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Are shrubs a necessary component of the habitat for *Ammospermophilus nelsoni* in the San Joaquin Desert?

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Abstract.—The San Joaquin antelope squirrel (*Ammospermophilus nelsoni*; SJAS) is a state-listed Threatened species in California that evolved in the shrublands of the San Joaquin Desert. Due to livestock overgrazing and fires, much of the desert has lost its shrub cover, which would be a conservation concern if shrubs are a necessary component of the habitat for squirrels. We established two 64-trap plots on the Lokern area of Kern County, California: one covered by saltbush scrub (*Atriplex* spp.) and another nearby without shrubs. We trapped quarterly starting in January 2019 and ending in November 2021 (12 trap sessions). When a squirrel was found in a trap, we permanently marked it with a passive integrated transponder (PIT) tag, recorded its trap location on the plot, and assessed its sex, weight (using a spring scale), age (young or adult), and reproductive condition. In the 3 years of trapping, we marked 90 SJAS on the shrub plot and 194 on the shrubless plot. On both plots, numbers of squirrels trended upward for the 3 years, with significantly higher numbers of SJAS on the shrubless plot in 2021. Survivorship did not differ significantly between plots, but we recorded more young squirrels on the shrubless plot. Although our plots were not replicated, our results and those of recent other studies show that shrubs are not a necessary component of the habitat for SJAS.

Resumen.—La ardilla antílope de San Joaquín (*Ammospermophilus nelsoni*; SJAS) es una especie que evolucionó en los matorrales del desierto de San Joaquín y que actualmente figura en la lista estatal de especies amenazadas de California. Debido al sobrepastoreo del ganado y a los incendios, gran parte del desierto ha perdido su cubierta arbustiva, lo que podría suponer un problema de conservación debido a que los arbustos son un componente necesario del hábitat de las ardillas. En este estudio, establecimos dos parcelas con 64 trampas en el área de Lokern en el condado de Kern, California: una cubierta por arbustos saltbush (*Atriplex* spp.) y otra cercana sin arbustos. Realizamos trampeos trimestrales que comenzaron en enero de 2019 y finalizaron en noviembre de 2021 (12 sesiones de trampeo). Cuando se encontró una ardilla en una trampa, la marcamos permanentemente con una etiqueta de transpondedor integrado pasivo (PIT), registrábamos la ubicación de la trampa en la que cayó, su sexo, peso (usando una báscula de resorte), edad (joven o adulta) y condición reproductiva. Durante los tres años de trampeo, marcamos 90 SJAS en la parcela con arbustos y 194 en la parcela sin arbustos. En ambas parcelas, la cantidad de ardillas tendió a incrementar durante los tres años, con un número significativamente mayor de SJAS en la parcela sin arbustos en 2021. La supervivencia no difirió significativamente entre parcelas, pero registramos más ardillas jóvenes en la parcela sin arbustos. Aunque nuestras parcelas no fueron replicadas, nuestros resultados y los de otros estudios recientes muestran que los arbustos no son un componente necesario del hábitat de las SJAS.

San Joaquin Antelope Squirrels (*Ammospermophilus nelsoni*; SJAS) inhabit the San Joaquin Desert of California from the San Joaquin Valley floor through the western foothills and into the Carrizo and Elkhorn plains and Cuyama and Panoche valleys (Best et al. 1990, Germano et al. 2011, Cypher et al. 2021). Most of the San Joaquin Desert originally supported large areas of shrubs (e.g., *Atriplex*, *Ephedra*, *Allenrolfea*, *Suaeda*; Griggs et al. 1992, Minnich 2008, Germano et al. 2011), but decades of overgrazing by livestock and subsequent grassland fires left large areas of remaining natural land devoid, or almost devoid, of shrub cover (Germano et al. 2012). Shrubs have been thought to be physiologically important to SJAS survival because they provide needed thermal cover (Heller and Henderson 1976). Authors of early field studies considered SJAS most numerous in areas with sparse to moderate shrub cover (Grinnell and Dixon 1918, Hawbecker 1953, 1958), but SJAS have been found in large expanses of land with few to no shrubs (Taylor 1916, Best et al. 1990, Harris and Stearns 1991, Cypher et al. 2021),

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Fig. 1. The plot with saltbush scrub (*Atriplex polycarpa* and *A. spinifera*) (top) and the plot without shrubs (bottom) where we captured San Joaquin antelope squirrels (*Ammospermophilus nelsoni*). Both plots are in the Lokern area, western Kern County, California.

especially where kangaroo rat (*Dipodomys* sp.) burrows are present. While Hawbecker (1953) believed that SJAS in areas without shrubs were nonbreeders, SJAS are widespread and persistent on the Carrizo Plains, where there are thousands of acres devoid of shrubs (USFWS 1998, Cypher et al. 2021). For conservation planning purposes, it is important to compare SJAS population size and demographics between shrubland and shrubless areas.

