



Interactions among rainfall, fire, forbs and non-native grasses predict occupancy dynamics for the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) in a Mediterranean-type ecosystem

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ABSTRACT

It is important to understand species-habitat relationships to implement effective adaptive management for rare species. However, it can be challenging to assess habitat associations and their relationships to abiotic stressors in dynamic habitats without the insights that can be gained from long-term monitoring. We report results from the first six years of extensive track tube monitoring of the largest two of three remaining extant populations of federally endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) in a coastal Mediterranean-type ecosystem on Marine Corps Base, Camp Pendleton in southern California, USA. We used dynamic occupancy and structural equation modeling to assess potential drivers of population trends that included habitat, fire history, rainfall, disturbance, and the presence of other small mammals. We found that the variables that best predicted mouse occupancy were moderate to high forb and perennial herb cover (40–80%), and moderate to high open ground (20–70%) and low non-native grass cover (<20%). Non-native grass cover (>20%) was also a strong predictor of lower PPM colonization and increased extinction probabilities, with the extent of non-native grass cover being strongly influenced by annual rainfall and recency of fire. Our study adds to the growing literature on effects of invasive annual grasses on native species in Mediterranean-type ecosystems. We suggest that habitat management could be based upon promotion of open forb and perennial herb dominated habitats with reduction of non-native grasses by prescribed fire and other methods. These types of spatial and temporal monitoring programs can support land managers by creating a monitoring and management feedback loop. They can reveal landscape and environmental variables associated with species persistence, inform habitat management goals, and help managers to assess the success of management actions on populations of conservation concern.

1. Introduction

Mediterranean-type ecosystems (MTE) are global biodiversity hotspots (Myers et al., 2000). These ecosystems are characterized by a mild climate and by increasing human density that has contributed to extensive habitat loss (Underwood et al., 2009). MTEs are also

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expected to be especially vulnerable to declines in species diversity from predicted climate changes from drought and increasing temperatures (Maiorano et al., 2011, Newbold et al., 2020). Despite this, there is a relatively small proportion of MTE protected habitats remaining (Hoekstra et al., 2005). For vulnerable species in MTEs, research can help to identify key habitats and inform efforts to protect and manage areas that support these species.

It can be challenging to assess habitat associations in MTEs because of multiple disturbances and abiotic stressors that influence habitat dynamics over space and time (Cox et al., 2014; Esler et al., 2018). In coastal southern California, one of the five Mediterranean biomes, several threatened and endangered species depend on dwindling coastal sage scrub habitats (Bolger et al., 1997; Conlisk et al., 2015; Tracey et al., 2018). Here, as in other MTEs, interactions between exotic species, rainfall and fire can influence vegetation characteristics and successional trajectories (Esler et al., 2018; Thomson et al., 2020). For example, wildfire results in loss of shrub cover in coastal sage scrub (Talluto and Suding, 2008; Keeley and Brennan, 2012), which may also lead to increased non-native grass cover (Fleming et al., 2009). However, recent wildfire can also reduce non-native grasses and promote growth of annual forb cover (Thomson et al., 2020). Prolonged drought can also reduce non-native grass cover, while drought-breaking rainfall can dramatically increase non-native grass cover (Diffendorfer et al., 2007; Puritty et al., 2019). Southern California is predicted to have increased fire danger, intensity of droughts and overall greater variability of rainfall (Swain et al., 2018; Dong et al., 2022), which may exacerbate vegetation changes and complicate conservation for endangered and endemic species that depend on these habitats.

One such species is the federally endangered Pacific pocket mouse (*Perognathus longimembris pacificus*; hereafter PPM), one of the smallest rodents of North America, weighing just 6–9 g (Reid, 2006). This solitary, nocturnal, burrow-dwelling rodent historically was patchily distributed along ~200 km of coastline in southern California, but habitat destruction and fragmentation from urban development and agriculture greatly reduced the number of populations (USFWS, 2020). After destruction of the last known population in 1972, PPM were assumed to be possibly extinct (Williams, 1986). However, two decades later they were incidentally rediscovered at a historic location at Dana Point with just a few dozen individuals at the time (USFWS, 1994). Three additional population sites were soon found on Marine Corps Base Camp Pendleton (MCBCP) in San Diego County, southern California, the smallest of which was presumed extirpated in the early 2000's (USFWS, 2020). The Dana Point and two MCBCP locations comprise the three currently known extant populations of this subspecies (USFWS, 2020). Ongoing recovery actions include efforts to establish additional populations and addressing information gaps such as how PPM are distributed across the landscape to identify suitable habitat for conservation and inform habitat management efforts for this species (USFWS, 2020).

PPM were initially live trapped on one to four fixed study grids on MCBCP where large fluctuations in density within and among years were documented (Miller and Pavelka, 2008). Generally low individual PPM capture probabilities make detection of large scale demographic trends in populations difficult and time intensive with the traditional method of live-trapping (Miller and Pavelka, 2008). Track tubes are an effective alternative to traditional live-trapping and are a noninvasive and cost-effective method to continuously monitor a large area without need for bi-nightly checks (Glennon et al., 2002, Loggins et al., 2010, Brehme et al., 2019). We monitored the two largest extant PPM populations using track tubes from 2012 to 2017 as part of a larger multifaceted long-term monitoring and research project at MCBCP to support decision making and habitat management for PPM (Brehme et al., 2011; 2018). This approach enabled us to track trends in the area occupied by PPM within MCBCP and to identify predictors of PPM occupancy, as well as localized colonization and extinction within and across populations (MacKenzie et al., 2018). To do so, we created a dynamic occupancy model to investigate potential drivers of population trends including habitat, fire history, climate, disturbance, and interactions with other small mammals. Next, we took the results of the occupancy model and created a piecewise structural equation model (SEM; Lefcheck, 2016). The SEM allowed us to conduct a confirmatory path analysis to further clarify the roles of fire and drought on vegetation cover that are important to PPM occupancy. We demonstrate how these two methods combined allow greater insight and additional support for the potential benefits of habitat management.

2. Methods

2.1. Study Sites

Study sites are within the Marine Corps Base Camp Pendleton (MCBCP), which is located in California roughly halfway between the cities of San Diego and Los Angeles. MCBCP is approximately 500 km² and is the largest of the last remaining expanses of undeveloped coastal areas in the region; as such it harbors several species at risk including PPM (INRMP, 2018). The topography is characterized by a narrow, sandy shoreline, seaside cliffs, coastal plains, low hills, canyons, and mountains that rise to elevations of approximately 823 m (INRMP, 2018). Habitats within the MCBCP include oak woodlands, coastal sage scrub, native and non-native grasslands, coastal dunes, riparian forest/woodland/scrub, and wetlands. The climate is semi-arid with an average of 26.3 cm of rainfall per year. Rainfall primarily falls between November–March but can be highly variable among years. Within the time frame of this study, rainfall varied between 12.9 and 33.0 cm, with lower than average rainfall from 2012 to 2015 and higher than average rainfall in 2016–2017 (Weather Underground, 2018).

