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

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A B S T R A C T

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).

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
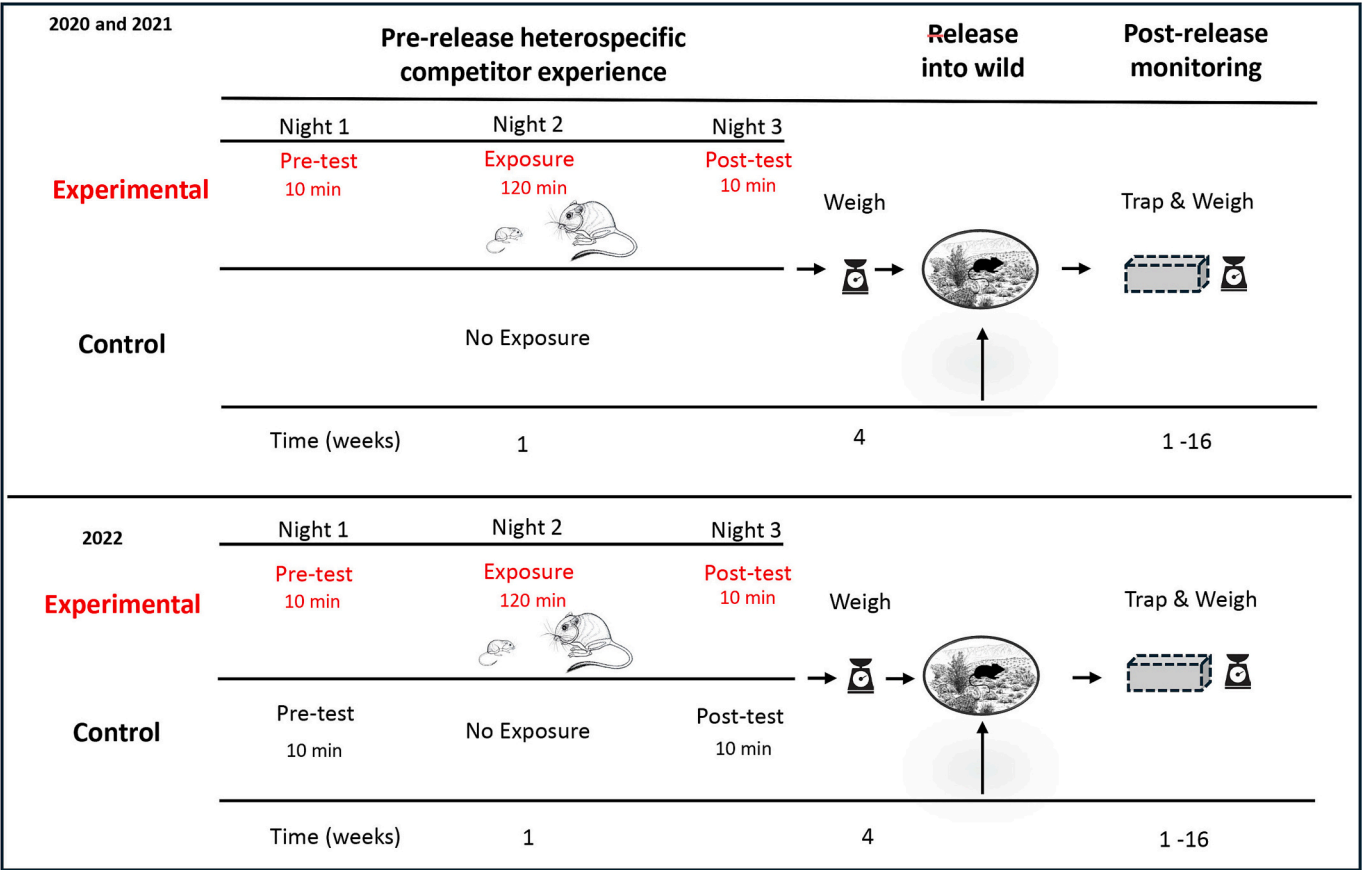

Fig. 1. Schematic of the experimental design and timeline illustrating different methods used in 2020 and 2021 with that used in 2022.

