, we developed recommendations for conserving SJAS throughout their range.

METHODS

Study Area

This project was conducted throughout the historic range of SJAS (Fig. 1). The habitats in which work was conducted included annual grasslands, saltbush scrub, alkali sink scrub, and ephedra scrub (USFWS 1998), all of which are within the region known as the San Joaquin Desert (Germano et al. 2011). The regional climate is Mediterranean in nature, and is characterized by hot, dry summers, and cool, wet winters with frequent fog. Based on data from Buttonwillow, CA, mean maximum and minimum temperatures are 36.9°C and 18.5°C in July, and 14.0°C and 1.4°C in December. Annual precipitation averages 14.3 cm and occurs primarily as rain falling between October and April (WRCC 2020). Topography is diverse within the range of SJAS and varies from flat valley bottoms to steep-sloped mountain ranges with elevations ranging from ca. 100 m to 1,200 m. Loss of natural habitat within the historic range of SJAS has been profound due to agricultural and urban development. Extensive areas of remaining habitat are subject to disturbances including hydrocarbon (oil, natural gas) extraction, off-road vehicle use, and cattle grazing (USFWS 1998; Kelly et al. 2005).

Surveys

We used automated camera stations to determine whether SJAS were present at a given site. We used Cuddeback (E3 Black Flash Trail Cameras; Non Typical, Green Bay, WI), Bushnell (models 119455, HD 119437, and HD 119477; Bushnell Outdoor Products, Overland Park, KS), and Reconyx (PC800 HyperFire Professional IR and Reconynx PC900 HyperFire Professional IR; Reconyx, Holmen, WI) field cameras. The cameras use an infrared sensor to detect movement and collect images at 5–20-megapixel resolution. At each station, a 1-m t-post was hammered into the ground, and the camera was mounted on the post using a bracket and zipties. To attract squirrels to the camera stations, we placed an approximately 1-kg piece of Premium Wild Bird Block or Flock Block (Purina, Gray Summit, MO) about 2 m in front of each camera. The block consisted of a mixture of grains, seeds, molasses, and other ingredients pressed into a solid block. At some sites, we caged the block in chicken wire and staked it to the ground to prevent removal by other species, such as coyotes (*Canis latrans*) or cattle.

We conducted surveys primarily on public lands administered by the U.S. Bureau of Land Management (BLM) and the California Department of Fish and Wildlife (CDFW), and on conservation lands administered by the Center for Natural Lands Management (CNLM) and The Wildlands Conservancy. For a few locations, we received permission to establish stations on private lands. Up to 20 camera stations were established at a time, depending on the amount of habitat available. We spaced stations at least 350 m (ca. 0.25 mi) apart. This is the approximate diameter of a SJAS home range based on an estimated average home range size of 10 ha reported by Harris and Stearns (1991). This spacing substantially reduced the potential for detecting a given individual at more than one station. SJAS are semi-colonial and therefore are unevenly distributed even in suitable habitat (Grinnell and Dixon 1918; Hawbecker 1953; Best et al. 1990). Therefore, multiple stations were established in most areas, frequently as a long transect through a region.

Our goal was to operate stations for at least 7 days at each location. Images collected by each camera were carefully examined to determine whether stations had been visited by SJAS. Detections of other species were recorded as well, particularly visits by California ground squirrels. Also, we noted the day of first detection for SJAS for each station.

Habitat Attributes

At each site where we established a camera station to survey for SJAS, we recorded a suite of habitat attributes (Table 1). We recorded information on shrubs, ground cover, topography, anthropogenic disturbances, kangaroo rat activity, California ground squirrel presence, and small mammal burrow (entrances ≥ 5 cm) abundance. Much of this information was qualitative so that a relatively large area (several hectares) could be characterized quickly (ca. 15 min). At each station, observations of kangaroo rat sign and of California ground squirrels and their sign were supplemented with detections of these species on the camera from that station.

We compared the proportional occurrence of each of the habitat attributes between stations with and without SJAS detections using contingency table analysis. For 2x2 analyses, a continuity correction was applied (Zar 1984). Some variables had more than two levels (e.g., shrub density, topography). For these variables, if the contingency table analysis indicated a significant difference in proportions, levels were compared pair-wise to assess which levels were different. A Cramer's V value and associated significance level were calculated along with each chi-square test to assess the strength of the association between the presence of SJAS and the presence of each habitat attribute. Cramer's V values range from 0 to 1 with "0" indicating no association and "1" indicating a strong association. We conducted statistical tests using IBM SPSS Statistics, Version 24 (IBM, Armonk, NY). We used an $\boldsymbol{\alpha}$ level of 0.1 as is increasingly common in ecological field studies to identify compelling trends that warrant further investigation (Gotelli and Ellison 2013).

Table 1. Habitat attributes assessed on sites surveyed for San Joaquin antelope squirrels in the San Joaquin Desert, California, USA.

Attribute	Measure
Shrubs	Present/absent
Estimated shrub density if present	Dense: < 2 m apart Medium: 2–10 m apart Sparse: > 10 m apart
Shrub species	List of species present
Estimated ground cover density	Dense: < 10% bare ground Medium: 10–30% bare ground Sparse: > 30% bare ground
Ground cover species	List of species with > 10% cover
Alkali scalds	Present/absent
Topography	Generally flat Gentle slopes (< 10%) Steep slopes (> 10%) Wash within 100 m
Anthropogenic disturbance	Present/absent (e.g., oil field or OHV activity)
Kangaroo rat activity	Present/absent (based on burrows and scats)
California ground squirrels	Present/absent (based on squirrel observations and burrows)
Abundance of burrows (entrances ≥ 5 cm)	Low: 0–2 burrows visible Medium: 3–5 burrows visible High: 6 or more burrows visible

Habitat Suitability Modeling

We produced a habitat suitability model for SJAS that incorporated results from the attribute analyses, particularly the dominant vegetation communities and the estimated ground cover density. For the model boundary, we used the southern portion of the San Joaquin Valley Recovery Planning area from the *Recovery Plan for Upland Species of the San Joaquin Valley* (Fig. 2 in USFWS 1998). For vegetation communities, we used a detailed vegetation layer from the CDFW Vegetation Classification and Mapping Program (VegCAMP) where available (CDFW 2010, 2015; CNPS 2013; California State University, Chico, Geographical Information Center 2016). Where VegCAMP data were not available, we used vegetation data derived from California Gap Analysis Project supplemented with newer land use data (University of California Santa Barbara Biogeography Lab 1998; CDOC 2014; California Council on Science and Technology 2015).