Although SJAS is a state-listed Threatened species, few studies have been conducted on permanently marked SJAS to determine population size and population demographics over several years, especially in relation to shrub occurrence. A notable exception is the study by Germano et al. (2012), which tracked populations of SJAS (and other species) for 10 years at the Lokern Natural Area of California. The focus of that study, however, was on the effect of cattle grazing on population abundance, and trapping only occurred once per year. A direct comparison of marked SJAS in shrub-dominated and shrubless habitats with multiple trapping sessions per year has not been conducted. Such a study would yield estimates of survivorship and timing of reproductive periods and recruitment of young.

The purpose of our study was to determine whether there is a difference in the population size and demographic characteristics of SJAS on a shrub-dominated site and a site with no shrubs. We carried out the study over 3 years using a 7.84-ha plot with shrubs and a 7.84-ha plot that was virtually devoid of shrubs in the Lokern Natural Area of Kern County, California. Population comparisons between the 2 plots contributes to our understanding of the role of shrubs in habitat suitability and habitat management for this squirrel.

METHODS

Study Sites

The shrub plot we used was located in Section 29, T32S, R23E MDPM (35.377695°N, 119.633924°W), where saltbush scrub (A*triplex polycarpa* and *A. spinifera*) is the dominant vegetation (Fig. 1); this plot was one of the plots used in our grazing study (Germano et al. 2012). While we had intended to use a shrubless plot at one of the previous grazing study plots, we encountered access permission problems and decided to instead conduct the shrubless study at a nearby parcel of conserved habitat. The shrubless plot was located approximately 8 km to the southeast of the shrub plot in Section 6, T30S, R23E, MDPM (35.352908°N, 119.552187°W). It had a very low occurrence of saltbush (or other shrubs) and a dominant plant cover of red brome (*Bromus madritensis rubens*), Arabian grass (*Schismus arabicus*), filaree (*Erodium cicutarium*), and other herbaceous species (Fig. 1). We used the rainfall totals for each rainfall year (July to June) from 2 gauges on the Lokern Natural Area, which were read after each rainfall event that year.

We conducted trapping sessions 4 times per year at both sites: spring, summer, fall, and winter from 2019 to 2021. As in the grazing study (Germano et al. 2012), each 8 × 8 plot consisted of 64 Tomahawk live traps spaced at 40-m intervals. We trapped each plot for 5 consecutive mornings during January, April, July, and October 2019, and February, May, August, and November during 2020 and 2021. We opened traps within approximately 1 h of sunrise (05:30 to 07:00 depending on the season), and we checked traps once or twice in a morning or conducted a second check in early afternoon on cool days. We covered all traps with shade cloth material to provide protection from the sun and baited traps with a mixture of wild bird seed and rolled oats.

When we found a squirrel in a trap, we permanently marked it with a passive integrated transponder (PIT) tag inserted dorsally, midbody. We also uniquely marked individuals on the pelage with a nontoxic marker to distinguish individuals during the trapping session, which allowed for identification of marked animals later in the session without the need to bag the animal to read the PIT tag. For each animal captured, we recorded trap location on the plot, sex, weight (using a spring scale), age (young or adult), reproductive condition, general condition, and capture markings. Typically, SJAS reproduce between January and March, and then young are aboveground in April (Hawbecker 1958, 1975). We defined young as animals weighing <100 g and those weighing <120 g with soft pelage who were not previously tagged when caught in February or May. We immediately released individuals at the point of capture after recording data.

Population Size Estimates

We compared annual population estimates of squirrels in 2019, 2020, and 2021 for the shrubless and shrub plots using the Schnabel method (Schnabel 1938, Chapman and Overton 1966). The equation for the Schnabel method is as follows:

$$\hat{N} = \frac{\sum(M_i C_i)}{\sum R_i},$$

where $\hat{N}$ is the estimate of population numbers, M_i is the number of marked squirrels in the ith session, C_i is the number of squirrels captured in the ith session, and R_i is the number of squirrels recaptured in the ith session.