MCBCP harbors the two largest of the three extant populations of PPM, the third lying to the north in Dana Point (12 ha). Within the Base, the populations are 1) Santa Margarita (885 ha), which is split into 2 subpopulations for analysis due to large variations in habitat and management: Oscar One (411 ha; hereby referred to as Oscar) and Edson (474 ha), and 2) South San Mateo (105 ha) approximately 20 km north of Santa Margarita (Fig. 1). All population sites are characterized as coastal sage scrub (CSS) habitats. However, Oscar contains patchy areas of sandy soils, sandy loam, and some clay soils. This area is largely dominated by non-native grasslands and open CSS, but also contains mature scrub in areas. Edson is largely open coastal sage scrub forland with some areas of dense non-native grasses. This site is dominated by more compact loamy sand and sandy clay loam soils and has a historically frequent fire regime

from both prescribed burns and wildfires. MCBCP conducted prescribed burns over half of Edson approximately every 3 years through 2011 and wildfires occurred in 2012 and 2014 across other portions of the site. The habitat in South San Mateo is largely open to closed CSS with abundant *Opuntia* and Cholla cacti. Soil here is dominated by sand and sandy loam.

2.2. Study Species

The Pacific pocket mouse (PPM) is one of several currently recognized subspecies of the little pocket mouse in the heteromyid rodent family (Williams et al., 1993). PPM have been historically found on southern California marine terraces and alluvial plains within 4 km of the coast. They have been typically associated with open patches of sandy soils within coastal sage scrub communities (von Bloeker, 1931), although vegetation characteristics, such as shrub and grass cover, vary considerably. Their diet is comprised primarily of small seeds from a diverse palette of annual forbs and perennial herbs (*Acmispon glaber*, *Calystegia* spp., *Centaurea melitensis*, *Corethrogyne filaginifolia*, *Croton californicus*, *Dienandra* sp., *Erodium* sp., *Gnaphalium* sp., *Heterotheca grandiflora*, *Phacelia* sp., *Pluchea sericea*, others) and seeds of some shrubs (*Artemisia californica*, *Eriogonum fasciculatum*) and grasses (*Avena* sp., *Bromus* sp., and *Stipa* sp.) (Meserve, 1976b; Germano, 1997; Iwanowicz et al., 2016; Vandergast et al., 2023). PPM obtain both metabolic water and energy from seeds and are highly efficient at minimizing evaporative water loss (French, 1993). PPM go into variable amounts of facultative torpor during the winter and in response to low resource conditions. Above ground activity is thought to coincide with seed availability, which may extend from March through September, but is most dependable in late April, May, and June (Meserve, 1976a; Shier, 2009; Brehme et al., 2014).

2.3. Field methods

An annual monitoring program was developed with input from small mammal biologists, PPM experts and statisticians (Brehme et al., 2011). From 2012–2017, we monitored 34 permanent spatially balanced and probabilistically chosen 1 ha grids across the three PPM population sites (9 in Oscar, 9 in Edson, and 15 in South San Mateo; Fig. 1) using specialized track tubes (Brehme et al., 2014; 2018). Track tubes are used to passively identify small animals by their footprints or “tracks” (Glennon et al. 2002; Loggins et al. 2010; Brehme et al., 2019). As small animals enter the tubes, presumably attracted to bait inside, they step onto an inked felt pad and leave their tracks on stationary paper inside the tube. PPM tracks are easily distinguished from other sympatric rodent species by both size and shape (Matsuda and Brehme, 2019). In each grid, two sizes of tracking tubes were used, 2.5 cm and 3.8 cm in diameter, both approximately 38 cm in length and placed in alternating rows. Although the 3.8 cm tube was originally shown to have greater probability of detecting PPM, the 2.5 cm tube excludes most other mice and may thus be better at detecting PPM in areas with high

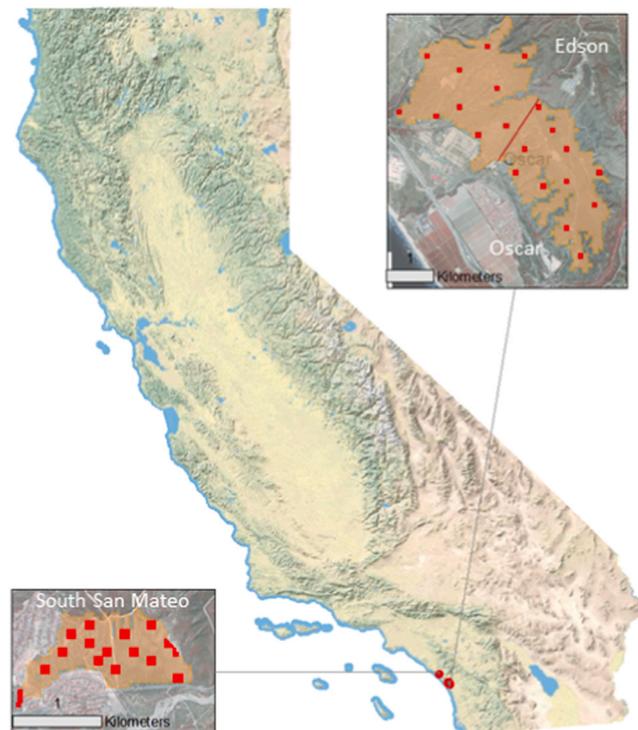


Fig. 1. Locations of PPM populations in California, USA. Insets show south San Mateo (lower left) and Santa Margarita (Oscar and Edson; upper right) population areas (orange) with permanent 1 ha sampling grids (red). Grey bars represent 1 km.

densities of other rodent species (Brehme et al., 2019). Thus, the combination of sizes was expected to offer the greatest ability to detect PPM when present.

A total of 64 tracking tubes were placed within each grid with one tracking tube in each 0.0156 ha (12.5 m x 12.5 m) subplot (Brehme et al., 2011). The size of the subplots is roughly equivalent to the core home range of PPM, ascertained by telemetry (Shier, 2009), to provide the closest relationship between occupancy and abundance and analysis at this scale provides conservative estimates for use in making regulatory and management decisions. Tubes were placed at the center of the plot near open sandy patches and/or small PPM sized burrows, if present. Prior to placement, each tube was rinsed with the local substrate several times to impart a natural scent shown to maximize PPM capture success (Brehme et al., 2019). Track tubes were baited with approximately a tablespoon of millet seed bait that was adhered to the center of the tracking paper with a small amount (< 100 uL) of non-toxic starch glue. This served to attach the first layer of bait to the tracking surface and allowed the tube to remain an effective attractant for a period of time, even if other mice or ants remove the loose seeds on top. Tracking tubes were checked every 2 weeks a total of eight times from March/April through July/August to coincide with the most reliable period of PPM activity prior to torpor. All tracking tubes were re-set, re-baited and re-inked as necessary. All tracking papers were evaluated for the presence of tracks from PPM, California pocket mice (*Chaetodipus californicus*), deer mice (*Peromyscus* spp.), and harvest mice (*Reithrodontomys megalotis*) (Matsuda and Brehme, 2019).

