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Los Angeles

Assessing the influence of interference competition between threatened heteromyid species

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Janine Nicole Straughan

2025

ABSTRACT OF THE DISSERTATION

Assessing the influence of interference competition between threatened heteromyid species

by

Janine Nicole Straughan
Doctor of Philosophy in Biology
University of California, Los Angeles, 2025
Professor Gregory F. Grether, Co-Chair
Professor Debra Marie Shier, Co-Chair

Interspecific competition plays a critical role in shaping species' space use and long-term persistence, making it an essential consideration in conservation planning. Dominant competitors can exclude subordinate species from preferred habitats and limit access to vital resources, potentially exacerbating extinction risk. Here, I explore the behavioral mechanisms and conservation implications of competition between threatened heteromyid species. In Chapter 1, in collaboration with the San Diego Zoo Wildlife Alliance, I evaluated whether providing conservation-bred, endangered Pacific pocket mice (*Perognathus longimembris pacificus*) experience with a dominant heterospecific competitor prior to translocation could enhance post-release success. *P.l. pacificus* is the smallest, most behaviorally subordinate, member of its native rodent community, competing both directly and indirectly for seeds. Competitor-experienced female mice had greater post-release weight gain, higher survival, and improved reproductive success relative to controls, demonstrating that exposure to ecologically relevant competitors can be a powerful, underutilized tool for improving translocation outcomes for subordinate species. In Chapters 2 and 3, I examined whether competition between two sympatric and ecologically similar kangaroo rats, Stephens' (*Dipodomys stephensi*) and the Dulzura kangaroo rat (*D. simulans*), drives their spatial segregation into different microhabitats. Field-based dyadic interactions revealed that *D. stephensi* is behaviorally dominant over *D. simulans*, and resident individuals have a higher probability of winning contests over intruders. To assess whether these behavioral dynamics translate into competitive displacement, I quantified spatial and temporal overlap in the wild. The two species had little spatial overlap and were strongly negatively correlated even after controlling for differences in habitat use, indicating that microhabitat segregation is likely driven by *D. stephensi* displacing *D. simulans*. As habitat loss continues to compress available space, *D. simulans* may become increasingly restricted to smaller, lower-quality habitat patches. These results highlight the importance of incorporating species interactions into translocation plans to avoid creating conditions for competitive displacement. Conserving habitat heterogeneity could support resource partitioning between these species and promote long-term coexistence. Collectively, my chapters demonstrate how interspecific competition can drive shifts in habitat use, influence translocation success, and reduce the persistence of at-risk species, underscoring the importance of explicitly considering interspecific competition when designing conservation strategies.

The dissertation of Janine Nicole Straughan is approved.

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2025

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PRESENTATIONS

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CHAPTER 1:

PRE-RELEASE EXPERIENCE WITH A HETEROSPECIFIC COMPETITOR INCREASES FITNESS OF A TRANSLOCATED ENDANGERED SPECIES

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Pre-release experience with a heterospecific competitor increases fitness of a translocated endangered species

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ABSTRACT

Translocation is a key conservation strategy, with breeding programs increasingly providing animals for release. Despite its growing use, translocation efforts frequently encounter limited success, particularly when captive-born animals are involved. Ex-situ environments may lack cues needed to develop survival behaviors, such as predator avoidance, foraging, and social skills. Although practitioners typically address the lack of predator avoidance through training or predator removal, competitor naivety remains largely overlooked, despite its potential to hinder population establishment by compromising access to resources. We examined the impact of pre-release competitor experience on the Pacific pocket mouse (*Perognathus longimembris pacificus*), one of southern California's most critically endangered mammals. The Pacific pocket mouse is the smallest, and most behaviorally subordinate species in a community of native rodents that compete for resources. We conducted a controlled experiment to test if providing captive-born mice pre-release experience with kangaroo rats (*Dipodomys simulans*) would improve translocation outcomes. We compared fitness and body condition of pocket mice between the two treatments and examined if behavioral change was exhibited before release. Competitor-experienced females gained more weight and had higher survival and reproductive success than controls, with female survival surpassing that of males in both groups. These findings suggest that incorporating competitor experience into conservation breeding programs could improve translocation success. As competition is a common challenge in natural ecosystems, this behavioral intervention could be applicable for a wide range of species.

1. Introduction

Conservation of species at-risk of extinction increasingly relies on translocation, the deliberate movement of animals between locations for conservation purposes (IUCN, 2013), to support their recovery (Seddon et al., 2014), with human-managed conservation breeding programs playing an expanding role in providing animals for translocation into the wild (Conde et al., 2011; Dawson et al., 2016). Despite the growing popularity of translocation, a significant proportion of these efforts are unsuccessful (Beck et al., 1994; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Morris et al., 2021; Wolf et al., 1998).

Early evaluations indicated that individuals born and raised in captivity are less likely to survive following translocation compared to wild-caught animals (Beck et al., 1994; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Maynard et al., 1995; Miller et al., 1994). Ineffective behavior of captive-born animals (poor survival skills) has long been thought to explain translocation failure (Kleiman, 1989). Scientists as far back as Darwin have recognized that captivity can radically alter animal behavior (Carlstead, 1996; Darwin, 1868; Lickliter and Ness, 1990; McPhee, 2003; Price, 1984). Captive environments tend to be predictable and unchanging, often lacking critical environmental cues (Rabin, 2003; Yoerg and Shier, 1997) or relevant challenges (Greggor et al., 2024). This can result in captive-born individuals failing to develop effective behavioral skills for survival following relocation. Consequently, skills associated with fitness, such as antipredator behavior, foraging ability, locomotion, and social behavior, including breeding and nesting and refuge use, may be suboptimal in animals reared under human care (Rabin, 2003).

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Antipredator training —conditioning animals to respond effectively to predators— has proven to be a successful method for addressing prey naivety in diverse taxa (Greggor et al., 2021; Greggor et al., 2019; Griffin et al., 2000; Moehrenschlager and Lloyd, 2016; Rowell et al., 2020; Shier, 2016; Shier and Owings, 2006, 2007; Tetzlaff et al., 2019). Such training may benefit from the use of live predators (Edwards et al., 2021; Rowell et al., 2020), as they are presumed to provide a particularly salient stimulus (Blumstein et al., 2019; Moseby et al., 2016; Shier, 2016; but see Rowell et al., 2020). Pre-release social integration has also been shown to improve social cohesion, site fidelity, and post-release survival (Greggor and Goldenberg, 2023; Shier, 2006; Shier and Swaisgood, 2012; Somers and Gusset, 2009). The increased implementation of pre-release behavioral interventions may help explain why animals' origin (i.e., captivity or wild) was not among the top predictors of survival in a recent meta-analysis (Morris et al., 2021). Nevertheless, the same review found that translocations of wild-caught animals resulted in substantially higher population growth rates than those of captive-bred animals (Morris et al., 2021), indicating that ex-situ protocols could be improved further. One type of behavioral intervention that is underexplored is improving how animals respond to interspecific competitors.

Interspecific competition comes in two mechanistically distinct forms (Pfennig and Pfennig, 2012). Exploitative competition occurs when two or more species deplete a shared, limiting resource (e.g., food, shelter), while interference competition involves costly interactions between individuals over access to a resource (e.g., aggression, dominance). Interference competition can be mitigated by changes in activity patterns that reduce interspecific encounter rates, such as spatial or temporal shifts in foraging activity, or by more direct behavioral responses, such as avoidance, hiding, or fleeing (e.g., Harmon et al., 2007; Pasch et al., 2013; Ziv et al., 1993). Behavioral mechanisms that can reduce exploitative competition include shifts in diet or predation risk tolerance (e.g., foraging farther from cover to reach undepleted patches). Just as behavioral responses to predators would be maladaptive in the absence of predators (Blumstein and Daniel, 2005), behavioral responses to interspecific competitors would be maladaptive in the absence of competing species. Thus, behavioral responses to competitors can be expected to be induced by exposure to competitors or their cues.

Competition between translocated individuals and other resident species is undoubtedly one of the impediments to establishing new, self-sustaining populations of at-risk species (Griffith et al., 1989). Predator exclusion can improve translocation success (Arkinstall et al., 2024; Sarah et al., 2018), and so might the exclusion of competitors. But considering that the ultimate goal is to return at-risk species to the ecosystem, interventions that facilitate integration are preferable. Just as animals raised ex-situ often lack effective defenses against natural predators (Griffin et al., 2000), they might also lack effective responses to competitors. Procedures to reduce prey naivety have become standard practice in some endangered species translocation programs (reviewed in Rowell et al., 2020), and similar techniques could be used to reduce 'competitor naivety'. For species that are subordinate to heterospecifics in competitive interactions, a lack of prior experience with competitors could be costly in terms of acquiring resources, setting up territories, and avoiding confrontations. Thus, providing captive-born animals with experience with competitors might also improve translocation success.

Here we present results from a controlled experiment designed to assess the impact of incorporating heterospecific competitor experience into the pre-translocation preparation of the Pacific pocket mouse (*Perognathus longimembris pacificus*), a federally endangered species (USFWS, 1998). More specifically, prior to a planned reintroduction of captive-born mice to the wild, we gave a random half of the mice exposure to the most dominant member of the same foraging guild present at the release site (Dulzura kangaroo rats, *Dipodomys simulans*). Following release, we collected data on survival, reproductive condition, and body weight by trapping the mice repeatedly throughout the active season and following years. To the best of our knowledge, this is the first time pre-release experience with heterospecific competitors has been tested as a conservation tool.

1.1. Study system

The Pacific pocket mouse is a small, relatively long-lived (up to 3–5 years in the wild; Miller et al., 2017) granivorous rodent in the family Heteromyidae. They are nocturnal and semi-subterranean, with peak breeding documented between February–June which can extend through September (Miller et al., 2017; Shier et al., 2025). Gestation is an average of 23 days, and females produce 0 to 3 litters in a breeding season with an average litter size at birth of 3.3 pups (Shier et al., 2025). The mice enter a physiological dormancy phase during the non-breeding months (Chew and Butterworth, 1964; Kenagy and Bartholomew, 1985; Miller et al., 2017; Shier et al., 2025). Pacific pocket mice are prey to diverse taxa, including coyotes (*Canis latrans*), foxes (*Vulpes* spp.), snakes (Viperidae and Colubridae), owls (Tytonidae and Strigidae), fire ants (*Solenopsis* spp.), tarantula (*Aphonophelma* spp.) (Miller et al., 2017) and possibly scorpion (Scorpiones) (Shier and King, pers. obs). Historical records indicate that Pacific pocket mice once inhabited coastal dune and scrub habitat from the El Segundo dunes in Los Angeles County, California to the Tijuana River mouth and valley at the US-Mexico border (Hall, 1981; Miller et al., 2017). Today only three isolated populations remain, with critically low effective population sizes, posing a threat to genetic diversity (Wilder et al., 2020) and species persistence (USFWS, 2020). The recovery plan for the species calls for the protection and maintenance of 10 independently viable populations to facilitate recovery by creating redundancy and thus, reducing the risk that a single catastrophic event could extirpate the remaining populations (USFWS, 1998, 2020). A consensus was reached among the regulatory agencies and species experts, that Pacific pocket mouse population parameters were at a critical level that justified establishment of a conservation breeding and translocation program.

The historic range of the Pacific pocket mouse overlaps broadly with several other small rodent species that are potential competitors for food and burrows. They are the smallest rodent in their community and within their foraging guild (Weight 6–9 g, Body length 52–69 mm; Brown and Harney, 1993; Chock et al., 2018; Miller et al., 2017). One competitor of Pacific pocket mice is the Dulzura kangaroo rat. Recent research on interspecific competition has shown the Dulzura kangaroo rat is the largest and most dominant competitor of *P. longimembris* (Weight: 50–94 g, Body length: 112–132 mm; Chock et al., 2018), suggesting it could exclude Pacific pocket mice from preferred habitat and other limited resources during settlement. However, it remains an open question whether the density of Dulzura kangaroo rats or other potential competitors in receiver sites designated for Pacific pocket mice directly impacts release success (i.e., survival and/or reproduction at the receiver site). The impact of competitor density on pocket mouse release success may depend on whether or not Pacific pocket mice (hereafter pocket mouse) have experience with the competitor. Early efforts to release captive-born pocket mice saw variable survival and reproductive fitness (King et al., 2019; Shier, 2017; Shier et al., 2016; Wang et al., 2018), to the extent that new techniques were needed to improve the persistence of new populations.

2. Materials & methods

2.1. Overview

To evaluate whether heterospecific competitor experience would be a valuable addition to the Pacific pocket mouse conservation breeding and translocation protocol, half of the pocket mice to be released in three consecutive years (2020–2022) were given an extended exposure to a live adult Dulzura kangaroo rat (hereafter kangaroo rat). Before release, behavior was quantified before and after extended exposure, and compared between exposed (competitor-experienced see below for details) and control mice. Following translocation, body condition, survival, and reproductive success of the experimental and control pocket mice was monitored by live-trapping (Fig. 1). The entire receiver site was encompassed by a dispersal barrier, and thus disappearances could be attributed to mortality.

2.2. Animals and housing

The pocket mice used in this experiment were born and housed in a conservation breeding facility (as were their parents). Animal rooms were equipped with skylights for the natural light-dark cycle and maintained at temperature and humidity ranges typical for coastal southern California. After weaning, the pocket mice were housed individually in clear, acrylic compartments (30 × 30 × 61 cm) with 5 cm of sand and a refuge consisting of a dark nest chamber (177 mL glass jar inserted into a 10.16 cm section of 6.35 cm diameter food-grade PVC tube with a cap on one end) with an artificial burrow entrance (15.24 cm section of 2.54 cm diameter PVC tube joined by a T-section). Compartments were perforated on their long sides (0.3 × 10 cm slots every 2.5 cm) and arranged such that each individual had visual, olfactory and auditory contact with at least one opposite-sex neighbor.

The kangaroo rats ($n = 13$) were collected from the wild and housed in a separate room from the pocket mice for a 14-day medical quarantine period. After being used in the experiment and within 30 days of collection, the kangaroo rats were returned to the wild (see Supplemental materials for details). Across the three years, 72 pocket mice were used in the experiment and transferred to the receiver site. We matched age and sex ratios where possible each year and divided pocket mice evenly between experimental and control treatment groups (16 females and 20 males in each group). One female in the competitor-experienced group died in acclimation and was removed from all fitness analyses. Seven additional pocket mice were run in the behavioral trials but were not released.

2.3. Experimental design and heterospecific competitor experience

The experimental treatment consisted of placing the pocket mouse in a plexiglass arena (122 × 61 × 30 cm) with a kangaroo rat on three consecutive nights (Fig. 1). On nights 1 and 3, the animals were observed together for 10 min and then immediately returned to their home cages. On night 2, they interacted for 2 h. The exposure period was set at two hours based on research showing that kangaroo rats can establish dominance relationships with previously unfamiliar conspecifics within this time frame (Shier and Randall, 2007). Data collected on nights 1 and 3 were intended to serve as a basis for comparing pre- and post-exposure behavior. Trials on nights 1 and 3 were recorded from above using an infrared video camera. The arena was illuminated with red light (outside nocturnal rodent visual sensitivity peaks, de Farias Rocha et al., 2016) to allow us to watch the animals without disturbing them and intervene if aggression occurred. While in years 1 and 2, mice in the control group were given no pre-release exposure to kangaroo rats, in year 3, mice in the control group were exposed to a kangaroo rat for 10 min on nights 1 and 3, for the purpose of testing for behavioral differences between treatments (See Fig. 1).

At the start of each trial, a kangaroo rat was placed in its artificial burrow at one end of the arena and the pocket mouse was placed in its artificial burrow at the other end. An observer sat quietly 1.5 m from the testing arena to watch for and immediately separate the animals if aggressive interactions escalated to physical contact. The floor of the arena was covered with 5 cm of sand, which was thoroughly mixed but not changed between trials. For the night 2 trials, objects were placed in

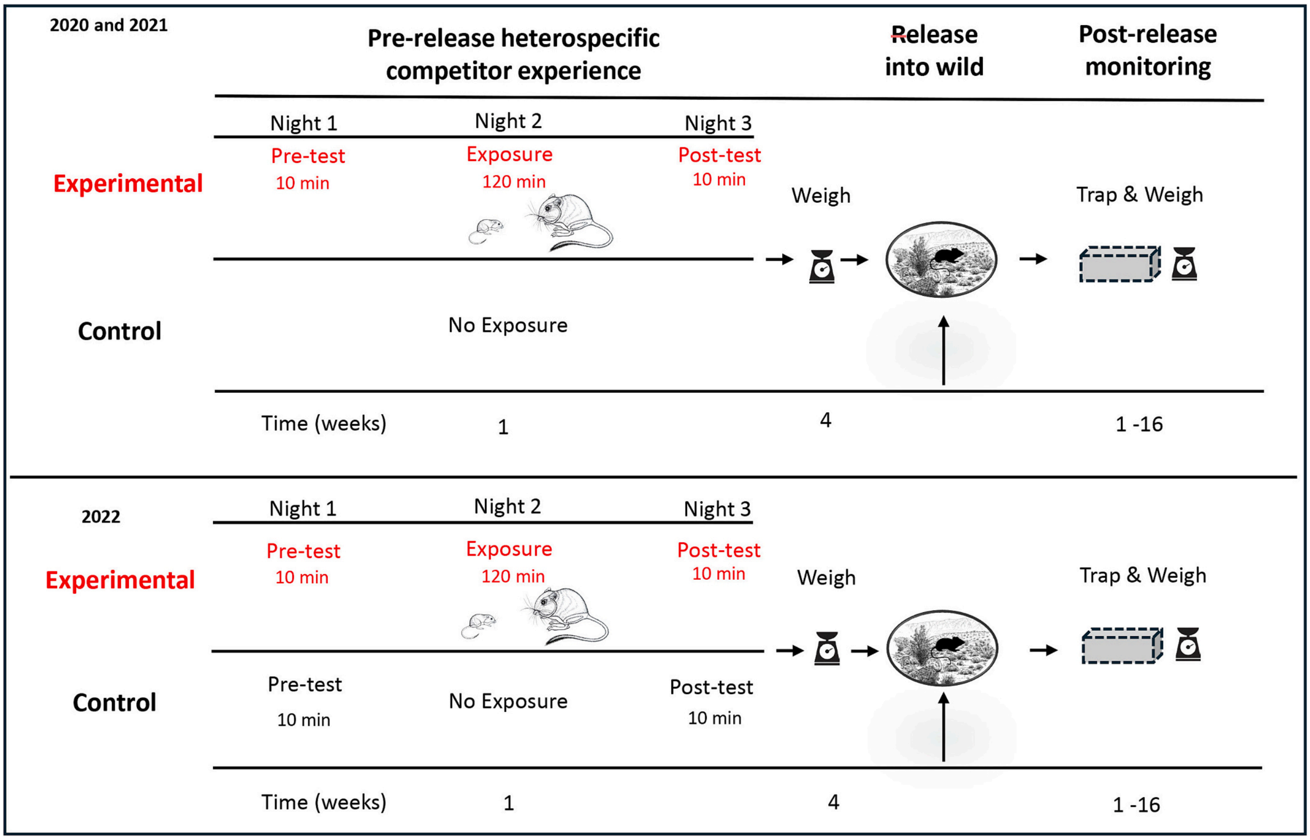

Fig. 1. Schematic of the experimental design and timeline illustrating different methods used in 2020 and 2021 with that used in 2022.

the arena to serve as refuges (e.g., sections of PVC, coconut shell, grass hut). In years 1 and 2, the animals could interact freely, but in year 3 the death of a pocket mouse necessitated the installation of a wire-mesh barrier across the middle of the arena to prevent physical contact in the remaining trials (13 of 28). All pocket mice (except 1) were exposed to at least two different kangaroo rats, and kangaroo rats were used in no more than four consecutive trials (no >25 over the course of several weeks). The intertrial interval was approximately 20 min. All trials were conducted within 3 weeks of translocating the pocket mice to the receiver site.

2.4. *Receiver site setup and management*

The receiver site was managed to meet pocket mouse habitat requirements established from extant populations (Brehme et al., 2023). To limit dispersal and allow pocket mice to acclimate to the new site (Germano, 2001; Shier, 2006; Shier and Swaisgood, 2012), the receiver site was prepared for "soft release". An acclimation chamber was constructed for each mouse (Fig. S1a). These chambers consisted of a below-ground cardboard and wood nest (Fig. S1b), and two biodegradable cardboard mailing tube artificial burrows which connected the nest to the surface (Fig. S1c). One artificial burrow connected the nest to the above-ground retention cage, while the other was capped at the surface during the acclimation period. This design allowed movement of pocket mice between the below-ground nest and the above-ground retention cage while preventing escape during the acclimation period (Shier, 2006; Shier and Swaisgood, 2012). Nest cameras were installed in a subset of the acclimation chambers to monitor the pocket mice below-ground. In years 1 and 2, pocket mice were translocated into a site unoccupied by the species, and acclimation chambers were placed approximately 5 m apart in a grid configuration. In year 3, we translocated mice into a low density pocket mouse occupied area within the receiver site. We confirmed locations of residents via trapping and placed the acclimation chambers in a quasi-grid maintaining a distance of at least 5 m from resident capture locations. We verified that no resident burrows were within 5 m of acclimation chambers via visual surveys. We also installed remote trigger infrared cameras (Cuddeback) within the receiver site enclosure to monitor pocket mouse activity during acclimation and following release.

The acclimation chamber grid was surrounded by a perimeter fence (Animex; 122–152 cm high) buried 30 cm below the surface to prevent pocket mice from leaving the receiver site and deter terrestrial predation attempts (Fig. S1d). We detected two snakes and removed one within the receiver site during the course of the experiment (number detected by year: 2020 = 0; 2021 = 1; 2022 = 1). The fence also facilitated effective management of heterospecific densities (Jarvis and Bennett, 1991). Because surveys prior to the first pocket mouse translocation indicated medium to high densities of potential heterospecific competitors, a decision was made to non-lethally reduce densities of these species within the perimeter fence at the receiver site to temporarily decrease competition for resources until pocket mice were established. After the perimeter fence was installed, we trapped and removed potential heterospecific competitors as needed to achieve low density (i.e., California pocket mice (*Chaetodipus californicus*); Dulzura kangaroo rat, Cactus mouse (*Peromyscus eremicus*), Deer mouse (*Peromyscus maniculatus*), and Western harvest mouse (*Reithrodontomys megalotis*); range of low densities 3–11/ha varies by species; Table S1). This process was repeated during post-release monitoring of pocket mice to maintain low densities of heterospecific competitors within the receiver site (see details below).

2.5. *Translocation, supplementation & post-release monitoring*

2.5.1. *Translocation*

We translocated pocket mice into a site in Laguna Coast Wilderness Park (33°N, −117°W, mean elevation 220 m) between April 25th and May 3rd each year. All pocket mice used in the experiment were sexually mature at the time of release (range: 1–4 yrs.; experimental mean ± sd: 2.2 ± 1.0 yrs.; control mean ± sd: 2.2 ± 0.9 yrs). Seven had been mated in captivity, with five confirmed pregnant immediately after release. We individually marked all pocket mice at the base of the tail with a light-activated microtransponder (500 × 500 × 100 μm P-chip; PharmaSeq, LLC, Monmouth Junction, NJ, USA); in case of microtransponder failure, tiny tissue samples (ear snips) were taken as a genetic reference.

We interspersed mice from each treatment equally across acclimation chambers at the site, and all of the mice in a given year were transferred to the site on the same night. During the 1-week acclimation period, we fed all pocket mice daily with a combination of their standard captive diet (inoculated finch seed mix and lettuce), and seeds of native plants present on the receiver site or found in Coastal sage scrub and documented to be consumed by pocket mice (Iwanowicz et al., 2016; Meserve, 1976; Vandergast et al., 2023). At the end of the acclimation period, we removed the above-ground portion of the acclimation chamber and uncapped the artificial burrow that led directly to the surface. The biodegradable below-ground nest and artificial burrows were left in place to provide temporary shelter for the mice.

2.5.2. *Supplementation*

To ensure the pocket mice had sufficient food resources post-release and could build seed caches before entering seasonal dormancy, we provided a mix of finch seed mix, native seeds, and lettuce for moisture at supplemental feeding stations. Non-native and non-locally sourced seeds were autoclaved before deployment at the receiver site to prevent germination and preserve the native vegetation community. Feeding stations designed to allow access only to pocket mouse sized rodents—25.4 cm long sections of 1.9 cm diameter food-grade PVC tubes—were staked into the ground and provisioned three evenings per week for the first month following release, one evening each week thereafter until the end of October, and then weekly (2020 and 2021) or biweekly (2022) until the next cohort was released the following year.

2.5.3. *Post-release monitoring*

To document all surviving mice, determine their condition (via weight) and mark any wild-born offspring that emerged on site, we conducted trapping surveys at least every four weeks up to 16 weeks post-release during the spring and summer. Additionally, we performed 1–2 bouts of trapping in the fall and/or winter to manage heterospecific densities, and at least one bout in the following spring to evaluate overwinter survival (details in Table S2). We continued trapping until no captive-born mice in this experiment remained alive. We used Sherman live-traps (22.9 cm; H.B. Sherman Traps, Tallahassee, FL, USA) with shortened doors to prevent tail injuries. We flagged trapping lines with approximately 5 m spacing across the receiver site, with one trap placed at each flag. We opened and baited traps with autoclaved finch seed (to prevent germination) before sunset, and checked traps twice during the night at approximately 2330 and 0330, with closure during the 0330 check. During trapping, we identified, weighed (g), and sexed each mouse and documented reproductive condition. For females, we documented pregnancy (abdomen swollen, body pear shaped, prominent nipples), lactation (red, distended nipples) and used estrous cycling via vulvar swelling to verify lack of pregnancy. We rated the degree of vulvar swelling on a four point scale (1 = not swollen, 4 = maximally swollen) developed for kangaroo rats (Yoerg, 1999) and adapted for pocket mice (Shier et al., 2025). We categorized male reproductive status using testes position (i.e., 0 = non-scrotal, 1 = partially scrotal, and 2 = scrotal).

This research followed guidelines by the American Society of Mammalogists (Sikes and Anim Care Use Comm Amer Soc, 2016), was approved under Institutional Animal Care and Use protocols (18-015 and 21-010) and permitted by the USFWS (10A1A 142435-6 and ESPER 0002526) and California Department of Fish and Wildlife (SC-002508).

2.6. *Statistical analyses*

All statistical analyses were conducted in the R programming environment (RCoreTeam, 2021).

To understand the impact of providing pocket mice with pre-release heterospecific experience on translocation success, we pursued three analyses. We first analyzed survival, using a Cox proportional hazards model with the 'survival' package (Therneau, 2020; Therneau and Grambsch, 2000) and clustered the data by year. Short-term survival (first active season–16 weeks) was measured based on recapture during live trapping efforts. Given that pocket mice are highly re-trappable, the population was closed (i.e., immigration and emigration limited by the fence and trapping conducted over three consecutive nights), and monitoring was conducted with a high density of traps, we concluded that pocket mice were deceased by the date of trapping if they were not caught in subsequent efforts. We confirmed this assumption by constructing robust design models (Kendall et al., 1995) in RMark (Kendall, 2001) to estimate detection probabilities for each year. Mean detection probability for a secondary sample (single trap check) varied between 0.5 and 0.69. This suggests that within a primary period (i.e., six trap checks) we have at least $1\text{-}(1\text{–}0.5)^6$ or 98 % chance of detecting an individual if it is present in our survey area. Within the Cox proportional hazards model, we included sex, age (years 1–4), whether the pocket mouse had been given heterospecific competitor experience (experimental treatment), and interaction terms between age and treatment and sex and treatment and clustered by year. We conducted model selection with the 'MuMIN' package (Barton, 2020), selecting sub models with $\Delta\text{AICc} < 2$ for model averaging. To understand the nature of interactions we ran pairwise contrasts with a Tukey method adjustment for multiple comparisons. Because there were several methodological differences between years 1 and 2 (2020 and 2021) and year 3 (2022), we analyzed the fitness data with and without year 3 (2022).