Using the most detailed vegetation classification available for a given location, we ranked upland vegetation communities from 1–4 (1 = best quality) based on habitat attribute data collected during the field surveys (Table 2). We tried to match habitat attributes on sites with SJAS to the descriptions of the vegetation classifications. We found that one vegetation classification (*Southwestern North American salt basin and high marsh*) was overly broad

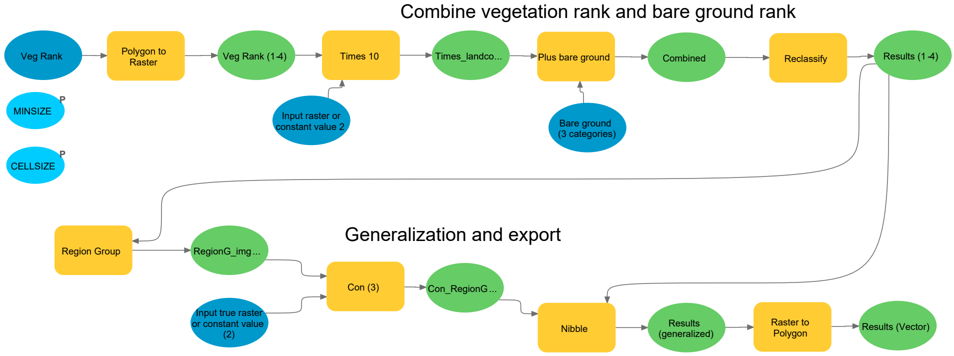

Figure 2. GIS model for combining vegetation and percent bare ground rankings to assess habitat suitability for the San Joaquin antelope squirrel.

Table 2. Vegetation classification rankings used to model habitat suitability for San Joaquin antelope squirrels. Classification levels are unique to the sources cited in the footnote; each is essentially a vegetation community or habitat type.

Rank	Vegetation classification[1]	Classification level
1	*Atriplex polycarpa*	Alliance
	Atriplex spinifera	Alliance
	Chenopod scrubs	Supplemental data
	Ephedra californica	Alliance
	Gutierrezia californica	Provisional Alliance
	Lycium andersonii	Alliance
	Monolopia (*lanceolata*)-*Coreopsis* (*calliopsidea*)	Provisional Alliance
	North American Warm Semi-Desert Cliff, Scree, and Other Rock Vegetation	Macrogroup
	Southwestern North American salt basin and high marsh/Desert Scrub	Group/soil
	Xeromorphic Scrub and Herb Vegetation (Semi-Desert)	Class
2	*Ambrosia salsola*	Alliance
	Amsinckia (*menziesii, tessellata*)	Alliance
	Atriplex canescens	Alliance
	Atriplex lentiformis	Alliance
	Atriplex vallicola - Lasthenia ferrisiae – Lepidium jaredii	Provisional Association
	Barren	Supplemental data
	California Annual and Perennial Grassland	Macrogroup
	California annual forb/grass vegetation	Group
	Centaurea (*virgata*)	Provisional Semi-Natural Alliance
	Coastal scrubs	Supplemental data

Table 2 continued

Rank	Vegetation classification[1]	Classification level
2	*Encelia* (*actoni, virginensis*)	Alliance
	Ephedra viridis	Alliance
	Ericameria linearifolia - Isomeris arborea	Provisional Alliance
	Ericameria linearifolia - Peritoma arborea	Provisional Alliance
	Ericameria nauseosa	Alliance
	Isocoma acradenia	Provisional Alliance
	Krascheninnikovia lanata	Alliance
	Lasthenia californica - Plantago erecta – Vulpia microstachys	Alliance
	Lepidospartum squamatum	Alliance
	Lupinus albifrons	Alliance
	Poa secunda	Alliance
	Southwestern North American salt basin and high marsh/Grassland	Group/soil
	subshrub scrubs	Supplemental data
	Valley and foothill grasslands	Supplemental data
3	*Allenrolfea occidentalis*	Alliance
	Corethrogyne filaginifolia	Provisional Alliance
	Eriogonum (*elongatum, nudum*)	Provisional Alliance
	Eriogonum fasciculatum	Alliance
	Great Basin scrubs	Supplemental data
	Interior dunes	Supplemental data
	Mediterranean California naturalized annual and perennial grassland	Group
	Nassella cernua	Provisional Alliance
	Riverine, Barren	-
	Salvia carduacea	Provisional Alliance
	Salvia leucophylla	Alliance
	Salvia mellifera	Alliance
	Southwestern North American salt basin and high marsh/Alkali sink	Group/soil
	Suaeda moquinii	Alliance
4	*Arctostaphylos glauca*	Alliance
	Artemisia californica	Alliance
	Artemisia californica - Eriogonum fasciculatum	Alliance
	Artemisia tridentata	Alliance
	Baccharis pilularis	Alliance
	Californian mixed annual/perennial freshwater vernal pool/swale/plain bottomland	Group
	Central and south coastal California seral scrub	Group
	Central and South Coastal Californian coastal sage scrub	Group
	Cercocarpus montanus	Alliance

Table 2 continued

Rank	Vegetation classification[1]	Classification level
4	Chaparral	Supplemental data
	Elymus glaucus	Alliance
	Frangula californica	Alliance
	Prunus fasciculata	Alliance
	Quercus john-tuckeri	Alliance
	Ribes quercetorum	Provisional Alliance

[1] Vegetation classifications based on CDFW 2010, 2015; CNPS 2013; California State University, Chico, Geographical Information Center 2016; U.C. Santa Barbara Biogeography Lab 1998; California Department of Conservation, Farmland Mapping and Monitoring Program 2014; California Council on Science and Technology 2015.

and included vegetation alliances that should be ranked differently. (An alliance is a category of vegetation classification which describes repeating patterns of plants across a landscape [CNPS 2013]). To solve this problem, we used a supplemental layer of historical vegetation based on reconnaissance-level soil surveys (Fig. 3 in Phillips and Cypher 2019) to identify which locations were generally in areas of *Valley saltbush scrub* (Rank = 1), *Grasslands* (Rank = 2), or other upland communities such as *Alkali Sink* (Rank = 3). In Table 2, these divisions are identified as Classification level = *Group/soil*.

For percentage of bare ground, we used a GIS layer derived from satellite imagery (USGS 2013). Based on the field surveys we grouped percentage of bare ground into three categories: 1 = > 30% bare ground, 2 = 10-30% bare ground, 3 = < 10% bare ground. We used GIS software (ArcGIS Pro *ModelBuilder*) to create a sequence of steps (Fig. 2) to combine the vegetation rankings with the three categories of bare ground. We then organized these into four categories of habitat quality (Table 3) from best (Rank 1) to worst (Rank 4). Data in the model were represented as a grid (or raster) of cells that were 90 x 90 m. To reduce small patches or thin, linear features in the output, we replaced cells that were in groupings of < 50 cells (40 ha) with the value of cells in neighboring, larger patches. This smoothing procedure provided a more meaningful representation of the data by eliminating fragments too small to influence SJAS presence.