In addition to surveying for PPM, habitat was surveyed every year during spring/early summer at each subplot to provide covariates for habitat modeling (Table A1). All habitat characteristics measured were hypothesized to be potentially important for PPM habitat suitability. They include measures of topography, soil, vegetation cover, and types of disturbance. Each spring, visual estimates of percent cover for vegetation (non-native grass, bare ground, forbs, native bunch grass, shrub/tree, woody debris/leaf litter) were recorded for each subplot. As a visual standard, computer generated percent cover cards were used as a reference in the field. Cover cards show representations of different percentages of cover (5%, 10%, 15%, 25%, 50%, and 75%) in three different configurations (scattered, partially scattered, clumped; Clark et al., 2014). To ensure consistency among observers, biologists worked together the first several days each year, and then the first subplot each subsequent day in the field. Habitat data were not collected at one grid in Edson in 2014, prior to a wildfire event. For this we used cover values from the previous year. Biologists also recorded the presence/absence of different types of disturbance (foot and vehicular traffic, military training), as well as roads, trails and infrastructure. An index variable to represent all types of disturbance in the subplot was calculated by combining the types of disturbances present (Table A1). Slope, aspect, and fire history (years since last fire and the number of fires in the previous 30 years) were calculated with GIS data provided by MCBCP. When no fire had occurred for at least 30 years or more, 30 was used as the maximum value. Proportions of sand and clay in the soil at each grid were determined by texture analysis of soil samples by the Brigham Young University Environmental Analytical Lab. Finally, total rainfall was calculated from the nearest weather station located in the MCBCP for each water year (October-September; KNFG).

2.4. Data analysis

Occupancy within and among all PPM populations and years from 2012 to 2017 was modeled at the subplot scale (0.016 ha) using the hierarchical logistic modeling program package *unmarked* (v. 0.9–9; Fiske and Chandler, 2011) in R (v4.1.3; R Core Team, 2021). The models enable the parameters [occupancy (ψ), detection probability (ρ), colonization (γ), extinction (ϵ)] to be estimated as a function of covariates. Occupancy is the probability PPM are present on a plot in the first year of monitoring. Colonization is the probability that plots become newly occupied by PPM after being unoccupied the previous year, while extinction is the probability that plots become unoccupied after being occupied by PPM the previous year. Finally, detection is the probability of detecting PPM on a single visit if present on a plot (e.g., MacKenzie et al., 2018).

A large number of potential correlates to PPM occupancy, colonization, and extinction (habitat and landscape variables, disturbance, other mice species, and disturbance) and probability of detection (presence of other mice, tube size) were evaluated (Table A1). The final candidate model set was created in a symmetrical secondary candidate set strategy with an information-theoretic approach (Burnham and Anderson 2002; Morin et al., 2020). First, individual covariates were screened for collinearity using the *psych* program in R (Revelle, 2016; Table A2), so as not to include covariates with strong correlations of $|r| > 0.5$ in the same model. We felt this step was important to avoid common issues with non-identifiability and unstable estimates which we have observed at these higher correlation levels (e.g., Dormann et al., 2013, Zuur and Ieno, 2016), although there are differing opinions on this issue (e.g., Achen 1982, Morrissey and Ruxton, 2018). To test between linear and quadratic relationships with model parameters (ψ , γ , ϵ), individual covariates with and without their squared terms were screened for best fit and to check for model convergence, with either the individual or individual plus squared term for each covariate advancing to the next submodel stage. Submodel sets for each parameter were created by comparing all individual covariates, as specified, and additive combinations of the top most predictive covariates (as correlations allowed using our criteria). Year and site were also not combined with landscape and environmental covariates that may better explain temporal or spatial variation in occupancy. Covariate interaction models of clay*rainfall and sand*rainfall for γ and ϵ were also specifically included according to a priori hypotheses that represented the potential effects of soil moisture retention on PPM extinction. As described by Morin et al. (2020), all models within 10 Δ AIC units of the top model for each parameter submodel dataset were then advanced into the final global candidate model set. Nagelkerke's R squared was computed in the program package *unmarked* to further evaluate the goodness fit of the final top models (Nagelkerke, 1991; Fiske and Chandler, 2011).

As a complementary analysis at the larger spatial scale of the grid (1.0 ha), we conducted a confirmatory path analysis with the R package '*piecewiseSEM*' to evaluate drivers (rainfall and fire) of habitat cover that in turn were hypothesized to influence PPM occupancy at the grid level (Lefcheck, 2016). To do so, we calculated the proportion of track tubes with PPM tracks within each 1 ha grid

for each year to represent the proportion area occupied by PPM. We did not use predicted occupancy for this analysis because the cumulative probability of detection is high (>0.94) after 8 sampling sessions per year (see Results), and the errors would not have been propagated. We also computed a mean of each covariate for all subplots within each grid for each year and included annual total rainfall. The a priori path model included 1) the mean years since last fire (YSLF) and annual rainfall predicts the log transformed mean percent cover of non-native grass, open ground, and forbs for each grid, and 2) the non-native grass, open ground, forbs as well as an interaction between non-native grass and YSLF influence the logit transformed proportion of track tubes with PPM tracks for each grid. All component models were fit with 'nlme' and included grid ID as a random effect (Pinheiro et al., 2022). The relationships among