To determine if pre-release experience with heterospecific competitors influenced female reproductive output in the short-term, we calculated the number of times each female was pregnant during the first 16 weeks following release (ranging from 0 to 2), after removing females that had copulated in the captive facility and may have been pregnant at the time of release. We used ordinal regression, implemented with the package 'MASS' with the function 'polr' and verified that the proportional odds assumption of ordinal regression was satisfied by running separate binomial models for comparisons between females that did and did not get pregnant, females that got pregnant at most once, and those that got pregnant twice.

We used Fisher's exact test to examine the relationship between experimental treatment and long-term survival (survival to 1 year following release).

Our final post-release analysis examined changes to weight from each mouse's pre-release baseline to determine if there was any indication as to why certain groups may have had a fitness advantage (e.g., changes in body condition). For each mouse, we calculated the maximum difference in weight (post minus pre-release) during the first 16 weeks following release, removing data from recaptures when females were notably pregnant. We analyzed these changes in weight with a Gaussian GLMM; including, experimental treatment, sex, and their interaction as factors. We used the "check_model" function in the 'performance' package to validate the model. We calculated R^2 using r.squaredGLMM function in the package 'MuMIn'.

We quantified pre-release behavior (Table S2) to determine behavioral mechanisms of any post-release results with the event-recording program BORIS (Friard and Gamba, 2016), focusing on time pocket mice spent in the PVC burrow, the probability of being displaced by a kangaroo rat, and the frequency of maintenance (i.e., grooming, digging and sandbathing) and vigilance (i.e., orienting towards the kangaroo rat or scanning) behaviors. Inter coder reliability was evaluated using the interclass correlation coefficient (ICC) calculated with the 'irr' package (Gamer et al., 2022).

For each behavior we conducted a generalized linear mixed model (GLMM) with the 'lme4' (Bates et al., 2015) package, examining the influence of experimental condition, sex, trial type, and their interactions, and how many trials the kangaroo rat had experienced at that point. The time spent in burrow and vigilance behavior were log transformed and analyzed with a Gaussian error distribution, whether pocket mice were displaced was analyzed with a binomial distribution, and the count of maintenance behavior was analyzed with a zero inflated, negative binomial model to account for overdispersion. We included the pocket mouse ID as random effect for each model. We determined the appropriateness of model fit using the 'DHARMa' package (Hartig, 2021). We simplified all models with the 'MuMIN' package (Barton, 2020), averaging submodels where $\Delta\text{AICc} < 2$ from the submodel with the lowest AICc value. We interpreted the impact of fixed effects by calculating parameter estimates and relative importance scores (RI), giving greater consideration to terms with $\text{RI} > 0.85$. For all models we also looked at subsets of the data, including only those from 2022 when there were pre and post trials run for experimental and control pocket mice, and only trials where no barrier was present. No new effects emerged when examining only the subsets of data, therefore, only the full data analyses are reported here.

3. Results

3.1. *Post-release fitness – first active season*

Across years we documented higher survival in pocket mice given pre-release experience with kangaroo rats compared to control mice (Fig. 2a). Both top-ranked models included competitor experience and sex. Whether a pocket mouse had been exposed to kangaroo rats pre-release was the best predictor of survival post-release (Table 1; Fig. 2b). Over the first active season post-release, competitor-experienced mice had a 78.6 % reduction in the rate of mortality compared to control mice. Females survived at higher rates than males, and there was an interaction between experimental treatment and sex (Table 1). Pairwise contrasts showed that competitor-experienced females had higher survival than control females (Tukey adjusted pairwise comparison: $z = 3.910$, $p < 0.001$), and males in either treatment group (Tukey adjusted pairwise comparison: experienced females vs male control: $z = 3.396$, $p = 0.004$; experienced female vs experienced male: $z = -2.668$, $p = 0.038$). The difference in survival between experimental and control males was in the same direction as with females, but not significant (Tukey adjusted pairwise comparison: $z = 1.074$, $p = 0.7$).

The model with the second lowest AIC included all four terms, competitor experience, sex, age, and competitor experience × sex. In that model, age was a highly significant predictor, indicating that younger mice had higher survival than older ones (Table 1).

Removing data from year 3, when pocket mice in the control group were briefly exposed to a kangaroo rat for behavioral testing, resulted in an increase in the magnitude of the effect the experimental treatment (from 78.5 % reduction in the mortality rate to 85.1 %) and age (from 15.5 % reduction in the mortality rate to 32.0 %) on survival. With year 3 removed, there was no difference in the survival time of control females and males in the experienced group (Tukey adjusted pairwise comparison: $z = 0.680$, $p = 0.9048$).

Competitor-experienced females had higher reproductive success than control females (Fig. 3). The odds of females in the experimental group having more pregnancies (2 vs 1 or 1 vs 0) was 10.44 times higher (2.35 times on the log odds scale) than that of control females.

3.2. *Long-term fitness*

Twice as many competitor-experienced mice (12 of 35, 34.3 %) than control mice (7 of 35; 16.7 %) lived beyond the first active season (>1 year: Fisher's exact test: $p = 0.028$, 95 % CI = 0.002–0.999). The two longest-lived mice (both females) were given pre-release competitor

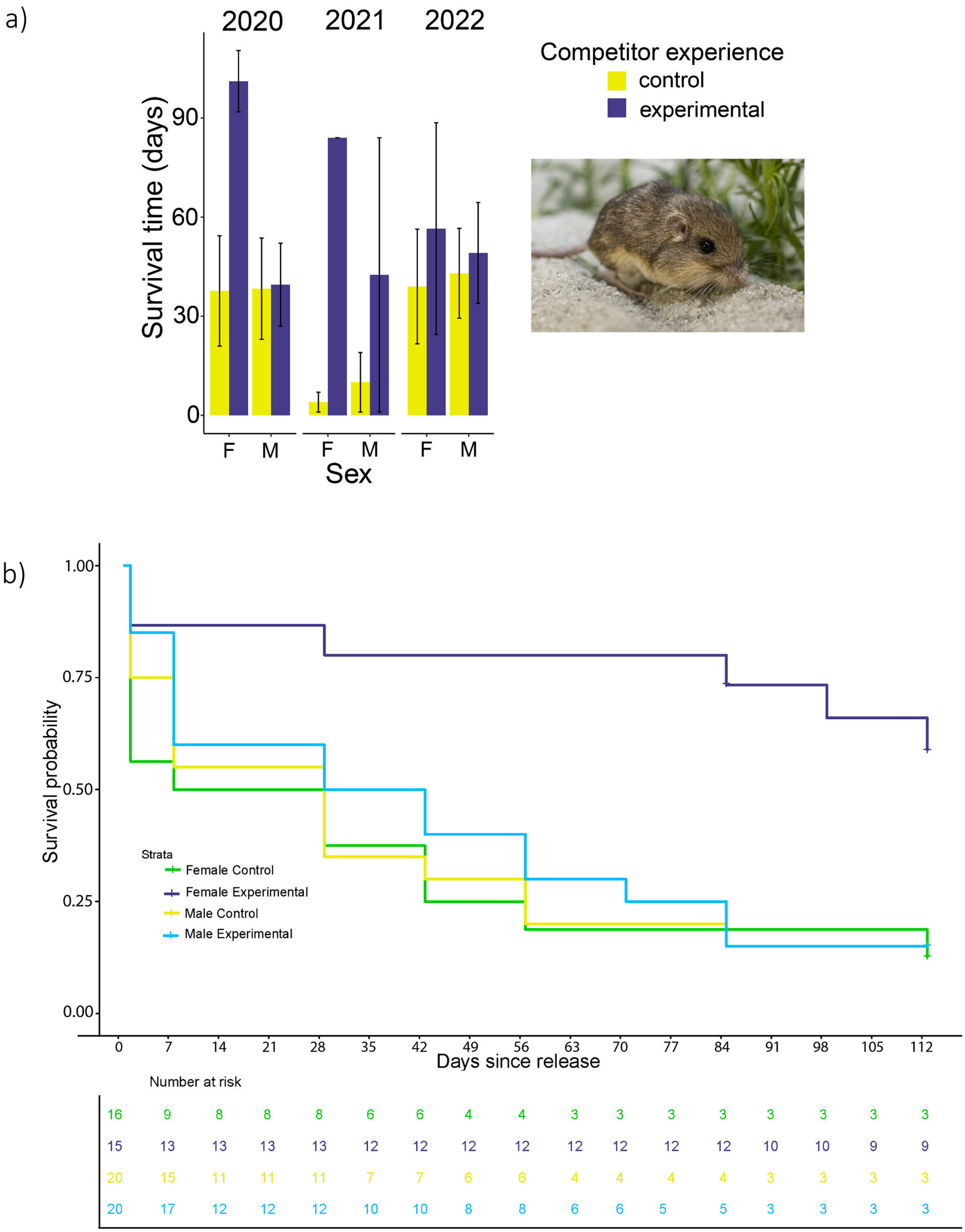

Fig. 2. Effects of pre-release competitor experience on survival. a) raw data showing survival time by year and experimental treatment (for females and males) and b) Kaplan Meier survival curve based on experimental group and sex.

Table 1
Survival model results.

Model	N par	AIC	ΔAICc	Weight
Survival ~ Competitor Experience + Sex + Competitor Experience × Sex + cluster (Release year)	4	394.35	0	0.67
Survival ~ Competitor Experience + Sex + Competitor Experience × Sex + Age + cluster (Release year)	5	395.77	1.42	0.33

Fixed effects	coef	SE	z	RI
Competitor Experience	−1.526	0.435	3.50	1.00
Sex (Male)	−0.129	0.032	4.00	1.00
Competitor Experience × Sex	1.38	0.467	2.96	1.00
Age	0.144	0.068	2.12	0.33

Survival models predict the likelihood of an event occurring, in this case a lack of recapture and presumed death. Coefficients with negative values suggest a decreased likelihood of that event (i.e., death) per day, positive values indicate a greater likelihood of the event. Two submodels were averaged to estimate the coefficients and relative importance (RI) scores. The conditional average is reported here. The full model also contained an interaction between age and competitor experience, which was not sufficiently predictive to end up in any of the top submodels.

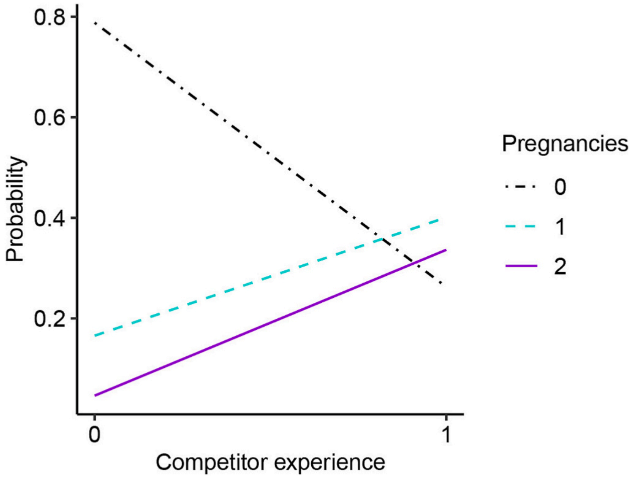

Fig. 3. Female reproductive success. Probability of having 0, 1 or 2 pregnancies during the first 16 weeks following release for experimental (1) and control (0) females. The odds of females in the experimental group having more pregnancies (1 vs 0 or 2 vs 1) were 10.44 times higher than that of control females.

experience and lived at the receiver site for nearly two years (697 days). Of the females that lived >1 year all but 1 (6 of 7) were given competitor experience prior to release and of those, 5 reproduced in their second active season. Only 1 control female survived >1 year and reproduced.

3.3. Body condition

Overall, pre-release competitor experience impacted weight change post-release from a pre-release baseline (Gaussian GLMM, $N = 49$ individuals, model $R^2 = 0.35$). Pocket mice given pre-release competitor experience gained more weight post-release compared with control mice ($t = 2.443$, $p = 0.019$). And, similar to the short-term survival results, there was an interaction between experimental treatment and sex with control females in the dataset gaining less weight than competitor-experienced females or males ($t = -2.018$, $p = 0.049$; Fig. 4).

3.4. Pre-release behavior

For the amount of time pocket mice spent in their burrow, three models were included in model averaging (based on dAIC), none of which included the interaction between trial type and experimental condition or the three-way interaction between sex, trial type, and experimental treatment. We found that regardless of treatment, pocket mice were more likely to spend time in the burrow during post-tests as compared to pre-tests (Gaussian GLMM, $N = 108$ trials, $\beta = -0.40 \pm 0.08$, $z = 5.02$, RI $= 1.00$; Fig. S2(A)), and that in-burrow behavior was influenced by how many times the kangaroo rat had been used in trials with pocket mice, with pocket mice spending less time in burrow the more trials kangaroo rats had with pocket mice ($\beta = -0.47 \pm 0.09$, $z = 5.04$, RI $= 1.00$). There was no impact of experimental treatment ($\beta = 0.13 \pm 0.09$, $z = 1.34$, RI $= 0.19$) or sex ($\beta = 0.16 \pm 0.09$, $z = 1.74$, RI $= 0.31$) on time spent in burrow.

Displacement and maintenance behavior models showed similar patterns. The averaged model for displacement contained 4 sub-models; while the averaged model for maintenance contained 2. None of the top sub models for either behavior included the interaction between trial type and experimental condition or the three-way interaction between trial type, experimental condition and sex. Regardless of treatment, pocket mice were less likely to be displaced by kangaroo rats (Binomial GLMM, $N = 108$ trials, $\beta = -1.28 \pm 0.54$, $z = 2.35$, RI $= 1.00$; Fig. S2(B)) and more likely to show maintenance behaviors (Zero inflated negative binomial GLMM, $N = 108$ trials, $\beta = 0.03 \pm 0.01$, $z = 2.30$, RI $= 1.00$; Fig. S2(C)) before the competitor experience as compared to the post test afterwards. Pocket mice were also less likely to be displaced by kangaroo rats ($\beta = -1.76 \pm 0.64$, $z = 2.73$, RI $= 1.00$; Fig. S3) and more likely to show maintenance behaviors ($\beta = 0.05 \pm 0.01$, $z = 3.80$, RI $= 1.00$) the more trials a kangaroo rat had with them. Females exhibited less maintenance behavior during trials than males ($\beta = -0.05 \pm 0.02$, $z = 2.92$, RI $= 0.39$), but there was no sex difference in the frequency of displacements ($\beta = -0.67 \pm 0.52$, $z = 1.27$, RI $= 0.44$). Finally, there was no impact of experimental treatment on either displacement or maintenance behaviors (displacement: $\beta = 1.04 \pm 0.60$, $z = 1.72$, RI $= 0.67$; maintenance $\beta = -0.02 \pm 0.02$, $z = 0.88$, RI $= 0.32$).

We did not find any predictors of vigilance worth considering. There were 12 submodels within ΔAIC < 2 of the null model, and no effect had an RI > 0.85 (Fig. S2(D)).

4. Discussion

The success of conservation breeding and release programs ultimately depends on whether individuals survive and reproduce in the wild following translocation. Many translocations fail, and funding for species recovery programs is limited. Determining which factors most strongly affect the outcome of translocations is thus of great importance (Morris et al., 2021; Taylor et al., 2017). We conducted an experiment to evaluate whether experience with heterospecific competitors would be a valuable addition to the pre-release preparation of pocket mice. We found clear short and long term survival and fitness benefits to providing competitor experience. Over the first active season for each release, the mortality rate of the experimental group was 79–85 % lower than that of the control group (Fig. 2), and females in the experimental group had more pregnancies than controls (Fig. 3). The positive effects on fitness continued beyond the first active season, with more experimental than control mice surviving and reproducing across multiple years. These results were so compelling that providing pocket mice experience with heterospecific competitors has become a standard part of the conservation breeding program and translocation program.

To the best of our knowledge, this was the first study to test for effects of pre-release competitor experience on fitness in the wild. Many conservation breeding programs include predator training (reviewed in Rowell et al., 2020), but our results suggest that experience with heterospecific competitors might also improve translocation outcomes.

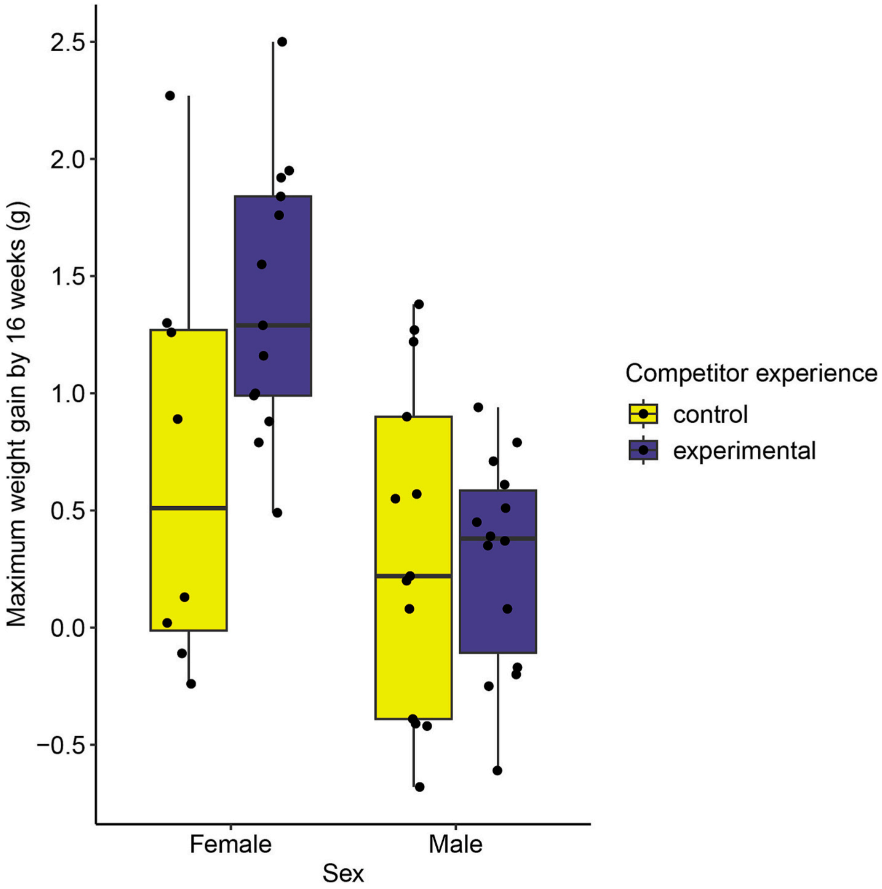

Fig. 4. Pocket mouse weight change data. Data showing changes to weight post-release from pre-release baseline. Competitor experienced females gained more weight than control females or males in either treatment; boxes show 25th–75th percentiles, whiskers show 1.5× the interquartile range, and the horizontal lines denote the median.

Considering that interspecific competition is ubiquitous in natural ecosystems and not limited to particular taxonomic groups or guilds, the potential for pre-release competitor experience to improve translocation outcomes is enormous.

Training naïve animals to fear predators has rather obvious survival benefits; how does experience with heterospecific competitors improve survival? The short answer is that more research is needed, but our results provided important clues. While competitor-experienced mice of both sexes had lower mortality rates and gained more weight than controls, on average, the treatment effects were more pronounced, and only statistically significant, for females (Table 1). We translocated captive pocket mice to the wild in the middle of the breeding season, the most energetically demanding time of year for females. Females can have multiple litters in a breeding season (Miller et al., 2017), but doing so requires meeting the energetic demands of pregnancy and lactation and the time demands of parental care. Having prior experience with kangaroo rats might have enabled females in the experimental group to forage efficiently enough to have multiple litters without going into energy deficit, while females in the control group were still learning how to cope with the dominant competitor. Foraging efficiently in the presence of a dominant competitor may be less crucial for male survival than female survival because males may have lower energetic demands during the breeding season. This could explain the interaction between treatment and sex in our experiment (Table 1). However, competition among males for mates is also energetically demanding. Evaluating whether competitor experience increases the fitness of males would require paternity data.

Alternatively, pre-release competitor experience may have facilitated settlement decisions. Dulzura kangaroo rats are the largest and most behaviorally dominant member of the foraging guild at the receiver site (Chock et al., 2018). Pocket mice could potentially avoid competing with kangaroo rats by shifting their foraging activity in space or time, but spatial niche partitioning is generally held to be more conducive to coexistence in complex foraging guilds with a high degrees of resource overlap (Brown and Harney, 1993; Brown and Heske, 1990; Brown and Zeng, 1989; Chock et al., 2022; Kelt, 2011; Reichman and Price, 1993; Zeng and Brown, 1987). Within coastal sage scrub habitat, Dulzura kangaroo rats are usually found in areas with low forb cover and high shrub cover (Chock et al., 2022), while pocket mice are found primarily in areas with high forb cover and low shrub cover (Brehme et al., 2023). Whether the differences in microhabitat use are a product of ongoing competitive interactions between the species (i.e., competitive displacement) is unknown, but perhaps pre-release experience with kangaroo rats affected pocket mouse settlement decisions such that the home ranges of mice in the experimental group overlapped less with kangaroo rats than did the home ranges of control mice. Testing this hypothesis would require data on the movement patterns of both species.

It is also possible that mice with competitor experience survived at higher rates than controls because they responded differently in direct encounters with kangaroo rats in the field. We examined pre-release behavioral data to test for differences between treatment groups in how the mice interacted with kangaroo rats. We found no behavioral differences between the treatment groups, but the length of the trials or the small size of the arena compared to natural home ranges may have obscured potential differences in how the mice responded to kangaroo rats. The brief exposure of mice in the control group to kangaroo rats (20 min, versus 160 min for the experimental group) in the third year of the experiment might explain why the difference between treatment groups in survival was smaller than in the two previous years (Fig. 2). This limited exposure to a heterospecific competitor might have been sufficient to improve fitness outcomes and suggests that shorter periods of competitor exposure could be implemented. Further research is needed to determine the minimum amount of exposure time required to maximize the fitness benefits. Another methodological difference could have driven differences between years. In the third year, mice were relocated into a site occupied at low density by resident conspecifics. While it has been posited that release into occupied habitat could reduce translocation success, it is unlikely that this methodological change explains the differences across years as there is no reason to expect the presence of resident conspecifics to reduce the survival time of experimental but not control mice.

Recently, it has been suggested that in-situ predator conditioning with low densities of predators may be more effective than pre-release predator training (Blumstein et al., 2019; Moseby et al., 2016). In-situ conditioning offers realistic encounters which are likely to hasten and reinforce learning for naive populations. But, the success of this strategy may be limited by the source and number of founders translocated. For animals bred and reared in ex-situ environments, release to the wild can entail many forms of novelty—exposure to weather, predators, competitors, wild habitats, location of food resources, and social interactions with conspecifics, and as a result translocated animals likely experience successive or simultaneous stressors that can be additive and impact cognitive function and fitness (Moberg, 2000; Teixeira et al., 2007). Providing pre-release experiences may familiarize founders with some aspects of life in the wild, reducing acute stress upon release (Teixeira et al., 2007) and easing the transition to wild environments (Tetzlaff et al., 2019). Our results demonstrate a large impact of pre-release competitor experience on post-relocation fitness despite reducing and maintaining low competitor densities at the receiver site throughout the study. This indicates that while in-situ conditioning could reinforce learning about competitors, pre-release experience had an important impact on initial success.

Conservation breeding and translocation programs can be last ditch efforts to recover critically endangered species when there is an inherent urgency to reverse the population trajectory. Given how resource intensive these programs are, it is imperative to work towards improving their efficiency. But often, conservation breeding and reintroduction programs face challenges due to limited funding and resources. As a result, breeding and release protocols are often established before optimal strategies can be fully researched (Flanagan et al., 2020). This need for immediate action despite uncertainty aligns with the adaptive management paradigm, where management decisions are made based on incomplete information and refined as controlled experiments yield new insights (Canessa et al., 2016). While an active adaptive management approach, which relies on strict experimentation, often involves testing approaches that may initially seem suboptimal (e.g., control groups, Williams, 2011), our findings illustrate the substantial conservation benefits that can result from such an approach.

With each additional pre-release management action (e.g., marking, health assessment, behavioral competency assessments and training, etc.), more time is needed to prepare animals for release, requiring more staff and funding. Thus, to be both effective and efficient, only the most impactful management actions should be implemented. In the Pacific pocket mouse recovery program, the next step will be to compare the efficacy of competitor experience to other pre-release management actions such as predator training, and resource (e.g., foraging and shelter) acquisition assessments to determine which combination of management actions are critical for translocation success. Similar assessments on the efficacy of competitor training amid the backdrop of existing protocols could benefit the many translocation programs whose species face competition post release.

CRediT authorship contribution statement

Debra M. Shier: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Janine N. Fischer:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Shauna N.D. King:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Alison L. Greggor:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis. **Gregory F. Grether:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Formal analysis, Conceptualization.

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Declaration of competing interest

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Relationships

There are no additional relationships to disclose.

Patents and intellectual property

There are no patents to disclose.

Other activities

There are no additional activities to disclose.

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Data availability

Data and code for this project will be deposited into a repository at acceptance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111193.

Data availability

Data for this paper can be found at: doi: 10.17632/vy62mnv5ff.2.

References

Arkinstall, C.M., FitzGibbon, S.I., Bradley, K.J., Moseby, K.E., Murray, P.J., 2024. High survivorship and rapid population growth of the greater bilby (*Macrotis lagotis*) reintroduced to a feral predator exclosure. Wildl. Res. 51.

Barton, K., 2020. MuMIn: Multi-Model Inference (R package).

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Beck, B.B., Rapaport, L.G., Price, M.R.S., Wilson, A.C., 1994. Reintroduction of captive-born animals. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation: Interactive Management of Wild and Captive Animals. Springer, Netherlands, Dordrecht, pp. 265–286.

Blumstein, D.T., Daniel, J.C., 2005. The loss of anti-predator behaviour following isolation on islands. Proc. R. Soc. B Biol. Sci. 272, 1663–1668.

Blumstein, D.T., Letnic, M., Moseby, K.E., 2019. In situ predator conditioning of naive prey prior to reintroduction. Philos. Trans. R. Soc. Lond. 374, 20180058.

Brehme, C.S., Thomsen, S.K., Adsit-Morris, D., Fisher, R.N., 2023. 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. Global Ecology and Conservation 47, e02640.

Brown, J.H., Harney, B.A., 1993. Population and community ecology of Heteromyid rodents in temperate habitats. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae. American Society of Mammalogists, Provo, Utah, pp. 618–651.

Brown, J.H., Heske, E.J., 1990. Control of a desert grassland transition by a keystone rodent guild. Science 250, 1705.

Brown, J.H., Zeng, Z., 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan desert Arizona USA. Ecology (Washington D C) 70, 1507–1525.

Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J.J., Southwell, D.M., Armstrong, D.P., Chadès, I., Lacy, R.C., Converse, S.J., 2016. Adaptive management for improving species conservation across the captive-wild spectrum. Biol. Conserv. 199, 123–131.

Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman, D. G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity. University of Chicago Press, Chicago, USA, pp. 317–333.