Variance is calculated as

$$\frac{\hat{1}}{N}.$$

Standard deviation is calculated as follows:

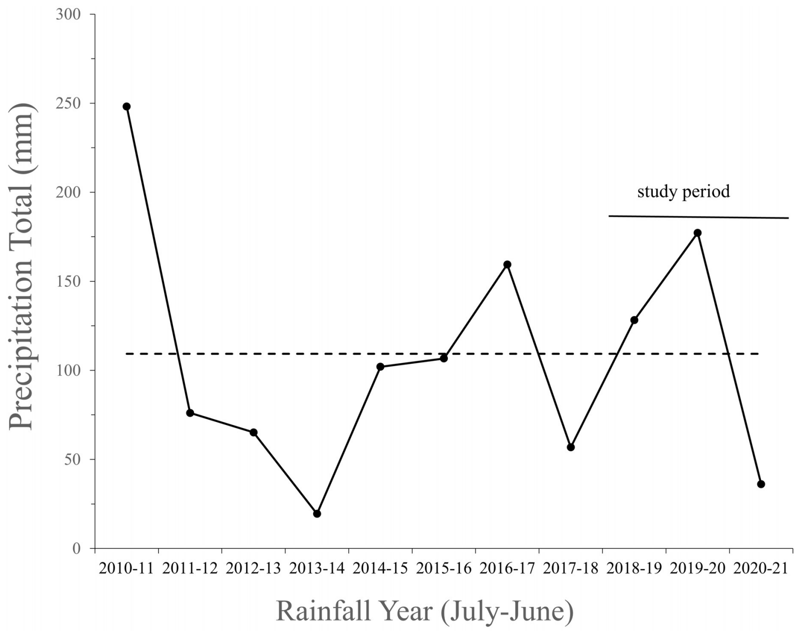

Fig. 2. Precipitation totals for Lokern, Kern County, California from 2010–2021. The dotted horizontal line is the 20-year average rainfall for 2001–2021.

$$s\frac{\hat{1}}{N} = \sqrt{\frac{\sum R_i}{\sum (M_i C_i)^2}}.$$

And the 95% confidence interval is calculated as

$$\frac{\hat{1}}{N} \pm 2s\frac{\hat{1}}{N},$$

for which the reciprocal term for each limit is computed. We determined a significant difference between plots if the mean of a plot did not intersect the 95% confidence interval of the other plot. We also determined the relationship between the number of squirrels caught in each session and the session date by using linear regression to establish whether there was a trend in the number of squirrels over the 3 years of the study. We compared regressions for each plot using analysis of covariance (ANCOVA), with session date as the covariate. We used $\alpha = 0.05$ for both tests.

Survival Estimates and Survivorship

We estimated annual survival of SJAS based on capture histories. Using March as the month of birth (Hawbecker 1958), for squirrels first caught as juveniles, we added the number of months back to March to the number of months an individual was caught on the plot to estimate its age. For squirrels caught as adults between January and March, we considered them to have been born in March of the preceding year. For example, we estimated the minimum longevity of an adult squirrel caught in April 2019 and last captured in May 2021 to be 3 years (38 months) old because it was caught in 2 successive years and would have been at least 1 year old when first caught.

For survivorship, we calculated recapture and demographic vital rates of SJAS using population encounter histories derived from individual encounter histories in Program MARK (White and Burnham 1999). We calculated apparent survival (Φ) and recapture rates (p) using the open population Cormack–Jolly–Seber (CJS) model in Program MARK (Lebreton et al. 1992, White and Burnham 1999). We generated CJS model sets for both shrubless and shrub plots based on group designation (adult male, adult female, young male, young female) to test whether Φ or p was best estimated independent of group or time, by group or time, or with a group × time interaction (generating 16 models). Model selection was based on Akaike information criterion (AICc) values, with lower values denoting greater parsimony (Burnham and

TABLE 1. The number of young (<100 g or <120 g based on soft pelage when an animal was caught in summer/fall sessions) and adult male (M) and female (F) San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) caught in the Lokern area, Kern County, California, during 4 trapping sessions per year in 2019, 2020, and 2021.