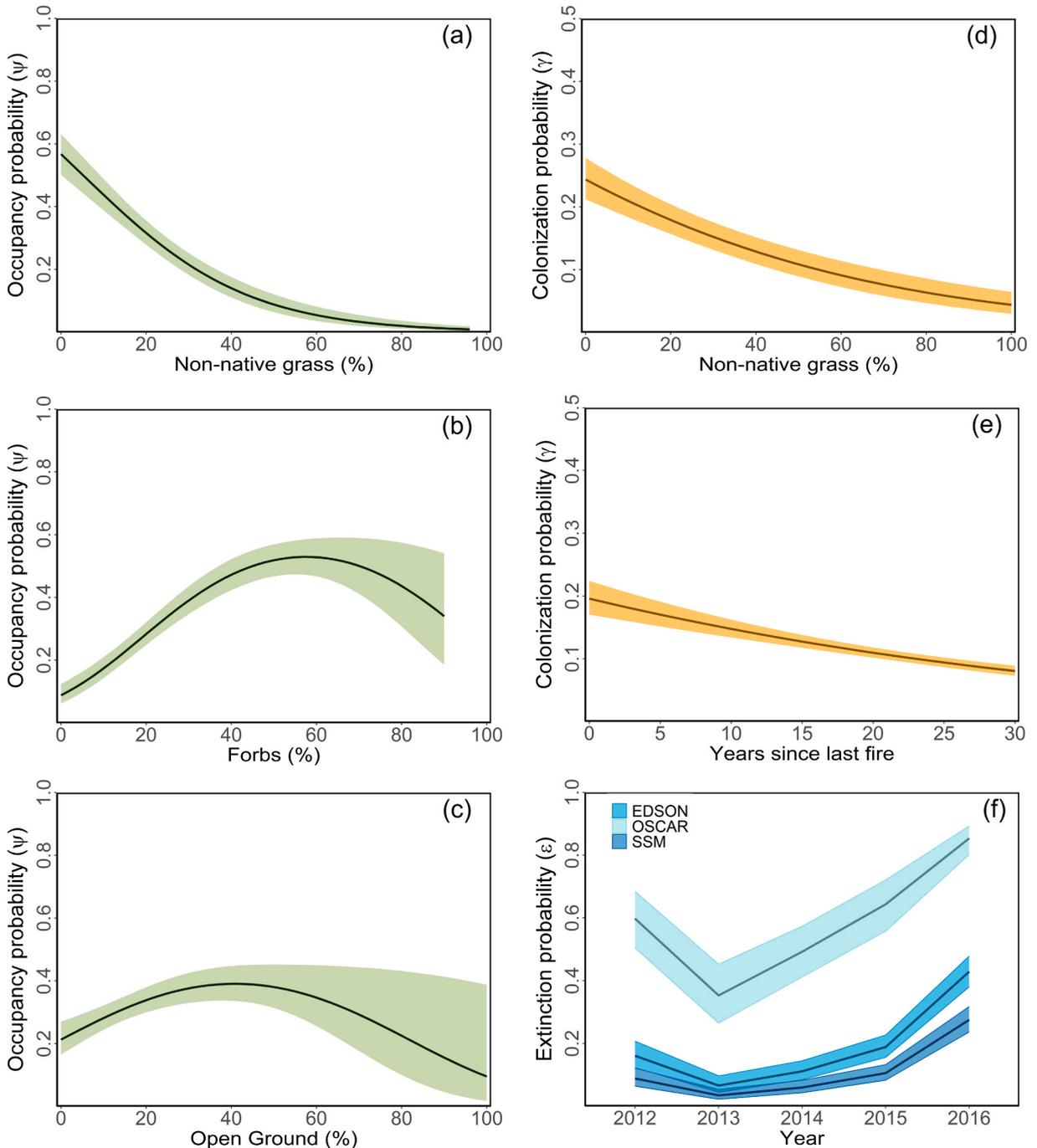


Fig. 2. Top predictors of PPM occupancy, colonization, and extinction across sites: Probability of PPM occupancy versus (a) non-native grass cover, (b) forb cover, and (c) open ground (green), probability of PPM colonization versus (d) non-native grass cover and (e) years since last fire (orange), and probability of PPM extinction by (f) site and year (blue).

non-native grass, forbs, and open ground cover were all modeled as correlated errors. The D-sep test was evaluated for non-significance ($p > 0.05$), which indicates whether the overall model was a good fit (Lefcheck, 2016). Standardized beta coefficients were used to compare effect sizes and directions for each path, and any non-significant pathways were retained.

3. Results

Overall, PPM occupancy varied substantially among population sites and years (Table A3, Figure A1). PPM occupancy averaged highest in Edson (mean 41% [$\pm 12\%$ SD]), compared to Oscar (8.6% [$\pm 4.5\%$ SD]) and South San Mateo (30% [$\pm 9\%$ SD]). Each site also had different trends over time and peaked in different years. PPM increased in Edson from 27.5% (SE=1.7%=640) in 2012 to a peak of 59.4% (SE=2.0%) in 2016, before declining dramatically to 30.6% (SE=1.8%) in 2017. In nearby Oscar, PPM increased from 9.6% (SE=1.3%) in 2012 to a peak of 16.5% in 2014 (SE=1.6%), and thereafter declined in the last three years with a low of only 2.4% (SE=0.6%) in 2016 and 5.4%(SE=0.9%) in 2017. In South San Mateo, PPM increased from 19.2% (SE=1.3%) in 2012 and peaked at 41.7% (SE=1.6%) in 2016, with a nonsignificant decline in 2017–39.1% (SE=1.5%).

The final candidate model set consisted of only two models, of which the highest ranking model had 100% of the weight and was the only model within 10 ΔAIC (Tables A4, A5; Nagelkerke $R^2 = 0.63$). In the top model, the probability of detecting PPM was influenced by track tube size and the presence of other rodents. During a single 2-week session, PPM had a lower probability of being detected in the narrower tubes (2.5 cm diameter; $p = 0.42$ (95% CI 0.41–0.43) than the larger tubes (3.8 cm diameter; $p = 0.54$ (95% CI 0.53–0.55)). Also, PPM detection probability averaged 0.58 (95% CI 0.57–0.59) when no other rodents were detected and 0.29 (95% CI 0.28–0.31) when other rodents were detected. However, over the course of 8 sessions, our cumulative probability of detecting PPM if present was 1.00 (95% CI 0.999–1.000) if no other rodents were present and 0.94 (95% CI 0.93–0.95) if other rodent species were detected in all sessions.

Across all population sites, variables that best predicted PPM occupancy were low non-native grass cover (<20%), moderate to high forb and perennial herb cover (40–80%), and moderate to high open ground (20–70%; Tables A4, A6b; Fig. 2a-c). Non-native grass cover was also a strong predictor of decreased colonization and increased extinction across sites (Table A6c&d, Fig. 2). With every 20% increase in non-native grass cover, the odds that PPM would colonize an unoccupied site decreased by 1.6 times (95% CI: 1.5–1.7) and the odds that PPM would be lost from a previously occupied site increased by 1.7 times (95% CI: 1.5–1.8). Therefore, the odds that PPM colonized a site with 100% non-native grass cover, was 10.9 times less likely (95% CI: 6.8–17.5) than a site with no non-native grass. Similarly, the odds that PPM would be extirpated from a site with 100% non-native grass cover, was 39.4 times more likely (95% CI: 19.2–80.9) than a site with no non-native grass. In addition to non-native grasses, colonization was negatively related to the number of years since the last fire (YSLF), which meant that colonization by PPM was more likely to occur the more recently an area had burned (Fig. 2e, Tables A4, A6c). Localized extinction was best predicted by site and year with the highest levels of extinction in the low