Chew, R.M., Butterworth, B.B., 1964. Ecology of rodents in Indian Cove (Mojave desert), Joshua Tree National Monument, California. J. Mammal. 45, 203–225.

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., Shier, D.M., Grether, G.F., 2022. Niche partitioning in an assemblage of granivorous rodents, and the challenge of community-level conservation. Oecologia 198, 553–565.

Conde, D.A., Flesness, N., Colchero, F., Jones, O.R., Scheuerlein, A., 2011. An emerging role of zoos to conserve biodiversity. Science 331, 1390–1391.

Darwin, C.R., 1868. The Variation of Animals and Plants Under Domestication. Johns Hopkinds University Press, Baltimore, MD.

Dawson, J., Patel, F., Griffiths, R.A., Young, R.P., 2016. Assessing the global zoo response to the amphibian crisis through 20-year trends in captive collections. Conserv. Biol. 30, 82–91.

de Farias Rocha, F.A., Gomes, B.D., de Lima Silveira, L.C., Martins, S.L., Aguiar, R.G., de Souza, J.M., Ventura, D.F., 2016. Spectral sensitivity M-measured with electroretinogram using a constant response method. PloS One 11, e0147318.

Edwards, M.C., Ford, C., Hoy, J.M., FitzGibbon, S., Murray, P.J., 2021. How to train your wildlife: a review of predator avoidance training. Appl. Anim. Behav. Sci. 234, 105170.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biol. Conserv. 96, 1–11.

Flanagan, A.M., Rutz, C., Farabaugh, S., Greggor, A.L., Masuda, B., Swaisgood, R.R., 2020. Inter-aviary distance and visual access influence conservation breeding outcomes in a territorial, endangered bird. Biol. Conserv. 242, 108429.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330.

Gamer, M., Lemon, J., Fellows, I., Singh, P., 2022. irr: Various Coefficients of Interrater Reliability and Agreement.

Germano, D.J., 2001. Assessing translocation and reintroduction as mitigation tools for Tipton kangaroo rats (*Dipodomys nitratoides nitratoides*). Transactions of the Western Section of the Wildlife Society 37, 71–76.

Greggor, A., Goldenberg, S., 2023. Manipulating animal social interactions to enhance translocation impact. Trends Ecol. Evol. 38, 316–319.

Greggor, A.L., Price, C.J., Shier, D.M., 2019. Examining the efficacy of anti-predator training for increasing survival in conservation translocations: a systematic review protocol. Environ. Evid. 8, 11.

Greggor, A., Masuda, B., Gaudioso, J., Nelson, J., White, J.T., Shier, D., Farabaugh, S., Swaisgood, R., 2021. Pre-release training, predator interactions and evidence for persistence of anti-predator behavior in reintroduced `alalā, Hawaiian crow. Global Ecology and Conservation 28, e01658.

Greggor, A.L., Merrick, M., Wisinski, C.L., Chock, R.Y., Shier, D.M., 2024. Conservation breeding and translocation Ch. 12. In: Wong, B., Ulrika, C. (Eds.), Behavioural Responses to a Changing World: Challenges and Applications. Oxford University Press, pp. 206–222.

Griffin, A.S., Blumstein, D.T., Evans, C.S., 2000. Training captive-bred or translocated animals to avoid predators. Conserv. Biol. 14, 1317–1326.

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. Science 245, 477–480.

Hall, E.R., 1981. The Mammals of North American, Second, edition edn. John Wiley and Sons, New York.

Harmon, L.J., Harmon, L.L., Jones, C.G., 2007. Competition and community structure in diurnal arboreal geckos (genus Phelsuma) in the Indian Ocean. Oikos 116, 1863–1878.

Hartig, F., 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.

IUCN, 2013. Guidelines for Reintroductions and Other Conservation Translocations. IUCN/Species Survival Commission, pp. 1–57.

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.

Jarvis, J.U.M., Bennett, N.C. (Eds.), 1991. Ecology and Behavior of the Family Bathyergidae. Princeton University Press, Princeton, NJ.

Kelt, D.A., 2011. Comparative ecology of desert small mammals: a selective review of the past 30 years. J. Mammal. 92, 1158–1178.

Kenagy, G.J., Bartholomew, G.A., 1985. Seasonal reproductive patterns in five coexisting California USA desert rodent species. Ecological monographs 55, 371–398.

Kendall, W., 2001. The Robust Design for Capture-Recapture Analysis Studies. Analysis Using Program MARK.

Kendall, W.L., Pollock, K.H., Brownie, C., 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51, 293–308.

King, S., Navarro, A., Montagne, J.P., Wang, T., Leivers, S., Shier, D.M., 2019. Conservation breeding and reintroduction of the Pacific pocket mouse (*Perognathus longimembris pacificus*). In: 2018 Annual Report. San Diego Zoo Institute for Conservation Research, pp. 1–68.

Kleiman, D.G., 1989. Reintroduction of captive mammals for conservation. Bioscience 39, 152–161.

Lickliter, R., Ness, J.W., 1990. Domestication and comparative psychology: status and strategy. J. Comp. Psychol. 104, 211–218.

Maynard, D.J., Flagg, T.A., Mahnken, C.V.M., 1995. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids. In: Schramm, H.L., Piper, R.G. (Eds.), American Fisheries Society Symposium; Uses and Effects of Cultured Fishes in Aquatic Ecosystems, pp. 307–314.

McPhee, M.E., 2003. Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. Biol. Conserv. 115, 71–77.

Meserve, P.L., 1976. Food relationships of a rodent fauna in a California USA coastal sage scrub community. J. Mammal. 57, 200–319.

Miller, B.D., Biggins, D., Hanebury, L., Vargas, A., 1994. Reintroduction of the black-footed ferret (*Mustela nigripes*). In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman and Hall, London, pp. 455–464.

Miller, W.B., Shier, D.M., Brehme, C.S., Tremor, S., 2017. Little pocket mouse (*Perognathus longimembris*). In: Tremor, S., Stokes, D., Spencer, W., Diffendorfer, J., Chivers, S. (Eds.), San Diego Mammal Atlas. Sunbelt Publications, Incorporated, San Diego, pp. 85–94.

Moberg, G.P., 2000. Biological response to stress: implications for animal welfare. In: Mench, G.P.M.a.J.A. (Ed.), The Biology of Animal Stress: Basic Priniciples and Implications for Animal Welfare. CABI publishing, Wallingford, pp. 1–21.

Moehrenschlager, A., Lloyd, N.A., 2016. Release considerations and techniques to improve conservation translocation success. In: Jachowski, D.S., Millspaugh, J.J., Angermeir, P.L., Slotow, R. (Eds.), Reintroduction of Fish and Wildlife Populations. University of California Press, Oakland, California, USA, pp. 245–280.

Morris, S.D., Brook, B.W., Moseby, K.E., Johnson, C.N., 2021. Factors affecting success of conservation translocations of terrestrial vertebrates: a global systematic review. Global Ecology and Conservation 28, e01630.

Moseby, K.E., Blumstein, D.T., Letnic, M., 2016. Harnessing natural selection to tackle the problem of prey naïveté. Evol. Appl. 9, 334–343.

Pasch, B., Bolker, B.M., Phelps, S.M., 2013. Interspecific dominance via vocal interactions mediates altitudinal zonation in neotropical singing mice. Am. Nat. 182, E161–E173.

Pfennig, D.W., Pfennig, K.S., 2012. Evolution's Wedge: Competition and the Origins of Diversity. University of California Press, Berkeley.

Price, E.O., 1984. Behavioral aspects of animal domestication. Q. Rev. Biol. 59, 1–32.

Rabin, L.A., 2003. Maintaining behavioural diversity in captivity for conservation: natural behaviour management. Anim. Welf. 12, 85–94.

RCoreTeam, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichman, O.J., Price, M.V., 1993. Ecological aspects of Heteromyid foraging. In: Brown, H.H.G.J.H. (Ed.), Biology of the Heteromyidae. American Society of Mammalogists, Shippensburg, PA, pp. 539–574.

Rowell, T.A.A.D., Magrath, M.J.L., Magrath, R.D., 2020. Predator-awareness training in terrestrial vertebrates: Progress, problems and possibilities. Biol. Conserv. 252, 108740.

Sarah, L., John, C.Z.W., Andrew, A.B., Russell, P., Jeremy, R., James, Q.R., Nicola, M., Michael, B., Brendan, W., Marcus, B., Joss, B., Peter, C., Nicholas, D., Chris, R.D., Graeme, R.G., Brydie, H., Chris, N.J., Peter, L., Mike, L., Adrian, M., Erin, E.M., Peter, M., Keith, M., Katherine, M., Manda, P., David, P., Katherine, T., 2018. Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. Wildl. Res. 45, 627–644.

Seddon, P.J., Griffiths, C.J., Soorae, P.S., Armstrong, D.P., 2014. Reversing defaunation: restoring species in a changing world. Science (Washington D C) 345, 406–412.

Shier, D.M., 2006. Effect of family support on the success of translocated black-tailed prairie dogs. Conserv. Biol. 20, 1780–1790.

Shier, D., 2016. Manipulating animal behavior to ensure reintroduction success. In: Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management, 21, p. 275.

Shier, D.M., 2017. Captive Breeding, Anti-predator Behavior and Reintroduction of the Pacific Pocket Mouse (*Perognathus longimembris pacificus*): 2015 Annual Report With Revised Genetics Section. San Diego Zoo Institute for Conservation Research, pp. 1–43.

Shier, D.M., Owings, D.H., 2006. Effects of predator training on behavior and post-release survival of captive prairie dogs (*Cynomys ludovicianus*). Biol. Conserv. 132, 126–135.

Shier, D.M., Owings, D.H., 2007. Effects of social learning on predator training and post-release survival in juvenile black-tailed prairie dogs (*Cynomys ludovicianus*). Anim. Behav. 73, 567–577.

Shier, D.M., Randall, J.A., 2007. Use of different signaling modalities to communicate status by dominant and subordinate Heermann's kangaroo rats (*Dipodomys heermanni)*. Behav. Ecol. Sociobiol. 61, 1023–1032.

Shier, D.M., Swaisgood, R.R., 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. Conserv. Biol. 26, 116–123.

Shier, D.M., Leivers, S., King, S., Chock, R., Montagne, J.P., 2016. Captive Breeding, Anti-predator Behavior and Reintroduction of the Pacific Pocket Mouse (*Perognathus longimembris pacificus*). For the period July 1, 2014–November 30, 2016. San Diego Zoo Institute for Conservation Research, pp. 1–146.

Shier, D.M., Greggor, A.L., Leivers, S., King, S.N.D., 2025. Using retrospective analyses to adaptively manage conservation breeding of an endangered rodent. Conservation Science and Practice 7, 1–15.

Sikes, R.S., Anim Care Use Comm Amer Soc, M., 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J. Mammal. 97, 663–688.

Somers, M.J., Gusset, M., 2009. The role of social behaviour in carnivore reintroductions. In: Reintroduction of Top-Order Predators, pp. 270–281.

Taylor, G., Canessa, S., Clarke, R.H., Ingwersen, D., Armstrong, D.P., Seddon, P.J., Ewen, J.G., 2017. Is reintroduction biology an effective applied science? Trends Ecol. Evol. 32, 873–880.

Teixeira, C.P., De Azevedo, C.S., Mendl, M., Cipreste, C.F., Young, R.J., 2007. Revisiting translocation and reintroduction programmes: the importance of considering stress. Anim. Behav. 73, 1–13.

Tetzlaff, S.J., Sperry, J.H., DeGregorio, B.A., 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. Biol. Conserv. 236, 324–331.

Therneau, T., 2020. A Package for Survival Analysis in R.

Therneau, T.M., Grambsch, P.M., 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York.

USFWS, 1998. Pacific Pocket Mouse (*Perognathus longimembris pacificus*) Recovery Plan, pp. 1–112. Portland, Oregon.

USFWS, 2020. In: Office, C.F.a.W. (Ed.), Pacific Pocket Mouse (*Perognathus longimembris pacificus*) 5-Year Review and Evaluation, pp. 1–34. Carlsbad, California.

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 forb rich diet that reflects local habitat availability. Ecol. Evol. 13, e10460.

Wang, T., King, S., Navarro, A., Leivers, S., Montagne, J.P., Shier, D.M., 2018. Captive Breeding, Anti-predator Behavior and Reintroduction of the Pacific Pocket Mouse (*Perognathus longimembris pacificus*): 2017 Annual Report, pp. 1–45. Escondido, CA.

Wilder, A.P., Navarro, A.Y., King, S.N.D., Miller, W.B., Thomas, S.M., Steiner, C.C., Ryder, O.A., Shier, D.M., 2020. Fitness costs associated with ancestry to isolated populations of an endangered species. Conserv. Genet. 21, 589–601.

Williams, B.K., 2011. Passive and active adaptive management: approaches and an example. J. Environ. Manage. 92, 1371–1378.

Wolf, C.M., Garland Jr., T., Griffith, B.J., 1998. Predictors of avian and mammalian translocation success: reanalysis and phylogenetically independent contrasts. Biol. Conserv. 86, 243–255.

Yoerg, S.I., 1999. Solitary is not asocial. Ethology 105, 317–333.

Yoerg, S.I., Shier, D.M., 1997. Maternal presence and rearing condition affect responses to a live predator in kangaroo rats, *Dipodomys heermanni arenae*. J. Comp. Psychol. 111, 362–369.

Zeng, Z., Brown, J.H., 1987. Population ecology of a desert rodent *Dipodomys merriami* in the Chihuahuan desert Arizona USA. Ecology (Washington D C) 68, 1328–1340.

Ziv, Y., Abramsky, Z., Kotler, B.P., Subach, A., 1993. Interference competition and temporal and habitat partitioning in two gerbil species. Oikos 66, 237–246.

SUPPLEMENTARY MATERIAL

Management Soft-release Protocol for Kangaroo Rats

To return kangaroo rats to their home territories, we held them in biodegradable artificial burrow (cardboard mailing tube; 61.0 cm long, 5.0 cm diameter, 0.3 cm thick). We spread water soluble nontoxic glue along the length of 1/3 of the inside of the artificial burrow, poured sand through the tube to provide traction and allowed it to dry. We installed an artificial burrow for each kangaroo rat near vegetation at their point of capture. The bottom of the burrow was left open to allow for access to soil. We used a PVC cap (5.0 cm diameter) to close the opening. Once installed, the base of the artificial burrow was approximately 30 cm below-ground sloped at 30° and the entrance rested just above ground-level (1 cm). If the collection site was sloped, we faced the burrow entrance downslope to prevent water from draining into the artificial burrow.. Artificial burrows were installed no more than 3 days before kangaroo rats were returned to the site to prevent soil moisture from degrading the cardboard in advance of use. On the evening of the transfer, we removed the PVC cap, placed nesting material (Carefresh ©), ~ 0.5g sterilized finch seed and a small piece of lettuce (~5 x 5 cm) into the bottom of the artificial burrow. We then placed each kangaroo rat into their respective artificial burrow and replaced the cap. We held the kangaroo rats in this artificial burrow for 24 hours and removed the caps at sunset to allow kangaroo rats the entire night to settle. Kangaroo rats could self-release from this chamber before caps were removed by digging out the bottom of the artificial burrow or chewing a hole in the side.

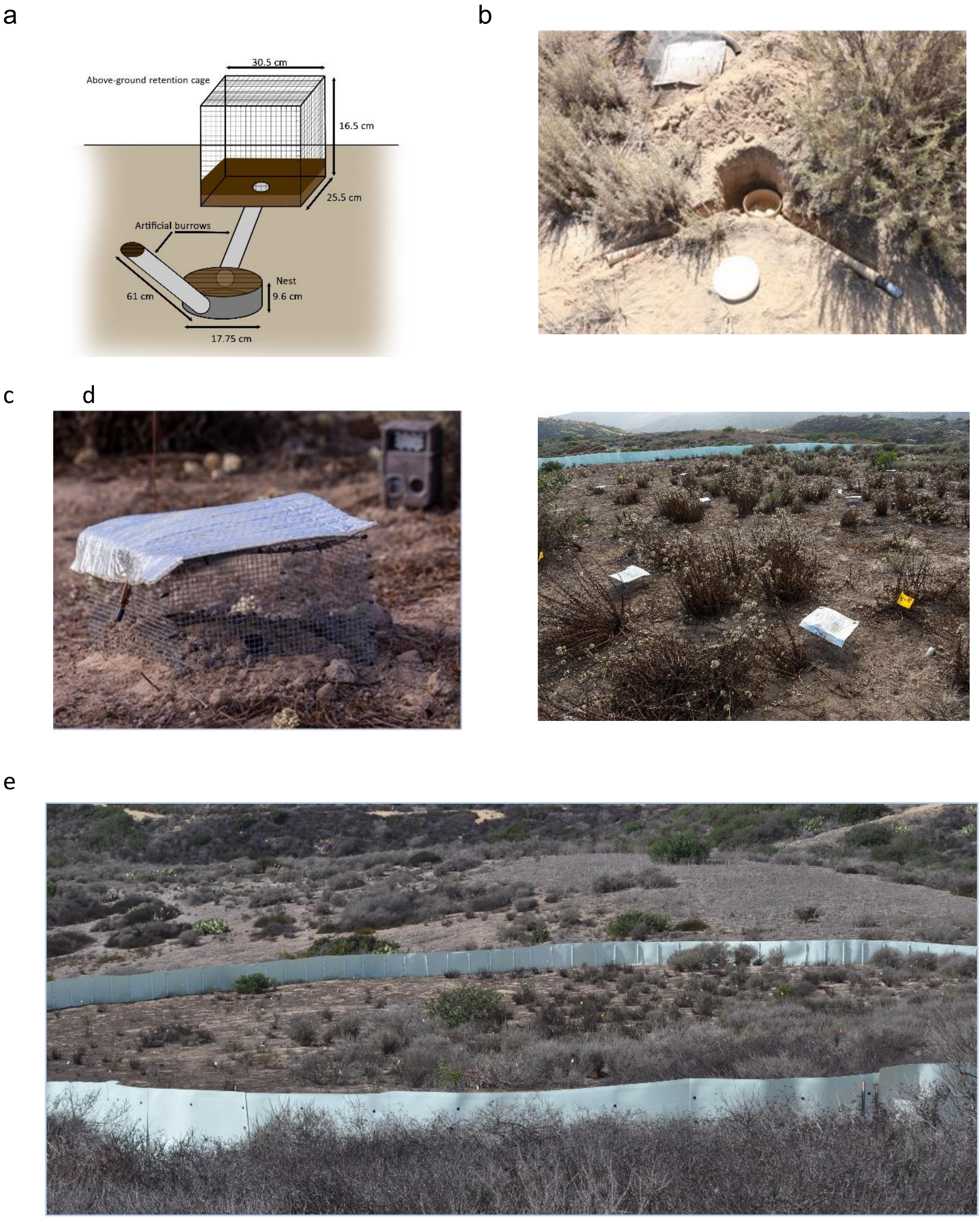

Figure S1. Receiver site setup. Acclimation chamber design (a), showing the below ground biodegradable nest and artificial burrows (b), the above-ground retention cage (c), the acclimation chamber spacing (d) and release site perimeter fence enclosed the 0.52

acre (.021 ha) receiver site in 2020, which was expanded to 1.06 (0.429) acres for the 2021 and 2022 releases (e).

Table S1. Density Categories for Potential Non-target Competitors.

	Density per hectare			
	Low	**Medium**	**High**	**Reference**
California pocket mice (*Chaetodipus californicus*)*	<7.26	7.26-13.52	>13.52	(M'Closkey 1972; Schwilk & Keeley 1998)
Dulzura kangaroo rat (*Dipodomys simulans*)	<12	12-18	>18	(Kelt et al. 2008)
Cactus mouse (*Peromyscus eremicus*)	<4	4-6.4	>6.4	(M'Closkey 1972; Meserve 1976)
Deer mouse (*Peromyscus maniculatus*)	<6.67	6.67-9.85	>9.85	(M'Closkey 1972; Meserve 1976; Schwilk & Keeley 1998)
Western harvest mouse (*Rethrodontomys megalotis*)	<10.97	10.97-21.94	>21.94	(Meserve 1976)

* Due to lack of published data on *Chaetodipus californicus*, San Diego pocket mouse*; Chaetodipus fallax* was used as reference for density categories

References for Table S1

Kelt DA, Wilson JA, E.S. K, Braswell JD, Deutschman D. 2008. Differential responses of two species of kangaroo rat (Dipodomys) to heavy rains: a humbling reappraisal. Journal of Mammalogy **89**:252-254.

M'Closkey RT. 1972. Temporal changes in populations and species diversity in a California rodent community. Journal of Mammalogy **53**:657-676.

Meserve PL. 1976. Habitat and resource utilization by rodents of a california USA coastal sage scrub community. Journal of Animal Ecology **45**:647-666.

Schwilk DW, Keeley JE. 1998. Rodent Populations after a Large Wildfire in California Chaparral and Coastal Sage Scrub. The Southwestern Naturalist **43**:480-483.

Table S2 Behaviors recorded during dyadic encounters

Behavior		**Description**
Aggressive	Displacement	Facing and approaching the dyad partner, whereupon the dyad partner withdraws
	Chase	Rapidly pursuing the dyad partner as it moves away
	Lunge Threat	A sudden strong movement or jump forward toward the dyad partner
	At burrow	Standing outside burrow occupied by dyad partner with head oriented toward or leaning into burrow entrance
	Fight	Contact initiated by animal that includes hitting with feet, biting, or bodies locked and rolling over
Submissive	Jump/avoid	Jumping upwards and back while facing the dyad partner
	Displaced	Moving away from approaching dyad partner
	Flee	Rapid movement away from dyad partner
	Withdraw	Movement away from the dyad partner at a pace slower than running
Other	Approach	Approaching within one body length of the dyad partner whereupon the dyad partner does not withdraw
	Digging	Pushing and pulling sand with feet
	Foot drumming	Striking of hind feet on the ground
	Freeze	Not moving body
	Grooming	Scratching with fore or hind feet and/or licking fur
	In burrow	Entire body inside of burrow
	Locomotion	Moving around the arena alone
	Oriented towards	Head oriented in general direction of the dyad partner
	Scanning/looking	Head rotating while the rest of the body stays still
	Sandbathing	Rubbing side or ventrum against the sand

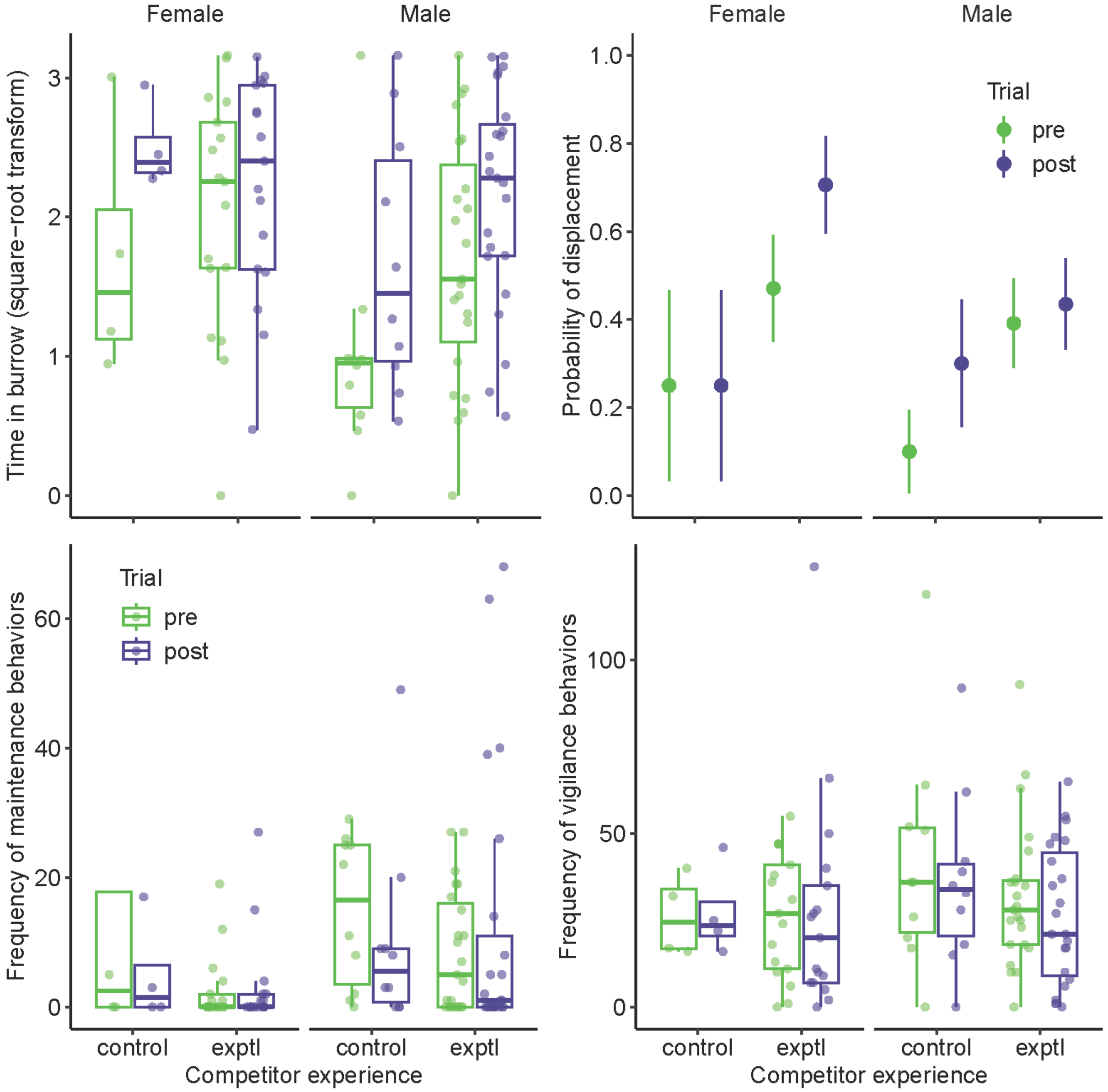

Figure S2. Summary of pre-release behavioral results. There was no interaction between the experimental condition and trial type or between sex, experimental condition and trial type in any behavior, suggesting a lack of documented effect of the competitor experience. Box plots (A, C, D) show median values (horizontal line in box) and 25th-75th percentiles of either the raw data (C) or square root transformed data (A, D). Whisker plot (B) shows the probability of the binomial outcome of getting displaced, with 95% confidence intervals.