RESULTS

Surveys

We established camera stations at 326 locations to determine if SJAS were present. The surveys were conducted from 13 December 2017 to 28 May 2019. The majority of the locations were in western Kern County and eastern San Luis Obispo County (Fig. 3). Additionally, there were a few stations (< 20) in each of southeastern Tulare County, western Kings County, western Fresno County, and eastern San Benito County. The mean number of days that stations were operational was 9.0 d (SE = 0.16, range 3–30) with a mode of 8 d. SJAS were detected at 160 locations (Fig. 3). Mean latency to first SJAS detection was 2.6 d (SE = 0.17, range 1–14) with a mode of 1 d.

SJAS were frequently detected at the stations in San Luis Obispo County and Kern County. Indeed, all but 2 of the stations with SJAS detections were in these two counties with one detection being recorded each in southwestern Fresno County and eastern San Benito County.

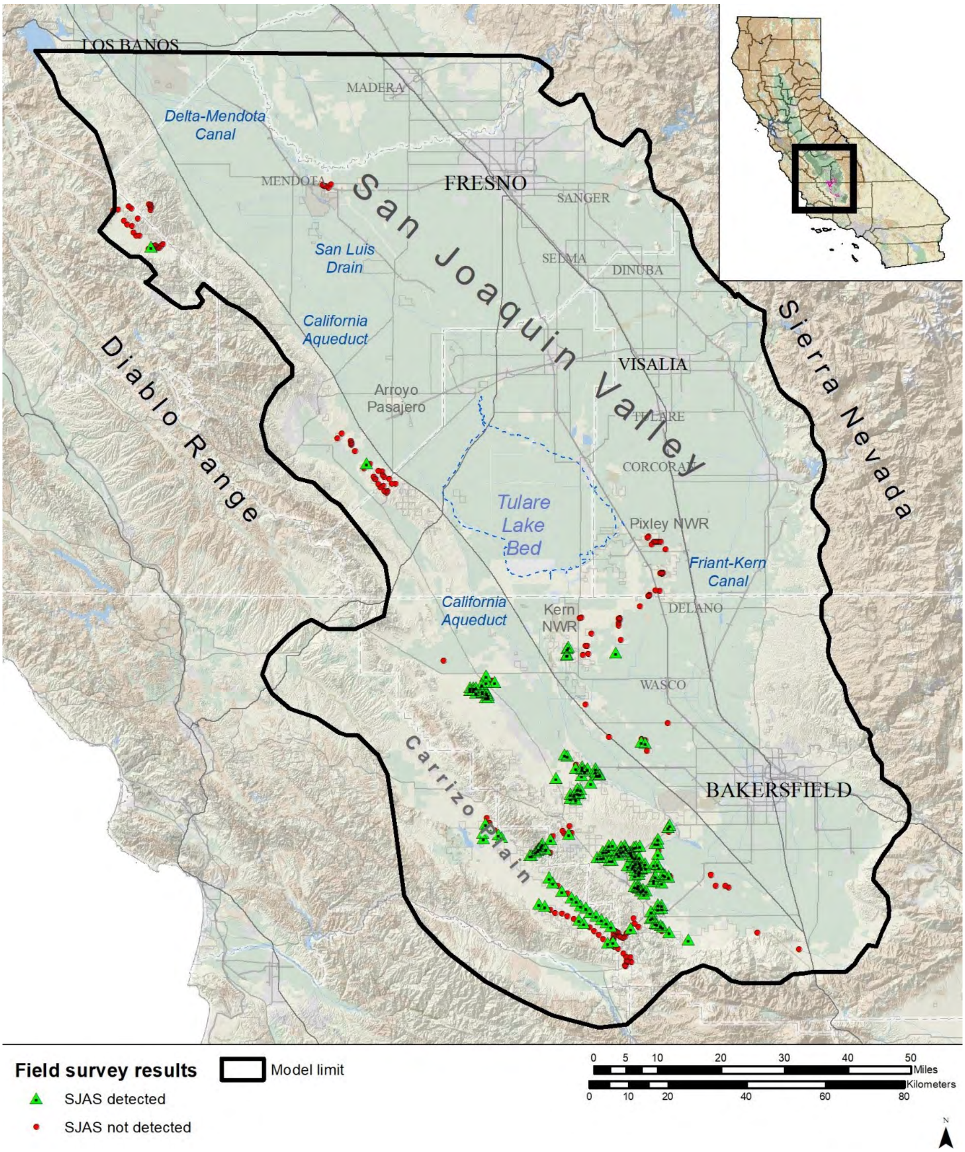

Figure 3. Results from camera stations (n = 326) established to survey for San Joaquin antelope squirrels (SJAS) in the San Joaquin Valley, California, USA.

Table 3. Habitat quality categories for San Joaquin antelope squirrels that combine vegetation rankings with categories of percentage of bare ground.

Habitat quality rank	Attributes
1 (highest quality)	Vegetation rank 1[1], > 30% bare ground
2 (moderately high quality)	Vegetation rank 1, 10–30% bare ground Vegetation rank 2, > 30% bare ground
3 (moderately low quality)	Vegetation rank 1, < 10% bare ground Vegetation rank 2, 10–30% bare ground
4 (low quality)	All other upland vegetation

[1]Vegetation ranks from Table 2.

Habitat Attributes

Habitat attribute data were collected at 319 locations surveyed for SJAS (Table 4). SJAS were not associated with shrubs in general or with shrub density, but when shrubs were present SJAS were associated with specific species. SJAS presence was strongly associated with small-leaved saltbushes, which primarily were desert saltbush (*Atriplex polycarpa*) but occasionally included spiny saltbush (*A. spinifera*). When saltbush was present, it usually was the dominant shrub. Other species observed where SJAS were detected included joint-fir (*Ephedra californica*) and matchweed (*Gutierrezia californica*). SJAS were negatively associated with iodine bush (*Allenrolfea occidentalis*), sinkweek (*Sueada* spp.), and alkali goldenbush (*Isocoma acradenia*).

Areas with SJAS were more likely to have sparse to medium ground cover (>10% bare ground) while areas without SJAS were more likely to have dense ground cover (0–10% bare ground) (Table 4). Arabian grass (*Schismus arabicus*) was present more frequently at locations where SJAS were detected compared to locations where SJAS were not detected, and when present at sites where SJAS were detected it tended to be a dominant species. Conversely, wild barley (*Hordeum* spp.) was present more frequently at locations where SJAS were not detected compared to locations where SJAS were present. The presence of red brome (*Bromus madritensis* ssp. *rubens*), amsinckia (*Amsinckia* spp.), and red-stemmed filaree (*Erodium cicutarium*) was similar between sites with and without SJAS.