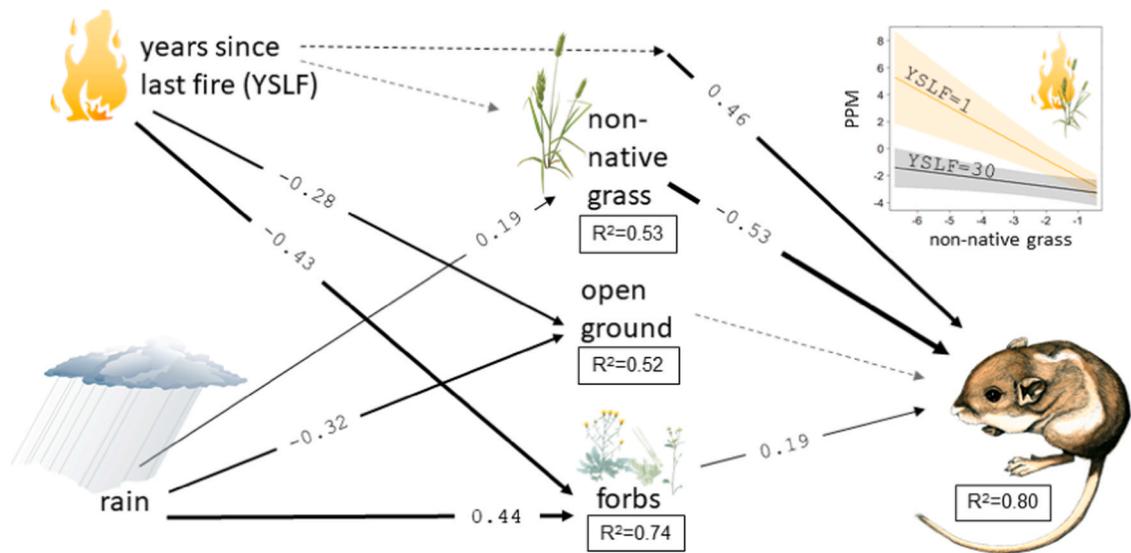


Fig. 3. Path model showing relationships between rainfall and the years since the last fire (YSLF) on three habitat variables that predict PPM occupancy. Arrow size is scaled to the magnitude of standardized coefficients and dashed arrows represent pathways that were non-significant. Coefficients for fire are negative, meaning that the cover of open ground and forbs decreases as the years since the last fire increases. The conditional pseudo R² for each is displayed in the boxes, which is the level of variance explained by both fixed and random effects. For clarity, correlated errors between non-native grass, open ground, and forbs are not displayed but these and other model summary details such as the raw coefficients and marginal pseudo R² values are included in Supplemental Table A10. Inset figure depicts the interaction between years since the last fire (YSLF) and the log transformed non-native grass cover on the logit transformed proportion of PPM in track tube grids, which is higher at low non-native grass cover when YSLF was more recent. PPM artwork by Tristan Edgarian. Other artwork is sourced from the Integration and Application Network (ian.umces.edu/media-library).

occupancy Oscar population (Fig. 2f).

Because site was the top predictor for basewide PPM extinction, we ran site specific models with the full set of habitat, landscape and competitor covariates for this parameter (Tables A7-A9). For Edson, fire was the top predictor of localized extinction, the only site with a substantial burn history in the past 25 years. PPM were predicted to have a very high probability of extinction if the habitat had not burned within 6–7 years, and were more likely to go extinct in areas with high levels of disturbance (Table A7, Figure A2a&b). It should be noted that although non-native grasses and frequent fire history were associated with a majority of the survey plots in Edson, the disturbance index was high in only a small proportion of plots and averaged only 0.06–0.12 among years (range 0–5) with only 1.5–4.1% of plots scoring at a value of 2 or greater. In nearby Oscar, year was the best predictor of extinction (Table A8, Figure A2c). Here, occupancy remained below 0.17 for all 6 years, which was likely too low to reliably estimate extinction dynamics (MacKenzie et al., 2018). Lastly, within the South San Mateo population, models indicated local extinction at this site was greater following higher rainfall, when forb cover was low (<25%) and in sites with high activity of grassland associated harvest mice (*R. megalotis*) (Table A9, Figure A2 d-f).

Finally, the results of the piecewise SEM suggested that the model was a good fit to the data (Fig. 3; Fisher's $C=2.76$, $df=4$, $p = 0.59$). The pathway from rainfall to both forb cover and non-native grass cover was positive (standardized $\beta = 0.43$, $p < 0.001$, standardized $\beta = 0.19$, $p < 0.001$, respectively), and was negative to open ground (standardized $\beta = -0.32$, $p < 0.001$). The number of years since last fire (YSLF) was negatively associated with forbs (standardized $\beta = -0.43$, $p < 0.001$), and with open ground (standardized $\beta = -0.28$, $p = 0.008$), while also weakly and non-significantly negatively associated with non-native grass (standardized $\beta = -0.07$, $p = 0.56$). This means that the more recently a fire has occurred, the greater the forb cover and open ground, with varying effects on non-native grass cover. The proportion of area occupied by PPM was positively associated with forb cover and weakly positively associated with open ground (standardized $\beta = 0.19$, $p < 0.001$, standardized $\beta = 0.08$, $p = 0.11$, respectively), but was much more strongly negatively impacted by non-native grass cover (standardized $\beta = -0.53$, $p < 0.001$). The interaction between non-native grass cover and years since last fire was also significant (standardized $\beta = 0.46$, $p < 0.001$), indicating that recent fire modifies the negative effect of non-native grass on PPM, and PPM are more likely to occur when recent fire results in reducing non-native grass cover (Fig. 3). Model summary details such as the raw coefficients and marginal pseudo R^2 values are included in Supplemental Table A10.

4. Discussion

Our results showed that track tube monitoring was effective in documenting status and trends within and among PPM populations on MCBCP. The use of track tubes also minimized the stress to PPM and habitat impacts from frequent visits required by live-trapping. The occupancy modeling framework provided insight into the habitat variables that may be important drivers of PPM occupancy, colonization and extinction in a dynamic Mediterranean-type ecosystem, and the results directly inform habitat management and restoration.

The top model indicated that PPM were more likely to occupy sites with medium to high levels of forb cover (40–80%) and open ground (20–70%), and less likely to occupy areas with moderate to high (generally >30%) cover of non-native grasses. PPM associations with forb cover and open ground can be explained by their life history. PPM have been shown to strongly select for diverse forb and perennial herb seeds in their diet (Meserve, 1976b; Iwanowicz, 2016; Vandergast et al., 2023). PPM and other heteromyid rodents also require open ground for high seed foraging efficiency and to use for dust bathing to remove ectoparasites, absorb oil, and communicate with conspecifics (Randall 1993).

Prior to the mid-1800's in California, grassland, forbland, and sage scrub habitats were largely open habitats dominated by native bunch grass and forbs (D'Antonio et al., 2007). Native perennial bunch grasses evolved deep root structures with space between individual plants to endure periods of drought that are typical in this Mediterranean ecosystem (Jackson et al., 1988). In the mid-1800's, European annual grasses invaded and dominated many of these habitats largely due to intensified agriculture and possibly livestock grazing (D'Antonio et al., 2007; Barry et al., 2006). These annual grasses have shallow root structures, germinate quickly after rainfall events, and grow in large contiguous stands (Parker and Schimel, 2010). Once invasion occurs, non-native grasses serve to further enrich nitrogen in soils which favors their continued growth and perpetuation over that of native bunch grasses and forbs species (Gillespie and Allen, 2004; Parker and Schimel, 2010).

From 2012–2017, non-native grasses encompassed approximately 5–40% of total habitat among PPM population sites in MCBCP (Figure A3). Non-native grass cover was a strong negative predictor of PPM occupancy and colonization across all sites, a positive predictor of localized extinction, and was strongly negatively associated with PPM in the piecewise SEM. Although small amounts of non-native grasses may be a seed resource for PPM in areas with less forb cover (Meserve, 1976a, 1976b; Brehme et al., 2014), concurrent resource selection studies across MCBCP in 2016–17 indicate that non-native grass seed makes up only a trace amount of their diet (Vandergast et al., 2023). Seeds from non-native *Bromus* grasses have also been reported to be less nutritious and avoided by other small mammal species (Kelrick et al. 1986; Lucero and Calloway 2018). Additionally, thick contiguous stands of non-native grasses and thatch likely hinder PPM movement and foraging success (Rieder et al., 2010). Therefore, non-native grass management and the promotion of an open forb dominated landscape is supported across all PPM habitats.

