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Long-term occupancy monitoring reveals value of moderate disturbance for an open-habitat specialist, the Stephens' kangaroo rat (*Dipodomys stephensi*)

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Abstract

For species of conservation concern, long-term monitoring is vital to properly characterize changes in population distribution and abundance over time. In addition, long-term monitoring guides management decisions by informing and evaluating the efficacy of management actions. A long-term monitoring initiative for the federally threatened Stephens' Kangaroo rat (*Dipodomys stephensi,* SKR) was established in 2005, across 628 hectares within Marine Corps Base Camp Pendleton (MCBCP), San Diego, California, USA. From 2005 to 2018, we tracked trends in area occupied by SKR, trends in relative SKR densities within occupied habitat, and modeled probabilities of SKR occupancy, colonization, extinction, with habitat, climate, and disturbance covariates. Area occupied by SKR increased almost 2-fold from 2005 to 2018 on MCBCP, while density in occupied habitat increased almost 3-fold. Increased area occupied was correlated with increases in estimated density among years, indicating SKR population growth occurs by expansion into suitable habitat patches, as well as increases in numbers within occupied habitat. SKR occupancy was positively associated with gentle slopes (<10%) and moderate open ground (40–80%) and forb cover (>40%). They were more likely to colonize previously unoccupied habitat when there were moderate levels of open ground (40–80%) and low shrub cover (<20%), while more likely to go locally extinct in areas with high slopes (>10%), less open ground (<20%), and increased non-native grass cover (>40%). Additionally, probabilities of SKR occupancy and colonization were higher in areas with moderate levels of disturbance, which was positively associated with open ground and forb cover. We conclude that long-term occupancy and density monitoring is effective in informing status and trends of spatially dynamic species and that moderate habitat-based disturbance is compatible with the management of SKR.

KEYWORDS

colonization, density, extinction, heteromyid, invasive grass, non-native grass, threatened species

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1 | INTRODUCTION

Effective management of populations of threatened and endangered species requires an understanding of species habitat use, population trends, and potential threats to populations (Campbell et al., 2002; Lindenmayer & Likens, 2010; Martin et al., 2007). This is particularly important for the management of species that are habitat specialists, where populations may be limited in size and spatial distribution (Wilkening et al., 2019). For these species, determining drivers of habitat selection and fluctuations in density, and how management affects habitat availability and population size is vital (Likens & Lindenmayer, 2018).

Long-term ecological studies of populations can be valuable for quantifying how spatial and demographic parameters change over time and for better understanding population dynamics in association with environmental change (e.g., Hughes et al., 2017; Likens & Lindenmayer, 2018; Lindenmayer et al., 2022). Long-term monitoring efforts are especially valuable when studying species that experience significant intra- and inter-annual variation in reproduction and survival and can provide more robust understanding of overall population trends (Meserve et al., 2003; Whitford, 1976). Rodent populations are known to have extremely high variability in abundance within and among years due to their high fecundity and short life spans (e.g., Krebs, 2013; Whitford, 1976). Long-term studies are essential to properly characterizing population dynamics (Hayes et al., 2017). Similarly, variation in the spatial distribution can result from meta-population dynamics and where availability of suitable habitat patches varies over space and time (i.e., Fahrig, 1992). As a result, long-term studies provide some of the most robust data on trends in populations, critical to evidence-based policy decisions (Lindenmayer et al., 2022).

Occupancy models can leverage long-term data to describe trends in populations over time (Broms et al., 2016; Kéry & Chandler, 2012; Royle & Kéry, 2007). Site-occupancy models estimate the proportion of a sampling area focal species occupy, while accounting for imperfect detection (Mackenzie et al., 2002, 2017). The models allow occupancy to be modeled as a function of landscape and habitat conditions, informing habitat management, conservation planning, and prioritization (De Wan et al., 2009; Mackenzie et al., 2017; Peterman et al., 2013). Dynamic occupancy models extend occupancy studies by including multiple sampling periods, allowing the estimation of colonization and extinction parameters, range dynamics, and responses to habitat change and disturbance (e.g., Bled et al., 2013; Broms et al., 2016; Gould, 2021; Royle & Kéry, 2007). Furthermore, spatial occupancy designs can provide high power to determine the effects of changes in habitat suitability, disturbance, and management on populations (Guillera-Arroita & Lahoz-Monfort, 2012; MacKenzie et al., 2017), making them powerful and cost-effective methods for monitoring species of conservation concern (e.g., MacKenzie et al., 2017).

In the United States, threatened and endangered species can occur on a patchwork of private, state-owned, and federally owned lands. The Department of Defense (DOD) oversees 35,600 km^2 of federal land in the United States and primarily manages for military training and testing (Vincent & Hanson, 2020). Consequently, managing for populations of endangered species on DOD land can be uniquely challenging (Boice, 2006). Marine Corps Base Camp Pendleton (MCBCP) is a military training site that encompasses the largest remaining expanse of undeveloped coastline and coastal habitat in southern California, USA. MCBCP has committed to fulfill stewardship and regulatory requirements for the natural resources on base, including monitoring and management for the federally threatened Stephens' kangaroo rat (*Dipodomys stephensi*, SKR; MCBCP 2018).

Stephens' kangaroo rat (SKR) is a medium-sized (ca. 65 g) nocturnal rodent of the family Heteromyidae. This species is listed as a threatened species by the U.S. Fish and Wildlife Service due to extensive habitat loss, degradation, and fragmentation (USFWS, 1997, 2021, 2022). SKR prefer open herbaceous and grassland habitat with minimal shrub cover and friable soils for digging and dust bathing (Bleich, 1977; Goldingay & Price, 1997; O'Farrell & Uptain, 1989; Thomas, 1975). SKR habitat is thought to be maintained via natural and unnatural disturbances (Kelt, Konno, & Wilson, 2005; Price et al., 1994; Price & Gilpin, 1996). In the absence of disturbance, vegetative succession can occur and has been associated with population decline (O'Farrell & Uptain, 1987, 1989).

Large fluctuations in distribution and density have been documented for SKR (e.g., Kelt, Wilson, & Konno, 2005; McClenaghan Jr. & Taylor, 1993; O'Farrell & Uptain, 1987, 1989; Price & Endo, 1989). SKR may follow patterns of meta-population dynamics, as declines in population sizes at some locations may be concurrent with increases at other locations (Burke et al., 1991; Diffendorfer & Deutschman, 2002; Fahrig, 1992; O'Farrell & Uptain, 1989; Price & Gilpin, 1996; Spencer, 2002). From 2005 to 2018, we monitored SKR population responses to changes in habitat, rainfall, environmental factors, fire, and military disturbance at MCBCP (Brehme et al., 2019). Our objectives were to (1) estimate trends in occupancy and density of SKR on MCBCP; (2) determine predictors of occupancy and localized colonization, and extinction events; and (3) evaluate the impacts of military training and disturbance on SKR populations.

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2 | METHODS

2.1 | Study site

MCBCP is located on approximately 50,585 ha (125,000 ac) of narrow, sandy shoreline, seaside cliffs, coastal plains, low hills, canyons, and mountains within the Peninsular Ranges physiographic province of California, USA. MCBCP provides habitat for the southwestern-most population of SKR, which, along with the neighboring Fallbrook Naval Weapons Station, was designated as one of four "conservation planning areas" developed to help with the conservation and recovery of SKR (USFWS, 1997).

Most land within the MCBCP experiences military-associated disturbances, including off-road troop movements, artillery fire, and bivouacking. Additionally, there is a high frequency of fire within MCBCP, especially within and near artillery firing and bombing ranges. Frequent fires may result in substantial changes in the vegetative composition of habitats, including the transformation of chaparral and coastal sage scrub communities into grasslands and forblands (Callaway & Davis, 1993; D'Antonio et al., 2007; Keeley, 2002; Zedler et al., 1983). Many areas on MCBCP may revert to shrubland or woodland habitats if disturbance were significantly reduced. Finally, there are many dirt roads, paths, and firebreaks that support the above activities.