Topography did not appear to influence the presence of SJAS. Sites with and without SJAS had similar proportions of flat, rolling, gentle slope (≤ 10%), and steep slope (> 10%) terrain (Table 4). Presence of washes also was similar between sites with and without SJAS. However, alkali scalds were less likely to be present on sites where SJAS were detected. Presence of habitat disturbances (e.g., oil field activities, off-road vehicle use) was similar between sites with and without SJAS. Presence of grazing also was similar, but when grazing was present on sites where SJAS were detected, it was much more likely to be by sheep than by cows.

Finally, kangaroo rats were more likely to be present on sites where SJAS were detected (Table 4). Also, burrows sufficiently large to permit entry by kangaroo rats and SJAS were more abundant on sites where SJAS were detected. Lastly, California ground squirrels were not present on most of the sites surveyed, but when they were present, SJAS were detected less frequently.

Table 4. Habitat attributes on sites with and without San Joaquin antelope squirrel (SJAS) detections during surveys conducted in the San Joaquin Valley, CA. Chi-square tests assessed attribute equality between sites with and without SJAS and Cramer's coefficient assessed the strength of the association.

Attribute	Sites w/ SJAS (n = 158)	Sites w/o SJAS (n = 161)	Chi-square test and Cramer's coefficient
Shrubs	Present: 114 (72.2%) Absent: 44 (27.8%)	Present: 112 (69.6%) Absent: 49 (30.4%)	$\chi^2 = 0.15$, 1 df, $p = 0.70$ $C = 0.028$, $p = 0.61$
Shrub density	Dense: 27 (17.1%) Medium: 67 (42.4%) Sparse: 64 (40.5%)	Dense: 17 (10.6%) Medium: 62 (38.5%) Sparse: 82 (50.9%)	$\chi^2 = 4.66$, 2 df, $p = 0.10$ $C = 0.121$, $p = 0.10$
Iodine bush	Dominant: 1 (0.6%) Not dominant: 2 (1.3%) Absent: 155 (98.1%)	Dominant: 9 (5.6%) Not dominant: 7 (4.3%) Absent: 145 (90.1%)	$\chi^2 = 9.48$, 2 df, $p < 0.01$ $C = 0.172$, $p < 0.01$
	Present: 3 (1.9%) Absent: 155 (98.1%)	Present: 16 (9.9%) Absent: 145 (90.1%)	$\chi^2 = 7.82$, 1 df, $p < 0.01$ $C = 0.170$, $p < 0.01$
Sinkweed	Dominant: 4 (2.5%) Not dominant: 6 (3.8%) Absent: 148 (93.7%)	Dominant: 10 (6.2%) Not dominant: 14 (8.7%) Absent: 137 (85.1%)	$\chi^2 = 6.17$, 2 df, $p = 0.05$ $C = 0.139$, $p = 0.05$
	Present: 10 (6.3%) Absent: 148 (93.7%)	Present: 24 (14.9%) Absent: 137 (85.1%)	$\chi^2 = 5.29$, 1 df, $p = 0.02$ $C = 0.139$, $p = 0.01$
Saltbush	Dominant: 87 (55.1%) Not dominant: 16 (10.1%) Absent: 55 (34.8%)	Dominant: 44 (27.3%) Not dominant: 11 (6.8%) Absent: 106 (65.8%)	$\chi^2 = 31.17$, 2 df, $p < 0.01$ $C = 0.313$, $p < 0.01$
	Present: 103 (65.2%) Absent: 55 (34.8%)	Present: 55 (34.2%) Absent: 106 (65.8%)	$\chi^2 = 29.48$, 1 df, $p < 0.01$ $C = 0.310$, $p < 0.01$
Goldenbush	Present: 5 (3.2%) Absent: 153 (96.8%)	Present: 21 (13.0%) Absent: 140 (87.0%)	$\chi^2 = 9.12$, 1 df, $p < 0.01$ $C = 0.181$, $p < 0.01$
Ground cover density	Dense: 15 (19.5%) Medium: 77 (48.7%) Sparse: 66 (41.8%)	Dense: 38 (23.6%) Medium: 66 (41.0%) Sparse: 57 (35.4%)	$\chi^2 = 11.46$, 2 df, $p < 0.01$ $C = 0.190$, $p < 0.01$
	Dense: 15 (9.5%) Med-Sparse: 143 (90.5%)	Dense: 38 (23.6%) Med-Sparse: 123 (76.4%)	$\chi^2 = 10.46$, 1 df, $p < 0.01$ $C = 0.190$, $p < 0.01$
Brome	Dominant: 80 (50.6%) Not dominant: 32 (20.3%) Absent: 46 (29.1%)	Dominant: 69 (42.9%) Not dominant: 35 (21.7%) Absent: 57 (35.4%)	$\chi^2 = 2.09$, 2 df, $p = 0.35$ $C = 0.081$, $p = 0.35$
Arabian grass	Dominant: 54 (34.2%) Not dominant: 45 (28.5%) Absent: 59 (37.3%)	Dominant: 10 (6.2%) Not dominant: 28 (17.4%) Absent: 123 (76.4%)	$\chi^2 = 56.69$, 2 df, $p < 0.01$ $C = 0.422$, $p < 0.01$
	Present: 99 (62.7%) Absent: 59 (37.3%)	Present: 38 (23.6%) Absent: 123 (76.4%)	$\chi^2 = 48.06$, 1 df, $p < 0.01$ $C = 0.394$, $p < 0.01$
Wild barley	Present: 9 (5.7%) Absent: 149 (94.38%)	Present: 33 (20.5%) Absent: 128 (79.5%)	$\chi^2 = 15.28$, 1 df, $p < 0.01$ $C = 0.219$, $p < 0.01$