Although annual rainfall was generally not a strong direct predictor of PPM occupancy dynamics across populations during this study, increased rainfall was associated with a greater probability of extinction in South San Mateo. Also, timing, frequency, and amount of rainfall can have substantial impacts on soil moisture, vegetation cover, and seed availability that may directly impact PPM. From 2012 through 2016 during a prolonged 5-year drought, the proportion area occupied by PPM within the MCBCP steadily increased by 78% (190–336 ha). Drought may benefit PPM habitat by reducing shallow rooted non-native grasses (Holmes and Rice,

1996), increasing native forb seed banks (LaForgia et al., 2018), and reducing competition from less drought resilient competitors, such as harvest mice (Chock et al., 2018; Prugh et al., 2018). In 2017, the first monitoring year with above average rainfall, we documented a loss of over 1/3 of the PPM population in a single year. While high rainfall may result in increased seed resources, high rainfall may negatively impact PPM by reducing open ground to unsuitably low levels needed for them to forage, by spoiling seed caches, or by negatively affecting the ability of PPM to retain body heat during their winter torpor (Valone et al., 1995). The piecewise SEM supported the link between higher rainfall in increasing forb and non-native grass cover, while reducing open ground (Fig. 3). It has been reported that soils lower in nitrogen and clay content may be more resilient to extreme increases in non-native grass and other vegetation cover in high rainfall years (Siemann et al., 2007; Bansal et al., 2013). Although soil texture or soil texture-rainfall interactions have not been a strong predictor of PPM occupancy dynamics in the sandy loam soils present on MCBCP, further studies on effects of soil properties, chemical composition, and soil horizons on PPM habitat and population dynamics are warranted.

Fire immediately clears vegetation and thatch, removes substantial quantities of nitrogen in the soil by volatilization and disproportionately reduces non-native grass seeds in the soil seed bank (Thomson et al., 2020). Thus, it serves to create open ground, reduce non-native grasses, and promote the growth of forbs and native bunch grasses (Cox and Allen, 2008; Valliere et al., 2020; Thomson et al., 2020). Both the occupancy and piecewise SEM models supported the relationship of recent fire with reduced non-native grass cover, increased open ground and forb cover, and PPM population expansion. In Edson, the only site with a substantial fire history, PPM were closely tied with the burn history, expanding and colonizing habitat after fire. PPM were much more likely to occupy and colonize sites that had recently burned while having more than 6 years since last fire was a strong predictor of local extinction across years. In addition to a regular prescribed burn history up through 2011, wildfires in 2012 and 2014 resulted in further PPM expansion at this site. Forbs are present in the highest densities and diversity in the first several years after fire (O'Leary and Westman, 1988; Thomson et al., 2020) and regular prescribed burns can be effective in restoring and maintaining native grassland and forbland habitats (Gillespie and Allen, 2004; Stromberg et al., 2007; Carlsen et al., 2017). These results support the positive role of fire in maintaining suitable open forb dominated habitat for PPM, as well as other open habitat specialists in grassland and coastal sage scrub habitats (Brehme et al., 2011; Litt and Steidl, 2011).

In response to these findings, MCBCP has enacted habitat management within these population sites in the form of prescribed burning and vegetation management to create more open forb dominated habitat within large areas of their population sites that do not conflict with military training. They have also supported creation of new suitable receiver sites for potential introduction of new populations on MCBCP. Continued monitoring and use of these modeling techniques will allow for assessment of these actions for long-term management of PPM and its habitat. Our results directly inform continued management of the habitat for species persistence and the selection of habitats suitable for reintroduction of PPM, both on and off MCBCP lands, to increase the number of extant populations in southern California for recovery of this critically endangered subspecies (USFWS, 2020, Chock et al., 2022). Finally, these findings may also inform the management of other open forb and native grassland specialist species in Mediterranean ecosystems.

5. Conclusions

Occupancy and SEM modeling of the two largest extant populations of the federally endangered PPM monitored using passive track tubes both indicate that their distribution, area occupied, and multi-year dynamics are positively associated with open ground, forbs (including perennial herbs), and recent fire, but negatively associated with non-native grasses. We suggest that management for PPM habitat could be based upon enhancement of forb growth and open ground and reduction of cover of non-native grasses. Non-native grasslands can be managed by controlled burning, herbicides, grazing, and addition of carbon (Stromberg et al., 2007; Parker and Schimel, 2010), but they likely require continued effort to maintain low levels of non-native grass (Cox and Allen, 2011; Carlsen et al., 2017). Re-establishment of native forbs may require seeding (Seabloom et al., 2003); however, studies are currently being conducted to understand the relative importance of native and non-native forb species in affecting PPM distribution, abundance and reproductive success.

Our results also show the value of long-term occupancy monitoring in informing status and trends of spatially and temporally dynamic species. Factors that affect PPM populations include those that cannot be controlled (e.g., climate, plant phenology, density dependence, natural predators) and those that can be controlled (e.g., habitat quality, vegetation cover and structure, important plant species). These long-term programs can directly benefit land managers by revealing factors that can be managed on the landscape associated with species distribution, persistence, expansion and contraction. Finally, these programs provide a feedback loop between monitoring and management to assess habitat management actions and disturbance on populations of conservation concern.

Authorship

CSB and RNF conceived the ideas and designed methodology; DAT and CSB collected the data; CSB and SKT analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02640](https://doi.org/10.1016/j.gecco.2023.e02640).