Year/plot/month	Young M	Young F	Adult M	Adult F	Total
2019					
No shrubs					
January			3	1	4
April			5	2	7
July		1	18	7	26
October			11	3	14
Shrubs					
January			1	2	3
April			3	1	4
July			13	12	25
October		2	5	6	13
2020					
No shrubs					
February			12	7	19
May	8	11	5	5	29
August			27	13	40
November			22	16	38
Shrubs					
February			11	10	21
May	5	10	6	6	28[a]
August		3	12	9	24
November			20	18	38
2021					
No Shrubs					
February			15	12	27
May	9	24	10	10	53
August			20	30	50
November			12	26	38
Shrubs					
February			20	21	41
May		1	10	15	26
August			8	15	23
November			13	13	26

[a]The total includes one individual for which age and sex were not recorded.

Anderson 2002), and we included ΔAICc (difference between model AICc and lowest AICc in the model set), ω (Akaike model weight), *k* (number of estimable parameters), and deviance (measure of model fit). After the top model, models considered explanatory were those with a ΔAICc < 2.

Traditionally, encounter rates are used to calculate the probability that an individual will leave a population. If the encounter rates are reversed, then the probability of an individual entering the population can be estimated (Pradel 1996), where lambda (λ) = rate of individuals entering a population or cohort. Using Pradel models, λ estimates the realized growth rates of the age class from which the encounter rates were generated but is not necessarily equivalent to the growth rate of the population. Still, it provides an important metric of the life-history characteristics of a population. Pradel's λ was estimated by Program MARK in conjunction with the CJS model described above.

RESULTS

Rainfall varied each year of the study, with above-average totals (July to June) in 2019 and 2020, but below-average totals in 2021 (Fig. 2). The number of squirrels we caught in the first year of trapping varied by session at both sites, with the highest number of individuals caught in July (Table 1). By 2020, when total numbers of squirrels were increasing (Fig. 3), the highest number we caught was still in the summer (August) on the plot without shrubs but was in May on the shrub plot (Table 1). The total number of individuals caught on the shrub plot peaked in February 2021 at 41 and then declined thereafter (Fig. 3). We caught the greatest number of squirrels on the shrubless

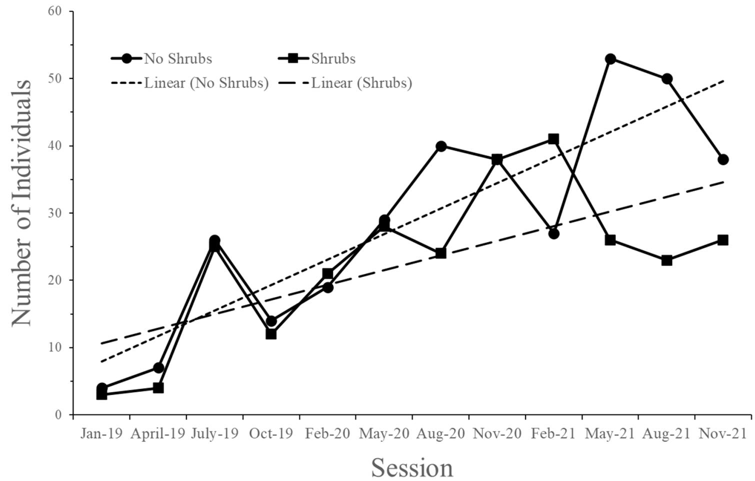

Fig. 3. The number (and population trends) of individual San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) caught per month from 2019 to 2021 on a plot with shrubs (squares) and a plot with no shrubs (closed circles) in the Lokern area, western Kern County, California.

plot in May 2021 (Table 1). Overall, we marked 90 SJAS on the shrub plot and 194 on the shrubless plot.

Reproduction

Reproductive activity varied by season on the plots (Table 2). The percentages of males and females in some stage of reproductive condition were similar between the shrub and shrubless plots (Table 2). We only caught 3 squirrels that we classified as young in 2019 (Table 1). The number of young we captured on the 2 plots in 2020 was much higher than in 2019, with 19 young caught in May on the shrubless plot, and 15 in May and 3 in August on the shrub plot (Table 1). In 2021, however, there was a stark difference in the number of young by plot, with 33 caught in May on the shrubless plot but only 1 caught on the shrub plot (Table 1).