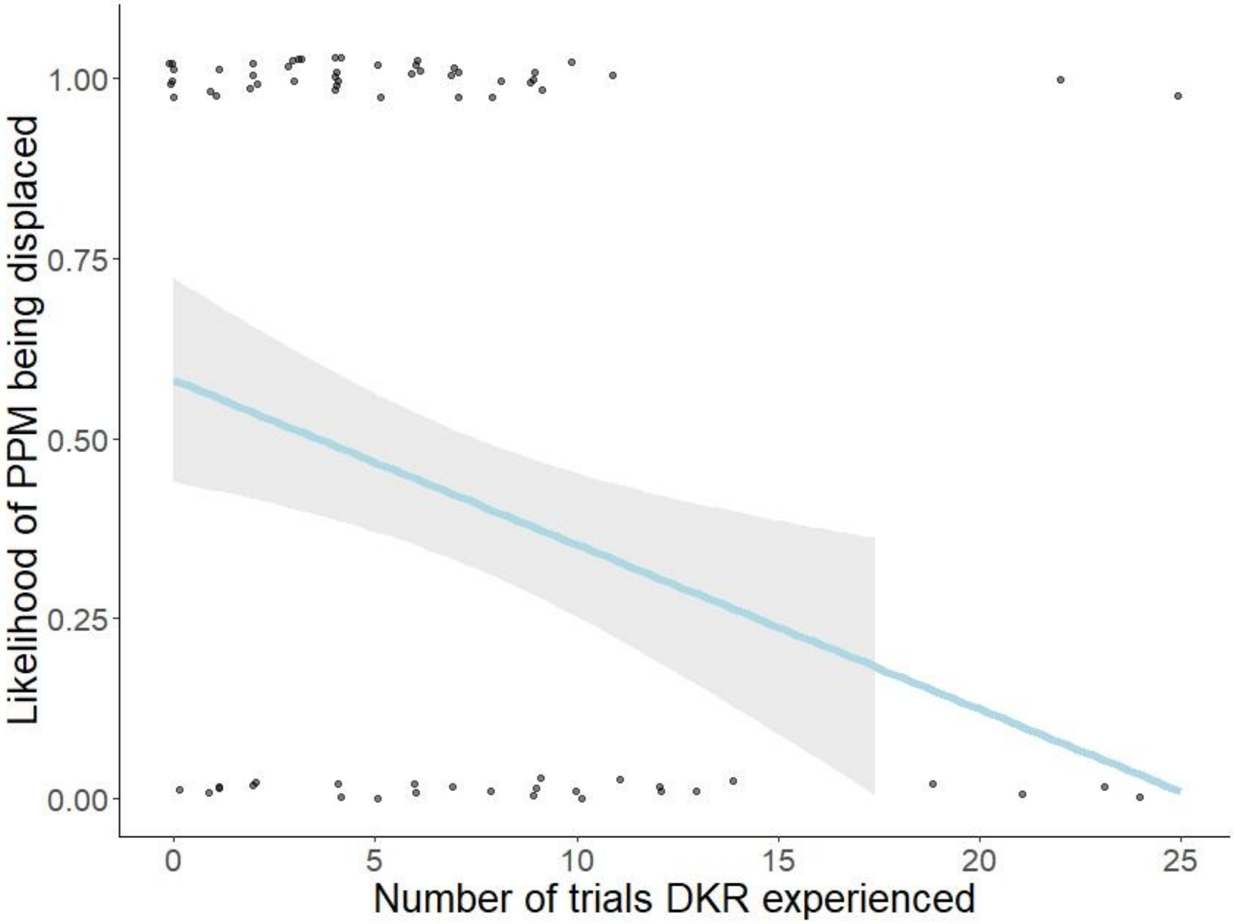

Figure S3. The likelihood that kangaroo rats displaced pocket mice during the trial as a function of the trial number. The more trials (pre, exposure and post) and experience a kangaroo rat had with pocket mice, the less likely they were to displace them. Line shows predicted values with shaded region covering 95% confidence interval. Dots show raw data points, with a binomial outcome.

CHAPTER 2:

ASSESSING THE INFLUENCE OF INTERFERENCE COMPETITION ON ECOLOGICALLY SIMILAR SPECIES THREATENED BY HABITAT LOSS

ABSTRACT

Understanding the strength and direction of species interactions is essential for managing co-occurring at-risk species in fragmented habitats. Habitat loss can intensify interference competition, potentially destabilizing community dynamics. The kangaroo rats *Dipodomys stephensi* and *D. simulans* are ecologically similar, sympatric species of conservation concern that overlap in habitat use. To assess how competition between them could influence their persistence, we tested whether one species dominates in direct interactions. We staged dyadic interactions between residents and intruders in the field and recorded the outcome of aggressive encounters. *D. stephensi* residents and intruders consistently dominated *D. simulans*, and *D. simulans* frequently avoided *D. stephensi*. These results suggest that *D. simulans* is at risk of being competitively displaced by *D. stephensi* as ongoing habitat loss increases spatial overlap between the species. Incorporating knowledge of behavioral interference into habitat management and translocation planning could improve conservation outcomes for these and other at-risk species.

INTRODUCTION

Earth is in the midst of a biodiversity crisis driven by habitat destruction, climate change, and other anthropogenic factors. These threats are causing unprecedented rates of species extinctions and population declines (Barnosky et al., 2011; Ceballos et al., 2015, 2017; Pimm et al., 2014). Anthropogenic threats are also altering species distributions, community compositions, and ecosystem functions (Angert et al., 2013; Tilman et al., 1994; Williams et al., 2022). Species' variable responses to environmental change (e.g. variation in range shifts and range contractions; Chen et al., 2011; Pacifici et al., 2020) are often mediated by species interactions, including competition, predation, and mutualism. Habitat loss and fragmentation can modify the strength and direction of various species interactions (Banks et al., 2007; Tylianakis et al., 2008). Species interactions, in turn, can affect mean population fitness, density, and distribution (Angert et al., 2013; Banks et al., 2007; Tilman et al., 1994). Thus, interspecific interactions play a crucial role in determining which species will persist in the face of environmental change.

Aggressive interference is one form of interspecific interaction that can shape species responses to landscape change (Grether et al., 2017). This type of interaction, which includes territorial displays, chasing, and physical conflict, influences species range dynamics (Patterson & Drury, 2023) and spatial and temporal habitat partitioning (Linnell & Strand, 2000; Ziv et al., 1993). Environmental changes can introduce new interference interactions or intensify the strength of aggressive interference between native competitors. For example, anthropogenic activities and climate change are causing species range shifts (Freeman et al., 2018) that increase contact between closely related species, sometimes leading to interference competition (e.g. Red and Arctic fox interference; Linnell et al., 1999; Tannerfeldt et al., 2002). Additionally, habitat loss and fragmentation can increase competition for limited resources and space, exacerbating the extinction risk for species that previously coexisted in larger, contiguous habitat patches (Bregman et al., 2015). Although there are many theoretical and empirical studies of interference competition, few studies have tested its influence on closely related, co-occurring threatened species - a critical gap in conservation research.

How species respond to habitat loss may depend, in part, on the strength and direction of interference competition. When interference is asymmetrical, the subordinate competitor may avoid or be displaced by the dominant competitor (Grether et al., 2013; Patterson & Drury, 2023). In some cases, this can result in niche partitioning that facilitates coexistence (Grether et al., 2013; Qvarnström et al., 2009). For example, in a study of desert gerbils (*Gerbillis*), two species preferred the same habitat type but coexisted because the subordinate species shifted its activity times and habitat use in the presence of the behaviorally dominant species (Ziv et al., 1993). Interference competitors, however, may coexist in a suboptimal state, where the subordinate species is restricted to smaller or lower quality habitat patches without access to critical resources (Grether et al., 2013; Jankowski et al., 2010; Martin & Martin, 2001). Such an exclusion can be especially detrimental to species of conservation concern which are at low population densities and may already face resource scarcity or habitat degradation.

The Stephens' kangaroo rat (*Dipodomys stephensi*) and the Dulzura kangaroo rat (*Dipodomys simulans*) are native California species of conservation concern that have been strongly affected by habitat loss and fragmentation. *D. stephensi* is federally listed as threatened under the Endangered Species Act (USFWS, 2022), while *D. simulans*, formerly part of *D. agilis* (Sullivan & Best, 1997), is considered vulnerable at the state level (CNDDB, 2024). These species are expected to compete for space and resources due to their overlapping ranges (USFWS, 2020; USGS 2018), close genetic relationship (Alexander & Riddle, 2005) similar morphology (Bleich, 1977; Lackey, 1967; Price et al., 1991), and solitary social structure (Longland & Dimitri, 2021). Some species of kangaroo rat are territorial (Randall, 1993; Randall et al., 2002; Ward & Randall, 1987), and there is evidence to suggest that *D. stephensi* is as well because they defend the core of their home range and communicate ownership (Shier, unpublished data). There is an active translocation effort for genetic rescue of the southernmost populations of *D. stephensi* (Shier et al., 2025), which involves relocating genetically diverse individuals into resident *D. stephensi* populations in areas also occupied by *D. simulans* (Shier et al., 2021; Shier & Swaisgood, 2012; USFWS, 2020). Where *D. stephensi* and *D. simulans* co-occur, they exhibit fine-scale spatial segregation: *D. stephensi* primarily inhabits open annual grasslands dominated by forbs, while *D. simulans* occupies coastal sage scrub (CSS) habitat (Goldingay & Price, 1997; Price et al., 1991). However, both species use the ecotone between these habitats, resulting in overlapping habitat use.

Competition between *D. stephensi* and *D. simulans* may be exacerbated by the continued loss of native grassland and CSS habitats. While some habitat is protected within a reserve system in southern California, much remains on private land and is at risk from continued urban and agricultural development (USFWS, 2020). Invasive grasses and increasing fire frequency in southern California pose additional threats by reducing suitable habitat for *D. stephensi* (Kelt et al., 2005; RECON, 1995; Shier & Swaisgood, 2012). Furthermore, the accumulation of dry biomass from invasive grasses, in combination with climate change (Goss et al., 2020; Swain, 2021), increases fire frequency beyond the tolerance of shrub species, resulting in the conversion of CSS to grassland (Talluto & Suding, 2008). This transition disproportionately impacts *D. simulans*, which depends on shrub cover for refuge and resources, while favoring *D. stephensi* populations that benefit from open habitats (Price et al., 1994a; Shier & Swaisgood, 2012). As habitat becomes more fragmented and homogenized, spatial overlap between the species is likely to increase, potentially intensifying interference competition and further constraining *D. simulans* populations.

Determining the dominance relationship between *D. stephensi* and *D. simulans* is essential for understanding how competition may constrain space use. In many species, dominance is predicted by body size (Blaustein & Risser, 1976; Chock et al., 2018; Langkilde & Shine, 2004; Martin & Ghalambor, 2014). A laboratory study found that *D. stephensi* was both heavier and dominant to *D. simulans* (Bleich & Price, 1995), suggesting that *D. stephensi* may competitively exclude *D. simulans*. However, laboratory studies often lack natural shelter, involve small enclosures, and may not accurately reflect wild encounters (Bleich & Price, 1995; Chappell, 1978). In the field, the size distributions of the species overlap broadly and many interactions occur within the core range of a territory holder. In such cases, residency can outweigh size in determining dominance among rodents (Stokes et al., 2012; Wolff et al., 1983) and territorial animals generally (Koivula et al., 1993; Smith & Parker, 1976).

Here, we tested whether the dominance relationship observed in laboratory studies also occurs under natural conditions. We staged dyadic interactions between *D. stephensi* and *D. simulans* in the field, with individuals of known residency status. We recorded contest outcomes to determine which species is dominant and whether dominance is influenced by body size or residency. We also noted avoidance behaviors that may contribute to spatial segregation. By directly testing interference competition in the wild, this study provides one of the first field-based assessment of dominance between two at-risk species. The results have direct implications for habitat management, translocation, and the co-management of *D. stephensi* and *D. simulans*.

METHODS

Overview and study site

Between 2021 and 2023, we staged 50 dyadic interactions between *D. stephensi* and *D. simulans* (Figure 1) at two sites in Riverside County: Southwestern Riverside County Multispecies Reserve (33.5863791, -117.0266333; n = 46) and Motte Rimrock Reserve (33.8041011, -117.2591999; n = 4). The habitat at both sites is composed of non-native grasslands, forblands, and coastal sage scrub (CSS). Experimental trials were conducted in the summer and/or fall of each year.

Figure 1. *Dipodomys stephensi* (left) and *Dipodomys simulans* (right) used in the staged interactions. *D. stephensi* primarily inhabits open annual grassland, while *D. simulans* occurs mostly in coastal sage scrub. The species are morphologically similar, but *D. simulans* has slightly larger and darker ears and a narrower face. Photo credits: G.F. Grether

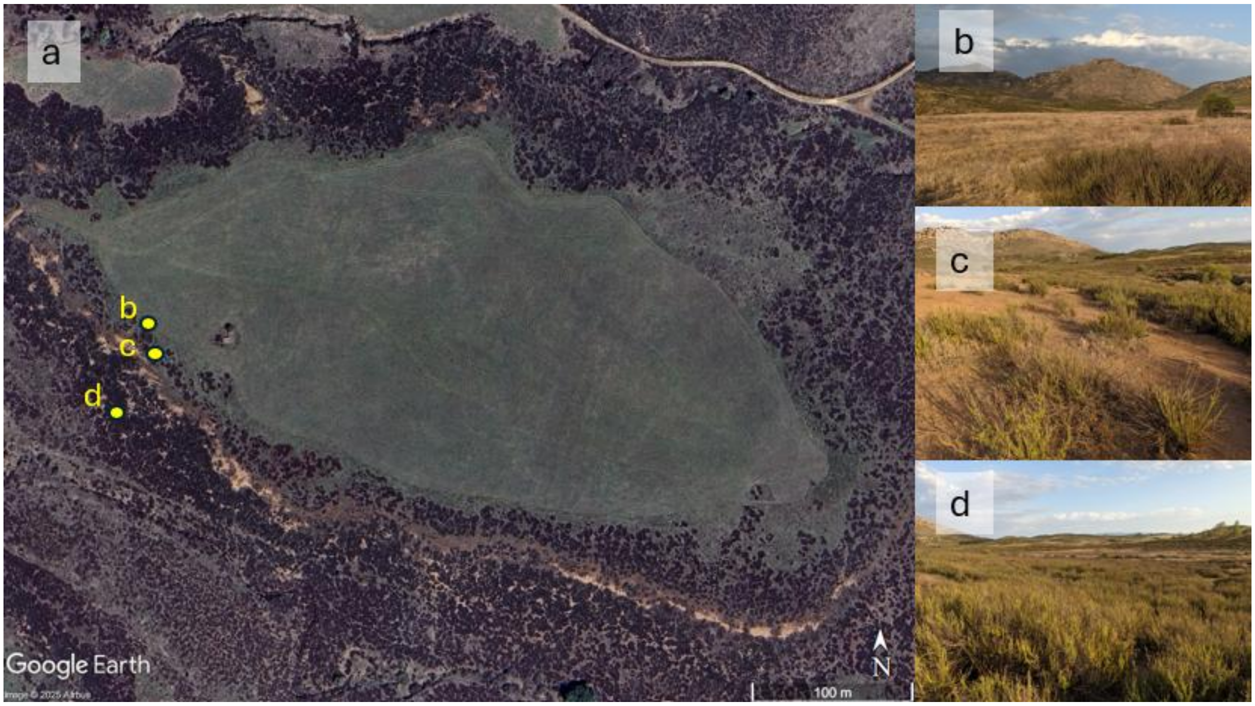

Figure 2. Habitat types found at the Southwestern Riverside County Multispecies Reserve (a) Aerial imagery of one of the study areas showing a plateau dominated by forbs and non-native grasses, surrounded by coastal sage scrub (CSS). Letters correspond to approximate locations of ground-level habitat photos: (b) grassland, (c) ecotone, and (d) CSS habitat.

Testing procedure

Each year, we established 4 - 5 noncontiguous trapping grids (16–182 traps per grid), spaced at least 130 m apart to minimize the likelihood that individuals were familiar with one another across grids (Price et al., 1994a). Grids were distributed across the different habitat types (Figure 2), with several spanning the ecotone between grassland and CSS habitat. Trap locations were spaced 10 m apart and marked with numbered flags. We used Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, U.S.A.) modified with a door gap to reduce tail injuries (Shier & Swaisgood, 2012).

Traps were baited with a commercial bird seed mixture (microwaved for 5 min to prevent germination) between 1800 - 2000 h and checked twice nightly (0200 – 0000 h and 0200 and 0400 h). Captured kangaroo rats were marked with uniquely numbered ear tags for individual identification. We tagged *D. stephensi* in their left ear and *D. simulans* in their right ear to facilitate distinguishing between the species. Some individuals also received a Passive Integrated Transponder (PIT) tag, which was inserted subcutaneously with sterile syringes (Sikes, 2016). This tagging method is known to be highly reliable and rarely results in injury (Williams et al., 1997). For each captured kangaroo rat, we recorded its ear tag or PIT tag ID, species, sex, weight, age (adult or juvenile), and the grid and trap number. Pregnant females were noted and excluded from trials. Individuals trapped at the same or adjacent locations at least three times were classified as residents at those locations (Shier & Swaisgood, 2012).

We staged dyadic interaction trials immediately after each trap check using a modified protocol from Chock et al. (2018). Individuals were not held for more than the interval between trap checks. Each trial paired one adult *D. stephensi* and one adult *D. simulans*. Trials occurred within the resident's home range; intruders were selected from a different trapping grid to ensure unfamiliarity. Both species served as residents and intruders. No individual was used in more than three trials, with a minimum of 24 h between trials, and residents were never paired with the same intruder. Pairings were randomly selected from nightly captures. For individuals used in multiple trials, some began as residents in their first trial and others as intruders.

The interaction trials took place in a clear Plexiglas arena (91 x 122 x 61 cm) with an open bottom, allowing the animals to remain on their natural substrate. Trials were conducted across the different habitat types, but the arena was always placed in relatively open areas without woody vegetation inside (e.g., between shrubs). We scattered mixed seed throughout the arena and added twigs and vegetation to two opposing corners to provide cover. In 2021 and 2022, we attached red lights to the upper four corners of the arena to increase the visibility of the kangaroo rats to the observer. In 2023, we instead attached infrared lights to two corners of the arena. An opaque partition initially divided the arena into halves, allowing the animals to acclimate separately for approximately 5 minutes. The partition was then removed, and the animals were allowed to interact for 10 minutes, after which they were released at their capture locations. Trials were closely monitored by the observer (J.N.S.) who sat quietly approximately 5 m away and intervened if fighting escalated to the point of risking injury. The animals appeared to acclimate quickly, as indicated by a lack of vigilant behavior and commencement of foraging and exploration. All trials were video-recorded with an infrared camcorder (LINNSE Camcorder) on a tripod.

Habitat survey

Because arenas were placed in open areas, direct habitat cues inside were minimal, though surrounding vegetation was visible through the clear walls of the arena. To test for the effect of habitat on the probability of winning, we conducted habitat surveys in a subset (80%) of the trap locations. We quantified vegetation cover in 10 x

10 m squares centered on each flagged trapping location by visually estimating the percent cover of shrubs at crown height.

Behavioral analysis

We used the event logging software BORIS (Friard & Gamba, 2016) to transcribe each video and record the occurrence of several behaviors (Table S1) associated with behavioral dominance (Shier & Randall, 2007). For all aggressive and submissive behaviors, we recorded counts, rather than duration, because the behaviors occur almost instantaneously. We determined the number of wins for each individual in each trial following the definitions used by Shier and Randall (2007). An individual was considered to win a given encounter if it displaced or behaved aggressively (lunge threat, fight, or chase) toward the opponent, followed by the opponent behaving submissively by moving away, fleeing, or jumping to avoid an attack.

We also quantified approach and avoidance movements using MTrackJ (Meijering, 2008) in ImageJ (Schneider et al., 2012) to overlay x and y axes on the video recording. The observer first selected a set of calibration points around the edge of the arena, and then the midpoint between the eyes was marked once per second for each individual. We distance-calibrated each coordinate location and calculated the change in distance initiated by each individual toward or away from the opponent. The sum of all positive values provided a measure of movement toward the opponent, and the sum of all negative values provided a measure of movement away from the opponent.

We removed time intervals (mean 6 s) where the observer interfered to prevent animals from escaping by digging under the arena walls and then standardized all videos to 9 min in length. Six videos shorter than 9 min were excluded from all analyses.

Statistical analysis

All statistical analyses were conducted in the R programming environment (v4.4.1; R Core Team 2024). The final data set contained 44 trials, with a total of 33 unique *D. stephensi* and 23 unique *D. simulans* used throughout the trials.

To examine how body weight, residency, and species identity influenced the probability of winning, we used conditional logistic regression with the *clogit* package (v0.9.6; Elff, 2022). Conditional logistic regression is an extension of logistic regression that stratifies on matching pairs. It was thus ideal for comparing the number of wins directly between dyad partners in each trial. We used the number of wins for each individual in each dyad as our dependent variable. The independent variables included species, body weight, sex, and residency status (resident or intruder). A random intercept was included for individual ID. Because we found that body weight was correlated with species, we normalized weight within each species using z-scores, such that each individual's weight was measured relative to the species' mean. An interaction term for species and residency could not be included because of the incomplete design (all trials were between residents and intruders). Interpretations of modeled results were the same regardless of whether videos <9 minutes were included (Table S2), whether trials differed by study site (Table S3), or the type of light used to illuminate the arena (Table S4), so we analyzed all trials together.

We calculated post-hoc pairwise contrasts using the *emmeans* package (v1.11.1-00001; Lenth, 2025) to compare the probability of winning between *D. stephensi* residents and *D. simulans* intruders and between *D. stephensi* intruders and *D. simulans* residents.

To test for a species difference in movement toward and away from the opponent, we used a Wilcoxon matched-pairs signed-rank test. Differences in the species' maintenance behaviors (digging and sandbathing), were tested using Wilcoxon matched-pairs signed-rank test and Fisher's exact test, respectively. Student's t-test was used to compare the species' mean body weights.

Our final data set included habitat data for 35 out of the 44 resident locations. This subset of the data was used to compare the percentage shrub cover at crown height between *D. stephensi* and *D. simulans* resident locations and to examine correlations between shrub cover and the probability of winning.

RESULTS

In individual encounters, *D. stephensi* had an 86% chance of defeating *D. simulans*, and residents had a 66% chance of defeating intruders (Table 1, Figure 3a; model results: species, $p < 0.001$; residency, $p = 0.004$). The effect size of species was larger than the effect size of residency, such that *D. stephensi* intruders had a 76% chance of beating *D. simulans* residents (Table 2; $t(39) = 2.77$, $p = 0.040$), and *D. stephensi* residents had a 92% chance of beating *D. simulans* intruders (Table 2; $t(39) = 4.93$, $p < 0.001$). The majority of *D. stephensi* aggressive behaviors consisted of chasing (36%) or displacing (40%), rather than lunging or physically attacking (Figure

S1). *D. simulans* usually responded to the approaching opponent by rapidly fleeing (82%) (Figure S2). *D. stephensi* exhibited more maintenance behaviors than *D. simulans*, such as digging (Figure S3; Wilcoxon matched-pairs signed-rank test: V = 826, p < 0.001) and sandbathing (Figure S3; Fisher's exact test: p = 0.026).

D. stephensi individuals were significantly heavier than *D. simulans* (Figure 3b; Student's t-test: t= 3.06, p = 0.004), but normalized weight was not a predictor of the probability of winning independent of species (Table 1; p = 0.54). Sex had no effect on the probability of winning (Table 1; p = 0.56).

D. simulans initiated more movement away from than towards *D. stephensi* (Figure 3c; Wilcoxon matched-pairs signed-rank test: V = 691, p <0.001). By contrast, *D. stephensi* initiated more movement towards *D. simulans* than away (Figure 3c; V = 170, p = 0.021).

In trials in which *D. stephensi* was the resident species, the habitat had a median shrub cover of 0.5% (Figure S4). In trials in which *D. simulans* was the resident species, the habitat had a median shrub cover of 55% (Figure S4). Because residency status was correlated with percent shrub cover, the effects of these two variables on the probability of winning are difficult to disentangle. However, we did not find a correlation between percent shrub cover and the probability of winning for either species (Figure S5).

Table 1. Conditional logistic regression results with the number of wins in each pair as the dependent variable, species, residency status, normalized weight, and sex as the independent variables, and individual as a random intercept. Means and SE are on the log-odds scale.

Model term	**Mean**	**SE**	**Odds ratio**	***p***
Species	1.83	0.37	6.22	<0.001
Residency status	0.66	0.23	1.94	0.004
Normalized weight	-0.14	0.27	0.87	0.616
Sex	0.29	0.52	1.34	0.576

Table 2. Pairwise contrasts comparing the probability of winning between *D. stephensi* residents versus *D. simulans* intruders, and *D. stephensi* intruders versus *D. simulans* residents. Means and SE are on the log-odds scale. df = 39.

Contrast	**Mean**	**SE**	**Odds ratio**	***t***	***p***
stephensi resident – *simulans* intruder	2.49	0.46	0.08	5.44	<0.001
stephensi intruder – *simulans* resident	1.17	0.42	3.21	2.78	0.040

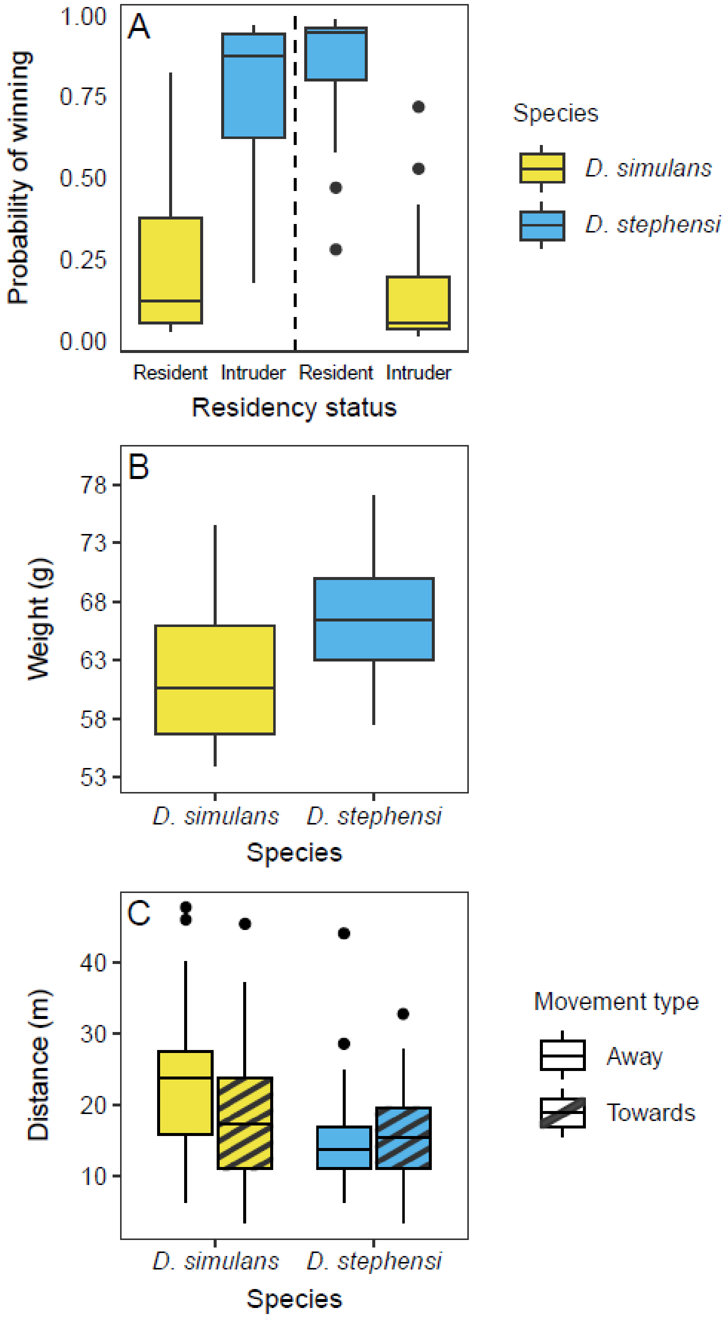

Figure 3. Outcomes and behaviors during staged dyadic interactions between *D. simulans* and *D. stephensi*. A) Probability of winning, by species and residency status. B) Body weight of individuals used in trials, by species. C) Net change in distance

initiated toward or away from the opponent during interactions. Whiskers of the boxplots extend to 1.5x the interquartile range, and any points beyond that are plotted as outliers.