In 2005, an SKR high-suitability monitoring area was established using previously mapped occupied habitat (Brehme, Clark, Rochester, & Fisher, 2011; Montgomery et al., 1997), which contains coastal sage scrub, grassland, and forbland habitats intertwined with military training areas. Dominant vegetation within the SKR monitoring area includes California sage (*Artemisia californica*), buckwheat (*Eriogonum fasciculatum*), laurel sumac (*Malosma laurina*), native Goldenbush (*Isocoma menziesii*), purple needlegrass (*Nassella* spp.), non-native brome grass (*Bromus* spp.), non-native oats (*Avena* spp.), non-native Storks bill filaree (*Erodium* spp.), ragweed (*Ambrosia psilostachya*), non-native black mustard (*Brassica* spp.), and California aster (*Lessingia filaginafolia*).

2.2 | Population monitoring

In 2005, we established 50 permanent, randomly selected plots (50 × 50 m) within the 740-ha monitoring area to estimate SKR occupancy and relative density, while 50 additional plots were randomly sampled outside of the monitoring area boundaries in potentially suitable habitat (Brehme et al., 2006). Due to low estimates of SKR occupancy and no additional SKR detections, the monitoring area was reduced to 628 ha in 2010 (Figure 1), and the number of permanent plots within the monitoring area was increased to 100 (Brehme, Clark, & Fisher, 2011, Table A1). Annually, we also sampled 25 random plots, within the monitoring area, to enhance spatial coverage for occupancy modeling, as well as 25 randomly chosen plots within the modeled potentially suitable habitat outside the monitoring area for discovery (Brehme, Clark, & Fisher, 2011).

2.3 | Habitat surveys

At each plot, habitat variables were recorded to use as covariates for occupancy modeling. We measured slope, soil compaction (SoilComp), open ground cover (OG), forb cover (Forbs), shrub cover (Shrub), non-native annual grass cover (AG), perennial grass cover (PG), proximity to roads (RdProx), road type (dirt, gravel, or paved), years since last fire (YSLF; up to 30 years), and fire interval over the past 30 years (FireInt: 30/ no. of years plot burned; Brehme et al., 2006). All habitat characteristics measured have been postulated to be important for SKR habitat suitability (Montgomery et al., 1997, 2005; O'Farrell & Uptain, 1987; USFWS, 1997).

We evaluated military disturbance across three measures, including: (1) flat compaction disturbance from foot traffic, bivouacking, and vehicle use (FlatD); (2) evidence of digging or rutted disturbances from vehicle usage in wet or moist conditions (RutD); and (3) presence of berms and targets (BermT). Scores for both the spatial extent of habitat disturbance (from 0 to >75% of habitat affected) and severity of disturbance were multiplied together to determine each disturbance index (Table 1). The spatial score was the median value of the index range divided by 10. The severity scores ranged from 0 to 5 for rutted disturbance and 0–6 for compaction-related disturbance. The presence of foot and tire tracks, depth of tracks (for rutted index), soil compaction, and presence or absence of plant growth at location of disturbance were used to score severity (see definitions in Table 1). The disturbance index for berms and targets was calculated using spatial extent only. Overall military disturbance (DIST) was the sum of all disturbance index values. Disturbance indices were included as continuous site covariates in the occupancy modeling.

2.4 | Kangaroo rat sign surveys

During habitat surveys, we conducted sign surveys to determine whether any kangaroo rat species may be present on the plot. If any sign was present or suspected, live-trapping was done to determine occupancy by SKR and/or the sympatric Dulzura kangaroo rat (*Dipodomys*

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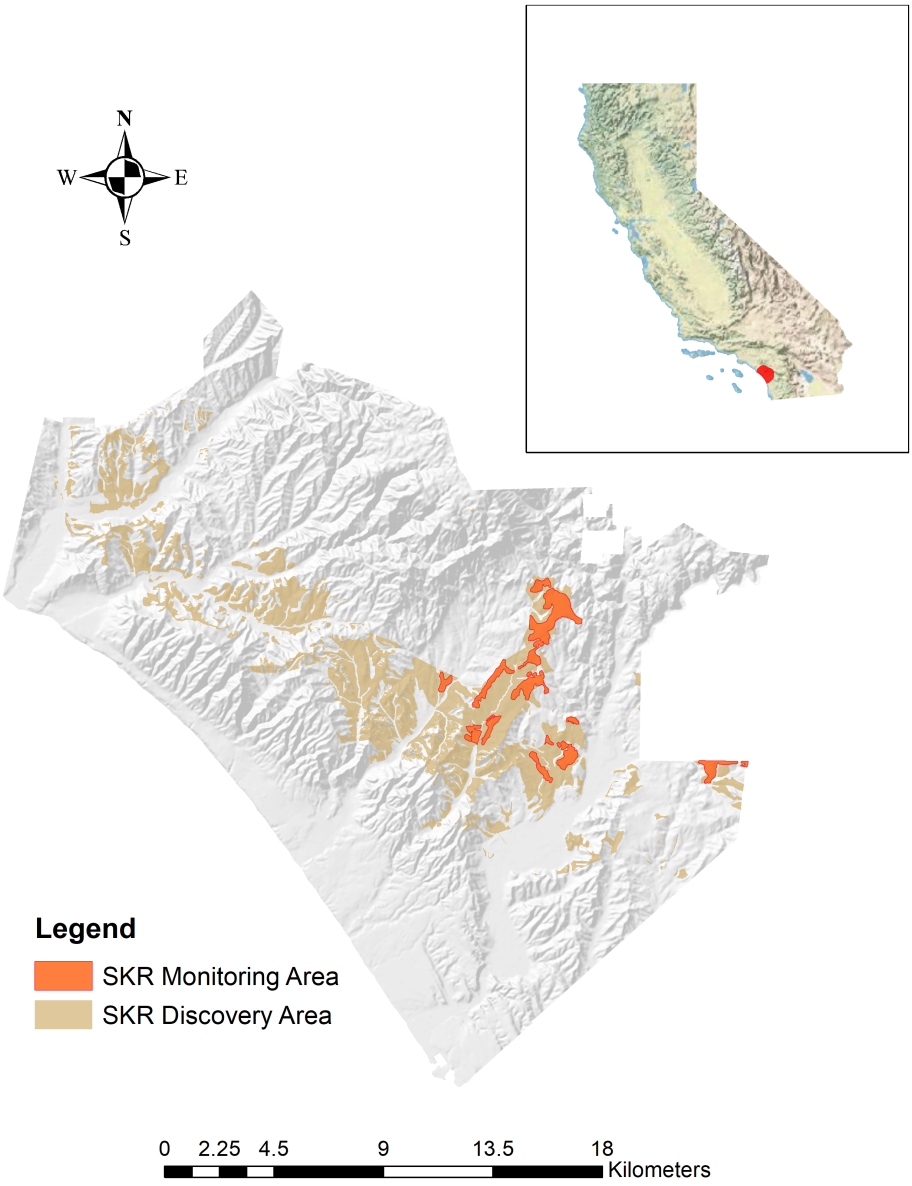


FIGURE 1 Stephens' kangaroo rat (*Dipodomys stephensi*) monitoring area within Marine Corps Base Camp Pendleton, San Diego County, CA, USA. Top right inset shows location (red) in California.

simulans; DKR). A complete search for active kangaroo rat sign (burrows, tracks, dust-bathing sites, scat, and runways) was conducted on each plot (Brehme et al., 2006). Plots were considered potentially occupied by SKR if they contained any kangaroo rat sign (burrows, scat, tracks) or if they contained or were adjacent to a dirt road (Brock & Kelt, 2004a). Because SKR burrows may be confused with burrows of other similar-sized animals, presumed gopher and squirrel burrows were examined carefully to identify evidence of kangaroo rats or other species (Brehme et al., 2006). If a sample plot did not contain any potential kangaroo rat sign, it was defined as "not detected," although this was relatively rare as we were purposefully liberal in our designations of potential kangaroo rat sign. All habitat surveys were conducted in the late summer and fall (September–November) when detectability of burrows is easier due to the disarticulation of annual herbs and grasses (Montgomery et al., 2005; O'Farrell & Uptain, 1987). To evaluate temporal closure within a season, we repeated sign surveys when revisiting a plot to conduct live-trapping and also resurveyed and live-trapped a subset of plots with no kangaroo rat sign.