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 $1-(1-0.5)^6$ 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 ΔAICc < 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 ΔAICc < 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 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
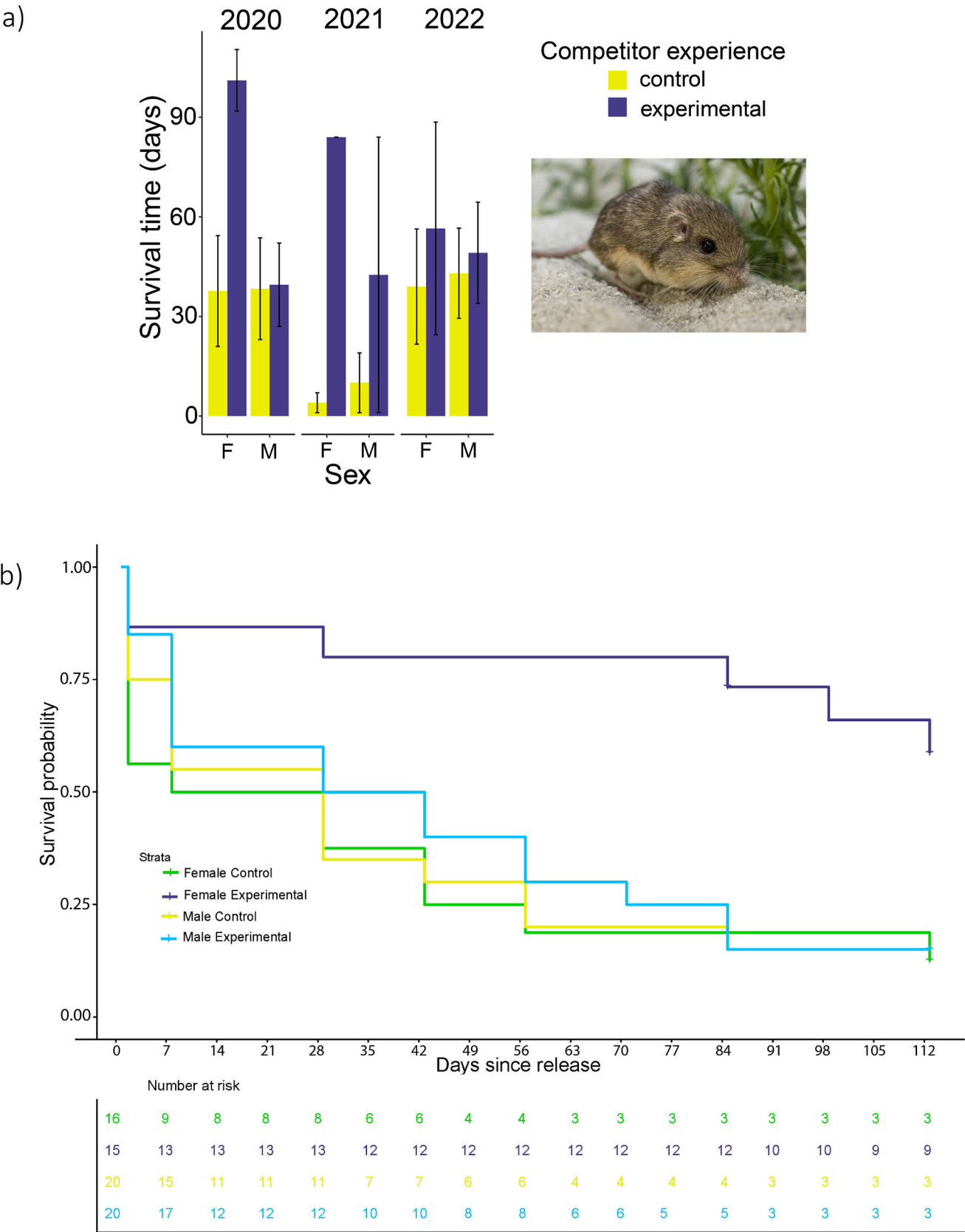
Fig. 2. Effects of pre-release competitor experience on survival. a) raw data showing survival time by year and experimental treatment (for females and males) and b) Kaplan Meier survival curve based on experimental group and sex.