DISCUSSION

Aggressive interference between species can strongly influence their distributions, habitat use, and persistence, making it a critical factor to consider in conservation planning. Understanding the dominance relationship between *D. stephensi* and *D. simulans* was important because the species' ranges overlap extensively and both species are threatened by development, wildfire, and invasive grasses. As the habitat becomes more fragmented and homogenized, direct encounters between the species are expected to increase, elevating the risk of competitive exclusion. In our field enclosure, *D. stephensi* dominated *D. simulans* regardless of residency status. Not only were *D. stephensi* more likely to win individual encounters, but most *D. simulans* movements were directed away from *D. stephensi*, suggesting active avoidance. These findings corroborate the results of a laboratory study (Bleich & Price, 1995), reinforcing the conclusion that *D. stephensi* is consistently dominant over *D. simulans* across contexts.

While species identity was the most important predictor of dominance, there was also a significant effect of residency status, with residents more likely to defeat intruders. This finding is consistent with established research showing that residency increases an individual's willingness to fight (Enquist & Leimar, 1987; Smith & Parker, 1976). Residents may be more motivated to defend their territory or range core due to prior investment in establishing a home range and familiarizing themselves with local resources (Arnott & Elwood, 2008; Smith & Parker, 1976; Takeuchi, 2006). The influence of residency on dominance varies among rodent species. For instance, residency did not predict dominance in a southern Californian rodent community where the species differed substantially in body size (Chock et al., 2018). However, in contests between similarly sized *Rattus* or *Peromyscus* species, residents consistently dominated intruders (Stokes et al., 2012; Wolff et al., 1983). In our study, both residency and species identity influenced contest outcomes, with *D. stephensi* residents having the highest probability of winning. This suggests that residency status plays a role in contest dynamics but that inherent species differences have a greater influence in this system.

Body size differences between species are often a primary determinant of dominance (Chock et al., 2018; Martin & Ghalambor, 2014). *D. stephensi* was significantly heavier than *D. simulans*; however, body weight did not predict contest outcomes. The lack of a strong body size effect in our trials may reflect the relatively small size difference between *D. stephensi* and *D. simulans* (~5 g or ~8%) (Faber & Baylis, 1993). Other factors, such as performance capacity or stamina (Lailvaux et al., 2004; Mowles et al., 2010), strength (Husak et al., 2006; Sneddon et al., 2000), hormone levels (Briffa & Sneddon, 2007), and behavioral traits such as aggressiveness and boldness (Courtene-Jones & Briffa, 2014; Wilson et al., 2013) may better explain why *D. stephensi* dominated *D. simulans*. These factors can influence how often individuals fight (Reaney & Backwell, 2007; Rudin & Briffa, 2012), how quickly they attack (Mowles et al., 2012) and how successful they are at defending a resource (Courtene-Jones & Briffa, 2014).

Habitat associations in our trials mirrored those reported in previous studies: *D. simulans* primarily occupied coastal sage scrub (CSS) habitat with greater than 40% shrub cover and *D. stephensi* primarily occupied habitat with less than 40% shrub cover (Burke et al., 1991; Price et al., 1991). These habitat associations raise the question of why the dominant *D. stephensi* has not expanded further into shrub-dominated habitat. Evidence from previous studies suggests that open habitats confer ecological advantages for *D. stephensi.* Their populations increase following shrub removal (Price et al., 1994b),they consume more grassland seeds (Lowe, 1997; Price et al., 1991), and their foraging strategy of moving quickly between clumped seed patches is better suited to open areas (Lemen & Rosenzweig, 1978; Price & Brown, 1983; Thompson, 1982). Moreover, dense vegetation may hinder bipedal locomotion (Lemen & Rosenzweig, 1978). Thus, ecological constraints and foraging advantages appear to maintain the strong association of *D. stephensi* with open habitats rather than promoting expansion into shrub-dominated areas.

The association of *D. simulans* with CSS habitat may result, at least in part, from displacement by and avoidance of *D. stephensi*. Alternatively, habitat partitioning could reflect divergent predation pressures. Shrub cover reduces exposure to aerial predators (Longland & Price, 1991), but may increase vulnerability to ambush by snakes (Randall, 1993; Webster & Webster, 1971). Morphological differences may shape predator detection strategies: *D. stephensi* has larger auditory bullae than *D. simulans* (Grinnell, 1992)*,* which may enhance their ability to detect low-frequency predator sounds (e.g., the swoop of an owl) (Webster, 1962). Venom resistance may also play a role; although untested in these species, at least one congener, *D. ordii*, exhibits resistance to rattlesnake venom (Balchan et al., 2024). In addition, exploitative competition with other rodent species associated with either grassland or CSS could further reinforce habitat segregation.

While these ecological and behavioral factors may help explain the current habitat segregation between the species, further work is needed to determine how general these patterns are across populations and landscapes. The majority of our trials took place at one reserve, the Southwestern Riverside County Multispecies Reserve. However, 4 trials were run at Motte Rimrock Reserve, approximately 32 km away, and the results from these trials followed the same trend as the rest. In all 4 trials that took place at Motte reserve, *D. stephensi* won the majority of encounters (88-100%) and was dominant over *D. simulans*. It is important to note that the behaviors that we observed in the arena might differ from how *D. stephensi* and *D. simulans* interact under more natural conditions. Although our arena was relatively large compared to those used in similar studies (Bleich & Price, 1995; Chock et al., 2018), spatial constraints may have increased the frequency and intensity of interactions. Nevertheless, given the strong effect of species identity in our study, we expect that *D. stephensi* dominates *D. simulans* under natural conditions as well.

Our findings have direct implications for the conservation and management of both species. Given that *D. stephensi* is dominant, the fitness of established populations of *D. stephensi* is unlikely to be greatly reduced by the presence of *D. simulans*. Our results similarly suggest that translocated *D. stephensi* would not be excluded by *D. simulans* residents. However, further research should explore how these species interact in the context of a translocation, where additional factors, such as increased stress of translocated individuals, may affect the outcome of interactions. Although exclusion of *D. simulans* from *D. stephensi* release sites is likely unnecessary, placing *D. stephensi* on the periphery, rather than center, of *D. simulans* populations might reduce the frequency of energetically costly fights. In general, stable coexistence is expected when habitat specialization and spatial heterogeneity allow species to partition resources (Boeye et al., 2014). However, increasing fire frequency —exacerbated by climate change— (Goss et al., 2020; Swain, 2021) is accelerating the conversion of CSS to invasive grassland (Talluto & Suding, 2008). This transition disproportionately impacts *D. simulans*, which relies on shrub-dominated habitat for cover and resources. As landscape heterogeneity declines, *D. simulans* may become increasingly restricted to shrinking habitat refugia, while *D. stephensi* gains ground in newly created grasslands. In such homogenized systems, behavioral avoidance of *D. stephensi* could reduce the time *D. simulans* spends foraging or engaging in essential maintenance behaviors, compounding the fitness costs of habitat loss. While recovery planning for *D. stephensi* remains a priority, co-management strategies that preserve CSS structure and reduce conflict zones will be critical to ensure long-term coexistence and mitigate unintended impacts on *D. simulans* populations.

CONCLUSIONS

We provide the first field-based evidence that *D. stephensi* is consistently dominant over *D. simulans* regardless of residency status. This finding has important implications for shared habitat management and conservation planning. *D. stephensi* appears to prefer open grassland habitat. *D. simulans*, however, may be restricted to

CSS habitat because it is being displaced by the dominant *D. stephensi*. Interactions between *D. simulans* and *D. stephensi* could be energetically costly and may further restrict *D. simulans* to smaller habitat patches as intense fires in southern California convert CSS to grassland habitat. Without targeted management that preserves or restores CSS structure, *D. simulans* populations may face continued decline driven by both environmental change and behavioral exclusion. By clarifying the dominance relationship between these species, our study provides a starting point for developing conservation strategies that account for species interactions in fragmented landscapes.

SUPPLEMENTARY MATERIAL

Table S1. Behaviors recorded in staged dyadic interactions

Behavior	Description
Aggressive behaviors	
Displacement	Facing and approaching the dyad partner, whereupon the dyad partner withdraws
Chase	Rapidly pursuing the dyad partner as it moves away
Lunge threat	A sudden strong movement or jump forward toward the dyad partner
Attack	Contact initiated by the focal animal that includes hitting with feet, biting, or bodies locked and rolling over
Submissive behaviors	
Jump/avoid	Jumping upwards and back while facing the dyad partner
Displaced	Moving away in response to approaching dyad partner (Chock et al. 2018)
Flee	Rapidly moving away from dyad partner
Withdraw	Moving away from dyad partner at a pace slower than fleeing
Other Behaviors	
Approach	Approaching within one body length of the other animal whereupon the dyad partner doesn't withdraw
Sandbathing	Rubbing side or ventrum against the sand (Randall 1981)
Digging	Pushing and pulling of sand with feet
Footdrumming	Striking of hind feet on the ground (Randall 1984)
Locomotion	Time spent moving around alone

References for Table S1.

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. *Animal Behaviour*, *137*, 197–204. https://doi.org/10.1016/j.anbehav.2018.01.015

Randall, J. A. (1981). Comparison of sandbathing and grooming in two species of kangaroo rat. *Animal Behavior*, *29*(4), 1213–1219. https://doi.org/10.1016/S0003-3472(81)80072-3

Randall, J. A. (1984). Territorial defense and advertisement by footdrumming in Bannertail kangaroo rats (Dipodomys spectabilis) at high and low population densities. *Behavioral Ecology and Sociobiology*, *16*(1), 11–20. **https://doi.org/10.1007/BF00293099**

Table S2. Conditional logistic regression results from the model that included all 9-minute videos and the 6 videos shorter than 9 minutes. Number of wins in each pair is the dependent variable, and species, residency status, normalized weight, and sex are the independent variables. Individual ID was included as a random intercept. Means and SE are on the log-odds scale.

Model term	**Estimate**	**SE**	**Odds ratio**	***p***
Species	1.97	0.36	7.15	p <0.001
Residency	0.40	0.20	1.50	0.044
Normalized weight	-0.05	0.26	0.95	0.856
Sex	0.12	0.49	1.12	0.812

Table S3. Conditional logistic regression results using data only collected at the Southwestern Riverside County Multispecies Reserve (n = 41). Number of wins in each pair is the dependent variable, and species, residency status, normalized weight, and sex are the independent variables. Individual ID was included as a random intercept. Means and SE are on the log-odds scale.

Model term	**Estimate**	**SE**	**Odds ratio**	***p***
Species	1.74	0.40	5.75	p <0.001
Residency status	0.72	0.24	2.06	0.003
Normalized weight	-0.07	0.30	0.93	0.814
Sex	0.16	0.56	1.17	0.773

Table S4. Conditional logistic regression results using data from only the videos that had infrared light on during the trial. Data from videos taken under red lights were not included. Number of wins in each pair is the dependent variable, and species, residency status, normalized weight, and sex are the independent variables. Individual ID was included as a random intercept. Means and SE are on the log-odds scale.

Model term	**Estimate**	**SE**	**Odds ratio**	***p***
Species	2.23	0.35	9.30	p <0.001
Residency status	0.85	0.25	2.34	0.001
Normalized weight	0.25	0.32	1.28	0.433
Sex	0.35	0.61	1.42	0.569

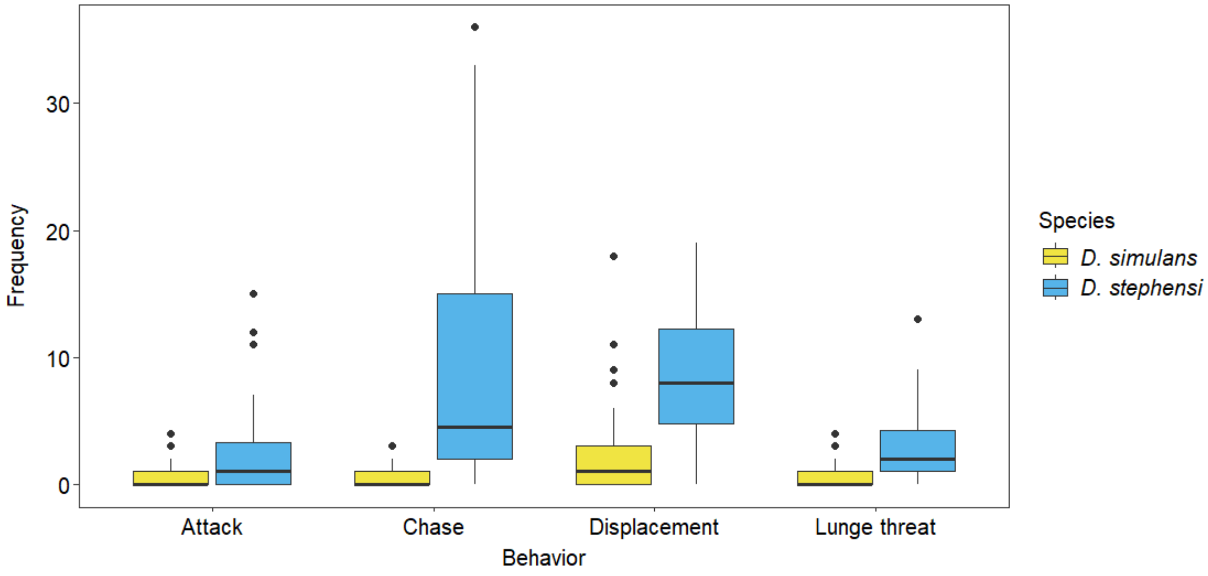

Figure S1. Frequency of aggressive behaviors and displacements displayed by *Dipodomys simulans* and *D. stephensi* during dyadic interaction trials.

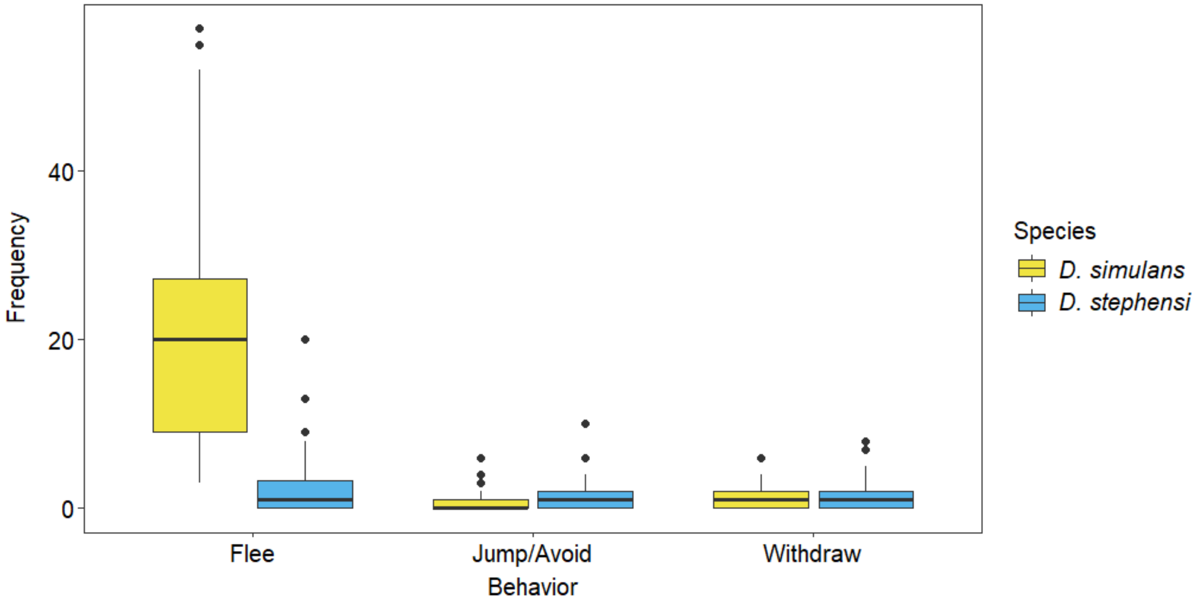

Figure S2. Frequency of submissive behaviors displayed by *Dipodomys simulans* and *D. stephensi* during dyadic interaction trials.

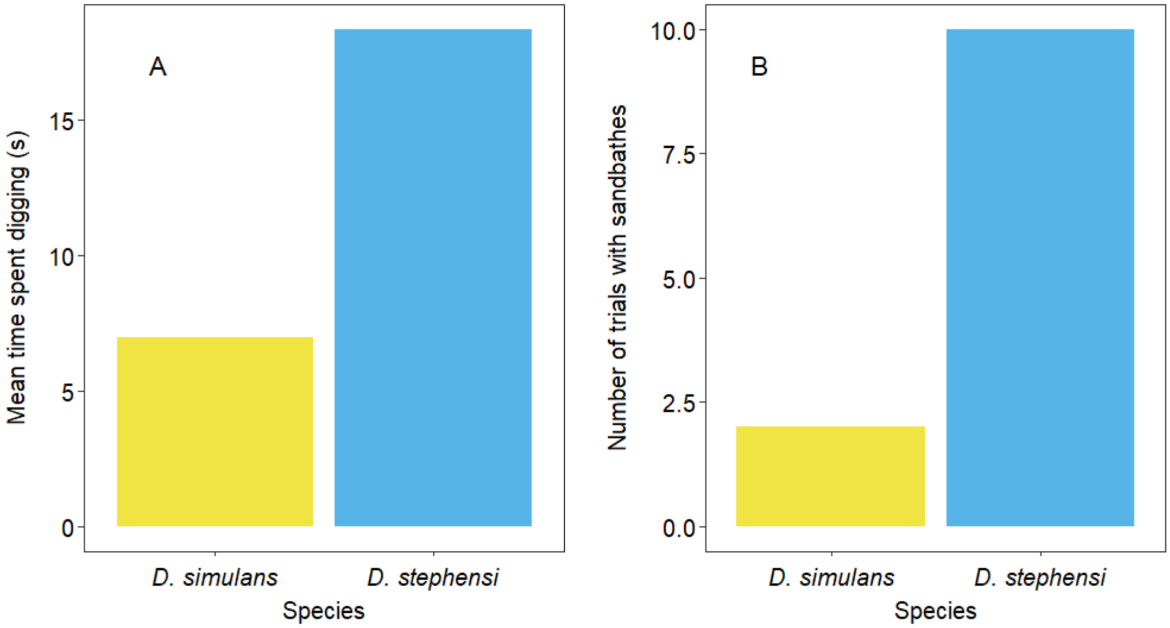

Figure S3. Maintenance behaviors by *Dipodomys simulans* and *D. stephensi* during interaction trials. (A) Mean time spent digging (seconds). (B) Number of trials in which the species sandbathed.

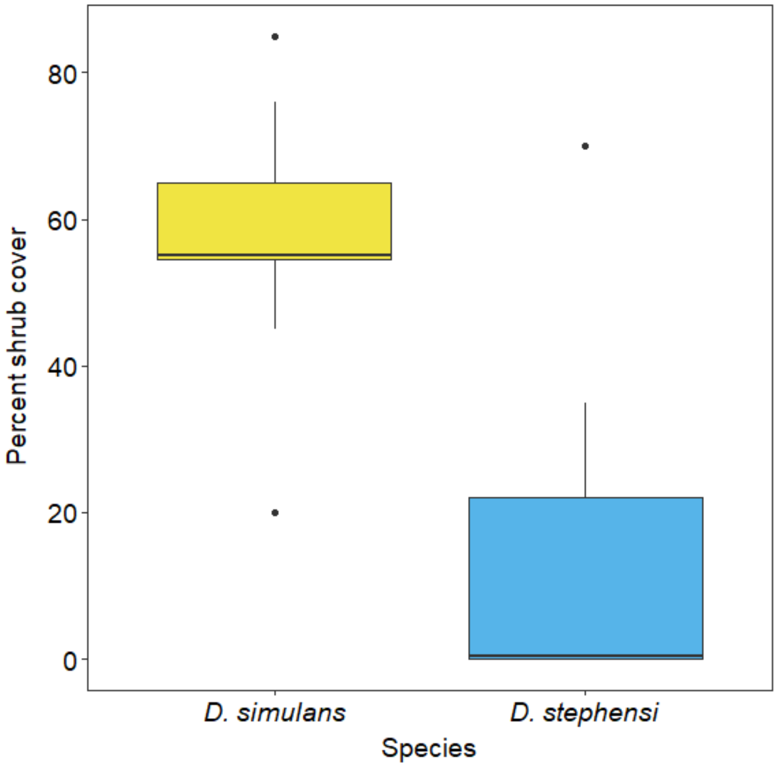

Figure S4. Percent shrub cover at crown height measured in 10 × 10 m plots centered on capture locations of resident *Dipodomys stephensi* and *D. simulans*.

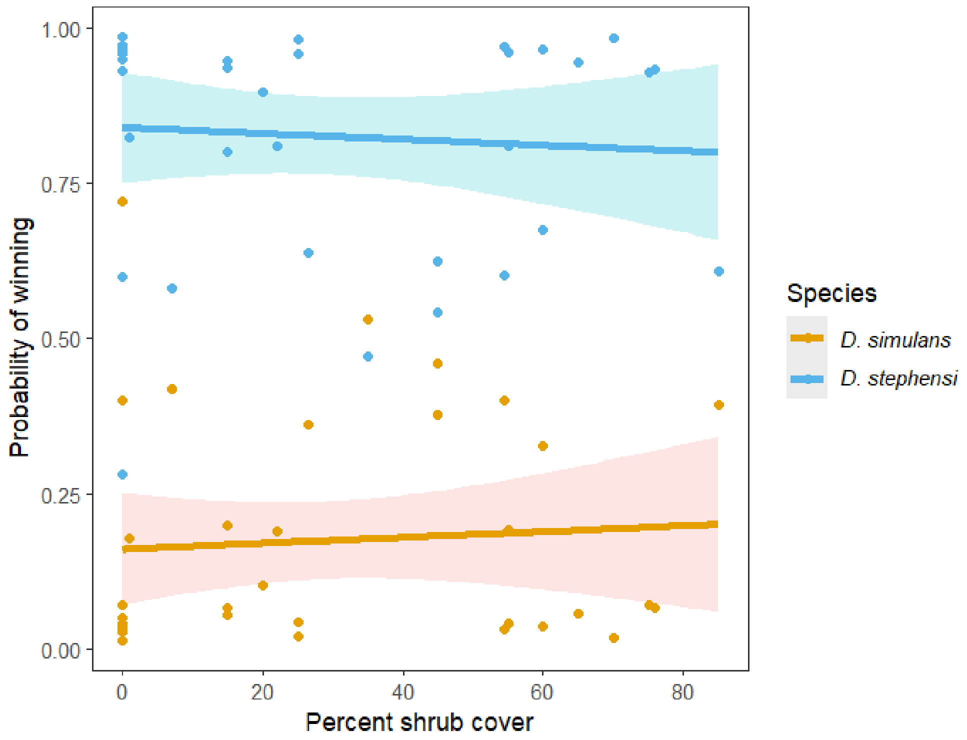

Figure S5. Probability of winning a dyadic encounter as a function of species identity and percent shrub cover at crown height at resident capture locations.

REFERENCES

Alexander, L. F., & Riddle, B. R. (2005). Phylogenetics of the new world rodent family Heteromyidae. *Journal of Mammalogy*, *86*(2), 366–379. https://doi.org/10.1644/BER-120.1

Angert, A. L., LaDeau, S. L., & Ostfeld, R. S. (2013). Climate change and species interactions: ways forward. *Annals of the New York Academy of Sciences*, *1297*(1), 1–7. https://doi.org/10.1111/NYAS.12286

Arnott, G., & Elwood, R. W. (2008). Information gathering and decision making about resource value in animal contests. *Animal Behaviour*, *76*(3), 529–542. https://doi.org/10.1016/J.ANBEHAV.2008.04.019

Balchan, N. R., Smith, C. F., & Mackessy S. P. (2024). A plethora of rodents: Rattlesnake predators generate unanticipated patterns of venom resistance in a grassland ecosystem. *Toxicon: X, 21*, 100179. https://doi.org/10.1016/j.toxcx.2023.100179.

Balchan NR, Smith CF, Mackessy SP. A plethora of rodents: Rattlesnake predators generate unanticipated patterns of venom resistance in a grassland ecosystem. Toxicon X. 2023 Dec 1;21:100179. doi: 10.1016/j.toxcx.2023.100179.

Banks, S. C., Piggott, M. P., Stow, A. J., & Taylor, A. C. (2007). Sex and sociality in a disconnected world: A review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology*, *85*(10), 1065–1079. https://doi.org/10.1139/Z07-094

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E.

A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*, 51–57. https://doi.org/10.1038/nature09678

Blaustein, A. R., & Risser, A. C. (1976). Interspecific interactions between three sympatric species of kangaroo rats (*Dipodomys*). *Animal Behaviour*, *24*(2), 381–385. https://doi.org/10.1016/S0003-3472(76)80047-4

Bleich, V. C. (1977). *Dipodomys stephensi*. *The American Society of Mammologists*, *73*, 1–3.

Bleich, V. C., & Price, M. V. (1995). Aggressive behavior of *Dipodomys stephensi*, an endangered species, and *Dipodomys agilis*, a sympatric congener. *Journal of Mammalogy*, *76*(2), 646–651. https://doi.org/10.2307/1382373

Boeye, J., Kubisch, A., & Bonte, D. (2014). Habitat structure mediates spatial segregation and therefore coexistence. *Landscape Ecology*, *29*, 593–604. https://doi.org/10.1007/s10980-014-0010-6

Bregman, T. P., Lees, A. C., Seddon, N., Macgregor, H. E. A., Darski, B., Aleixo, A., Bonsall, M. B., & Tobias, J. A. (2015). Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology*, *96*(10), 2692–2704. https://doi.org/10.1890/14-1731.1

Briffa, M., & Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Functional Ecology*, *21*(4), 627–637. https://doi.org/10.1111/J.1365-2435.2006.01188.x

Burke, R. L., Tasse, J., Badgley, C., Jones, S. R., Fishbein, N., Phillips, S., & Soule, M. E. (1991). Conservation of the Stephens' Kangaroo Rat (*Dipodomys stephensi*):

Planning for persistence. *Bulletin of the Southern California Academy of Sciences*, *90*(1), 10–40.

California Natural Diversity Database (CNDDB). (2024). *Special Animals List*.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5). https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Chappell, M. A. (1978). Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*). *Ecology*, *59*(3), 565–579. https://doi.org/10.2307/1936586

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/ 10.1126/science.1206432. PMID: 21852500.

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. *Animal Behaviour*, *137*, 197–204. https://doi.org/10.1016/j.anbehav.2018.01.015

Courtene-Jones, W., & Briffa, M. (2014). Boldness and asymmetric contests: role- and outcome-dependent effects of fighting in hermit crabs. *Behavioral Ecology*, *25*(5), 1073–1082. https://doi.org/10.1093/beheco/aru085

Elff M (2022). mclogit: Multinomial Logit Models, with or without Random Effects or Overdispersion. R package version 0.9.6. https://CRAN.R-project.org/package=mclogit.