Population Size Estimates

The estimated number of SJAS on the shrubless plot varied from 38.7 to 94.5 individuals and increased in each successive year of the study (Table 3). On the shrub plot, the estimated number of SJAS was highest in 2020 (86.6 individuals), but declined significantly in 2021 (Table 3). By 2021, there were significantly more SJAS estimated to be on the shrubless plot than on the shrub plot (Table 3). Despite these differences in estimated annual numbers on each plot, the trend in numbers of SJAS caught quarterly significantly increased over the 3-year study on both plots (no shrubs: slope = 3.787, $F_{1,10} = 29.47$, $P < 0.001$, $r^2 = 0.747$; shrubs: slope = 2.192, $F_{1,10} = 8.638$, $P = 0.015$, $r^2 = 0.463$; Fig. 4) and the regressions did not differ significantly (slopes: $F_{1,20} = 2.438$, $P = 0.134$; elevations: $F_{1,20} = 2.864$, $P = 0.105$).

Survival and Survivorship

Of the 284 SJAS we caught across both plots, 81.0% ($n = 230$) were recorded for a time period of ≤1 year (1–4 consecutive sessions), and of these, 35.9% ($n = 102$) were caught only in 1 session. We captured 1 adult female for 2.25 years, as well as 1 adult male and 1 adult female for 2 years on the shrub plot. We estimated these squirrels' minimum longevities, based on when they were first captured, as 3 years, 3 years, and 2.75 years, respectively. The longest time spans during which we caught SJAS on the shrubless plot were 2 years and 1.75 years (both adult males). Minimum longevity for these males was 2.75 years for both.

The best models (ΔAICc < 2) to describe survivorship and recapture rates for SJAS on the shrubless plot included static survivorship and recapture rate by group and static survivorship and static recapture rate (Table 4). There was only one model that described survivorship and recapture rate for SJAS on the shrub plot: static survivorship and recapture rate by group and time (Table 4). Apparent static quarterly survivorship

TABLE 2. The percentages of adult San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) found in reproductive condition at a shrubless and shrub plot in the Lokern area, western Kern County, California, during 4 trapping sessions in 2019, 2020, and 2021. For males, PS = partially scrotal and S = scrotal. For females, E = estrous, P = pregnant, L = lactating, and PL = postlactating.

	Males			Females				
Plot/month and year	*n*	%PS	%S	*n*	%E	%P	%L	%PL
No shrubs								
January 2019	3	0	66.7	1	100	0	0	0
April 2019	5	0	0	2	0	0	50.0	0
July 2019	19	5.26	0	6	0	0	0	0
October 2019	11	9.01	90.9	3	0	0	0	0
February 2020	12	66.7	0	6	0	100	0	0
May 2020	5	20.0	0	5	0	0	0	40.0
August 2020	27	0	0	13	0	0	0	0
November 2020	22	13.6	72.7	16	0	0	0	0
February 2021	15	53.3	33.3	12	0	100	0	0
May 2021	10	10.0	0	10	0	0	0	0
August 2021	20	5.00	0	30	0	0	0	0
November 2021	12	33.3	58.3	26	0	0	0	0
Shrubs								
January 2019	1	100	0	2	0	100	0	0
April 2019	3	33.3	0	1	0	0	0	0
July 2019	13	0	0	12	0	0	0	0
October 2019	5	20.0	80.0	7	0	0	0	0
February 2020	12	25.0	25.0	14	0	85.7	14.3	0
May 2020	6	0	0	6	0	0	0	33.3
August 2020	12	0	0	9	0	0	0	0
November 2020	19	15.8	84.2	18	0	0	0	0
February 2021	19	10.5	89.5	22	18.2	13.6	0	0
May 2021	10	0	20.0	14	0	0	0	0
August 2021	8	0	12.5	15	0	0	0	0
November 2021	13	7.69	92.3	14	0	0	0	0

TABLE 3. Schnabel estimates of population numbers (lower and upper 95% confidence limits in parentheses) for San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) in a shrubless and shrub plot in the Lokern area, Kern County, California, during a 3-year study. Within a year (rows), population numbers between shrubless and shrub plots differed significantly only in 2021. Within a plot (columns), numbers are significantly different if letter suffixes are not the same.