Table 4. continued

Attribute	Sites w/ SJAS (n = 158)	Sites w/o SJAS (n = 161)	Chi-square test and Cramer's coefficient
Fiddleneck	Present: 14 (8.9%) Absent: 144 (91.1%)	Present: 23 (14.3%) Absent: 138 (85.7%)	$\chi^2 = 1.79$, 1 df, $p = 0.18$ $C = 0.085$, $p = 0.13$
Red-stemmed filaree	Dominant: 14 (8.9%) Not dominant: 97 (61.4%) Absent: 47 (29.7%)	Dominant: 11 (6.8%) Not dominant: 95 (59.0%) Absent: 55 (34.2%)	$\chi^2 = 0.98$, 2 df, $p = 0.61$ $C = 0.055$, $p = 0.61$
Topography	Flat: 79 (50.0%) Rolling: 34 (21.5%) Gentle slope: 21 (13.3%) Steep slope: 24 (15.2%)	Flat: 78 (48.4%) Rolling: 37 (23.0%) Gentle slope: 21 (13.0%) Steep slope: 25 (15.5%)	$\chi^2 = 0.13$, 3 df, $p = 0.99$ $C = 0.020$, $p = 0.99$
Washes	Present: 29 (18.4%) Absent: 129 (81.6%)	Present: 19 (18.8%) Absent: 142 (88.2%)	$\chi^2 = 2.19$, 1 df, $p = 0.14$ $C = 0.092$, $p = 0.10$
Scalds	Present: 7 (4.4%) Absent: 151 (95.6%)	Present: 38 (23.6%) Absent: 123 (76.4%)	$\chi^2 = 22.63$, 1 df, $p < 0.01$ $C = 0.275$, $p < 0.01$
Disturbance	Present: 97 (61.4%) Absent: 61 (38.6%)	Present: 101 (62.7%) Absent: 60 (37.3%)	$\chi^2 = 0.02$, 1 df, $p = 0.90$ $C = 0.014$, $p = 0.81$
Grazing	Cow: 28 (17.7%) Sheep: 53 (33.5%) No grazing: 77 (48.7%)	Cow: 51 (31.7%) Sheep: 18 (11.2%) No grazing: 92 (57.1%)	$\chi^2 = 25.26$, 2 df, $p < 0.01$ $C = 0.281$, $p < 0.01$
	Grazing: 81 (51.3%) No grazing: 77 (48.7%)	Grazing: 69 (42.9%) No grazing: 92 (57.1%)	$\chi^2 = 1.94$, 1 df, $p = 0.16$ $C = 0.084$, $p = 0.13$
Kangaroo rats	Present: 152 (96.2%) Absent: 6 (3.8%)	Present: 119 (73.9%) Absent: 42 (26.1%)	$\chi^2 = 29.27$, 1 df, $p < 0.01$ $C = 0.312$, $p < 0.01$
Burrow density	High: 62 (39.2%) Medium: 34 (21.6%) Low: 62 (39.2%)	High: 32 (19.9%) Medium: 27 (16.8%) Low: 102 (63.4%)	$\chi^2 = 20.11$, 2 df, $p < 0.01$ $C = 0.251$, $p < 0.01$
	High-Med: 96 (60.8%) Low: 62 (39.2%)	High-Med: 59 (36.6%) Low: 102 (63.4%)	$\chi^2 = 17.61$, 1 df, $p < 0.01$ $C = 0.241$, $p < 0.01$
California ground squirrels	Present: 4 (2.5%) Absent: 154 (97.5%)	Present: 16 (9.9%) Absent: 145 (90.1%)	$\chi^2 = 6.24$, 1 df, $p = 0.01$ $C = 0.153$, $p = 0.01$

Habitat Suitability Modeling

Within the SJAS habitat suitability model boundary, we identified approximately 1,348 km^2 of high-quality habitat, 4,583 km^2 of moderately high-quality habitat, 3,388 km^2 of moderately low-quality habitat, and 1,365 km^2 of low-quality habitat (Fig. 4). When we compared the results from field surveys with output from the model, we found that 58% of sites where SJAS were detected were in the highest quality habitat and 32% were in moderately high-quality habitat. The remaining 10% were in moderately low- or low-quality habitat, and in most cases these locations were in ecotone zones near higher quality habitat.

DISCUSSION

SJAS Survey Technique

Automated camera stations appeared to be an effective technique for detecting SJAS presence. The stations were easy to install and we found that about 20 stations could be established in the course of a day, depending upon station spacing. A location was surveyed continuously during the period that the station was operational. Continuous camera operation