Enquist, M., & Leimar, O. (1987). Evolution of fighting behaviour: The effect of variation In resource value. *Journal of Theoretical Biology, 127*(2), 187-205. https://doi.org/10.1016/S0022-5193(87)80130-3

Faber, D. B., & Baylis, J. R. (1993). Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). *Animal Behaviour*, *45*(2), 289–299. https://doi.org/10.1006/anbe.1993.1033

Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(47), 11982–11987. https://doi.org/10.1073/pnas.1804224115

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Goldingay, R. L., & Price, M. V. (1997). Influence of season and a sympatric congener on habitat use by Stephens’ kangaroo rat. *Conservation Biology*, *11*(3), 708–717. https://doi.org/10.1046/j.1523-1739.1997.95480.x

Goss, M., Swain, D. L., Abatzoglou, J. T., Sarhadi, A., Kolden, C. A., Williams, A. P., &

Diffenbaugh, N. S. (2020). Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. *Environmental Research Letters*, *15*(9). https://doi.org/10.1088/1748-9326/ab83a7

Grether, G. F., Anderson, C. N., Drury, J. P., Kirschel, A. N. G., Losin, N., Okamoto, K., & Peiman, K. S. (2013). The evolutionary consequences of interspecific aggression. *Annals of the New York Academy of Sciences*, *1289*(1), 48–68. https://doi.org/10.1111/nyas.12082

Grether, G. F., Peiman, K. S., Tobias, J. A., & Robinson, B. W. (2017). Causes and consequences of behavioral interference between species. *Trends in Ecology and Evolution, 32*(10), 760–772. https://doi.org/10.1016/j.tree.2017.07.004

Grinnell, J. (1922). A geographical study of the kangaroo rats of California. *University of California Publications in Zoology*, 24, 1-124

Hammond, T.T., Curtis, M.J., Jacobs, L.E., Tobler, M.W., Swaisgood, R.R. & Shier, D.M. (2021). Behavior and detection method influence detection probability of a translocated, endangered amphibian. *Animal Conservation*, *24*(3), 401-411. https://doi.org/10.1111/acv.12645

Husak, J. F., Lappin, A. K., Fox, S. F., & Lemos-Espinal, J. A. (2006). Bite-force performance predicts dominance in male venerable collared lizards (Crotaphytus antiquus). *Copeia*, *2*, 301–306. https://doi.org/10.1643/0045-8511(2006)6[301:BPPDIM]2.0.CO;2

Jankowski, J. E., Robinson, S. K., & Levey, D. J. (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, *91*(7), 1877–1884. https://doi.org/10.1890/09-2063.1

Kelt, D. A., Konno, E. S., & Wilson, J. A. (2005). Habitat management for the endangered Stephens' Kangaroo Rat: The effect of mowing and grazing. *The Journal of Wildlife Managment*, *69*(1), 424–429. http://www.jstor.org/stable/3803619

Koivula, K., Lahti, K., Orell, M., & Rytkönen, S. (1993). Prior residency as a key determinant of social dominance in the willow tit (*Parus montanus*). *Behavioral Ecology and Sociobiology*, *33*, 283–287. https://doi.org/10.1007/BF02027126

Lackey, J. A. (1967). Biosystematics of Heermanni group kangaroo rats in southern California. *Transactions of the San Diego Society of Natural History*, *14*(22), 313–344.

Lailvaux, S. P., Herrel, A., VanHooydonck, B., Meyers, J. J., & Irschick, D. J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (Anolis carolinensis). *Proceedings of the Royal Society B: Biological Sciences*, *271*(1556), 2501–2508. https://doi.org/10.1098/RSPB.2004.2891

Langkilde, T., & Shine, R. (2004). Competing for crevices: Interspecific conflict influences retreat-site selection in montane lizards. *Oecologia*, *140*(4), 684–691. https://doi.org/10.1007/s00442-004-1640-1

Lemen, C. A., & Rosenzweig, M. L. (1978). Microhabitat selection in two species of heteromyid rodents. *Oecologia*, *33*(2), 127–135. https://doi.org/10.1007/BF00344843

Lenth R (2025). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.11.1-00001, https://rvlenth.github.io/emmeans/.

Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, *6*(4), 169–176. https://doi.org/10.1046/j.1472-4642.2000.00069.x

Linnell, J. D. C., Strand, O., & Landa, A. (1999). Use of dens by red Vulpes vulpes and arctic Alopex lagopus foxes in alpine environments: Can inter-specific competition explain the non-recovery of Norwegian arctic fox populations? *Wildlife Biology*, *5*(3), 167–176. https://doi.org/10.2981/wlb.1999.021

Longland, W. S., & Dimitri, L. A. (2021). Kangaroo rats: Ecosystem engineers on western rangelands. *Rangelands*, *43*(2), 72–80. https://doi.org/10.1016/J.RALA.2020.10.004

Longland, W. S., & Price, M. V. (1991). Direct observations of owls and Heteromyid rodents: Can predation risk explain microhabitat use? *Ecology*, *72*(6), 2261–2273.

Lowe, M. (1997). Diet of Stephens' Kangaroo Rat, *Dipodomys stephensi*. *The Southwestern Naturalist*, *42*(3), 358–361.

Martin, P. R., & Ghalambor, C. K. (2014). When David beats goliath: The advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLoS ONE*, *9*(9). https://doi.org/10.1371/journal.pone.0108741

Martin, P. R., & Martin, T. E. (2001). Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. *Ecology*, *82*(1), 189–206. https://doi.org/10.1890/0012-9658(2001)082[0189:EAFCOS]2.0.CO;2

Mowles, S. L., Cotton, P. A., & Briffa, M. (2010). Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, *80*(2), 277–282. https://doi.org/10.1016/J.ANBEHAV.2010.05.004

Mowles, S. L., Cotton, P. A., & Briffa, M. (2012). Consistent crustaceans: The identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology*, *66*(7), 1087–1094. https://doi.org/10.1007/s00265-012-1359-7

Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E. M., Woinarski, J. C. Z., & Di Marco, M. (2020). Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications 11*, 1–9. https://doi.org/10.1038/s41467-020-16684-w

Patterson, C. W., & Drury, J. P. (2023). Interspecific behavioural interference and range dynamics: current insights and future directions. *Biological Reviews*, *98*(6), 2012–2027. https://doi.org/10.1111/brv.12993

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M, Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/ 10.1126/science.1246752. PMID: 24876501.

Price, M. V., & Brown, J. H. (1983). Patterns of morphology and resource use in North American desert rodent communities. *Great Basin Naturalist Memoirs*, *7*, 8–9. https://scholarsarchive.byu.edu/gbnm/vol7/iss1/8

Price, M. V, Goldingay, R. L., Szychowski, L. S., & Waser, N. M. (1994a). Managing habitat for the endangered Stephens' Kangaroo Rat (*Dipodomys stephensi*): Effects of shrub removal. *American Midland Naturalist*, *131*(1), 9–16. https://doi.org/10.2307/2426603

Price, M. V, Kelly, P. A., & Goldingay, R. L. (1994b). Distances moved by Stephens' Kangaroo Rat (*Dipodomys stephensi* Merriam) and implications for conservation.

American Society of Mammologists, *75*(4), 929–939. https://doi.org/10.2307/1382474

Price, M. V, Longland, W. S., & Goldingay, R. L. (1991). Niche relationships of *Dipodomys agilis* and *D. stephensi*: Two sympatric kangaroo rats of similar size. *The American Midland Naturalist*, *126*(1), 172–186. https://doi.org/10.2307/2426161

Qvarnström, A., Wiley, C., Svedin, N., & Vallin, N. (2009). Life-history divergence facilitates regional coexistence of competing Ficedula flycatchers. *Ecology*, *90*(7), 1948–1957. https://doi.org/10.1890/08-0494.1

Randall, J. A. (1993). Behavioral adaptations of desert rodents (Heteromyidae). *Animal Behaviour*, *45*, 263–287.

Randall, J. A., Hekkala, E. R., Cooper, L. D., & Barfield, J. (2002). Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. *Animal Behaviour*, *64*(1), 11–21. https://doi.org/10.1006/ANBE.2002.3029

R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reaney, L. T., & Backwell, P. R. Y. (2007). Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behavioral Ecology*, *18*(3), 521–525. https://doi.org/10.1093/BEHECO/ARM014

RECON. 1995. Stephens' kangaroo rat literature review. Pages 1–39 in Riverside County Habitat Conservation Agency, editor. Habitat conservation plan for the Stephens' kangaroo rat in western Riverside County, California. Volume II.

Technical reports. Riverside County Habitat Conservation Agency, Riverside, California.

Rudin, F. S., & Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1735), 1904–1910. https://doi.org/10.1098/RSPB.2011.2418

Shier, D.M., Chock, R.Y., Zellmer, A.J., Wilder, A.P., Chaille, A.Y., Shomo, B., Ryder, O.A., and Steiner, C. (2025). Conservation in the Anthropocene: Using genetics to understand the past and manage for the future of the endangered Stephens' kangaroo rat. *Evolutionary Applications*, *18*(8), e70152. https://doi.org/10.1111/eva.70152.

Shier, D. M., Navarro, A. Y., Tobler, M., Thomas, S. M., King, S. N. D., Mullaney, C. B., & Ryder, O. A. (2021). Genetic and ecological evidence of long-term translocation success of the federally endangered Stephens' kangaroo rat. *Conservation Science and Practice*, *3*(9), e478. https://doi.org/10.1111/CSP2.478

Shier, D. M., & Randall, J. A. (2007). Use of different signaling modalities to communicate status by dominant and subordinate Heermann's kangaroo rats (*Dipodomys heermanni*). *Behavioral Ecology and Sociobiology*, *61*(7), 1023–1032. https://doi.org/10.1007/s00265-006-0335-5

Shier, D. M., & Swaisgood, R. R. (2012). Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology*, *26*(1), 116–123. https://doi.org/10.1111/j.1523-1739.2011.01748.x

Sikes, R. S., & the Animal Care and Use Committee of the American Society of Mammologists. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. In *Journal of Mammalogy* (Vol. 97, Issue 3, pp. 663–688). https://doi.org/10.1093/jmammal/gyw078

Smith, J. M., & Parker, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour*, *24*(1), 159–175. https://doi.org/10.1016/S0003-3472(76)80110-8

Sneddon, L. U., Huntingford, F. A., Taylor, A. C., & Orr, J. F. (2000). Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). *Journal of Zoology*, *250*(3), 397–403. https://doi.org/10.1111/J.1469-7998.2000.TB00783.X

Stokes, V. L., Banks, P. B., & Pech, R. P. (2012). Influence of residency and social odors in interactions between competing native and alien rodents. *Behavioral Ecology and Sociobiology*, *66*(2), 329–338. https://doi.org/10.1007/s00265-011-1280-5

Sullivan, R. M., & Best, T. L. (1997). Systematics and morphologic variation in two chromosomal forms of the Agile Kangaroo Rat (*Dipodomys agilis*). *Journal of Mammalogy*, *78*(3), 775–797. https://doi.org/10.2307/1382936

Swain, D. L. (2021). A shorter, sharper rainy season amplifies California wildfire risk. *Geophysical Research Letters*, *48*, e2021GL092843. https://doi.org/10.1029/2021GL092843

Takeuchi, T. (2006). Matter of size or matter of residency experience? Territorial contest in a green hairstreak, *Chrysozephyrus smaragdinus* (Lepidoptera: Lycaenidae). *Ethology*, *112*(3), 293–299. https://doi.org/10.1111/J.1439-0310.2006.01140.X

Talluto, M. V., & Suding, K. N. (2008). Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology*, *23*(7), 803–815. https://doi.org/10.1007/S10980-008-9238-3/FIGURES/3

Tannerfeldt, M., Elmhagen, B., & Angerbjörn, A. (2002). Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, *132*(2), 213–220. https://doi.org/10.1007/s00442-002-0967-8

Thompson, S. D. (1982). Microhabitat utilization and foraging behavior of bipedal and quadrupedal Hetermoyid rodents. *Ecology*, *63*(5), 1303–1312. https://doi.org/10.2307/1938858

Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature 1994 371:6492*, *371*(6492), 65–66. https://doi.org/10.1038/371065a0

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/J.1461-0248.2008.01250.X

U.S. Fish and Wildlife Service (USFWS). (2020). Species Report for the Stephens' kangaroo rat (*Dipodomys stephensi*). Version 1.1, July 30, 2020. U.S. Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California. xi -125.

U.S. Fish and Wildlife Service (USFWS). (2022). Reclassification of Stephens' Kangaroo Rat from endangered to threatened with a section 4(d) rule. *Federal Register*, 87(33), 8967-8981.

U.S. Geological Survey (USGS) - Gap Analysis Project (GAP), 2018, Dulzura Kangaroo Rat (*Dipodomys simulans*) mDZRAx_CONUS_2001v1 Range Map: U.S. Geological Survey data release, https://doi.org/10.5066/F7DJ5DS1.

Ward, D. W., & Randall, J. A. (1987). Territorial defense in the bannertail kangaroo rat (*Dipodomys spectabilis*): footdrumming and visual threats. *Behavioral Ecology and Sociobiology*, *20*(5), 323–328. https://doi.org/10.1007/BF00300678

Webster, D. B. (1962). A function of the enlarged middle-ear cavities of the kangaroo rat (Dipodomys). *Physiological Zoology, 35*(3), 248-255. http://www.jstor.org/stable/30152809

Webster D. B., & Webster M. (1971) Adaptive value of hearing and vision in kangaroo rat predator avoidance. *Brain Behavior and Evolution, 4*(4), 310–322. https://doi.org/10.1159/000125441

Williams, D., Tordoff, W. I., & Germano, D. (1997). Evaluation of methods for permanently marking kangaroo rats (Dipodomys: Heteromyidae). In T. Yates, W. Gannon, & D. Wilson (Eds.), *Life among the muses: papers in honor of James S. Findley* (Spec Publ, p. 290). papers3://publication/uuid/40A1EF7F-B379-436D-872B-6AB897D03482

Williams, J. J., Freeman, R., Spooner, F., & Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology*, *28*(3), 797–815. https://doi.org/10.1111/GCB.15978

Wilson, A. J., Grimmer, A., & Rosenthal, G. G. (2013). Causes and consequences of contest outcome: Aggressiveness, dominance and growth in the sheepshead swordtail, *Xiphophorus birchmanni*. *Behavioral Ecology and Sociobiology*, *67*(7), 1151–1161. https://doi.org/10.1007/S00265-013-1540-7

Wolff, J. O., Freeberg, M. H., & Dueser, R. D. (1983). Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). *Behavioral Ecology and Sociobiology*, *12*(3), 237–242. https://doi.org/10.1007/BF00290776

Ziv, Y., Abramsky, Z., Kotler, B. P., & Subach, A. (1993). Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos*, *66*(2), 237–246. https://doi.org/10.2307/3544810

CHAPTER 3:

COMPETITION DRIVES SPATIAL SEGREGATION BETWEEN TWO THREATENED RODENT SPECIES

ABSTRACT

Interspecific competition can be an important driver of resource partitioning between ecologically similar species, but it is often difficult to disentangle the effects of competition from evolved habitat preferences. Understanding how competition influences space use and activity patterns is especially important in the face of rapid environmental changes that constrain species' distributions and increase contact between competitors. The kangaroo rats *Dipodomys stephensi* and *D. simulans* are ecologically similar, sympatric species of conservation concern that overlap in habitat use and compete for seeds both exploitatively and through direct aggressive interference. These species partially segregate into different microhabitat types, but it was unclear whether the spatial segregation results from ongoing interspecific competition. We used a passive monitoring system along a natural habitat gradient to quantify the species' space use and activity patterns throughout the year. We quantified temporal segregation and individual-level spatial overlap and used joint species distribution modeling to test for negative species associations independent of habitat covariates. We found no evidence for temporal segregation, but even after accounting for differences in habitat use, the species' spatial distributions were almost perfectly negatively correlated (> -0.99), indicating that interspecific competition contributes strongly to spatial segregation. These results highlight the need for conservation plans, such as translocations, population augmentation, and habitat management, to explicitly consider both habitat requirements and species interactions. Managers should prioritize conserving habitat heterogeneity to support resource partitioning between these species and promote long-term coexistence.

INTRODUCTION

Understanding how ecologically similar species coexist despite shared resource requirements has long been a central question in ecology (Hutchinson, 1961; Leibold and Mcpeek, 2006; MacArthur and Levins, 1964). When species overlap in resource use, competition can occur through exploitation, in which shared resources are depleted, or interference, which involves direct and often costly interactions such as territorial exclusion and allelopathy (Grether et al., 2017). Although classic theory predicts competitive exclusion when interspecific competition is strong (Amarasekare, 2002), contemporary coexistence theory demonstrates that species can persist when stabilizing mechanisms favor niche differentiation or when intraspecific exceeds interspecific competition (Chesson, 2000; Grether and Okamoto, 2022; Hillerislambers et al., 2012).

Competition frequently leads to partitioning of habitat, food, or time, and such niche differentiation is often necessary for coexistence. Desert small mammals provide well-known examples: two *Gerbillus* species prefer the same microhabitat, but shift microhabitat use and activity times in sympatry (Ziv et al., 1993), and *Microtus ochrogaster* modify their spatial and temporal patterns when a dominant interspecific competitor is breeding (Glass and Slade, 1980). Spatial avoidance can also occur at fine scales; for instance, subordinate carnivores reduce use of areas heavily used by dominant species even when broad habitat use overlaps (Berger and Gese, 2007; Dröge et al., 2017). These examples highlight that competition can structure space use across multiple behavioral and ecological dimensions.

The role of competition in shaping space use has become increasingly important to understand as habitat loss, invasive plants, altered fire regimes, and climate change restructure species distributions. Environmental change can compress species into smaller patches, force novel species assemblages, and intensify competitive interactions (Bregman et al., 2015; Freeman et al., 2018; Linnell et al., 1999). Even when resources remain sufficient, interference can reduce access for subordinate species, lowering fitness and population persistence (Grether et al., 2013). Identifying when and how competition shapes species distributions is therefore essential for anticipating community responses to rapid global change.

Two threatened sympatric heteromyid rodents in southern California, the Stephens' kangaroo rat (*Dipodomys stephensi*) and the Dulzura kangaroo rat (*D. simulans*), provide an ideal system for evaluating how competition influences space use. The species occur across a mosaic of forb dominated annual grassland and coastal sage scrub (CSS), habitats degraded and fragmented by development, invasive grasses, and fire (USFWS 2020, Talluto 2008). *D. stephensi* is listed as threatened under state and federal Endangered Species Acts (USFWS 2022; CNDDB 2024), and *D. simulans*, formerly part of *D. agilis* (Sullivan and Best, 1997), is considered vulnerable at the state level (CNDDB, 2024). Both species are solitary, nocturnal granivores (Longland and Dimitri, 2021) that vary subtly in morphology and behavior (Price et al., 1991), making competition for space and food highly likely where their distributions overlap.

Previous studies have shown partial habitat segregation where the species co-occur: *D. stephensi* primarily occupies annual grasslands while *D. simulans* is more common in coastal sage scrub (CSS), with both species using the intervening ecotone (Goldingay and Price, 1997; Price et al., 1991). *D. stephensi* consistently dominates *D. simulans* in direct encounters in the laboratory (Bleich and Price, 1995) and field (see Chapter 2) and *D. simulans* actively avoids *D. stephensi* (see Chapter 2). But the extent to which habitat segregation is caused by ongoing competitive displacement versus evolved differences in habitat preferences is unknown. This distinction may be crucial for conservation management. If habitat segregation between these species is entirely a product of divergence in habitat preferences in the evolutionary past, the focus should be on protecting or restoring both habitats. However, if habitat segregation is driven by ongoing interference competition, that would likely mean that the presence of *D. stephensi* restricts *D. simulans* to a fraction of its remaining available habitat. In fact, *D. simulans* has been reported to prefer open habitat in areas where it does not overlap geographically with *D. stephensi* (Price and Waser, 1984). If *D. stephensi* limits the habitat use of *D. simulans* in sympatry*,* more research would be needed to develop a co-management plan that takes the competitive asymmetry into account.

To evaluate whether *D. stephensi* actively displaces *D. simulans* from suitable habitat at locations where the species co-occur, we obtained year-round data on fine-scale space use and activity of both species across a natural habitat gradient. Experimental removals are the classic way to test for effects of contemporary interspecific competition (Schoener, 1983) but less invasive methods are required for at-risk species. We evaluated the potential for active competition using joint species distribution models (JSDMs), an approach that models species responses to environmental factors and infers biotic interactions through model residuals (Pollock et al., 2014; Tikhonov et al., 2020). We also quantified individual-level spatial overlap with conspecifics and heterospecifics and tested for temporal partitioning in nocturnal activity. By integrating behavioral, spatial, and temporal dimensions of habitat use, our study provides insight into the mechanisms that promote coexistence and informs the management of two co-occurring at-risk species whose interactions are likely to intensify under ongoing habitat change.

METHODS

Study site

This study was conducted in 2022-2023 at the Southwestern Riverside County Multispecies Reserve (117.025°W, 33.580°N) in southern California. We selected a 1.43 ha area (130 m x 110 m) occupied by both *D. stephensi* and *D. simulans*. The site encompassed a habitat gradient from annual grassland to coastal sage scrub (CSS) on the margin of an old-field plateau (Fig. 1). Vegetation included annual forbs, non-native grasses, and native shrubs such as *Eriogonum fasciculatum*.

Passive Monitoring system

We used a passive Small Scale Monitoring System (Biomark, Boise, ID, U.S.A.) to detect the locations of individual kangaroo rats implanted with uniquely coded Passive Integrated Transponder (PIT) tags. Each PIT tag was 8 mm long and encoded a unique 15-digit identification number. Tags were activated by 25 cm circular antennas that continuously broadcast a radio frequency which triggered a tag’s response when within the detection radius (~ 12 cm). Antennas recorded detections once per second, including the tag ID, antenna number, and timestamp.

Site set-up and trapping

We established a 12 x 10 grid with 10 m spacing, marked with numbered stake flags (Fig. 1). The grid was divided into four subsections, and 30 antennas were deployed at a time in a 3 x 10 grid configuration within one subsection. The short axis of the antenna grid ran parallel to the habitat gradient, while the long axis spanned grassland to CSS. Antennas were relocated approximately monthly until all four subsections had been sampled. Sampling was conducted during two seasonal periods, nonbreeding season (September 24th 2022 - February 28th 2023) and breeding season (April 26th 2023 – August 23rd 2023), to account for potential seasonal changes in home range (Kelly and Price 1992), vegetation, and foraging (Reichman and Price 1993, pp.548-549). The breeding season for *D. stephensi* typically extends from late spring to early summer (Bleich, 1977; Burke et al., 1991), though higher than average rainfall in 2023 likely extended the breeding season.

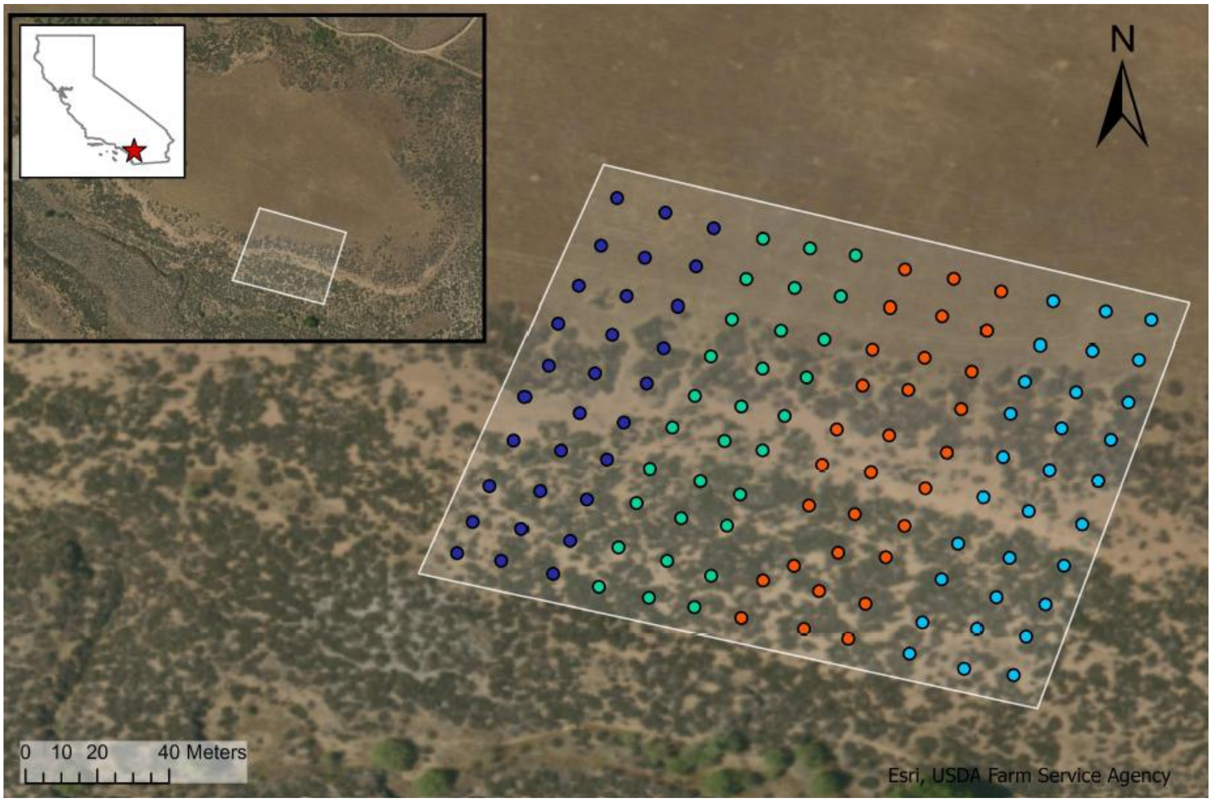

Figure 1. Study grid at the Southwestern Riverside County Multispecies Reserve. The white outline shows the 110 × 130 m study site. 30 antennas (represented by same-colored dots) were deployed at a time in a 3 x 10 grid configuration, which varied slightly due to shrub obstruction, and relocated approximately monthly to different sampling subsections. Insets: reserve location (red star) in southern California and study grid location within the plateau.

We live-trapped kangaroo rats to implant PIT tags. The trapping grid included all flagged locations on the study grid, as well as 1-2 additional perimeter lines (10 m spacing). We trapped for 5 nights prior to the start of the study, and for 2-4 nights every 1-2 months thereafter to tag any newly captured individuals. During each trapping session, we set a Sherman live trap (H.B. Sherman Traps, Inc., Tallahassee, FL, U.S.A.), modified with a door gap to prevent tail injuries (Shier and Swaisgood, 2012), at each flagged location. Traps were baited with sterilized commercial birdseed between 1800 and 2000 h and checked twice nightly (2200-0000 h; 0200-0400 h). Kangaroo rats were sexed, weighed to the nearest 0.1 g, and implanted subcutaneously with an 8 mm PIT tag between the scapulae using sterile syringes (Sikes and the Animal Care and Use Committee of the American Society of Mammologists, 2016; Williams et al., 1997). Some individuals also received a uniquely numbered ear tag. Individuals weighing > 50 g were classified as adults (Shier, 2008).

Habitat surveys

We conducted habitat surveys in both seasons to quantify microhabitat characteristics associated with antenna locations. Within 10 x 10 m quadrats centered on each antenna, we visually estimated the percentage cover of open ground, woody debris or leaf litter, forbs, embedded litter (dead plants still rooted in ground), grasses, rocks, cactus, and shrubs at crown height (Brehme et al., 2016). We also recorded the three most dominant forb species, the presence or absence of harvester ant (*Pogonomyrmex californicus*) nests, and the distance from the antenna to the nearest shrub cover. Surveys were completed within 1-3 months of antenna data collection for each grid subsection to capture seasonal changes in vegetation and ant activity.

To reduce dimensionality, forb species were grouped by family or subtribe, and rare groups (<25% occurrence across the 120 antenna sites) were excluded. Rock cover was merged with open ground, while cactus was excluded due to rarity.

At each antenna, we recorded the presence or absence of heterospecific rodents (*Neotoma bryanti*, *Peromyscus maniculatus*, *Chaetodipus fallax*, *Thomomys bottae*) from concurrent trapping data.