2.5 | Trapping surveys

Each year, we live-trapped all sample plots containing potential kangaroo rat sign for two to four consecutive nights (4–8 trap events; midnight and morning checks). On each plot, we placed 25 live-traps (15 measuring 10.2 × 11.4 × 38.1 cm and 10 measuring 7.6 × 8.9 × 30.5 cm) in a 5 × 5 array, spaced approximately 10 m apart. We placed traps next to burrow entrances, dust-bathing sites, or within runways, when adjacent to trapping points, to maximize capture success (O'Farrell, 1992).

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TABLE 1 Military disturbance index scores and spatial extent used to quantify habitat disturbances for Stephen's kangaroo rat (*Dipodomys stephensi*) at MCB Camp Pendleton, 2011–2017.

Rutted Disturbance Spatial Extent (%)	Score
0	0
1-10	0.5
11-25	1.8
26-50	3.8
50-74	6.3
≥75	8.8

multiplied by (X)

Rutted Surface > 1 inch deep	Score
None	0
Historic ruts <2" with grown over plants	1
New ruts <2", with plants	3
New ruts <3", no plants	4
Deep Ruts >3" deep old	3
Deep Ruts >3" deep new, no plants	5
max score - all deep ruts	44

Flat Disturbance Spatial Extent (%)	Score
0	0
1-10	0.5
11-25	1.8
26-50	3.8
50-74	6.3
≥75	8.8

multiplied by (X)

Flat Surface- Disturbance Level	Score
None	0
Light disturbance high plants	1
Med disturbance low plants	2
Heavy dirt road/bivuoc. No plants	4
Paved road	6
max score - all pavement	52.8

Berm / Target- Spatial Extent (%)	Score
0	0
1-10	8
11-25	16
26-50	24
50-74	32
≥75	40
max score - all berms and / or targets	40

Rutted Surface Disturbance	SE*RS score
Compact / Flat Surface Disturbance	SE*FLAT score
Berm / Target Surface Disturbance	SE score
Overall Military Disturbance	SUM of above

Note: Higher disturbance index scores correspond to areas with more disturbances. The overall disturbance level was the sum of rutted, flat, and berm disturbance scores.

Trapping was largely conducted during the fall and winter months (October–January), when capture probabilities for SKR are highest (Brehme & Fisher, 2009; O'Farrell & Uptain, 1987), and to better target adult population, which are more likely to remain at a site over time (lower dispersal rate, higher survival) than juvenile

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SKR (McClenaghan Jr. & Taylor, 1993; Price & Kelly, 1994). The monitoring occurred over calendar years 2005/6–2017/18 and is referred to in text as 2005–2018 for simplicity. Trapping was primarily conducted during new or part moon phases, as full moon periods are associated with lower detection probability of kangaroo rats (Brehme & Fisher, 2009; Kaufman & Kaufman, 1982; Price et al., 1984). All trapping was conducted by experienced small mammal researchers with U.S. Fish and Wildlife (USFWS) and California Department of Fish and Wildlife (CDFW) permits for trapping SKR (USFWS Permit TE-045994-19; CDFW MOU SCP838). All traps were set prior to sunset, using heat inactivated rolled oats and birdseed as bait. Traps were checked around midnight and again in the morning each trap-night. Individuals were marked using ear tags and assessed for age, sex, and reproductive condition before releasing.

2.6 | Data analysis

2.6.1 | Correlations

Pearson's correlations among multiple covariates were conducted using the package "psych" (v2.2.9; Revelle, 2022) in R (v4.1.3; R Core Team, 2021) using the Holm correction for multiple comparisons (Holm, 1979). Pairwise correlations among SKR occupancy, density in occupied plots, and rainfall (July–June; NOAA NCEI, 2021: range 9.8–57.1 cm) were conducted using the base package "stats" in R.

2.6.2 | Proportion area occupied

We estimated occupancy probability using static and dynamic occupancy models in the package Unmarked in R (v0.9–9; Kéry & Chandler, 2012). We estimated percent area occupied (PAO) for each year using a static occupancy model, which is equivalent to using a multi-year model with year-specific occupancy and detection probabilities. For the dataset from 2011 to 2018 where we monitored 100 permanent plots, we used dynamic occupancy models (MacKenzie et al., 2003) to model covariates predictive of occupancy (Ψ), detection probabilities (p), as well as localized colonization (γ) and extinction (ε) among years. For this, we first modeled Ψ using all permanent, random, and discovery plot data from all years to best inform this parameter. We then modeled γ and ε using data from the 100 permanent plots.

We compared models where p was constant or varied by each individual trapping session (t). Because small mammals may be more likely to enter a trap after a period of acclimation (e.g., Brehme & Fisher, 2009), we also included a model where p differed between the first session and all subsequent sessions (Night 1).

We compared models where Ψ, γ, and ε varied in response to site-level environmental variables. We evaluated models in which Ψ, γ, and ε were constant, varied with slope, soil compaction, disturbance (indices of military disturbance, years since last fire, fire frequency 1974–present), proximity to roads (road_prox; dirt, gravel, and paved), presence of DKR, presence of squirrel burrows, and different types and amounts of vegetative cover (shrubs, perennial grass, annual grass, forbs, open ground, and open ground+forbs). For γ and ε, we also included annual rainfall totals for rain years preceding SKR surveys (July–June; NOAA NCEI, 2021: range 9.8–57.1 cm). For all analyses, all covariates were analyzed independently or including squared terms to determine the best fit for each covariate. Models with combinations of covariates that increased the fit of the models (>2 AIC) were then compared for final model selection. Covariates that were highly correlated in the first year of sampling (Pearson's $r > 0.4$ and $p < 0.05$) were not combined to model parameters. We applied sequential-by-submodel selection, where we determined the best detection model, and then modeled state models with the best fitting detection model fixed (Morin et al., 2020). For model selection and inference, we followed the information-theoretic approach with model averaging used when top model weights were less than 95% (Burnham & Anderson, 2002).

Cumulative probabilities of detection were calculated by subtracting the product of probabilities an SKR was not detected ($1-p$) during each successive trap event from 1 through n (Equation 1).

$$\text{Cumulative } p = 1-(1-p_1)\times(1-p_2)\times\ldots\times(1-p_n) \quad (1)$$

where p = detection probability and n = trap event.

2.6.3 | Model assumptions and tests

Two critical assumptions exist for our study: (1) there is a near-perfect probability of detecting the absence of active kangaroo rat sign (i.e., the plot is "unoccupied" if no potential sign is detected) and (2) the state of occupancy (occupied vs. unoccupied) does not change between sign surveys and live-trapping. We test assumption 1 by live-trapping a subset of plots each year, where no potential sign was detected. To test assumption 2, we resurveyed plots for potential sign when setting traps. To minimize violations of assumption 2, we surveyed in the fall and

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winter, after we expected most juveniles have dispersed and reproductive activity has ceased, and by conducting burrow searches and trapping as close in time as logistically possible.