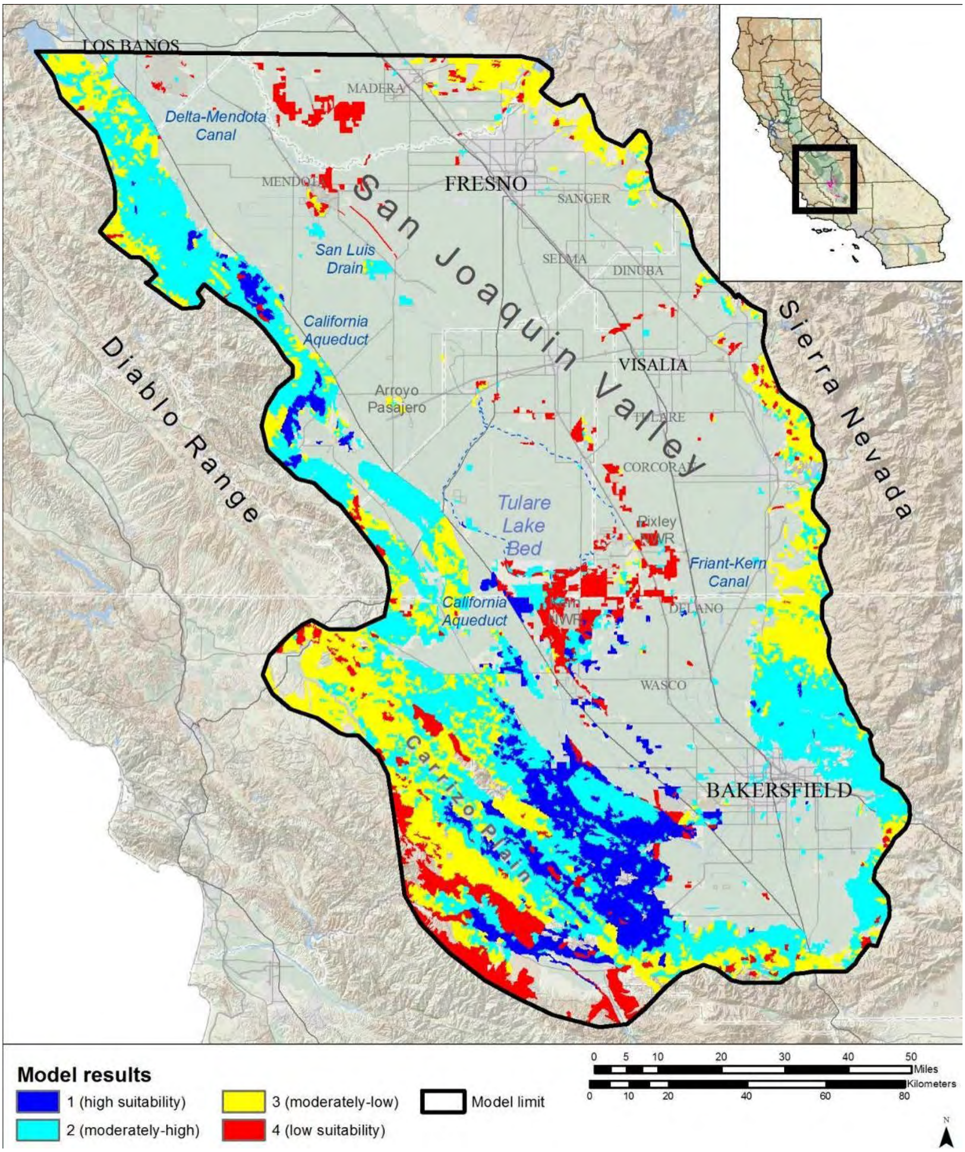

Figure 4. Results of habitat suitability modeling analysis for the San Joaquin antelope squirrel (SJAS) in California, USA.

over multiple days helps avoid false-negative determinations resulting from variations in SJAS activity levels due to time of day or daily weather. For example, SJAS may reduce activity for several hours during mid-day on days when temperatures exceed about 32° C and for entire days when temperatures fall below about 10° C (Best et al. 1990). The strategy of deploying multiple cameras in a given general area is prudent as even within suitable habitat, the distribution of SJAS can be patchy (Grinnell and Dixon 1918; Hawbecker 1953; Best et al. 1990).

Visual encounter surveys conducted by foot or vehicle can cover large areas, but detections are limited to the brief time that observers are searching a given location. Thus, the potential for false-negative determinations is much higher than that for cameras. Live-trapping is another common survey technique for SJAS. However, trapping is labor intensive as traps must be set and then are typically checked multiple times per day to avoid heat stress to captured animals. The effective survey period is limited to the time that the traps are open. Also, as with any live-trapping, there always is some degree of risk of injury or death to animals during trapping.

The camera station survey approach does entail an initial investment in cameras, but thecost is generally not prohibitive. Cameras that can operate continuously and reliably for at least a week are readily available and can be purchased for under $150 each. Other costs (approximately $15-$20) include posts and attachment materials, batteries, SD cards, and bait block. The posts, SD cards, and possibly some of the attachment materials can be used multiple times. Also, we commonly recovered and reused all or some of the bait block, particularly from stations where SJAS were not detected. We considered the camera stations to be an effective and cost-effective strategy for detecting SJAS in a given area.

Habitat Attributes

The habitat attribute data warrant certain caveats. As mentioned in the methods, the protocol for assessing habitat attributes at each camera station location was designed such that the information could be collected rapidly, usually within about 15 min. Most attributes were characterized as present or absent, or were assigned to one of 3-4 ordinal bins. Thus, the data essentially are coarse scale in nature. Another caveat is that the camera station detection data potentially included some false-negative determinations. SJAS sometimes were detected at some stations but not at other nearby stations with seemingly similar habitat conditions. The reasons for these non-detections are unknown but could include a temporarily vacant home range, camera stations unknowingly placed too far from escape cover, or some other habitat attribute that we did not recognize as important to SJAS. Also, as mentioned previously, the distribution of SJAS even within suitable habitat can be patchy (Grinnell and Dixon 1918). Consequently, the habitat attributes from any stations with false-negative findings would have been grouped with stations without SJAS detections, thereby increasing the difficulty of detecting significant differences between stations with and without SJAS detections.

Despite the caveats above, several significant differences were found between stations with and without SJAS detections. Shrubs were absent on over a quarter of the sites where SJAS were detected. SJAS use shrubs for escape cover and thermal regulation in hot weather, but can use burrows for the same purposes when shrubs are not present. Harris and Stearns (1991) found that SJAS densities on the Elkhorn Plain actually were considerably higher in areas without shrubs and that giant kangaroo rat (*D. ingens*) burrows were abundant in these areas. Dense shrubs may actually exclude SJAS (Grinnell and Dixon 1918; Hawbecker 1975). Shrubs may not be a required habitat feature for SJAS, although Hawbecker (1975) suggested that females using burrows under shrubs may have higher reproductive success.

When shrubs were present, overwhelmingly they were desert saltbush or jointfir. These species are the dominant shrubs in arid saltbush scrub and ephedra scrub communities that occur on the more well-drained sandier soils preferred by SJAS (Hawbecker 1975). Conversely, SJAS were infrequently detected in areas with iodine bush, sinkweed, and alkali goldenbush. These are the dominant shrubs in alkali sink communities. These results are consistent with range-wide habitat characterizations by Grinnell and Dixon (1918) and Hawbecker (1975) who reported that SJAS were closely associated with desert saltbush and jointfir.

SJAS also were detected more frequently in areas with lower ground cover. Over 90% of detections were in areas with > 10% bare ground and over 40% of detections were in areas with > 30% bare ground. SJAS are relatively small animals and have difficulty moving through dense ground cover (Germano et al. 2001). In particular, they rely on speed to reach cover and elude predators, and predation risk likely increases with herbaceous ground cover density. At two separate study sites in Kern County, SJAS abundance increased with decreasing ground cover (Cypher 2001; Germano et al. 2012). Arabian grass was a common dominant ground cover in locations with SJAS detections. This grass forms a low, sparse cover and prefers more arid sites where it is not outcompeted by species that require more mesic conditions, such as wild barley. Wild barley tends to form a dense cover and SJAS were rarely detected at locations where this species was present. The lack of association with red brome, amsinckia, and red-stemmed filaree likely was due to these plants being ubiquitous throughout the San Joaquin Valley region.

The lower SJAS detection rates in locations with iodine bush, sinkweed, alkali goldenbush, wild barley, and alkali scalds all indicate that alkali sink habitats, where these species and features are commonly found, are not optimal habitats for SJAS. We found that this habitat was typically only used where it was in close proximity to arid upland scrub habitat, or more commonly, locations that were in transition zones between arid upland scrub and alkali sink habitats. Our results are consistent with and further confirm those of previous researchers that also noted the suboptimal nature of alkali sink habitat for SJAS (Grinnell and Dixon 1918; Hawbecker 1953, 1975; Harris and Stearns 1991). Areas with alkali sink communities tend to occur in more low lying areas of the San Joaquin Valley with heavy clay soils where burrowing may be more difficult, the water table commonly is just a few centimeters below the surface, soils are saturated during the winter rainy season, and periodic flooding occurs. Consequently, SJAS were only detected on the valley floor in two locations (Semitropic Ridge area and Buttonwillow Ecological Reserve), both of which have habitat transitional between alkali sink and arid upland scrub habitat growing on slightly higher areas (e.g., sand ridges, hummocks).