Approximately 300 g of soil were collected near each antenna after removing surface organic matter and sampling to a depth of ~20 cm. Samples were oven-dried, weighed, and sifted through 2 mm mesh sieves to separate the gravel. We then used the Bouyoucos Hydrometer Method (Gee and Bauder 1986) to determine the percentage of sand, silt, and clay. Soil texture variables were reduced to orthogonal axes via a principal component analysis (PCA).

Soil compaction was measured with a penetrometer (AgraTronix Soil Compaction Tester model #08180; 68.6 cm length probe, 1.27 cm diameter tip, Streetsboro, OH, U.S.A) following Chock et al. (2020). Four measurements were taken at the corners of a 1 x 1 m quadrat centered on each antenna location and averaged. We recorded the depth (cm) at which point the probe reached at 21 bar pressure, the threshold known to restrict root penetration and likely restrict kangaroo rat burrowing.

Burrow ownership

We identified burrow locations for a subset of kangaroo rats using a combination of radio telemetry and direct nocturnal observations. For telemetry, kangaroo rats were fitted with VHF radio-transmitter backpacks (Model Bd-2C; Shier and Swaisgood, 2012), held for 24 h to confirm normal locomotion and foraging behavior, and released at their capture location the following night. Over three consecutive mornings, individuals were tracked using handheld antennas, and burrow locations were assigned if detections occurred at the same location on ≥ 2 occasions.

For visual observations, a subset of individuals were marked with uniquely colored reflective tape on their ear tags. Using night-vision googles, we (J.N.S.) confirmed burrow ownership by observing tagged individuals transporting seeds into burrow entrances. Visual determinations of burrow ownership were limited to grassland where burrow entrances were unobstructed.

Statistical analysis

We conducted all statistical analyses in R (v4.4.1; R Core Team 2024), with mapping in ArcGIS Pro 3.5.0 (Esri Inc. 2025). To minimize pseudoreplication, repeated detections of the same individual at a single antenna within a 1-minute interval were collapsed to a single record. Data from trapping nights and the nights immediately following trapping were excluded to avoid potential behavior effects of baiting.

Spatial segregation

We estimated species differences in space use from the frequency of detections per antenna. The data was rescaled to account for variation among subsections in sampling duration. Specifically, we divided the number of antenna detections by the number of sampling days (21-51 days) and multiplied by the minimum number of sampling days in each season (breeding: 21 days, nonbreeding: 28 days). The rescaled detections were rounded to integers, with non-zero values <0.5 set to one to retain rare detections.

To distinguish habitat selection from species interactions, we used joint species distribution models (JSDMs) implemented through the hierarchical modeling of species communities (HMSC; Ovaskainen et al. 2017) approach with R package *Hmsc* (Tikhonov et al., 2022). HMSC uses a hierarchical Bayesian linear model to predict species occurrences using fixed effects (environmental covariates) and random effects, with random effects structured using latent variables to capture residual associations between the species (Ovaskainen et al., 2017). Residual associations explain variation in species occurrences that cannot be attributed to the environment covariates (Ovaskainen et al., 2017). HMSC is an ideal approach for spatial studies because the latent factors can be spatially structured to account for spatial autocorrelation among observations (Ovaskainen et al., 2017).

We ran separate models for the nonbreeding and breeding season to examine whether habitat selection and species associations differed across seasons. The response variable was the rescaled detections, and predictor variables were habitat survey metrics. To allow for curvilinear relationships between detections and numeric habitat variables, the HMSC models included both linear and quadratic terms.

We used a Poisson-lognormal distribution within our HMSC models to account for over-dispersed count data. Antenna coordinate locations were included as a random effect (spatial latent factor). For each season, we ran both a full model including the spatial latent variables, and an environment-only model without the spatial latent variables. We applied the default priors of the HMSC package (Tikhonov et al., 2020). Following the methods outlined in Ovaskainen and Abrego (2020), four MCMC chains were run for 375,000 iterations, discarding the first 125,000 as burn-in and thinning by

1,000, yielding 250 posterior samples per chain (1,000 posterior samples in total). MCMC convergence was examined using the Gelman-Rubin statistic ($\hat{R}$) of the model parameters. Model fit was evaluated by k-fold cross validation with k = 4, as recommended by Tikhonov et al. (2020), with folds randomly chosen. We recognize that a spatial fold would be more rigorous for model comparison, but we are only trying to assess the adequacy of fit for a single model. We determined pseudo R^2 values, computed as the squared Spearman correlation between observed and predicted values.

We used variance partitioning to assess the proportion of explained variance in *D. stephensi* and *D. simulans* rescaled detections explained by spatial random effects and environmental covariates Following the conventions of the *Hmsc* package, the Probability of Direction (pd) was determined for all parameters; environmental covariates and species residuals correlations with pd > 0.95 were considered to have high statistical support (Tikhonov et al., 2020).

To quantify fine-scale spatial overlap between individual kangaroo rats, we examined how many of the antenna locations used by each individual overlapped with conspecifics or heterospecifics. We compared how spatial overlap differed between heterospecifics and conspecifics, species, and season, using the well-established frequentist method of binomial generalized linear model (GLM) with the *lme4* package (Bates et al., 2015). The dependent variable was the number of overlapping antennas out of the total antenna locations for each individual, and the independent variables were species, season, overlap type (conspecific or heterospecific overlap), and their interactions. Post-hoc pairwise contrasts were calculated using the *emmeans* package

(Lenth, 2025). We chose to report p-values, but interference is based on 95% confidence intervals.

Temporal partitioning

We tested for temporal segregation using the common approach of kernel density estimates of detection times with the *overlap* package (Meredith et al., 2024). Detection timestamps were converted to radians, and kernel density functions were fit to each species. We calculated overlap coefficients (Δ_4) - ranging from 0 (no overlap) to 1 (complete overlap) (Ridout and Linkie, 2009) and generated confidence intervals by bootstrapping 999 estimates of activity for each species (Meredith et al., 2024).

RESULTS

Across both seasons, we detected a total of 40 unique individuals: 32 *D. stephensi* and 8 *D. simulans*. During the nonbreeding season, 14 *D. stephensi* and 5 *D. simulans* were detected, and during the breeding season, 23 *D. stephensi* and 5 *D. simulans* were detected.

JSDM

The MCMC convergence of the models was satisfactory for all parameters, as indicated by mean parameter $\hat{R}$ values less than 1.1 (Gelman and Rubin, 1992). The full models demonstrated a relatively high fit, with mean pseudo R^2 values of 0.78 for explanatory power and 0.38 for predictive power in the breeding season and 0.74 for explanatory power and 0.43 for predictive power in the nonbreeding season. By contrast, the environmental-only models had mean pseudo R^2 values of 0.50 for explanatory power and 0.28 for predictive power in the breeding season and 0.56 for explanatory power and 0.34 for predictive power in the nonbreeding season.

In the full models, a greater proportion of the variance (as measured by pseudo R^2) was explained by spatial random effects in the breeding season (0.46) than the nonbreeding season (0.39), suggesting stronger spatial structuring when densities were higher (Fig. 3). Within seasons, *D. stephensi* had less variance explained by environmental variables (breeding: 0.35; nonbreeding 0.50) than *D. simulans* (breeding: 0.72; nonbreeding: 0.71), consistent with less restricted habitat use by *D. stephensi* (Fig. 3).

After controlling for environmental variables, the posterior mean of the residual correlation between the species was nearly -1.0, indicating almost complete spatial segregation in both the full breeding (mean: -0.9996, $p(\text{mean} < 0) = 1$) and nonbreeding model (mean: -0.9909; $p(\text{mean} < 0) = 0.9975$; Fig. 2).

There was high statistical support (between 0.96 – 1 posterior probability) for both species selecting for and against several habitat variables (Tables S1-S4). In the nonbreeding season full model, *D. simulans* was positively associated with open ground, which was most prevalent in the ecotone and CSS. *D. stephensi* was negatively associated with the quadratic terms for open ground and grass, suggesting preference for intermediate levels of both variables. In the breeding season full model, *D. simulans* was negatively associated with the quadratic terms for embedded litter and soil texture PC1 (representing high sand content), suggesting an association with intermediate levels of sand and embedded litter. In contrast, *D. stephensi* occurrence increased with distance to shrub cover, consistent with its use of open habitats.

Individual spatial overlap

At the individual level, both species overlapped significantly less with heterospecifics than with conspecifics (Fig. 4, Table 1. mean = -2.00, 95% CI: [-2.81, -1.25], $p < 0.0001$); mean overlap with heterospecifics was only 14.58%, whereas mean overlap with conspecifics was 85.21%. *D. stephensi* overlapped more with other individuals overall (mean =0.91, 95% CI: [0.25, 1.58], $p = 0.007$). There was a significant interaction between species and overlap type (mean = -1.46, 95% CI: [-2.52, -0.40, $p = 0.007$), such that D. simulans conspecifics overlapped less than D. simulans conspecifics ($z = -4.74$, $p <0.001$), but there was no significant difference between the species in regards to overlap with heterospecifics ($z = 1.58$, $p = 0.39$). These patterns confirm that both species segregate spatially at fine scales, with limited overlap of activity centers between *D. stephensi* and *D. simulans*.

Temporal partitioning

There was no evidence of temporal segregation. The two species' nocturnal activity patterns overlapped extensively in both the breeding season ($\Delta_4 = 0.90$, 95% CI: [0.85,0.96]) and nonbreeding season ($\Delta_4 = 0.83$, 95% CI: [0.76-0.88]). Both species were active from dusk to dawn, typically between 1600–0600 h in the nonbreeding season and 2000–0600 h in the breeding season. Activity peaked shortly after sunset for both species and declined toward sunrise. (Fig. 5).

Burrow locations

Burrow mapping revealed clear habitat segregation between the two species. *D. stephensi* burrows were located primarily in grassland and ecotone habitats (three confirmed by telemetry, eight by direct observation). *D. simulans* burrows were located exclusively in CSS (two confirmed by telemetry), with no *D. simulans* burrows observed during observations of grassland areas. These patterns corroborate the JSDM results showing negative spatial associations and distinct microhabitat use.

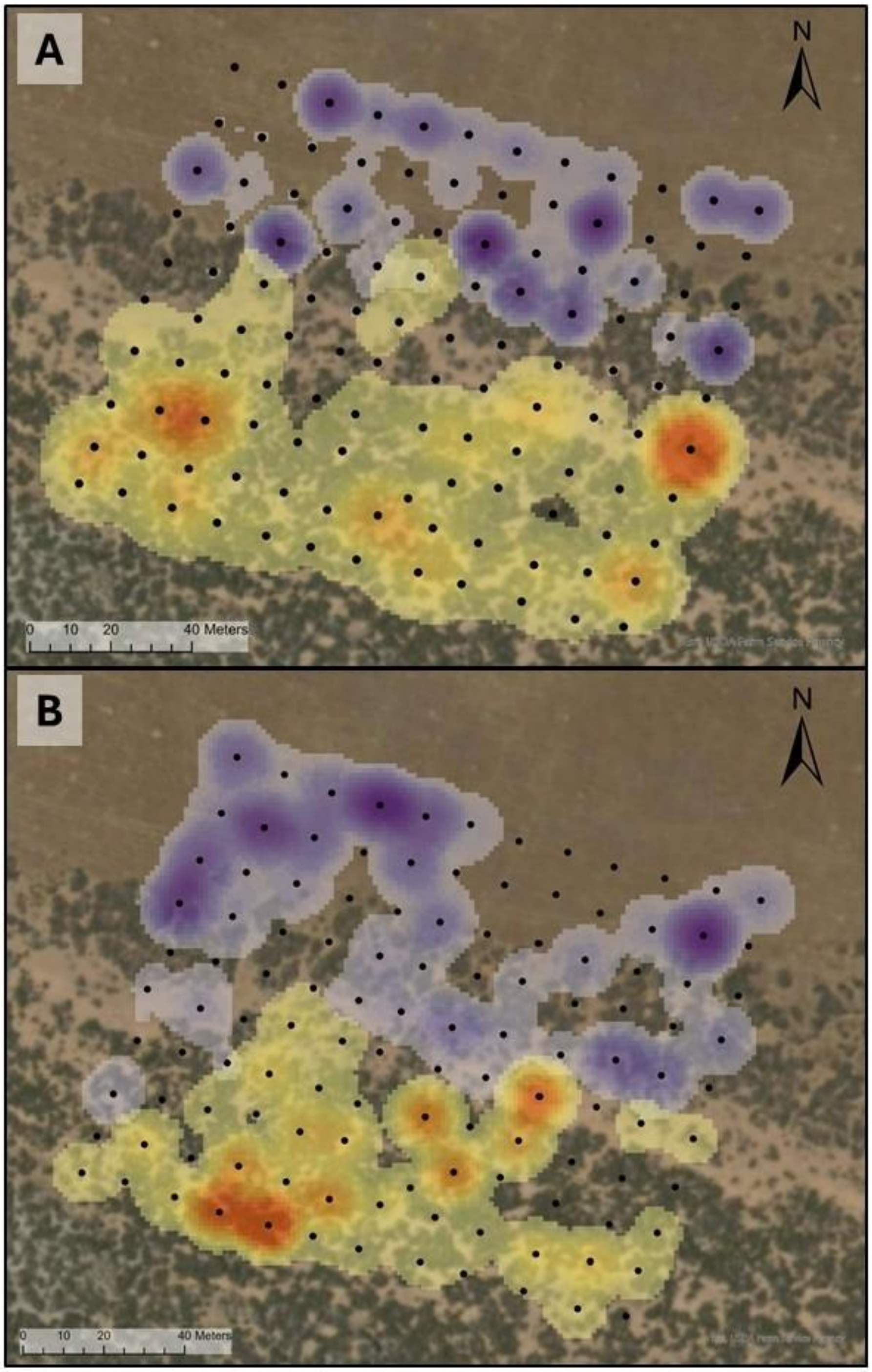

Figure 2. Distribution of *D. stephensi* (purple) and *D. simulans* (orange) in the (A) nonbreeding and (B) breeding seasons. Colored areas show the 95% kernel density

estimates of each species' detections; darker areas represent higher densities of detections. Black dots indicate the antenna grid.

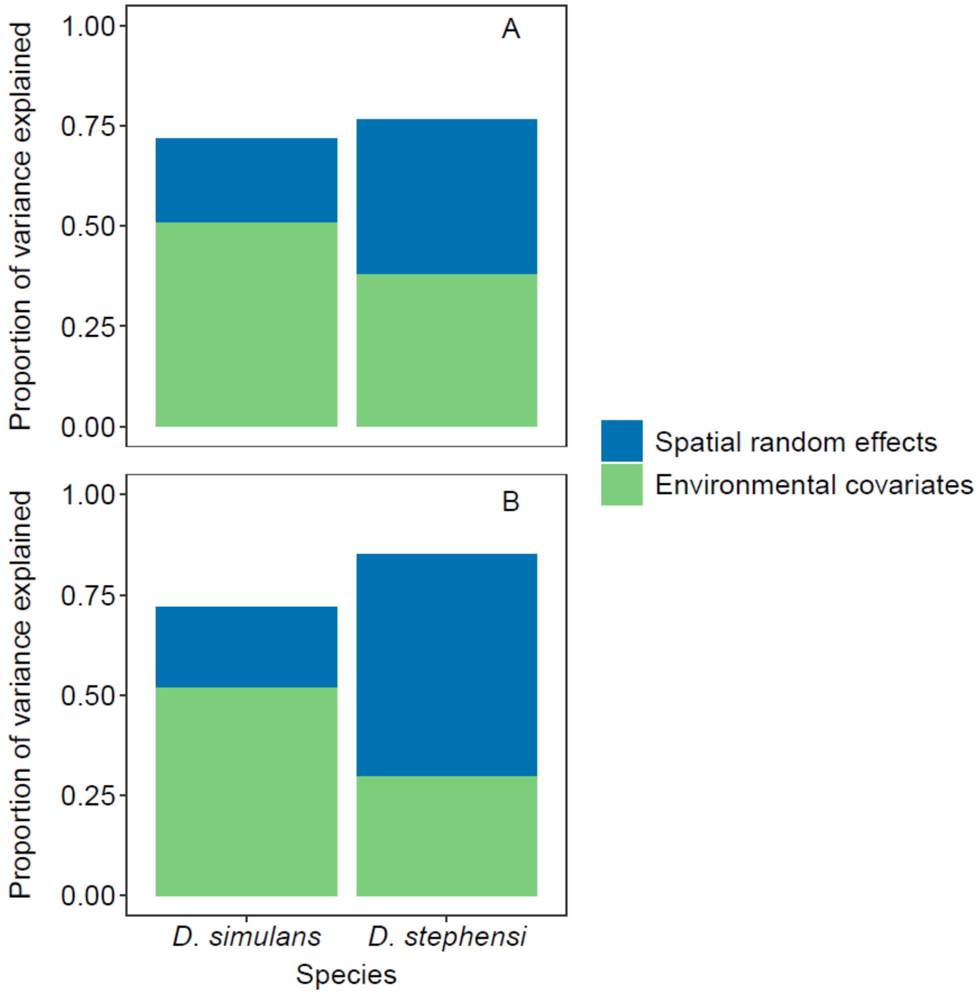

Figure 3. Proportion of variance in *D. stephensi* and *D. simulans* rescaled detections explained by spatial random effects and environmental covariates for (A) nonbreeding and (B) breeding seasons.

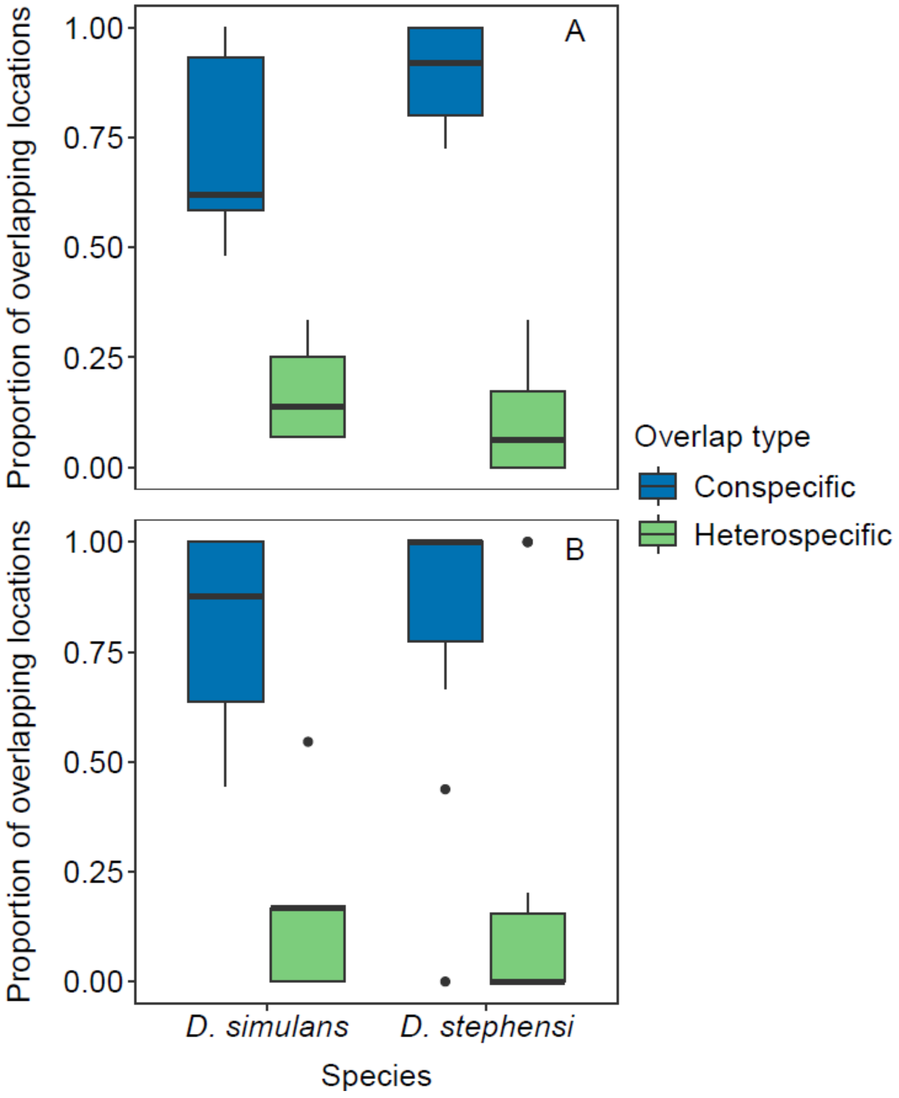

Figure 4. Proportion of individual space-use overlap of *D. stephensi* and *D. simulans* with conspecifics and heterospecifics for (A) nonbreeding and (B) breeding seasons. Whiskers of the boxplots extend to 1.5x the interquartile range, and any points beyond that are plotted as outliers.

Table 1. Binomial GLM results with the number of overlapping antennas out of the total antenna locations for each individual as the dependent variable, and species, season, overlap type (conspecific or heterospecific overlap), and their interactions as the independent variables. Means and SE are on the log-odds scale.

Model term	Mean	SE	2.5% CI	97.5% CI	Odds ratio	*p*
Species	0.91	0.34	0.25	1.58	2.49	0.007
Season	0.12	0.33	-0.53	0.77	1.13	0.718
Overlap type	-2.00	0.39	-2.81	-1.25	0.13	<0.0001
Species*Season	0.49	0.49	-0.46	1.45	1.63	0.318
Species*Overlap type	-1.46	0.54	-2.52	-0.40	0.23	0.007
Season*Overlap type	-0.46	0.54	-1.52	0.61	0.63	0.397
Species*Season* Overlap type	-0.33	0.77	-1.84	1.17	0.72	0.667

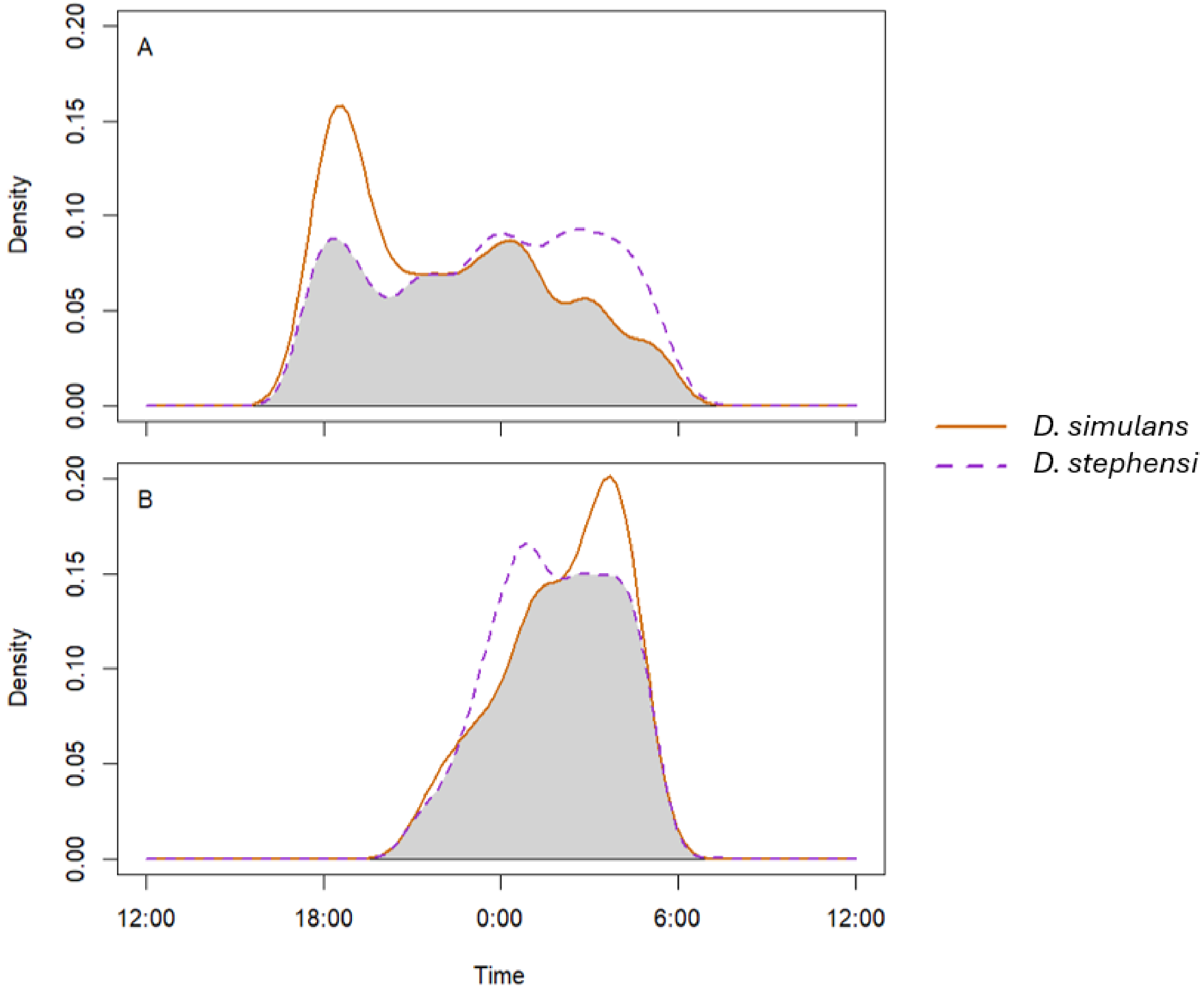

Figure 5. Temporal overlap between *D. stephensi* and *D. simulans* in the (A) nonbreeding season and (B) breeding season. The kernel density functions for each species' activity periods is plotted, with *D. simulans* outlined in orange, *D. stephensi* outlined in a dashed purple line, and areas of overlap shaded grey.

DISCUSSION

Interspecific competition strongly influences habitat use and activity (Grether et al., 2017), making it a critical consideration in the co-management of threatened species.

For species facing habitat destruction, such as *D. stephensi* and *D. simulans*, active competition can further constrict space use, reduce access to critical resources, and accelerate species decline. Using fine-scale PIT-tag monitoring and joint species distribution models, we assessed species associations, individual spatial overlap, and nightly activity patterns across a natural habitat gradient. Our results indicate strong spatial segregation between the species, even after accounting for habitat characteristics, and no temporal segregation. These findings indicate that interference competition, rather than habitat preference alone, plays a central role in structuring their distributions.

Multiple lines of evidence point to interference competition as a major mechanism structuring the distributions of these species. Individual-level spatial analyses revealed significantly lower overlap between heterospecifics than conspecifics across the habitat gradient (Fig. 4). Kangaroo rats tend to be solitary and many species are territorial (Longland and Dimitri, 2021), thus fine-scale spatial avoidance at the level of home-range cores is likely due to territorial defense or threat displays towards heterospecifics. The JSDM results further support this conclusion: the species showed a nearly perfect negative residual correlation even after controlling for habitat features, and the environment-only model had a much poorer fit, indicating that the species interaction substantially improved the full model's ability to explain patterns of space use. The negative correlations between species could be caused by exploitative competition if one species reduced resource levels (e.g. seeds) below the giving up density of the other, thereby forcing it to forage elsewhere (Rosenzweig, 1981). However, as shown in Chapter 2 and previous laboratory studies (Bleich and Price, 1995), *D. stephensi* is behaviorally dominant and can displace *D. simulans*. Thus, interference competition is the most likely mechanism driving the species' spatial segregation.