2.6.4 | Density estimation

We calculated annual density indices for SKR across years using the Huggins full closed capture models in RMark (Huggins, 1989; Laake, 2013; White & Burnham, 1999). These models allow for inclusion of heterogeneous encounter probabilities (pi) and inclusion of individual covariates to model probability of initial capture (p) and probability of recapture (c). Estimates of population size (N) are then conditioned out of the likelihood (Huggins, 1989). We tested models with and without heterogeneous encounter probabilities, where capture probability was constant, varied by year, time, night vs. morning trapping sessions, and between the first session and all subsequent sessions. To test for a positive or negative behavioral response to being trapped (i.e., "trap happy" or "trap shy"), we compared models where p and c were equal versus unequal. Open population models were not run due to low recapture rates among years. We followed the information-theoretic approach for final model selection and adjusted standard errors using the square root of the variance inflation factor $\hat{c}$ (Burnham & Anderson, 2002; White et al., 2001). Cumulative probabilities of capture were calculated in the same manner as cumulative detection probabilities (Equation 1). Density indices of SKR within occupied habitat (No. SKR/0.25 ha) were calculated using the abundance estimates divided by total number of occupied plots for each year.

3 | RESULTS

3.1 | Trends in area occupied and density between 2005 and 2018

Long-term results indicate the amount of habitat occupied by SKR ranged from a low estimate of 85 ha in 2006 to 248 ha in 2016 (Figure 2a, Table A2). The density of SKR within occupied plots ranged from 2.3 to 8.5 SKR/0.25 ha. Trends and precision in density estimates from 2005 to 2018 were slightly more variable annually (Figure 2b). Across all 13 monitoring years, mean occupancy and density within occupied habitats were positively correlated (Pearson $r = .64$, $p = .02$).

Across years, the probability of detecting SKR was lower on the first night ($p = .33$, SE = 0.03) than on subsequent morning and night checks ($p = .75$, SE = 0.01), with cumulative detection estimates of 1.0 after 2–3 trap nights, while cumulative individual capture probabilities over the survey period averaged 0.65 (0.20). The top closed capture model across all years included heterogeneity in capture probabilities within and among years, and time-specific shared capture and recapture probabilities.

3.2 | Multi-year integrated habitat occupancy models

The model that best explained spatial and temporal dynamics of SKR from 2011 to 2018 indicated more compact soils, gentle slopes (<10 degrees), and high proportions of open ground and forbs were the best predictors for SKR occupancy on MCBCP (Table A3). The odds of SKR occupying a plot increased 2.7 times (95% CI: 1.5–4.6) for every 20 lbs. per square inch (psi) increase in soil compaction and decreased 2.0 times (95% CI: 1.3–3.2) for every 5-degree increase in slope (Figure 3a,b). The relationship between SKR occupancy with open ground was nonlinear, with the highest occupancy between 40 and 80% open ground. The odds of SKR occupying a plot also increased 2.4 times (95% CI: 1.6–3.5) for every 20% increase in forb cover (Figure 3c,d). The third highest single-covariate model showed that the odds of SKR occupancy was 2.9 times (95% CI: 1.7–4.9) greater where sympatric DKR were also present across the landscape.

While 6% of plots remained occupied and 54% of plots remained unoccupied throughout the monitoring period, 40% of the monitoring plots changed state (local colonization and extinction events) during our monitoring efforts among years. Among the 100 permanent plots, SKR colonized 4–7 plots annually (mean = 5.6). SKR were more likely to colonize areas with >40% open ground and <20% shrub cover (Table A4). The odds of SKR colonizing a plot (that was unoccupied the previous year) was 2.2 times greater (95% CI: 1.6–3.0) for every 20% increase in open ground and 2.1 times lower (95% CI: 1.1–4.1) with every 20% increase in shrub cover (Figure 4a,b).

Concurrently with colonization, SKR also went locally extinct (changed from occupied to unoccupied) in 2–8 plots per year (mean = 5.6). Multiple competing models showed that SKR were more likely to become locally extinct in areas with <20% open ground, > 40% non-native grass cover, and with slopes >10 degrees (Table A5). For each 20% increase in open ground, the odds of local extinction decreased 1.5 times (95% CI: 0.9–2.5), and for every 20% increase in annual grass cover (0% vs. 20%, 20% vs. 40%, etc.), the odds of local extinction increased 3.2 times (95% CI: 1.5–6.9; Figure 4c,d).

Rainfall was negatively associated with SKR colonization from 2011 to 2018, during which rainfall varied between 13 and 33 cm per year. For every 10 cm increase

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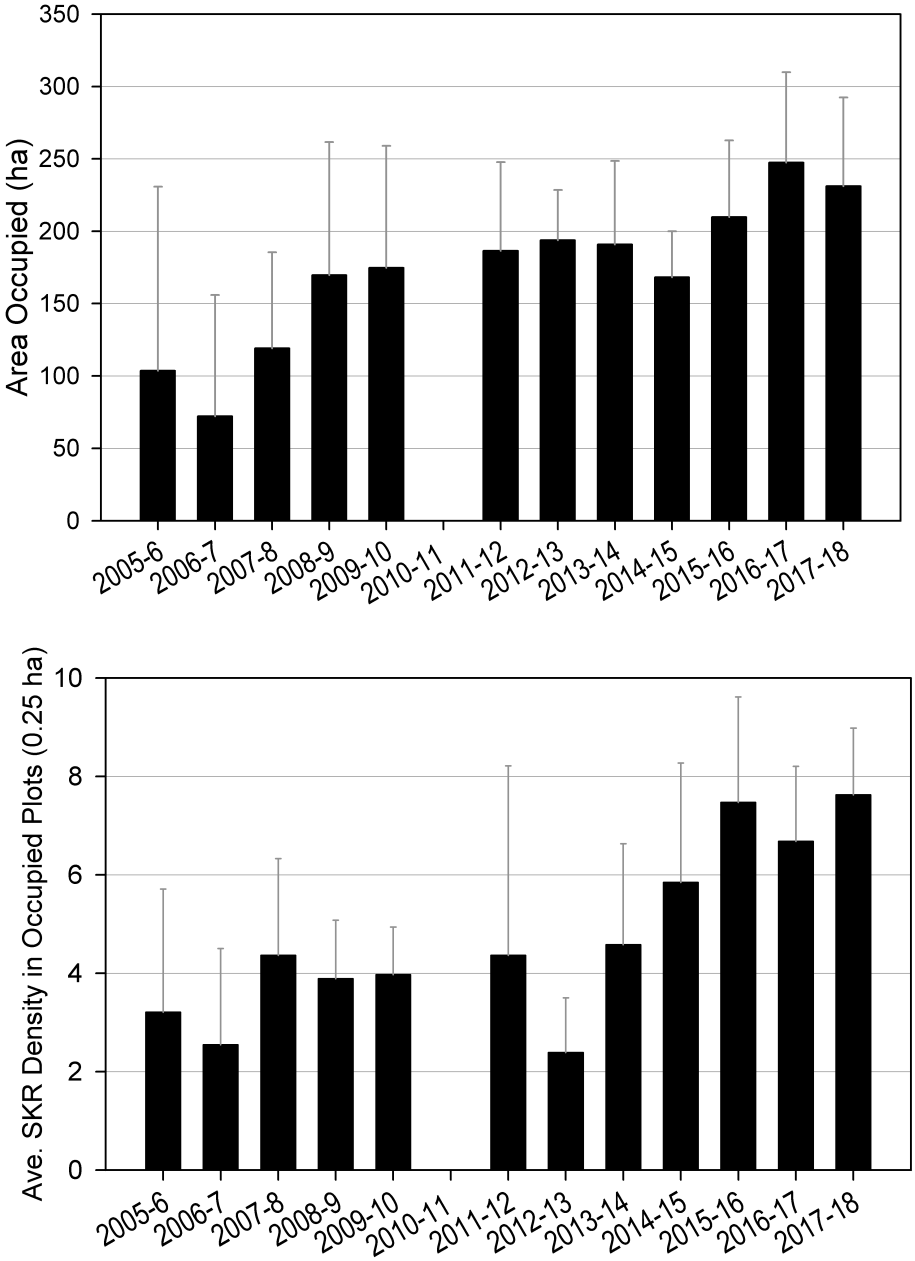


FIGURE 2 Trends in total area occupied (a) and density (b) of Stephens' kangaroo rat (*Dipodomys stephensi*) within Marine Corps Base Camp Pendleton, San Diego County, CA. monitoring area from 2005 to 2018. Error bars indicate the upper and lower 95% confidence intervals for individual year estimates.

in seasonal rainfall, the odds of colonization decreased 1.8 times (95% CI: 1.0–3.1). Rainfall was not predictive of extinction (AIC < null model); however, the coefficient was negative. Over the longer period from 2005 to 2018, there was no significant correlation between rainfall and area occupied by SKR ($r = -.04$, $p = .91$) or density of SKR within occupied habitats ($r = -.07$, $p = .83$).