Topographic ruggedness and slope did not appear to influence SJAS presence. However, the locations where we established camera stations did not have slopes exceeding 30%, and it is possible that locations with steeper slopes may be less suitable for SJAS (Hawbecker 1975). Harris and Stearns (1991) found SJAS on slopes of up to 20 degrees. Also, topography may influence SJAS in other ways. In particular, vegetation characteristics can vary with elevation and aspect with ground cover being denser at higher elevations and on more northerly facing slopes (Cypher 2001).

Presence of SJAS did not appear to be affected by habitat disturbances. These disturbances consisted primarily of infrastructure related to oil and gas production, such as pipelines and well pads. However, in the areas where we established camera stations, these features typically affected < 10% of the habitat and an abundance of intact habitat remained available. In a study of oil field effects on vertebrate communities in the southwestern San Joaquin Valley (Fiehler et al. 2017), SJAS continued to be present on plots with about a third of the habitat disturbed by oil field features (e.g., roads, well pads, pipelines, storage tanks, and other facilities).

Presence of SJAS also did not appear to be affected by grazing. When grazing was occurring on sites where SJAS were detected, the grazers usually were sheep, although this may have been due to a sampling bias. To some extent, we avoided areas where cattle were abundant as these animals, out of curiosity, commonly investigate and disturb camera stations, sometimes to the point of destroying them. However, on a site near Blackwell's Corner in northern Kern County that was being grazed by cattle, SJAS were abundant and were detected on 16 out of 20 camera stations operated on that site. Harris and Stearns (1991) also observed SJAS in areas that were heavily grazed by cattle. Germano et al. (a,b) found that SJAS home range size and demographic attributes were similar between grazed and ungrazed areas. Hawbecker (1975) even suggested that SJAS might benefit from the presence of cattle by feeding on the abundant insects attracted to cattle excrement.

The association between SJAS presence and kangaroo rat presence was not surprising. Kangaroo rats also are arid-adapted rodents that prefer areas with sparser ground cover (Goldengay et al. 1997; Cypher 2001; Germano et al. 2012). Thus, kangaroo rats and SJAS share similar habitat preferences. Furthermore, SJAS may benefit from the presence of kangaroo rats. Although SJAS can create their own burrows (Grinnell and Dixon 1918), Hawbecker (1947, 1953) reported that SJAS mostly use burrows created by kangaroo rats. Hawbecker (1953) concluded that the presence of SJAS was likely strongly influenced by the presence of kangaroo rats, particularly Heermann's kangaroo rats (*D. heermanni*) and giant kangaroo rats. These are larger kangaroo rats and SJAS can fit into their burrows with little or no modification (Hawbecker 1947). Harris and Stearns (1991) also reported an association in occurrence between SJAS and giant kangaroo rats. Consistent with these observations, we found that burrow abundance was typically higher in areas where SJAS were detected and that most of these burrows were made by kangaroo rats. Also, SJAS do not necessarily use a single "home burrow," but instead use multiple burrows as they forage throughout their home range (Hawbecker 1975). Thus, higher burrow abundance benefits SJAS.

The negative association between SJAS and California ground squirrels also was not surprising as this relationship has been noted previously (Taylor 1916; Grinnell and Dixon 1918; Hawbecker 1975; Harris and Stearns 1991). The nature of this negative association is not well understood. In areas where the two species co-occur, California ground squirrels may locally displace SJAS. Harris and Stearns (1991) observed California ground squirrels simply moving into SJAS burrow complexes and the resident SJAS moving to other nearby burrows. No aggression was observed. Similarly, we observed both species feeding together on the bait block at one of our stations. The two species may have different habitat preferences with SJAS preferring more arid areas with sparser vegetation and California ground squirrels preferring more mesic areas with denser vegetation (Grinnell and Dixon 1918; Jameson and Peeters 1988). Also, anthropogenic habitat disturbance appears to favor California ground squirrels as evidenced by their abundance in agricultural areas, urban areas, and even highly disturbed oil field areas (Fiehler et al. 2017). Such disturbance may allow this species to colonize areas that traditionally were SJAS habitat, as reportedly occurred in the Panoche region (Hawbecker 1975).

Suitability Modeling

In developing our SJAS habitat suitability model, we used the best available information (e.g., Hawbecker 1975; Best 1990; Harris and Stearns 1991; USFWS 1998) along with preferred habitat attributes based on findings from our surveys. However, we caution that as with any suitability model, the results do not guarantee that SJAS are present or absent at any given location. Instead, modeling results should be viewed as an estimate of the potential for SJAS to occur on given lands; higher suitability rankings indicate a higher probability of SJAS occurrence. Surveys to determine the presence of SJAS or at least to assess habitat conditions should be conducted on any parcel prior to initiating conservation (e.g., acquisition) or habitat-disturbing activities.

Williams (1981) estimated that the historic range of the SJAS encompassed approximately 1,398,600 ha and that by 1979 just 274,200 ha remained, of which only 41,300 ha (15%) was fair to good quality habitat. These estimates were for the San Joaquin Valley proper. Our habitat suitability modeling effort indicated that approximately 593,100 ha of high or moderately high-quality habitat were still present within the historic range of SJAS, which includes the San Joaquin Valley, Carrizo Plain region, and Cuyama Valley. An almost equal quantity (475,300 ha) of low and moderately low-quality habitat also was present. Possibly, some of this lower quality habitat could be enhanced to improve suitability for SJAS.

The largest quantities of remaining high and moderately high-quality habitat are located in western Kern County and eastern San Luis Obispo County. Considerable high and moderately high-quality habitat also occurs in a band along the western edge of the San Joaquin Valley from the Kern County line north into western Merced County. Significant areas of high-quality habitat occur in the Coalinga area and also on the eastern toe of the Coast Ranges south of the Panoche region. Also, a large area of mostly moderately high quality habitat occurs along the southeastern margin of the San Joaquin Valley from about Poso Creek just north of Bakersfield down to about Pastoria Creek in the very southeastern corner of the valley on Tejon Ranch lands. A number of small fragments of high-quality habitat occur on the valley floor, primarily toward the drier west side. Many of these fragments are < 40 ha and may be too small to support a self-sustaining population of SJAS.