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.
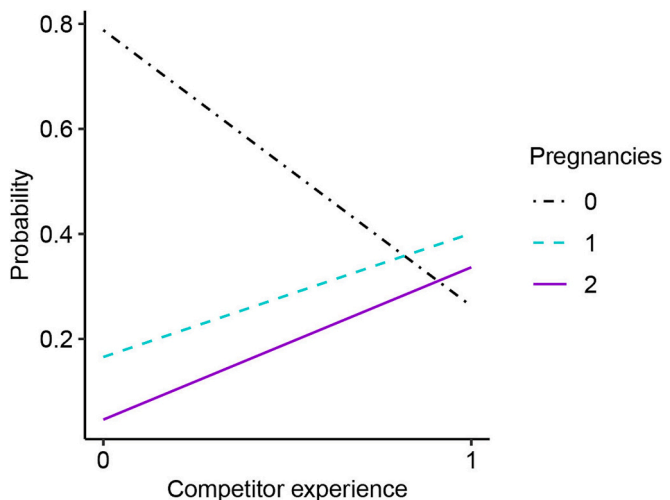
Fig. 3. Female reproductive success. Probability of having 0, 1 or 2 pregnancies during the first 16 weeks following release for experimental (1) and control (0) females. The odds of females in the experimental group having more pregnancies (1 vs 0 or 2 vs 1) were 10.44 times higher than that of control 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, $β = −0.40 ± 0.08$, $z = 5.02$, 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 ($β = −0.47 ± 0.09$, $z = 5.04$, RI = 1.00). There was no impact of experimental treatment ($β = 0.13 ± 0.09$, $z = 1.34$, RI = 0.19) or sex ($β = 0.16 ± 0.09$, $z = 1.74$, 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, $β = −1.28 ± 0.54$, $z = 2.35$, RI = 1.00; Fig. S2(B)) and more likely to show maintenance behaviors (Zero inflated negative binomial GLMM, N = 108 trials, $β = 0.03 ± 0.01$, $z = 2.30$, 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 ($β = −1.76 ± 0.64$, $z = 2.73$, RI = 1.00; Fig. S3) and more likely to show maintenance behaviors ($β = 0.05 ± 0.01$, $z = 3.80$, RI = 1.00) the more trials a kangaroo rat had with them. Females exhibited less maintenance behavior during trials than males ($β = −0.05 ± 0.02$, $z = 2.92$, RI = 0.39), but there was no sex difference in the frequency of displacements ($β = −0.67 ± 0.52$, $z = 1.27$, RI = 0.44). Finally, there was no impact of experimental treatment on either displacement or maintenance behaviors (displacement: $β = 1.04 ± 0.60$, $z = 1.72$, RI = 0.67; maintenance $β = −0.02 ± 0.02$, $z = 0.88$, 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.
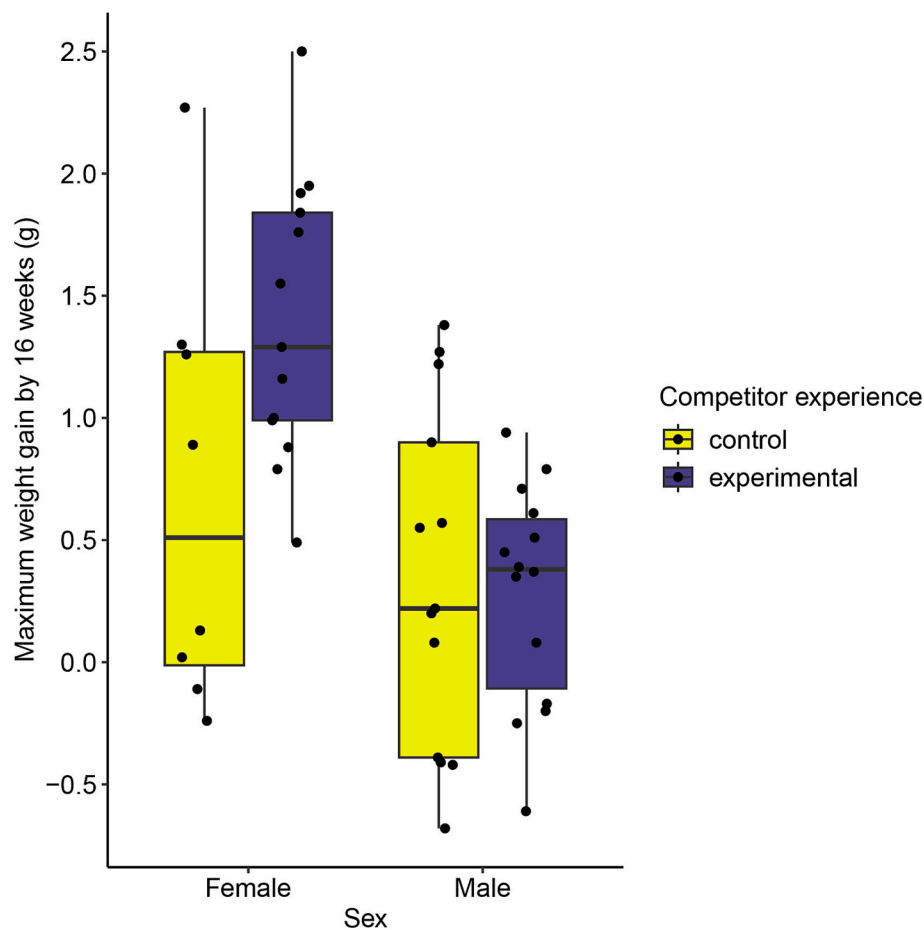
Fig. 4. Pocket mouse weight change data. Data showing changes to weight post-release from pre-release baseline. Competitor experienced females gained more weight than control females or males in either treatment; boxes show 25th–75th percentiles, whiskers show 1.5× the interquartile range, and the horizontal 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.

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.

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.

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