Year	No shrubs	Shrubs
2019	38.7 (26.3, 73.1) a	46.4 (28.9, 116.8) a, b
2020	84.1 (66.1, 115.6) b	86.6 (66.2, 125.3) a
2021	94.5 (77.4, 121.3) b	52.3 (41.9, 69.5) b

(*F*) on the shrubless plot varied from 0.872 to 0.890 across age and sex groups, but differences were not significant (Table 5). Similarly, there were no significant differences in survivorship among age and sex groups on the shrub plot, with rates varying from 0.916 for adult males to 0.969 for young female squirrels (Table 5). Survivorship of females (adult and young) on the shrub plot, however, were significantly higher than all but young males on the shrubless plot (Table 5).

The quarterly recapture rates (*p*) of young males (0.647) on the shrubless plot, and adult males (0.645) and adult females (0.634) on the shrub plot did not differ significantly (Table 5). These rates were significantly lower than the recapture rates for adults and young females on the shrubless plot and for young on the shrub plot (Table 5). All sex and age groupings of SJAS showed increasing populations ($\lambda > 1.0$). Lambda values were significantly higher for young of both sexes on the shrubless plot than for adults on the shrubless plot and all groups on the shrub plot (Table 5). Lambda values for both adult sexes on the shrub plot were significantly lower than all but adult males on the shrubless plot (Table 5).

DISCUSSION

The number of squirrels that we captured on the shrubless plot was either the same or exceeded the number caught on the shrub plot. Also, the trend showed an increase of squirrel numbers over the 3 years of study on the

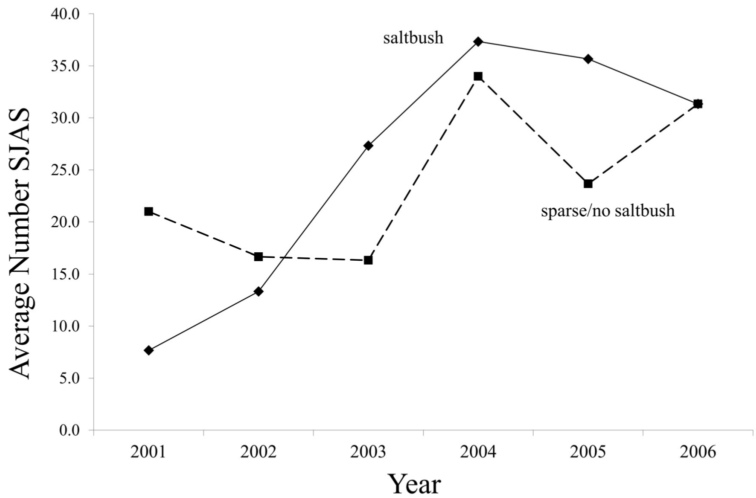

Fig. 4. The average number of San Joaquin antelope squirrels (*Ammospermophilus nelsoni*; SJAS), caught on 3 plots with saltbush shrubs (*Atriplex* sp.) and on 3 plots with few to no saltbush during a grazing study (Germano et al. 2012) in the Lokern area, Kern County, California (unpublished data).

TABLE 4. Cormack–Jolly–Seber model set (first 5 of 16 for each plot type) analyzing the effects of group (adult male, adult female, young male, and young female) and time on apparent survivorship (Φ) and recapture rates (*p*) of San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) caught quarterly in a shrubless and shrub plot from January 2019 to November 2021 in the San Joaquin Desert of California. Abbreviations: t = time, g = group, (.) = static value, AIC = Akaike information criterion, ΔAICc = difference between model AICc and lowest AICc in the model set, ω = Akaike model weight, *k* = number of estimable parameters, and deviance = measure of model fit.

Model	AICc	ΔAICc	ω	*k*	Deviance
No shrubs					
Φ(.) *p*(g)	639.7552	0	1.53227	5	209.4598
Φ(.) *p*(.)	640.8685	1.1133	0.30506	2	216.6934
Φ(g) *p*(.)	644.5283	4.7731	0.04894	5	214.2329
Φ(t) *p*(.)	644.9148	5.1596	0.04034	12	199.9755
Φ(t) *p*(g)	645.1855	5.4303	0.03523	15	193.8094
Shrubs					
Φ(.) *p*(g × t)	424.3926	0	1.00000	1	221.9378
Φ(.) *p*(t)	473.5023	49.1097	<0.00001	12	247.5729
Φ(g) *p*(t)	475.3756	50.9830	<0.00001	15	242.6089
Φ(.) *p*(g)	481.4589	57.0663	<0.00001	5	270.7445
Φ(.) *p*(.)	482.6045	58.2119	<0.00001	2	278.1131