Distribution

The historic range of the SJAS is described as extending from western Merced County south along the western side of the San Joaquin Valley, across the southern valley in Kern County, north along the eastern side of the valley to southern Tulare County, and in the Carrizo Plain and Cuyama Valley (Williams 1981; USFWS 1998). Harris and Stearns (1991) reported that the current range was still similar in extent to the historic range, but that less of the range was occupied due to habitat loss. Williams (1981) concluded that SJAS had mostly been extirpated on the floor of the San Joaquin Valley. The Carrizo Plain and Elkhorn Plain in eastern San Luis Obispo County and the Elk Hills-Lokern area in western Kern County were considered strongholds for remaining SJAS populations (Grinnell and Dixon 1918; Harris and Stearns 1991).

During our survey effort, SJAS were commonly detected at the stations in the Carrizo Plain region. The Carrizo Plain is recognized as a core area for imperiled arid upland species, including SJAS, that are endemic to the San Joaquin Desert region (USFWS 1998). The Temblor Range bounds the Carrizo Plain on the east and roughly follows the border between San Luis Obispo County and Kern County. We ran transects of cameras over this range along Crocker Grade Road located about mid-range and along Elkhorn Grade Road at the southern end of the range, primarily in an effort to determine the effect of rugged topography on SJAS. We obtained few detections of SJAS along the Elkhorn Grade transect, but SJAS were detected at most of the camera stations on the Crocker Grade transect. SJAS seemed less limited by terrain along this transect and more limited by the denser vegetation, particularly non-native grasses, which were present on north and east facing slopes. In western Kern County, SJAS were detected at most of the stations established in the Midway Valley, Buena Vista Valley, Buena Vista Hills, Lokern area, and Blackwells Corner area. All of these areas are within a second core area identified in the recovery plan for imperiled arid upland species (USFWS 1998).

At the southern end of the San Joaquin Valley, SJAS were only detected in a saltbush scrub community in the northwestern corner of the Wind Wolves Preserve where they also had been detected in the past (Cypher et al. 2011). Most of the remaining habitat at the south end of the valley is on the toe of the Transverse ranges and has dense grass, or is alkali sink habitat. SJAS were only detected at 1 of 26 sites surveyed in the Kettleman Hills on the west side of the San Joaquin Valley at the border between Fresno County and Kings County. These sites were characterized by moderate to dense ground cover of primarily non-native grasses.

The Panoche Valley region is recognized as a third core area for listed species in the recovery plan for upland species of the San Joaquin Valley (USFWS 1998). SJAS were only detected at 1 station out of 25 in this region. The location was on the Silver Creek Ranch that is now part of the Panoche Valley Preserve managed by CNLM. CNLM staff report that SJAS are abundant and widespread on the Preserve (B. Teton, CNLM, personal communication). SJAS also were observed at a location approximately 10 km north of Silver Creek Ranch in 2017 (B. Cypher, personal observation).

Near Kern National Wildlife Refuge in northern Kern County, SJAS were mostly detected on an approximately 4-km long sand ridge, called Semitropic Ridge, south of the refuge. This ridge is a relictual dune complex that is 1–3 m higher than the surrounding land and has sandier soil and supports a saltbush scrub vegetation community. Otherwise, SJAS were detected at only one of the numerous other survey sites to the east and northeast up to Pixley National Wildlife Refuge. These sites are in lower lying areas that primarily support intact or degraded alkali sink vegetation communities and also are more prone to occasional flooding.

Similarly, SJAS were detected on the Buttonwillow Ecological Reserve in Kern County. Similar to Semitropic Ridge, this area was ecotonal between alkali sink and saltbush scrub communities, but saltbush was the dominant shrub at sites where SJAS were detected. SJAS were not detected at any other sites on the valley floor.

SJAS potentially are present in other areas that were not surveyed during this project, primarily due to lack of access (i.e., private lands). One such area is the Cuyama Valley in southeastern San Luis Obispo County. Harris and Stearns (1991) conducted surveys in this area in 1988 and commonly detected SJAS on the north side of the Cuyama River along the base of the Caliente Range. A thin band of high-quality saltbush scrub habitat still remains and SJAS may still be present. North of Kern County, a mostly continuous band of good quality habitat extends north along the western margin of the San Joaquin Valley. Based on our model, relatively large areas with highly suitable habitat are present west and north of the city of Coalinga, and just southeast of Panoche Valley between the Coast Ranges and the California Aqueduct. The band of suitable habitat continues up into western Merced County.

Scattered patches of saltbush scrub habitat persist along the southeastern margin of the San Joaquin Valley and SJAS were present at one time in this area (Hawbecker 1975). Grinnell and Dixon (1918) reported seeing SJAS "in grain fields at the base of the Tehachapi Mountains" and 35 individual SJAS were collected from a location northeast of Bakersfield in 1911. However, no extant populations of SJAS are currently known from the eastern side of the San Joaquin Valley. We did not conduct surveys in this region primarily because biologists have had access to much of this area in recent years and there have been no reports of SJAS sightings.

Conclusions and Recommendations

Based on our survey results supplemented with recent opportunistic observations, SJAS are present in the Carrizo Plain region and along the western margin of the San Joaquin Valley from the southwestern corner of the valley north to about the Merced County line. They are locally abundant in the Carrizo Plain, western Kern County, and Panoche Valley regions, all of which have been identified as core areas for rare arid upland species including SJAS (USFWS 1998). SJAS primarily occur in locations with arid upland shrub scrub communities, typically with saltbush or jointfir as the dominant shrubs (although the presence of shrubs is not required) and with sparse ground cover. Alkali sink habitat appears to constitute suboptimal habitat for SJAS. SJAS are present at only a few locations on the floor of the San Joaquin Valley because so little natural habitat remains, and most is alkali sink habitat. These valley floor populations are relatively small and isolated, and therefore they are at increased risk of extirpation from catastrophic or stochastic events.

SJAS currently persist in a metapopulation structure consisting of populations of varying size and connectivity. Goals for SJAS conservation should include conserving as much of the remaining unprotected higher quality habitat as possible, expanding buffers around occupied habitat, and increasing connectivity between habitat patches to facilitate genetic and demographic flow, all of which will help maintain more optimal metapopulation dynamics and reduce extinction risk. In light of the continuing loss of habitat within the range of the SJAS, continued protections for this species under the California Endangered Species Act are warranted.

We offer the following recommendations based on our results:

1. Conduct additional surveys for SJAS, particularly on lands that have not been surveyed previously.
2. Conserve any unprotected lands where SJAS have been detected or that contain high quality habitat based on suitability modeling.
3. Manage vegetation if necessary (e.g., grazing) to reduce dense herbaceous ground cover and improve suitability for SJAS.
4. Identify strategies for restoring habitat on previously disturbed lands to render them suitable for occupation by SJAS.
5. Translocate SJAS from appropriate source populations to restored habitat or unoccupied conserved parcels with suitable habitat, if effective translocation strategies can be identified.

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