References

- Barry, S., Larson, S., George, M., 2006. California native grasslands: a historical perspective a guide for developing realistic restoration objectives. *J. Environ. Manag.* 91 (12), 2404–2423.
- Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Potenza, P., McCalvin, C., Tran, D., Mazzoni, S., Soule, M.E., 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecol. Appl.* 7 (2), 552–563.
- Brehme, C.S., Clark, D.R., Rochester, C.J., Fisher, R.N., 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. *Fire Ecol.* 7 (2), 81–98.
- Brehme, C.S., Adsit-Morris, D.T., Edgarian, T.K., and Fisher, R.N. 2018. Marine Corps Base, Camp Pendleton Pacific Pocket Mouse Monitoring Results and Trend Analysis for 2017. Prepared for Environmental Security Department, Marine Corps Base, Camp Pendleton. 71p.
- Brehme, C.S., Sebes, J., Matsuda, T., Clark, D., Fisher, R.N., 2014. MCBCP Pacific Pocket Mouse Monitoring Results for 2013 and Multi-year Trend Analysis from 2012 to 2013. Prepared for AC/S Environmental Security, Marine Corps Base, Camp Pendleton, p. 69.
- Brehme, C.S., Matsuda, T.A., Adsit-Morris, D.T., Clark, D.R., Sebes, J.B., Burlaza, M.A.T., Fisher, R.N., 2019. Track tube construction and field protocol for small mammal surveys with emphasis on the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*). *US Geol. Surv. Tech. Methods* 2A 15.
- Brehme, C.S., J.A. Tracey, and R.N. Fisher in collaboration with Burnham, K., Meserve, P., Spencer, D., Deutschman, W., Miller, and M. Pavelka 2011. Pacific Pocket Mouse Monitoring Protocol for Marine Corps Base Camp Pendleton. Prepared for Wildlife Management Branch, AC/S Environmental Security, Marine Corps Base, Camp Pendleton. 52pp.
- Carlsen, T.M., Espeland, E.K., Paterson, L.E., MacQueen, D.H., 2017. Optimal prescribed burn frequency to manage foundation California perennial grass species and enhance native flora. *Biodivers. Conserv.* 26 (11), 2627–2656.
- Chock, R.Y., Shier, D.M., Grether, G.F., 2018. Body size, not phylogenetic relationship or residency, drives interspecific dominance in a little pocket mouse community. *Anim. Behav.* 137, 197–204.
- Chock, R.Y., Miller, W.B., King, S.N., Brehme, C.S., Fisher, R.N., Sin, H., Wilcox, P., Terp, J., Tremor, S., Major, M.R., Merrill, K., 2022. Quantitative SWOT analysis: a structured and collaborative approach to reintroduction site selection for the endangered Pacific pocket mouse. *J. Nat. Conserv.*, 126268
- Clark, D.R., Burlaza, M.A., Brehme, C.S., 2014. Pacific Pocket Mouse Habitat Protocol. *U. S. Geol. Surv.* 34pp.
- Conlisk, E., Syphard, A.D., Franklin, J., Regan, H.M., 2015. Predicting the impact of fire on a vulnerable multi-species community using a dynamic vegetation model. *Ecol. Model.* 301, 27–39.
- R. Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>. R version 4.1.3 (2022-03-10).
- Cox, R.D., Allen, E.B., 2008. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecol.* 198 (1), 37–46.
- Cox, R.D., Allen, E.B., 2011. The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland. *Plant Ecol.* 212 (10), 1699–1707.
- Cox, R.D., Preston, K.L., Johnson, R.F., Minnich, R.A., Allen, E.B., 2014. Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA. *Glob. Ecol. Conserv.* 2, 190–203.
- D'Antonio, C.M., Malstrom, C., Reynolds, S.A., Gerlach, J., 2007. Ecology of invasive non-native species in California grassland. In: Stromberg, M.R., Corbin, J.D., Antonio, C.M. (Eds.), *California grasslands: ecology and management*. Univ of California Press.
- Diffendorfer, J.E., Fleming, G.M., Duggan, J.M., Chapman, R.E., Rahn, M.E., Mitrovich, M.J., 2007. Developing terrestrial, multi-taxon indices of biological integrity: An example from coastal sage scrub. *Biol. Conserv.* 140, 130–141.
- Dong, C., Williams, A.P., Abatzoglou, J.T., Lin, K., Okin, G.S., Gillespie, T.W., Long, D., Lin, Y.H., Hall, A., MacDonald, G.M., 2022. The season for large fires in Southern California is projected to lengthen in a changing climate. *Commun. Earth Environ.* 3 (1), 22.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1), 27–46.
- Esler, K.J., Jacobsen, A.L., Pratt, R.B., 2018. *The biology of Mediterranean-type ecosystems*. Oxford University Press.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23.