shrubless plot, although the slopes of the regression lines of the 2 plots were not significantly different. We also found that there was a greater number of young born on the shrubless plot in the last year of the study and that survivorship estimates were about the same or higher on the shrubless plot for both sexes compared to the shrub plot. Finally, estimates of population growth (λ) for the 3 years was higher for male and female young on the shrubless plot than for any other group on the shrub plot. We are not suggesting that areas with shrubs are worse for SJAS than areas without shrubs, but our data indicate that shrubs may not be a necessary component of habitat for this threatened species. We recognize that we cannot make broad statements about the importance of shrubs for this species because we do not have replicated plots, but the data are suggestive. During our grazing study from 1997 to 2006, however, we found significantly greater numbers of SJAS on plots reinvaded by saltbush than on plots with sparse or no shrubs (Germano et al. 2012). In that study, though, there were many SJAS on plots with sparse or no shrubs, and sometimes averages on shrubless plots were the same or higher in some years than on shrub

TABLE 5. Apparent static quarterly survivorship (Φ), recapture rate (*p*), and lambda (λ) (lower and upper 95% confidence limits in parentheses) for adult and young male and female San Joaquin antelope squirrels (*Ammospermophilus nelsoni*) caught in a shrubless plot and a plot with shrubs in the San Joaquin Desert of California. Squirrels were captured from January 2019 to November 2021. Mean life-history traits (down a column) that do not have the same letter suffixes differ significantly (based on means not intersecting confidence intervals)

Group	Φ	*p*	λ
No Shrubs			
Adult male	0.889 (0.855, 0.916) a	0.906 (0.810, 0.956) a	1.023 (1.002, 1.043) a, b
Adult female	0.885 (0.840, 0.918) a	0.926 (0.806, 0.977) a	1.043 (1.017, 1.069) b, c
Young male	0.872 (0.749, 0.940) a, b	0.647 (0.347, 0.869) b	1.086 (1.036, 1.138) d
Young female	0.890 (0.846, 0.923) a	0.894 (0.753, 0.959) a	1.087 (1.057, 1.119) d
Shrubs			
Adult male	0.916 (0.879, 0.943) a, b	0.645 (0.520, 0.753) b	1.002 (0.979, 1.026) a
Adult female	0.932 (0.893, 0.958) b	0.634 (0.504, 0.748) b	1.004 (0.979, 1.031) a
Young male	0.953 (0.715, 0.994) a, b	0.788 (0.326, 0.966) a	1.029 (0.934, 1.133) a, c
Young female	0.969 (0.915, 0.989) b	0.841 (0.673, 0.931) a	1.030 (0.989, 1.073) a, c

plots (Fig. 4), which reinforces the conclusion that shrubs are not obligatory for robust populations of SJAS in their range.

Hawbecker (1953) thought that SJAS were dependent on habitat with widely spaced shrubs, even though he studied squirrels near Los Banos and Mendota on the valley floor of the San Joaquin Desert without shrubs. He concluded that sites without shrubs were poor habitat because he saw only a few females with young running about during the breeding season. SJAS are very wary of humans, however, and usually hide in burrows long before they are spotted (personal observation). We suspect that population sizes and reproduction of SJAS at these 2 shrubless sites were not significantly lower than at sites Hawbecker studied with shrubs. In fact, the earliest reports of SJAS habitat use from a study conducted in the southern end of the San Joaquin Valley found that the squirrels preferred open, exposed areas covered mostly by foxtail grasses (Taylor 1916). On the Elkhorn Plain and in the Panoche Valley, Harris and Stearns (1991) found the highest densities of SJAS in open ephedra scrub with fairly large, widely spaced shrubs, but densities were also high in open, shrubless, grassy sites with kangaroo rats. They concluded that, although unexpected, density estimates of SJAS suggested that shrub cover was not necessary, with burrow systems of kangaroo rats providing sufficient cover.