3.3 | Relationship between SKR and disturbance

SKR occupancy probability was associated with low to moderately high levels of overall disturbance (Figure 5a,b). Index values from field surveys ranged from 0 to 44 (max = 53), and occupancy probability was greatest at intermediate levels of disturbance (5–30). Very low levels of disturbance (<5) and very high levels of disturbance (>30) were less suitable for SKR. Overall disturbance was most strongly correlated with the compaction disturbance index ($r = .99$, $p < .001$), with varying levels of compaction from foot traffic and vehicles being far more common among the sample plots than rut ($r = .12$, $p = .03$) and berm ($r = .08$, $p = .138$)-related disturbance.

SKR colonization was also positively associated with increased levels of overall disturbance and negatively related to increase time since fire events (Figure 5c,d). SKR were 1.8 times (95% CI: 1.2–2.7) more likely to colonize habitat for every 5 units increase in disturbance score. Similarly, colonization probability was greater in more

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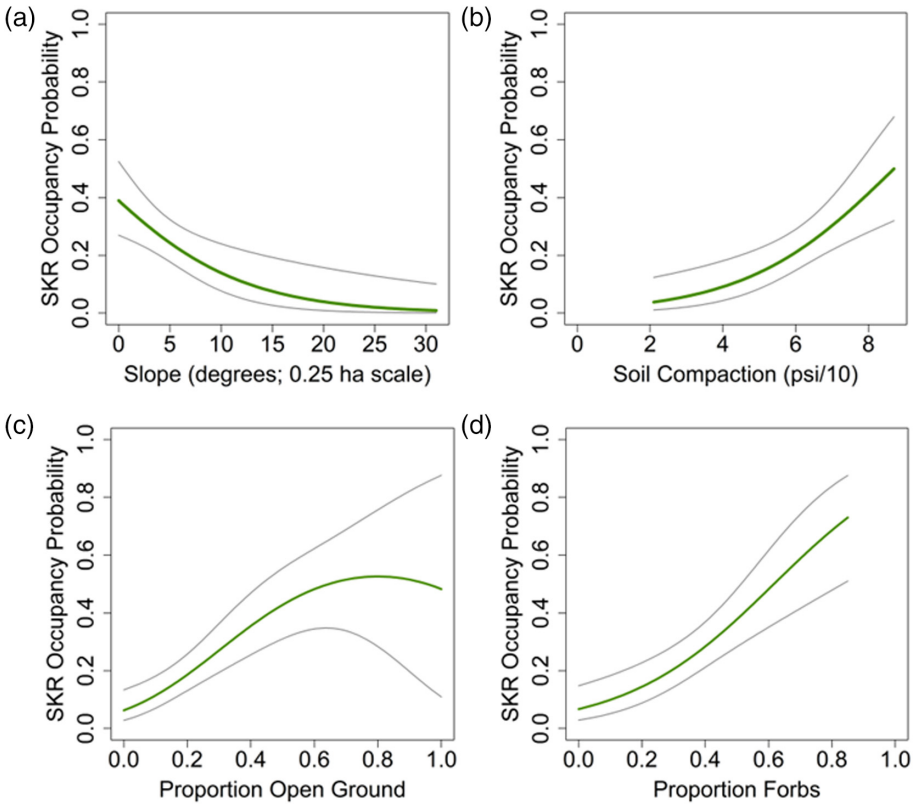


FIGURE 3 Predicted patch occupancy of Stephens' kangaroo rat (SKR; *Dipodomys stephensi*) in relation to soil compaction (a), slope (b), and open ground and forbs (c). Gray lines indicate the 95% confidence intervals.

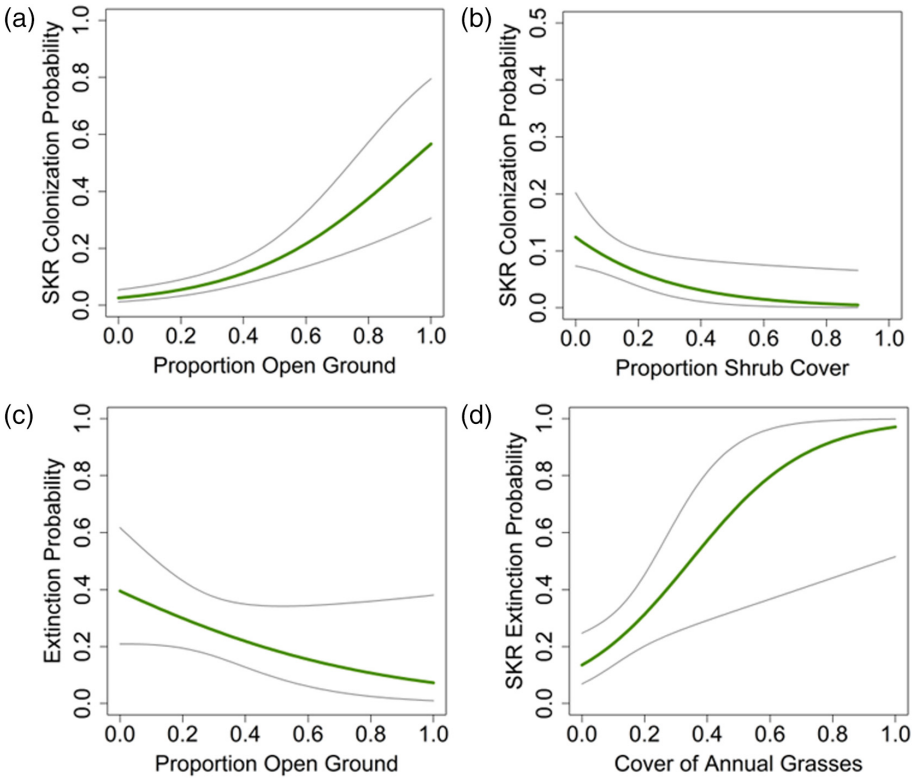


FIGURE 4 Predicted changes in Stephens' kangaroo rat (SKR; *Dipodomys stephensi*) colonization (a, b) and extinction probability (c, d) in relation to land cover on the United States Marine Corps Base Camp Pendleton, San Diego County, CA. Gray lines indicate the 95% confidence intervals.

recently burned habitat and declined 1.9 times (95% CI: 1.2–3.1) for every 10-year increase in years since last fire.