Importantly, the strength of spatial structuring increased during the breeding season. Spatial random effects explained more variance during the breeding season than in the nonbreeding season, and *D. stephensi* in particular exhibited especially strong spatial clustering (Fig. 3). This pattern suggests that competition intensifies when energetic demands and reproductive activities are highest. Similar patterns have been reported in at least one other rodent system, where there was stronger spatial segregation during the reproductive season, likely as a result of the dominant species showing higher levels of aggression while reproductively active (Glass and Slade, 1980).

Although the species share the same general habitat mosaic, they differ in fine-scale habitat associations. Consistent with previous work on co-occurring populations, *D. stephensi* and *D. simulans* mainly used and burrowed in grassland and CSS, respectively (Bleich, 1977; Lackey, 1967; Price et al., 1991). Despite these habitat associations, it is difficult to determine which environmental variables are limiting factors for each species without conducting manipulative experiments or studying habitat use where only one species is present. The species' conservation status limits removal experiments, and there are no areas where *D. stephensi* is present without adjacent *D. simulans* populations. However, previous studies have suggested that both species are disturbance specialists that prefer habitats without dense vegetation (Brehme et al., 2011; Brock and Kelt, 2004; Kelt et al., 2005). *D. simulans* densities increase in open post-fire habitats in areas without *D. stephensi* (Brehme et al., 2011; Price and Waser, 1984), and *D. stephensi* increase following both fire and shrub removal (Price et al., 1995, 1994). Thus, D. stephensi likely prefers open grassland and CSS habitat, and *D. simulans* may only shift into dense CSS habitat in the presence of *D. stephensi* to avoid costly interference interactions. Similar mechanisms occur in other rodent systems, where subordinate species shift into marginal habitat or forage at different times in the presence of dominant competitors (Gutman and Dayan, 2005; Ziv et al., 1993). The absence of temporal segregation in our study indicates that modifying nightly activity timing is not a strategy available to *D. stephensi* and *D. simulans*, likely due to shared physiological constraints and similar exposure to predation risk. Thus, spatial partitioning appears to be the primary axis along which competition is expressed.

While our study provides evidence for ongoing competition shaping space use, further research is needed. The negative residual correlation between the species could be due to missing environmental variables or biotic interactions with other species at the site. However, we attempted to account for all important factors by including environmental variables previously used in studies of these and related species (Brehme et al., 2016; Chock et al., 2022, 2020; Price et al., 1991). We also included the presence of other prominent granivores (*Pogonomyrmex* Harvester ants and other rodent species) as variables, although we would expect interactions between *D. stephensi* and *D. simulans* to have the strongest effect on space use, because competition is more likely among closely related and ecologically similar species (Elsen et al., 2017; Pigot et al. 2016).

Our findings have significant implications for the persistence of both species in landscapes undergoing rapid transformation. Kangaroo rat habitat is being fragmented and lost due to continued urban and agricultural development (USFWS, 2020). Furthermore, grassland and CSS systems in southern California are being reshaped by interacting pressures, including invasive annual grasses that increase litter and suppress native forbs, and altered fire regimes that promote type-conversion to nonnative grasslands (Talluto and Suding, 2008). These habitat changes are likely compressing available habitat for each species and altering competitive dynamics.

D*. stephensi* is particularly vulnerable to invasive grass thatch accumulation, shrub encroachment, and reduced forb diversity that diminish the suitability of its native grassland habitat (Kelt et al., 2005; Price et al., 1994). As these changes progress, *D. stephensi* may be forced into structurally denser habitat where encounters with *D. simulans* become unavoidable. This shift could lead to increased energetic costs for both species and potential displacement of *D. simulans* from CSS–ecotone interfaces. Although *D. simulans* is more tolerant of structurally complex habitats, its bipedal locomotion is more suited for traveling over open ground (Lemen and Rosenzweig, 1978). Therefore, being displaced into extremely dense cover may reduce foraging efficiency, as has been shown for other kangaroo rat species (Lemen and Rosenzweig, 1978; Price, 1978). Thus, both species are susceptible to different forms of habitat degradation, and the consequences of environmental change for each species will depend on how changing conditions alter the potential for overlap—and therefore competition—between them.

The strong role of competition in structuring habitat use highlights the need for conservation strategies that explicitly consider both habitat heterogeneity and species interactions. Maintaining a mosaic of open native grassland and adjacent CSS is essential for allowing the species to segregate spatially. Management actions that inadvertently homogenize habitat—such as widespread shrub removal, prolonged grassland thatch accumulation, or post-fire management that allows rapid vegetation transitions—could intensify competition by limiting the availability of distinct habitat refugia. Restoration efforts for *D. stephensi* should prioritize the retention and expansion of open microhabitats, while management for *D. simulans* must ensure that CSS retains sufficient structural complexity.

Translocation and population augmentation plans should also incorporate species interactions. Releasing *D. stephensi* into patches where *D. simulans* is already established, could create conditions for competitive displacement, especially considering that *D. stephensi* is dominant over *D. simulans* regardless of residency status (see Chapter 2). As *D. stephensi* densities increase, some may shift into shrub-covered habitats, as we saw in the breeding season. Managers should place *D. stephensi* in areas with lower densities of *D. simulans*, or on the periphery, rather than center, of *D. simulans* populations, to reduce competition. Monitoring competitive dynamics through PIT-tag arrays or similar fine-scale tools may help managers adaptively evaluate whether restored sites support coexistence or whether additional habitat modification is needed.

Overall, our findings demonstrate that interspecific competition, rather than habitat preference alone, is a major driver of spatial segregation between *D. stephensi* and *D. simulans*. Despite strong overlap in temporal activity, the species partition space at fine scales, likely through behavioral avoidance mechanisms. These results underscore the importance of conserving habitat heterogeneity, anticipating shifts in competitive dynamics under environmental change, and explicitly incorporating species interactions into conservation planning. As southern California ecosystems continue to transform under climate change, invasive species, and expanding human land use, careful management will be required to ensure the long-term viability of both species.

SUPPLEMENT

Table S1. JSDM results for *D. stephensi* in the breeding season. Environment parameter means, lower and upper credible intervals (CI), and Probability of Direction support levels (probability of parameters being positive or negative) are shown. Covariates with ≥ 0.95 posterior probability of being negative or positive are bolded.

Covariate	Mean	Lower CI	Upper CI	Support Positive	Support Negative
Open	0.0086	-0.092	0.11	0.57	0.43
Open^2	-0.0014	-0.0036	0.00064	0.1	0.9
Leaf litter/Woody debris	-0.034	-0.11	0.037	0.17	0.83
Leaf litter/Woody debris^2	-0.00016	-0.0011	0.00078	0.38	0.62
Forb	0.051	-0.06	0.15	0.83	0.17
Forb^2	-0.0012	-0.0038	0.0015	0.2	0.8
Embedded litter	0.052	-0.052	0.15	0.86	0.14
Embedded litter^2	-0.0017	-0.0039	0.00062	0.08	0.92
Grass	-0.025	-0.12	0.075	0.31	0.69
Grass^2	-0.00037	-0.0024	0.0016	0.35	0.65
Shrub	-0.037	-0.094	0.022	0.11	0.89
Shrub^2	2.00 E-05	-7.00 E-04	0.00072	0.53	0.47
Distance to shrub	**0.57**	**-0.0013**	**1.2**	**0.97**	**0.026**
Distance to shrub^2	-0.035	-0.11	0.037	0.19	0.81
Ant nests	-0.27	-0.93	0.4	0.23	0.77
Heterospecifics	0.4	-0.4	1.2	0.83	0.17
Soil compaction	-0.00055	-0.024	0.024	0.49	0.51
Soil compaction^2	-3.50 E-05	-0.00021	0.00014	0.35	0.65
Soil PC1	-0.15	-0.5	0.21	0.2	0.8
Soil PC1^2	-0.094	-0.23	0.022	0.054	0.95
Soil PC2	-0.15	-0.6	0.26	0.25	0.75
Soil PC2^2	-0.14	-0.32	0.034	0.052	0.95
Daucus pusillus	0.0027	-0.061	0.068	0.53	0.47
Daucus pusillus^2	0.00065	-0.00089	0.0022	0.8	0.2
Dienandra paniculate	0.06	-0.031	0.15	0.9	0.1
Dienandra paniculate^2	-0.0013	-0.0036	0.0015	0.14	0.86
Eschscholzia californica	-0.021	-0.11	0.071	0.31	0.69
Eschscholzia californica^2	0.00044	-0.0014	0.0024	0.66	0.34
Eriogonum gracile	0.019	-0.058	0.099	0.66	0.34
Eriogonum gracile^2	-0.00015	-0.0011	0.00079	0.39	0.61
Gnaphaliinae	-0.00016	-0.038	0.042	0.5	0.5
Gnaphaliinae^2	3.40 E-05	-0.00037	0.00045	0.57	0.43

Table S2. JSDM results for *D. simulans* in the breeding season. Environment parameter means, lower and upper credible intervals (CI), and Probability of Direction support levels (probability of parameters being positive or negative) are shown. Covariates with ≥ 0.95 posterior probability of being negative or positive are bolded.

Covariate	Mean	Lower CI	Upper CI	Support Positive	Support Negative
Open	0.026	-0.076	0.13	0.71	0.29
Open^2	-0.00028	-0.0022	0.0018	0.38	0.62
Leaf litter/Woody debris	-0.033	-0.11	0.038	0.18	0.82
Leaf litter/Woody debris^2	-0.00025	-0.0014	0.00079	0.32	0.68
Forb	0.02	-0.087	0.11	0.66	0.34
Forb^2	-0.0013	-0.0047	0.002	0.22	0.78
Embedded litter	0.073	-0.029	0.17	0.9	0.1
Embedded litter^2	**-0.0026**	**-0.0049**	**-0.00014**	**0.02**	**0.98**
Grass	-0.045	-0.13	0.048	0.15	0.85
Grass^2	-0.0011	-0.0037	0.0014	0.18	0.82
Shrub	-0.031	-0.093	0.031	0.16	0.84
Shrub^2	0.00024	-4.00 E-04	0.00087	0.77	0.23
Distance to shrub	0.47	-0.14	1.1	0.94	0.064
Distance to shrub^2	-0.046	-0.14	0.035	0.15	0.85
Ant nests	-0.019	-0.68	0.69	0.46	0.54
Heterospecifics	0.28	-0.32	0.84	0.84	0.16
Soil compaction	-0.0042	-0.027	0.016	0.38	0.62
Soil compaction^2	4.30 E-06	-0.00016	0.00018	0.52	0.48
Soil PC1	-0.18	-0.49	0.11	0.12	0.88
Soil PC1^2	**-0.08**	**-0.15**	**-0.016**	**0.003**	**1**
Soil PC2	-0.082	-0.4	0.29	0.31	0.69
Soil PC2^2	-0.15	-0.35	0.059	0.088	0.91
Daucus pusillus	0.0077	-0.051	0.07	0.59	0.41
Daucus pusillus^2	0.00018	-0.0011	0.0014	0.62	0.38
Dienandra paniculate	0.059	-0.035	0.15	0.88	0.12
Dienandra paniculate^2	-0.0021	-0.0051	0.00075	0.066	0.93
Eschscholzia californica	0.016	-0.066	0.098	0.64	0.36
Eschscholzia californica^2	0.00033	-0.0023	0.0029	0.59	0.41
Eriogonum gracile	0.00055	-0.08	0.087	0.51	0.49
Eriogonum gracile^2	-0.00039	-0.0016	0.00085	0.25	0.75
Gnaphaliinae	0.017	-0.025	0.062	0.76	0.24
Gnaphaliinae^2	2.00 E-04	-0.00017	6.00 E-04	0.84	0.16

Table S3. JSDM results for *D. stephensi* in the non-breeding season. Environment parameter means, lower and upper credible intervals (CI), and Probability of Direction support levels (probability of parameters being positive or negative) are shown. Covariates with ≥ 0.95 posterior probability of being negative or positive are bolded.

Covariate	Mean	Lower CI	Upper CI	Support Positive	Support Negative
Open	0.071	-0.024	0.16	0.94	0.063
Open^2	**-0.0014**	**-0.0031**	**0.00016**	**0.037**	**0.96**
Leaf litter/Woody debris	0.041	-0.071	0.14	0.77	0.23
Leaf litter/Woody debris^2	-0.00018	-0.0028	0.0024	0.45	0.55
Forb	0.026	-0.041	0.099	0.76	0.24
Forb^2	-4.70 E-05	-0.00096	0.00092	0.46	0.54
Grass	0.074	-0.021	0.17	0.93	0.073
Grass^2	**-0.0014**	**-0.003**	**0.00014**	**0.036**	**0.96**
Shrub	-0.007	-0.065	0.06	0.4	0.6
Shrub^2	0.00014	-0.00061	0.00091	0.66	0.34
Distance to shrub	0.012	-0.56	0.57	0.52	0.48
Distance to shrub^2	0.0048	-0.061	0.069	0.56	0.44
Ant nests	-0.1	-0.87	0.65	0.41	0.59
Heterospecifics	-0.27	-1.1	0.6	0.26	0.74
Soil compaction	0.02	-0.0098	0.05	0.91	0.086
Soil compaction^2	-6.20 E-06	-0.00019	0.00018	0.48	0.52
Soil PC1	-0.2	-0.59	0.2	0.16	0.84
Soil PC1^2	-0.044	-0.16	0.053	0.23	0.77
Soil PC2	-0.029	-0.49	0.45	0.43	0.57
Soil PC2^2	0.02	-0.11	0.17	0.6	0.4
Daucus pusillus	-0.02	-0.077	0.035	0.26	0.74
Daucus pusillus^2	-0.00029	-0.0012	0.00049	0.25	0.75
Erodium	0.012	-0.032	0.053	0.71	0.29
Erodium^2	-6.80 E-05	-0.00065	0.00047	0.41	0.59
Eschscholzia californica	0.018	-0.038	0.076	0.74	0.26
Eschscholzia californica^2	-8.90 E-05	-0.00098	0.00083	0.42	0.58
Pectocarya linearis ssp. Ferocula	-0.026	-0.07	0.016	0.13	0.87
Pectocarya linearis ssp. Ferocula^2	3.00 E-04	-0.00029	0.00086	0.85	0.15
Gnaphaliinae	0.0063	-0.039	0.05	0.6	0.4
Gnaphaliinae^2	2.60 E-05	-0.00044	0.00051	0.54	0.46

Table S4. JSDM results for *D. simulans* in the non-breeding season. Environment parameter means, lower and upper credible intervals (CI), and Probability of Direction support levels (probability of parameters being positive or negative) are shown. Covariates with ≥ 0.95 posterior probability of being negative or positive are bolded.

Covariate	Mean	Lower CI	Upper CI	Support Positive	Support Negative
Open	**0.12**	**0.018**	**0.22**	**0.99**	**0.014**
Open^2	-0.00059	-0.002	0.00083	0.22	0.78
Leaf litter/Woody debris	0.014	-0.094	0.12	0.61	0.39
Leaf litter/Woody debris^2	0.00014	-0.002	0.0024	0.56	0.44
Forb	0.016	-0.05	0.084	0.69	0.31
Forb^2	-0.00032	-0.0014	0.00078	0.28	0.72
Grass	0.077	-0.019	0.16	0.94	0.055
Grass^2	-0.0014	-0.0031	0.00044	0.068	0.93
Shrub	-0.0041	-0.061	0.057	0.44	0.56
Shrub^2	0.00027	-0.00038	9.00 E-04	0.8	0.2
Distance to shrub	-0.14	-0.72	0.4	0.31	0.69
Distance to shrub^2	-0.013	-0.087	0.067	0.36	0.64
Ant nests	0.13	-0.6	0.87	0.65	0.35
Heterospecifics	-0.28	-0.94	0.38	0.2	0.8
Soil compaction	0.014	-0.01	0.04	0.86	0.14
Soil compaction^2	-7.80 E-05	-0.00027	1.00 E-04	0.2	0.8
Soil PC1	-0.18	-0.53	0.2	0.16	0.84
Soil PC1^2	-0.012	-0.071	0.056	0.34	0.66
Soil PC2	-0.082	-0.43	0.24	0.31	0.69
Soil PC2^2	-0.00076	-0.18	0.15	0.52	0.48
Daucus pusillus	0.0027	-0.045	0.048	0.54	0.46
Daucus pusillus^2	-9.40 E-05	-0.00069	0.00045	0.38	0.62
Erodium	0.0074	-0.032	0.051	0.64	0.36
Erodium^2	-0.00021	-9.00 E-04	0.00042	0.28	0.72
Eschscholzia californica	0.0087	-0.054	0.067	0.63	0.37
Eschscholzia californica^2	-0.00041	-0.0014	0.00055	0.2	0.8
Pectocarya linearis ssp. Ferocula	-0.025	-0.062	0.015	0.11	0.89
Pectocarya linearis ssp. Ferocula^2	0.00034	-0.00015	0.00084	0.92	0.083
Gnaphaliinae	0.011	-0.034	0.057	0.68	0.32
Gnaphaliinae^2	-0.00012	-0.00054	3.00 E-04	0.29	0.71

REFERENCES

Amarasekare, P., 2002. Interference competition and species coexistence. Proceedings of the Royal Society B: Biological Sciences 269, 2541–2550. https://doi.org/10.1098/rspb.2002.2181

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1-48. doi:10.18637/jss.v067.i01.

Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76, 1075–1085. https://doi.org/10.1111/j.1365-2656.2007.01287.x

Bleich, V.C., 1977. Dipodomys stephensi. The American Society of Mammologists 1–3.

Bleich, V.C., Price, M. V, 1995. Aggressive behavior of *Dipodomys stephensi*, an endangered species, and *Dipodomys agilis*, a sympatric congener. Journal of Mammalogy 76, 646–651.

Bregman, T.P., Lees, A.C., Seddon, N., Macgregor, H.E.A., Darski, B., Aleixo, A., Bonsall, M.B., Tobias, J.A., 2015. Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. Ecology 96, 2692–2704. https://doi.org/10.1890/14-1731.1

Brehme, C.S., Clark, D.R., Burlaza, M.A., Fisher, R.N., 2016. Pacific Pocket Mouse Habitat Protocol.

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 Ecology 7, 81–98. https://doi.org/10.4996/fireecology.0702081

Brock, R.E., Kelt, D.A., 2004. Keystone effects of the endangered Stephens’ kangaroo rat (*Dipodomys stephensi*). Biological Conservation 116, 131–139. https://doi.org/10.1016/S0006-3207(03)00184-8

Burke, R.L., Tasse, J., Badgley, C., Jones, S.R., Fishbein, N., Phillips, S., Soule, M.E., 1991. Conservation of the Stephens’ Kangaroo Rat (*Dipodomys stephensi*): Planning for Persistence. Bulletin of the Southern California Academy of Sciences 90, 10–40.

California Natural Diversity Database (CNDDB), 2024. Special Animals List. Sacramento, CA.

Chesson, P., 2000. Mechansisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31, 343–366.

Chock, R.Y., McCullough Hennessy, S., Wang, T.B., Gray, E., Shier, D.M., 2020. A multi-model approach to guide habitat conservation and restoration for the endangered San Bernardino kangaroo rat. Global Ecology and Conservation 21. https://doi.org/10.1016/j.gecco.2019.e00881

Chock, R.Y., Shier, D.M., Grether, G.F., 2022. Niche partitioning in an assemblage of granivorous rodents, and the challenge of community-level conservation. Oecologia. https://doi.org/10.1007/s00442-021-05104-5

Cribari-Neto F, Zeileis A., 2010. “Beta Regression in R.” Journal of Statistical Software, 34, 1-24. doi:10.18637/jss.v034.i02

Dröge, E., Creel, S., Becker, M.S., M’soka, J., 2017. Spatial and temporal avoidance of risk within a large carnivore guild. Ecology and Evolution 7, 189–199. https://doi.org/10.1002/ECE3.2616

Esri Inc., 2025. *ArcGIS Pro* (Version 3.5.0). Esri Inc. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V., Fitzpatrick, J.W., 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proceedings of the National Academy of Sciences of the United States of America 115, 11982–11987. https://doi.org/10.1073/pnas.1804224115

Gee GW, Bauder JW.,1986. Particle size analysis. In: Klute A (ed) Methods of soil analysis, Part 1. Physical and mineralogical methods. Agronomy Monograph No. 9, 2nd ed. Soil Science Society.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7, 457–511.

Glass, G.E., Slade, N.A., 1980. The Effect of Sigmodon Hispidus on Spatial and Temporal Activity of Microtus Ochrogaster: Evidence for Competition. Ecology 61, 358–370. https://doi.org/10.2307/1935194

Goldingay, R.L., Price, M. V., 1997. Influence of season and a sympatric congener on habitat use by Stephens' kangaroo rat. Conservation Biology 11, 708–717. https://doi.org/10.1046/j.1523-1739.1997.95480.x

Grether, G.F., Anderson, C.N., Drury, J.P., Kirschel, A.N.G., Losin, N., Okamoto, K., Peiman, K.S., 2013. The evolutionary consequences of interspecific aggression. Annuals of the New York Academy of Sciences 1289, 48–68. https://doi.org/10.1111/nyas.12082

Grether, G.F., Okamoto, K.W., 2022. Eco-evolutionary dynamics of interference competition. Ecology Letters 25, 2167–2176. https://doi.org/10.1111/ELE.14091

Grether, G.F., Peiman, K.S., Tobias, J.A., Robinson, B.W., 2017. Causes and Consequences of Behavioral Interference between Species. Trends in Ecology and Evolution. https://doi.org/10.1016/j.tree.2017.07.004

Gutman, R., Dayan, T., 2005. Temporal partitioning: An experiment with two species of spiny mice. Ecology 86, 164–173. https://doi.org/10.1890/03-0369

Hillerislambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. Annual Reviews of Ecology, Evolution, and Systematics 43, 227–275. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hutchinson, G.E., 1961. The Paradox of the Plankton. The American Naturalist 95, 137–145.

Kelly, P. A., and M. V. Price. 1992. Home range use of Stephen's kangaroo rats: implications for density estimation.

Kelt, D.A., Konno, E.S., Wilson, J.A., 2005. Habitat Management for the Endangered Stephens ' Kangaroo Rat : The Effect of Mowing and Grazing. The Journal of Wildlife Management 69, 424–429.

Leibold, M.A., Mcpeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410. https://doi.org/10.1890/0012-9658(2006)87

Lemen, C.A., Rosenzweig, M.L., 1978. Microhabitat selection in two species of heteromyid rodents. Oecologia 33, 127–135. https://doi.org/10.1007/BF00344843/METRICS

Lenth, R., 2025. emmeans: Estimated marginal means, aka least-squares means. R package version 1.11.2. doi:10.32614/CRAN.package.emmeans

Linnell, J.D.C., Strand, O., Landa, A., 1999. Use of dens by red *Vulpes vulpes* and arctic *Alopex lagopus* foxes in alpine environments: Can inter-specific competition explain the non-recovery of Norwegian arctic fox populations? Wildlife Biology 5, 167–176. https://doi.org/10.2981/wlb.1999.021

Longland, W.S., Dimitri, L.A., 2021. Kangaroo rats: Ecosystem engineers on western rangelands. Rangelands 43, 72–80. https://doi.org/10.1016/J.RALA.2020.10.004

MacArthur, R., Levins, R., 1964. Competition, Habitat Selection, and Character Displacement in a Patchy Environment. Proceedings of the National Academy of Sciences of the United States of America 51, 1207–1210. https://doi.org/10.1073/pnas.51.6.1207

Meredith M, Ridout M, Campbell LA. 2024. Overlap: Estimates of Coefficient of Overlapping for Animal Activity Patterns. R package version 0.3.9. doi:10.32614/CRAN.package.overlap,

Ovaskainen, O. and Abrego, N. 2020. Joint species distribution modelling - with applications in R. Cambridge University Press.

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., Abrego, N., 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20, 561–576. https://doi.org/10.1111/ele.12757

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., Vesk, P.A., Mccarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution 5, 397–406. https://doi.org/10.1111/2041-210X.12180

Price, M. V, 1978. The role of microhabitat in structuring desert rodent communities. Ecology 59, 910–921.

Price, M. V, Goldingay, R.L., Szychowski, L.S., Waser, N.M., 1994. Managing Habitat for the Endangered Stephens' Kangaroo Rat (Dipodomys stephensi): Effects of Shrub Removal. The American Midland Naturalist 131, 9–16. https://doi.org/10.2307/2426603

Price, M. V, Longland, W.S., Goldingay, R.L., 1991. Niche Relationships of Dipodomys agilis and D. stephensi: Two Sympatric Kangaroo Rats of Similar Size. The American Midland Naturalist 126, 172–186.

Price, M. V, Waser, N.M., 1984. On the Relative Abundance of Species: Postfire Changes in a Coastal Sage Scrub Rodent Community. Ecology 4, 1161-1169.

Price, M. V., Waser, N.M., Taylor, K.E., Pluff, K.L., 1995. Fire as a management tool for Stephens' kangaroo rat and other small mammal species. Brushfires in California Wildlands: Ecology and Resource Management, 51–61.

Reichman, O.J. and M.V. Price. 1993. Ecological aspects of heteromyid foraging. Pp. 539–574. In *Biology of the Heteromyidae* [H. H. Genoways and J. H. Brown, eds.]. Special Publication 10, The American Society of Mammalogists.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agriculture, Biological and Environmental Statistics 14, 322–337. https://doi.org/10.1198/JABES.2009.08038/METRICS

Rosenzweig, M.L., 1981. A Theory of Habitat Selection. Ecology 62, 327–335. https://doi.org/10.2307/1936707

Schoener, T.W., 1983. Field experiments on interspecific competition. The American Naturalist 122, 240–285.

Shier, D.M., 2008. Behavioral ecology and translocation of the endangered Stephens' kangaroo rat (*Dipodomys stephensi*), Report to U.S.F.W.S. for the 2008 calendar year. Escondido, California.

Shier, D.M., Swaisgood, R.R., 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. Conservation Biology 26, 116–123. https://doi.org/10.1111/j.1523-1739.2011.01748.x

Sikes, R.S., the Animal Care and Use Committee of the American Society of Mammologists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy. https://doi.org/10.1093/jmammal/gyw078

Sullivan, R.M., Best, T.L., 1997. Systematics and Morphologic Variation in Two Chromosomal Forms of the Agile Kangaroo Rat (*Dipodomys agilis*). Journal of Mammalogy 78, 775–797. https://doi.org/10.2307/1382936

Talluto, M. V., Suding, K.N., 2008. Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. Landscape Ecology 23, 803–815. https://doi.org/10.1007/S10980-008-9238-3/FIGURES/3

Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M.J., Oksanen, J., Ovaskainen, O., 2020. Joint species distribution modelling with the r-package

Hmsc. Methods in Ecology and Evolution 11, 442–447. https://doi.org/10.1111/2041-210X.13345

U.S. Fish and Wildlife Service (USFWS). 2020. Species report for Stephens' kangaroo rat (*Dipodomys stephensi*).

U.S. Fish and Wildlife Service (USFWS). 2022. Reclassification of Stephens' Kangaroo Rat from endangered to threatened with a section 4(d) rule. Federal Register 87, 8967-8981.

Williams, D., Tordoff, W.I., Germano, D., 1997. Evaluation of methods for permanently marking kangaroo rats (Dipodomys: Heteromyidae), in: Yates, T., Gannon, W., Wilson, D. (Eds.), Life among the Muses: Papers in Honor of James S. Findley. Museum of Southwestern Biology, Albuquerque, NM, p. 290.

Ziv, Y., Abramsky, Z., Kotler, B.P., Subach, A., 1993. Interference Competition and Temporal and Habitat Partitioning in Two Gerbil Species. Oikos 66, 237–246.