A recent range-wide study of SJAS presence/absence (Cypher et al. 2021) found that squirrels were not associated with shrubs in general or with shrub densities, and SJAS also were associated with kangaroo rat burrows. Another small squirrel, the Uinta Ground Squirrel (*Urocitellus armatus*), also appears not to be dependent on shrub cover in its habitat; when shrubs were experimentally removed from a 1.25-ha study plot in Wyoming, the population size, sex ratios, and age structure were not affected (Parmenter and MacMahon 1983). An important conservation point is that SJAS recovery and long-term occupancy of areas in the San Joaquin Desert are not likely dependent on revegetating areas with shrubs, which is expensive (>$2500 per ha on the Carrizo Plain; Ben Munger, personal communication) and not always successful (personal observation). In an experiment to test reseeding saltbush in the Lokern Natural Area, saltbush became established in only 2 of 7 test plots (Randi McCormick personal communication). Management agencies that produce habitat suitability models for SJAS should consider shrubs as facultative (not obligatory) habitat features, and landscape conservation planning and habitat acquisitions should not disregard shrubless parcels that exhibit robust kangaroo rat activity, because such parcels can support equivalent numbers of SJAS.

During our study, reproductive activity was limited to fall and winter months for males, and for the most part only to winter (January or February) for females, although a few females were found postlactating in spring. We cannot be more precise because we only trapped 4 times per year. These times of reproductive activity are the same as those found in the past for SJAS (Hawbecker 1958, 1975). For the most part, we found the greatest number of young in May, perhaps indicating only one bout of reproduction per year, but a few young were found in summer on the shrub plot. Hawbecker (1958) believed that SJAS bred only once per year; however, during our grazing study, we found several years in which a second litter of young was produced (Germano et al. 2021). Unlike our current study, the grazing study occurred over 10 years, and second litters did not occur every year. SJAS appear in most years to breed once, but sometimes 2 litters may be produced in a year, no doubt dependent on yearly rainfall, food production, and SJAS densities.

Survival across years in our study was almost exactly the same as that found by Hawbecker (1958) for SJAS. He found that 80.4% (193 of 240) of SJAS that he captured over his 7-year study were not caught again after 9 months, whereas we found that 81.0% were not captured after 1 year. Similar rates of yearly survival were found in the 10-year grazing study on the Lokern, where 77.3% of SJAS were caught in only 1 year during annual trapping (Germano et al. 2012). The greatest longevities of SJAS that we found (3 years) were exceeded by both the study by Hawbecker (1958) and the Lokern grazing study (Germano et al. 2021): Hawbecker (1958) found several squirrels living to 4 years and 1 lived at least to 5 years 8 months, and during the grazing study, 11 SJAS lived at least to 4 years and 2 lived at least to 5 years. We likely would have found several squirrels living past 3 years if we had continued our trapping. Our quarterly estimates of survivorship give a first approximation of annual survivorship of 0.578 to 0.882 across sex, age group, and plots if quarterly survivorship did not vary within a year. Estimates of annual survivorship of SJAS based on 10 years of annual trapping at the grazing study site, however, varied from 0.317 to 0.404 (Germano et al. 2021). Our quarterly estimates may indicate greater survivorship of SJAS at this site than during the grazing study, but the differences in the duration of time used to estimate survivorship makes a comparison unreliable.

Activity does not seem to be greatly different across seasons. Once the population numbers increased from the beginning of our trapping, we caught many squirrels in November and February, even though nighttime temperatures were in the single digits (°C). We opened traps by about 08:00 and started checking them from about 11:00 to 12:30, when temperatures had risen to 15–20 °C, at least. Based on our 4 trapping sessions, SJAS are active above ground all year, which is what Hawbecker (1958) concluded. Also, low rainfall in 2020–2021 did not affect the number of squirrels we found. Based on rainfall recorded at Lokern, the July–June total was 128.2. mm (5.05 inches) in 2018–2019, 177.2 mm (6.98 inches) in 2019–2020, and 36.1 mm (1.42 inches) in 2020–2021. The 20-year average at the Lokern Natural Area was 109.3 mm (4.30 inches), and rainfall in the preceding year (2017–2018) was 56.8 mm (2.24 inches). Therefore, even though in 2 of 4 years the site received well below average rainfall, enough rain seems to have fallen at the correct times in the last year of our study to produce food sufficient to sustain a growing population. Also, SJAS are omnivorous (Hawbecker 1947, Harris 2019), which means that some food resources are available to them even after one dry year. If climate change alters the rainfall pattern and amounts in the San Joaquin Desert, however, continued dry years may adversely affect SJAS.

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