The overall military training index was positively correlated to open ground ($r = .47$, $p < .001$), dirt road proximity ($r = .42$, $p < .001$), soil compaction ($r = .19$, $p = .057$), and native bunch grass cover ($p = .003$). Number of years since last fire was positively correlated to shrub cover ($r = .32$, $p < .001$) and negatively correlated

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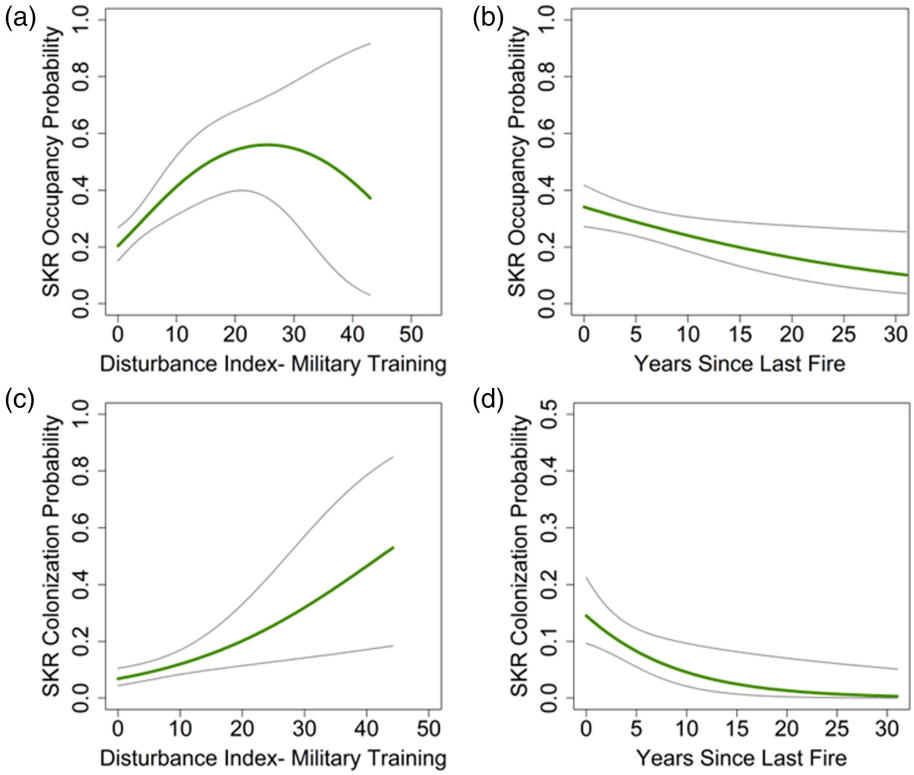


FIGURE 5 Predicted patch occupancy and colonization probability of Stephens' Kangaroo rat (*Dipodomys stephensi*) relative to overall disturbance levels and years since last fire, associated with military training on the United States Marine Corps Base Camp Pendleton, San Diego County, CA. Gray lines indicate the 95% confidence intervals. Green mean lines indicate the covariate had a positive effect on SKR populations. Red mean lines indicate the covariates had a negative effect on SKR populations.

to open ground ($r = -.23$, $p = .003$) and forb cover ($r = -.18$, $p = .094$). Finally, open ground was negatively correlated with all forms of vegetative cover, and was particularly strong with non-native grass cover ($r = -.43$, $p < .001$).

3.4 | Model assumptions

The survey method was 100% effective at detecting the absence of SKR when sites were unoccupied. Across all years, we randomly trapped 99 plots with no detected signs of SKR and failed to capture a single SKR during those surveys. All plots that had kangaroo rat sign or possible sign (burrows, tracks, and scat) after the habitat/sign survey continued to show sign or potential sign at the beginning of the trapping period. We documented no evidence of plots changing status between habitat/sign surveys and trapping.

4 | DISCUSSION

Long-term results indicate the area occupied by SKR increased almost 2-fold and SKR density within occupied habitat increased almost 3-fold from 2005 to 2018 on MCBCP. Among years, area occupied and density were positively correlated. This suggests that SKR population growth occurs by expansion into suitable habitat patches, as well as increases in numbers within occupied patches. Our results suggest that SKR are spatially and temporally dynamic, as they can move among habitat patches based upon local and heterogeneous changes in habitat suitability over relatively short time-scales. By sampling a large number of plots over a short period of time for this highly detectable species, this has been an efficient program to monitor SKR status and trends and to quantify changes in their habitat, relative densities, and distribution. Density estimates were generally more variable and less precise across years, so area occupied has been a more stable monitoring metric than density to assess long-term trends. Occupancy modeling results have enabled MCBCP to assess the responses of SKR to annual changes in habitat conditions to directly inform habitat-based management goals, responses to purposeful management actions, and unplanned disturbance for this species. This program is currently being used as a model for range-wide monitoring of this species (Spencer et al., 2021).

Our results confirm SKR are spatially dynamic and prefer low-slope open forb-dominated habitats while avoiding non-native grass and shrub habitats (Bleich, 1977; Goldingay & Price, 1997; O'Farrell & Uptain, 1989; Thomas, 1975). The models showed that open ground was a significant predictor of all parameters of SKR population dynamics (occupancy, colonization, and extinction). The greatest probability of SKR occupancy

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was in areas with between 40 and 80% open ground. SKR were more likely to colonize habitat with >40% open ground and to become locally extirpated with <20% open ground. Open habitat is thought to be important for SKR to efficiently move and forage within their habitat (Brock & Kelt, 2004a, 2004b; Genoways & Brown, 1993; Price et al., 1994), and many other local rodent species avoid open habitats, resulting in potentially less competition for seed resources (e.g., Brehme, Clark, Rochester, & Fisher, 2011; Kelt, Wilson, & Konno, 2005; Price et al., 1991). SKR occupancy was also positively associated with forb cover, a primary dietary seed source (e.g., Genoways & Brown, 1993; Lowe, 1997). Furthermore, surveys were conducted in the fall and winter months after many spring forbs had died and disarticulated, so open ground may further indirectly capture the effects of spring forb cover on SKR populations. Therefore, positive associations between SKR population dynamics and open ground and forb cover are likely driven by a combination of habitat suitability, foraging efficiency, decreased competition, and preferred seed availability.

It has been theorized that rainfall should be positively correlated to SKR population increases based on other southern California heteromyid species that are associated with shrubland habitats (*Chaetodipus fallax*, *Dipodomys simulans*; Price & Endo, 1989, Burke et al., 1991). However, we found no evidence of this relationship, as has been reported by Kelt, Konno, and Wilson (2005). Rather, rainfall was negatively associated with SKR colonization since 2011, and there was no correlation between rainfall and occupancy or density across the entire 13-year period. Although higher rainfall years may have a positive effect on SKR by increasing seed resources, our results indicate that high rainfall may also have a negative effect by increasing vegetative cover (especially by shrubs and non-native grasses), decreasing the availability of open ground, and reducing habitat suitability.

SKR were more likely to be extirpated from areas with greater than 40% non-native grass cover. In comparison with California native bunch grass (i.e., *Nasella pulchra*), non-native European grasses (i.e., *Bromus* and *Avena* spp.) tend to grow in thick stands that may impede kangaroo rat movement and foraging (USFWS, 1997). In forblands with low cover of non-native grasses (<10%), SKR may be a keystone species by maintaining open ground and forb diversity through seed predation and burrowing (Brock & Kelt, 2004b). However, there is evidence that non-native grass seeds are less nutritious and may be avoided by many small mammals, including heteromyids (Kelrick et al., 1986; Lucero & Callaway, 2018; Vandergast et al., 2023). Although SKR are known to include some non-native grasses in their diet (e.g., Lowe, 1997), a lack of preference for these seeds would suggest that SKR may not have a keystone effect in areas with abundant non-native grasses. Historically, SKR likely inhabited natural bunch grass and forbland habitats, which would have provided both open ground and seed resources most suitable for SKR (Price & Endo, 1989). However, following habitat loss and the introduction of European grasses in the mid-1800s (Barry et al., 2006; D'Antonio et al., 2007; Price & Endo, 1989), SKR have been primarily associated with non-native grasslands and forblands that contain open ground from disturbance (see Price & Endo, 1989; Thomas, 1975; USFWS, 1997).

Through the period of monitoring, SKR were also positively associated with conditions associated with habitat disturbance. Soil compaction, military disturbance index, and fire were all positive predictors of occupancy and/or colonization of newly disturbed habitats. SKR largely occur within heavily used impact areas and artillery ranges on MCBCP, where the availability of suitable open ground habitat was highly correlated to military training-associated disturbance. In the absence of disturbance, vegetative succession of dense grasses or shrubs can create habitats that are not suitable for SKR. These late-successional conditions were associated with decreased colonization and increased extinction on MCBCP and have been reported by others to lead to rapid declines in population size (O'Farrell & Uptain, 1987, 1989; Price & Endo, 1989; USFWS, 1997).