- Fleming, G.M., Diffendorfer, J.E., Zedler, P.H., 2009. The relative importance of disturbance and exotic-plant abundance in California coastal sage scrub. *Ecol. Appl.* 19 (8), 2210–2227.
- French, A.R., 1993. Physiological ecology of the Heteromyidae: economics of energy and water utilization. In: Genoways, H.H., Brown, J.H. (Eds.), *Biology of the Heteromyidae*, The American Society of Mammalogists, pp. 509–538.
- Germano, D.J. 1997. Distribution and habitat affinities of the Pacific pocket mouse. Draft final report for California Department of Fish and Game, contract no. FG5129WM.
- Gillespie, I.G., Allen, E.B., 2004. Fire and competition in a southern California grassland: impacts on the rare forb *Erodium macrophyllum*. *J. Appl. Ecol.* 41, 643–652.
- Glennon, M.J., Porter, W.F., Demers, C.L., 2002. An alternative field technique for estimating diversity of small-mammal populations. *J. Mammal.* 83 (3), 734–742.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.* 8 (1), 23–29.
- Holmes, T.H., Rice, K.J., 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Ann. Bot.* 78 (2), 233–243.
- [INRMP] Joint Integrated Natural Resources Management Plan for Marine Corps Base and Marine Corps Air Station Camp Pendleton, California, 2018. Prepared for: U.S. Marine Corps Base and U.S. Marine Corps Air Station Camp Pendleton, California. 791 pp.
- Iwanowicz, D.D., Vandergast, A.G., Cornman, R.S., Adams, C.R., Kohn, J.R., Fisher, R.N., Brehme, C.S., 2016. Metabarcoding of Fecal Samples to Determine Herbivore Diets: A Case Study of the Endangered Pacific Pocket Mouse. *PLoS One* 11 (11), e0165366.
- Jackson, L.E., Strauss, R.B., Firestone, M.K., Bartolome, J.W., 1988. Plant and soil N dynamics in California annual grassland. *Plant Soil* 110, 9–17.
- Keeley, J.E., Brennan, T.J., 2012. Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia* 169, 1043–1052.
- LaForgia, M.L., Spasojevic, M.J., Case, E.J., Latimer, A.M., Harrison, S.P., 2018. Seed banks of native forbs, but not exotic grasses, increase during extreme drought. *Ecology* 99 (4), 896–903.
- Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7 (5), 573–579.
- Litt, A.R., Steidl, R.J., 2011. Interactive effects of fire and nonnative plants on small mammals in Grasslands: effets interactifs du Feu et des Plantes Non Indigènes sur les Petits Mammifères dans les Prairies. *Wildl. Monogr.* 176 (1), 1–31.
- Loggins, R.E., Gore, J.A., Brown, L.L., Slaby, L.A., Leone, E.H., 2010. A modified track tube for detecting beach mice. *J. Wildl. Manag.* 74 (5), 1154–1159.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2018. Burlington, Massachusetts, USA. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.
- Maiorano, L., Faluccci, A., Zimmermann, N.E., Psomas, A., Pottier, J., Baisero, D., Rondinini, C., Guisan, A., Boitani, L., 2011. The future of terrestrial mammals in the Mediterranean basin under climate change. *Philos. Trans. R. Soc. B: Biol. Sci.* 366 (1578), 2681–2692.
- Matsuda, T.A., and Brehme, C.S. 2019. Guide To The Identification Of Pacific Pocket Mouse Tracks And Other Common Mice In Marine Corps Base, Camp Pendleton, North Coast San Diego County. Appendix 1 In Track tube construction and field protocol for small mammal surveys with emphasis on the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*): U.S. Geological Survey Techniques and Methods, book 2, chap. A15, 18 p., plus appendix, <https://doi.org/10.3133/tm2A15>.
- Meserve, P.L., 1976a. Habitat and resource utilization by rodents of a California coastal sage scrub community. *J. Anim. Ecol.* 46 647–666.
- Meserve, P.L., 1976b. Food relationships of rodent fauna in a California coastal sage scrub community. *J. Mammal.* 57, 300–372.
- Miller, W.B. and M. Pavelka. 2008. Monitoring of the Pacific pocket mouse (*Perognathus longimembris pacificus*) population in the Oscar One training area on Marine Corps Base, Camp Pendleton 2003–2006. Draft Report. Prepared for Wildlife Management Branch, AC/S Environmental Security, Marine Corps Base Camp Pendleton.
- Morin, D.J., Yackulic, C.B., Diffendorfer, J.E., Lesmeister, D.B., Nielsen, C.K., Reid, J., Schaub, E.M., 2020. Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere* 11 (1), e02997.
- Morrissey, M.B., Ruxton, G.D., 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. *Philos., Theory, Pract. Biol.* 10.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772), 853–858.
- Nagelkerke, N.J., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78 (3), 691–692.
- Newbold, T., Oppenheimer, P., Etard, A., Williams, J.J., 2020. Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nat. Ecol. Evol.* 4 (12), 1630–1638.
- O’Leary, J.F., Westman, W.E., 1988. Regional disturbance effects on herb succession patterns in coastal sage scrub. *J. Biogeogr.* 15, 775–786.
- Parker, S.S., Schimel, J.P., 2010. Invasive grasses increase nitrogen availability in California grassland soils. *Invasive Plant Sci. Manag.* 3 (1), 40–47.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Core Team, R., 2022. nlme: linear and nonlinear mixed effects models. R. Package Version 3, 1–155.
- Prugh, L.R., Deguines, N., Grinath, J.B., Suding, K.N., Bean, W.T., Stafford, R., Brashares, J.S., 2018. Ecological winners and losers of extreme drought in California. *Nat. Clim. Change* 8 (9), 819–824.
- Purity, C.E., Esch, E.H., Castro, S.P., et al., 2019. Drought in Southern California coastal sage scrub reduces herbaceous biomass of exotic species more than native species, but exotic growth recovers quickly when drought ends. *Plant Ecol.* 220, 151–169.
- Reid, F., 2006. Peterson field guide to mammals of North America. Houghton Mifflin Harcourt.
- Revelle, W. 2016. psych: Procedures for Personality and Psychological Research, Northwestern University, Evanston, Illinois, USA, Version 2.1.9.
- Rieder, J.P., Newbold, T.A.S., Ostoja, S.M., 2010. Structural changes in vegetation coincident with annual grass invasion negatively impacts sprint velocity of small vertebrates. *Biol. Invasions* 12 (8), 2429–2439.
- Seabloom, E.W., Borer, E.T., Boucher, V.L., Burton, R.S., Cottingham, K.L., Goldwasser, L., Gram, W.K., Kendall, B.E., Micheli, F., 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecol. Appl.* 13 (3), 575–592.
- Shier, D. 2009 Behavioral ecology and translocation of the endangered Pacific little pocket mouse (*Perognathus longimembris pacificus*). Interagency Agreement between U.S. Fish and Wildlife Service and CRES, Zoological Society of San Diego.
- Siemann, E., Rogers, W.E., Grace, J.B., 2007. Effects of nutrient loading and extreme rainfall events on coastal tallgrass prairies: invasion intensity, vegetation responses, and carbon and nitrogen distribution. *Glob. Change Biol.* 13 (10), 2184–2192.
- Stromberg, M.R., J.D. Corbin, C.M. D’Antonio 2007. California Grasslands: Ecology and Management. University of California Press. 407p.
- Swain, D.L., Langenbrunner, B., Neelin, J.D., Hall, A., 2018. Increasing precipitation volatility in twenty-first-century California. *Nat. Clim. Change* 8 (5), 427–433.
- Talluto, M.V., Suding, K.N., 2008. Historical change in coastal sage scrub in southern California in relation to fire frequency and air pollution. *Landsc. Ecol.* 23, 2008.
- Thomson, D.M., Bonapart, A.D., King, R.A., Schultz, E.L., Startin, C.R., 2020. Long-term monitoring of a highly invaded annual grassland community through drought, before and after an unintentional fire. *J. Veg. Sci.* 31 (2), 307–318.
- Tracey, J.A., Rochester, C.J., Hathaway, S.A., Preston, K.L., Syphard, A.D., Vandergast, A.G., Diffendorfer, J.E., Franklin, J., MacKenzie, J.B., Oberbauer, T.A., Tremor, S., Winchell, C.S., Fisher, R.N., 2018. Prioritizing conserved areas threatened by wildfire and fragmentation for monitoring and management. *PLoS ONE* 13 (9), e0200203.
- U.S. Fish and Wildlife Service (USFWS), 1994. Endangered and Threatened Wildlife and Plants: Determination of Endangered Status for the Pacific Pocket Mouse. In: Federal Register, pp. 49752–49764.
- U.S. Fish and Wildlife Service (USFWS), 2020. Pacific Pocket Mouse (*Perognathus longimembris pacificus*) 5-Year Review: Summary and Evaluation. Report by U.S. Fish and Wildlife Service Carlsbad Fish and Wildlife Office, Carlsbad, California.
- U.S. Fish Wildlife Service (USFWS) Recovery Plan for the Pacific Pocket Mouse 1998 Portland, OR 112pp.
- Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the Mediterranean biome. *Divers. Distrib.* 15 (2), 188–197.
- Valliere, J.M., Bucciarelli, G.M., Bytnerowicz, A., Fenn, M.E., Irvine, I.C., Johnson, R.F., Allen, E.B., 2020. Declines in native forb richness of an imperiled plant community across an anthropogenic nitrogen deposition gradient. *Ecosphere* 11 (2), e03032.
- Valone, T.J., Brown, J.H., Jacobi, C.L., 1995. Catastrophic decline of a desert rodent, *Dipodomys spectabilis*: insights from a long-term study. *J. Mammal.* 76 (2), 428–436.

- Vandergast, A.G., Brehme, C.S., Iwanowicz, D., Cornman, R.S., Adsit-Morris, D., Fisher, R.N., 2023. Fecal metabarcoding of the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) reveals a diverse and for rich diet that reflects local habitat availability. *Ecol. Evol.* 13 (9), e10460.
- von Bloeker, J.C., 1931. *Perognathus pacificus* from the type locality. *J. Mammal.* 12 (4), 369–372.
- Weather Underground, 2018. Monthly weather history. Ocean. Muni Station 2023. [https://www.wunderground.com/history/monthly/us/ca/oceanside/KOKB/date/\[year-month\]](https://www.wunderground.com/history/monthly/us/ca/oceanside/KOKB/date/[year-month]).
- Williams, D.F., 1986. California department of fish and game, wildlife Mgt. Admin. Report. *Mamm. Species Spec. Concern Calif.* 112, 86-1.
- Williams, D.F., H.H. Genoways, and J.K. Braun. 1993. Taxonomy. pp. 38–196. In: H.H. Genoways and J.H. Brown (eds.), *Biology of the Heteromyidae*. Special Publication, The American Society of Mammalogists.
- Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.* 7, 636–645. <https://doi.org/10.1111/2041-210X.12577>.