Disturbances that result in moderate levels of soil compaction may also increase seed foraging efficiency for SKR and better support their burrow structures (Brock & Kelt, 2004a). Foot traffic, vehicle traffic, and frequent fires on MCBCP serve to decrease cover of shrubs and non-native grasses and thus maintain the open ground and forb-dominated habitat. Because their burrows are sufficiently deep (23–46 cm; O'Farrell & Uptain, 1987), SKR are likely able to survive most fires and other surface disturbances and readily colonize newly disturbed habitat. Dirt roads may also facilitate SKR movement (Brock & Kelt, 2004a; O'Farrell & Uptain, 1989) and were positively associated with occupancy. However, SKR require some vegetative cover to provide dietary seed resources, so very high levels of repeated disturbance that prevent seed establishment and plant growth over large areas would likely reduce SKR habitat suitability. This was evidenced by the negative trends modeled for SKR with disturbance levels characterized as "very high" (complete loss of vegetation cover). Therefore, disturbance via military training, fire management, and vegetation management up to a level that still supports sufficient forb and native grass growth over non-native grasses and shrubs would be expected to benefit SKR.

Overall, these findings indicate that effective SKR management can be accomplished without infringing

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upon the objectives of MCBCP and that the impacts of most training operations have been largely positive in maintaining or increasing SKR habitat suitability. Outside MCBCP, prescribed fire, mowing, vegetation thinning, and grazing have been effectively used as sources of disturbance to manage SKR habitat (e.g., Kelt, Wilson, & Konno, 2005; Price et al., 1994; Shier et al., 2021; Spencer et al., 2021, Brian Shomo, 2023). Across their range, maintaining suitable habitat and connectivity within and among sub-populations is important for SKR conservation (Price & Endo, 1989; Spencer et al., 2021; USFWS, 1997). Also, regular habitat management may be particularly important for isolated populations that are not able to disperse to nearby more suitable habitats. Additional studies on SKR population dynamics, responses to habitat management, and seasonal dietary needs of SKR throughout their range could enhance understanding of this species and further inform habitat restoration techniques and goals.

5 | CONCLUSION

Results show the value of long-term occupancy and density monitoring in informing status and trends of spatially dynamic species, particularly in response to spatially dynamic habitat conditions and where densities may fluctuate greatly within and among years. Spatial occupancy monitoring programs can directly benefit land managers by creating a cost-effective monitoring and management feedback loop by revealing factors on the landscape associated with species persistence, localized colonization, and extinction, and by determining the effects of habitat management and disturbance impacts on populations of conservation concern.

AUTHOR CONTRIBUTIONS

Cheryl Brehme and Robert Fisher conceived and have implemented the monitoring design on MCBCP since 2005 (with others acknowledged). Philip Gould and Cheryl Brehme prepared the manuscript. Cheryl Brehme conducted the analyses, created figures, and revised the manuscript. Denise Clark (2010–present) and Cheryl Brehme (2005–2010) led the field project and collected and managed data (with others acknowledged). All authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data used in this analysis are available upon request from James Asmus, Upland Management Head, Environmental Security, Marine Corps Base Camp Pendleton, Box 555008, Bldg 2648, Camp Pendleton, CA 92055.

ETHICS STATEMENT

This research followed ethical standards. Field surveys and animal marking were done under U.S. Federal Permit TE-045994 and California Department of Fish and Wildlife Entity Permit #838.

PERMISSION TO REPRODUCE MATERIALS FROM OTHER SOURCES

None.

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APPENDIX A

TABLE A1 Monitoring protocol elements for Stephens' kangaroo rat (*Dipodomys stephensi*) on Marine Corps Base Camp Pendleton, California.

Protocol element	Purpose(s)	Procedure(s)	Timing
Habitat suitability model	To determine spatial extent of occupied habitat to define annual SKR monitoring area	Current knowledge of SKR habitat associations and distribution on MCBCP	2005, 2011
	To define discovery area	Use of GIS layers to map potentially suitable SKR habitat (soils, slope, vegetation, impact area boundaries)	2005, 2011
Sample allocation	Optimize sample allocation for highest power to detect changes over time and greatest coverage of known SKR habitat over time	125 plots in monitoring area (100 permanent and 25 new every year)	Yearly
	Discovery of new populations	25 plots in discovery area (new each year)	Yearly
Sampling protocol	To monitor trends in potential habitat areas occupied by SKR, estimated density within and among strata	Burrow/Sign Searches + Live-trapping in randomly chosen permanent sample plots (0.25 ha)	Yearly
Burrow/sign search and habitat characterization	To determine presence or absence of kangaroo rats	Complete survey of sample plots for any potential kangaroo rat burrows or sign	Late summer and fall (Oct–Nov), yearly
—	To collect habitat covariate data to model, better understand and predict SKR habitat relationships	Survey habitat characteristics thought to be associated with SKR presence	—
Live-trapping surveys	To confirm presence or absence of SKR. Produce metric of density. Calculate detection and capture probabilities for models	Live-trap for 2+ nights with standard 25 trap grid	Fall (Oct–Dec)
Analyses	Total area (ha) of habitat on MCBCP occupied by SKR. Probabilities of SKR occupancy within and among strata	Program Unmarked in R (occupancy): Program RMark (density index)	Yearly (all)
—	Density within and among strata		—
—	Multi-year: patch occupancy and extinction (i.e., metapop. growth rate)		
—	Model habitat and other covariates for value in predicting SKR occupancy, detection, density, colonization, and extinction		

Brehme et al. 2006, Brehme et al. 2011.

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TABLE A2 Trends in the occupancy and relative density of Stephens' kangaroo rat (*Dipodomys stephensi*) within Marine Corps Base Camp Pendleton, California, 628 ha monitoring area, from 2005 to 2018.

SKR fall/winter monitoring period	Monitoring area (ha)	Proportion area occupied (se)	Total hectares occupied (ha, se)	Density in occupied plots (SKR/0.25 ha, se)
2005–6	740	0.165 (0.076)	122.2 (56.0)	2.7 (1.0)
2006–7	740	0.115 (0.049)	85.0 (35.9)	4.5 (4.2)
2007–8	740	0.190 (0.045)	140.3 (33.8)	4.0 (1.1)
2008–9	740	0.270 (0.066)	199.9 (48.8)	4.5 (1.4)
2009–10	740	0.278 (0.061)	205.9 (45.3)	4.1 (0.9)
2010–11	Refinement of monitoring area and addition of plots			—
2011–12	628	0.297 (0.050)	186.5 (31.4)	4.1 (1.8)
2012–13	628	0.309 (0.044)	193.7 (27.7)	2.3 (0.6)
2013–14	628	0.304 (0.047)	190.9 (29.5)	4.7 (1.6)
2014–15	628	0.268 (0.042)	168.1 (26.3)	6.2 (2.1)
2015–16	628	0.334 (0.043)	209.7 (27.2)	6.8 (2.6)
2016–17	628	0.394 (0.051)	247.4 (32.0)	8.3 (2.5)
2017–18	628	0.368 (0.050)	231.1 (31.4)	8.5 (1.9)

Note: 15% of unoccupied habitat was removed from the monitoring area 2011+.

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TABLE A3 Model comparison all years: occupancy.

Model[1]	negLogLike	nPars	*n*	AIC	Delta	AICwt	
p(Night1)psi(SoilComp +Slope + OG^2 + Forbs)	989.33	10	338	1998.66	0.00	0.99	Top model
p(Night1)psi(SoilComp +OG^2 + Forbs)	994.92	9	338	2007.84	9.18	0.01	
p(Night1)psi(Slope + OG^2 + Forbs)	996.04	10	338	2012.08	13.42	0.00	
p(Night1)psi(Slope + DKR)	1004.43	7	338	2022.87	24.21	0.00	
p(Night1)psi(OG^2+ Forbs)	1003.58	8	338	2023.16	24.50	0.00	
p(Night1)psi(SoilComp+ Slope)	1005.98	7	338	2025.95	27.29	0.00	
p(Night1)psi(SoilComp+ DKR)	1006.04	7	338	2026.08	27.42	0.00	
p(Night1)psi(SoilComp+ Forbs)	1006.40	7	338	2026.79	28.13	0.00	
p(Night1)psi(Slope + OG^2)	1006.35	8	338	2028.71	30.05	0.00	
p(Night1)psi(SoilComp+ AG)	1007.54	7	338	2029.07	30.41	0.00	
p(Night1)psi(Slope + AG)	1008.75	7	338	2031.49	32.83	0.00	
p(Night1)psi(SoilComp+ OG^2)	1008.67	8	338	2033.33	34.67	0.00	
p(Night1)psi(DKR+ Forbs)	1010.77	7	338	2035.54	36.88	0.00	
p(Night1)psi(Slope + Forbs)	1011.23	7	338	2036.47	37.81	0.00	
p(Night1)psi(DKR+ OG^2)	1011.75	8	338	2039.51	40.85	0.00	
p(Night1)psi(DKR+ AG)	1012.99	7	338	2039.99	41.33	0.00	
p(Night1)psi(SoilComp10)	1014.18	6	338	2040.35	41.69	0.00	
p(Night1)psi(Slope)	1014.80	6	338	2041.60	42.94	0.00	
p(Night1)psi(AG+ Forbs)	1014.57	7	338	2043.14	44.48	0.00	
p(Night1)psi(DKR)	1017.34	6	338	2046.68	48.02	0.00	
p(Night1)psi(OG^2+ AG)	1015.48	8	338	2046.97	48.31	0.00	
p(Night1)psi(OG^2)	1017.70	7	338	2049.40	50.74	0.00	
p(Night1)psi(AG)	1018.73	6	338	2049.47	50.81	0.00	
p(Night1)psi(Forbs)	1019.02	6	338	2050.04	51.38	0.00	
p(Night1)psi(DIST^2)	1018.19	7	338	2050.38	51.72	0.00	
p(Night1)psi(Squirrel)	1019.51	6	338	2051.03	52.37	0.00	
p(Night1)psi(Paved)	1020.02	6	338	2052.04	53.38	0.00	
p(Night1)psi(Shrub)	1020.59	6	338	2053.19	54.53	0.00	
p(Night1)psi(FLATD)	1020.79	6	338	2053.59	54.93	0.00	
p(Night1)psi(Dirt)	1021.31	6	338	2054.61	55.95	0.00	
p(Night1)psi(Gravel)	1021.52	6	338	2055.04	56.38	0.00	
p(Night1)psi(RdProx)	1022.11	6	338	2056.22	57.56	0.00	
p(Night1)psi(YSLF)	1022.21	6	338	2056.43	57.77	0.00	
p(Night1)psi(PG^2)	1022.79	7	338	2059.58	60.92	0.00	
p(Night1)psi(FireInt)	1024.09	6	338	2060.19	61.53	0.00	
p(Night1)psi(.)	1025.38	5	338	2060.75	62.09	0.00	Null model
p(Night1)psi(SunIndex)	1024.98	6	338	2061.96	63.30	0.00	
p(Night1)psi(BERMT)	1025.36	6	338	2062.73	64.07	0.00	

[1]Only combinations of covariates with >2 AIC values above lower parameterized models are shown.

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TABLE A4 Model comparison all years: colonization.

Model[1]	negLogLike	nPars	n	AIC	Delta	AICwt	
p(Night1)col(OG+ Shrub)	695.06	8	91	1406.11	0.00	0.98	Top model
p(Night1)col(OG)	701.31	6	91	1414.62	8.51	0.01	
p(Night1)col(YSLF + Shrub)	701.53	7	91	1417.06	10.95	0.00	
p(Night1)col(Shrub)	706.57	6	91	1425.14	19.03	0.00	
p(Night1)col(YSLF)	706.99	6	91	1425.98	19.87	0.00	
p(Night1)col(Soil)	710.70	6	91	1433.41	27.30	0.00	
p(Night1)col(Paved)	711.41	6	91	1434.82	28.71	0.00	
p(Night1)col(Rain)	711.72	6	91	1435.44	29.32	0.00	
p(Night1)col(AG)	712.00	6	91	1436.00	29.89	0.00	
p(Night1)col(DIST)	712.12	6	91	1436.23	30.12	0.00	
p(Night1)col(FlatD)	712.26	6	91	1436.52	30.40	0.00	
p(Night1)col(BermT)	713.04	6	91	1438.07	31.96	0.00	
p(Night1)col(.)	714.10	5	91	1438.20	32.09	0.00	Null model
p(Night1)col(FireInt)	713.19	6	91	1438.38	32.27	0.00	
p(Night1)col(Slope)	713.62	6	91	1439.23	33.12	0.00	
p(Night1)col(RdProx)	713.65	6	91	1439.29	33.18	0.00	
p(Night1)col(Forbs)	713.75	6	91	1439.51	33.39	0.00	
p(Night1)col(RutD)	713.78	6	91	1439.57	33.46	0.00	
p(Night1)col(Gravel)	713.94	6	91	1439.89	33.78	0.00	
p(Night1)col(SunIndex)	714.10	6	91	1440.20	34.08	0.00	
p(Night1)col(PG)	714.10	6	91	1440.20	34.09	0.00	
p(Night1)col(Dirt)	714.10	6	91	1440.20	34.09	0.00	

[1]Only combinations of covariates with >2 AIC values above lower parameterized models are shown.

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TABLE A5 Model comparison all years: extinction.

Model[1]	negLogLike	nPars	*n*	AIC	Delta	AICwt	
p(Night1)ext(OpenGrd+ AG)	705.04	7	91	1424.09	0.00	0.42	Top model
p(Night1)ext(AG + Slope_10)	705.41	7	91	1424.83	0.74	0.29	Top model
p(Night1)ext(AG)	706.47	6	91	1424.93	0.84	0.28	Top model
p(Night1)ext(OG)	710.12	6	91	1432.25	8.16	0.01	
p(Night1)ext(RdProx)	710.97	6	91	1433.95	9.86	0.00	
p(Night1)ext(Dirt)	711.40	6	91	1434.80	10.71	0.00	
p(Night1)ext(Slope)	712.39	6	91	1436.77	12.68	0.00	
p(Night1)ext(SoilComp)	712.46	6	91	1436.92	12.83	0.00	
p(Night1)ext(.)	714.10	5	91	1438.20	14.11	0.00	
p(Night1)ext(PG)	713.40	6	91	1438.80	14.71	0.00	Null model
p(Night1)ext(Forbs)	713.61	6	91	1439.22	15.13	0.00	
p(Night1)ext(FlatD)	713.74	6	91	1439.49	15.40	0.00	
p(Night1)ext(Shrub)	713.80	6	91	1439.60	15.51	0.00	
p(Night1)ext(DIST)	713.80	6	91	1439.61	15.52	0.00	
p(Night1)ext(YSLF)	713.81	6	91	1439.63	15.54	0.00	
p(Night1)ext(Gravel)	713.83	6	91	1439.67	15.58	0.00	
p(Night1)ext(RutD)	713.85	6	91	1439.71	15.62	0.00	
p(Night1)ext(FireInt)	713.92	6	91	1439.84	15.75	0.00	
p(Night1)ext(Paved)	713.95	6	91	1439.91	15.82	0.00	
p(Night1)ext(Rain)	829.33	5	91	1668.65	244.56	0.00	
p(Night1)ext(OG+ AG)	705.04	7	91	1424.09	0.00	0.42	
p(Night1)ext(AG + Slope)	705.41	7	91	1424.83	0.74	0.29	

[1]Only combinations of covariates with >2 AIC values above lower parameterized models are shown.

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