

**UCLA**

**UCLA Electronic Theses and Dissertations**

**Title**

Interspecific competition and conservation of Pacific pocket mice (*Perognathus longimembris pacificus*)

**Permalink**

<https://escholarship.org/uc/item/6pw455n8>

**Author**

Chock, Rachel

**Publication Date**

2018

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

Interspecific competition and conservation of  
Pacific pocket mice (*Perognathus longimembris pacificus*)

A dissertation submitted in partial satisfaction of the  
requirements for the degree Doctor of Philosophy  
in Biology

by

Rachel Yi-Ling Chock

2018

© Copyright by  
Rachel Yi-Ling Chock  
2018

## ABSTRACT OF THE DISSERTATION

Interspecific competition and conservation of  
Pacific pocket mice (*Perognathus longimembris pacificus*)

By

Rachel Yi-Ling Chock

Doctor of Philosophy in Biology

University of California, Los Angeles, 2018

Professor Debra Marie Grether Shier, Co-Chair

Professor Gregory F. Grether, Co-Chair

Reintroduction programs for endangered species rarely take competitive interactions between species into account. The endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) is being reintroduced to parts of its former range where multiple species of native rodents have overlapping diets. The species in this foraging guild compete for seeds both exploitatively and through direct interference interactions. I conducted simulated territory intrusion experiments between *P. longimembris* and four sympatric species, and determined that pocket mice, the smallest species, are subordinate to all larger species. Body size asymmetries strongly predicted dominance, regardless of phylogenetic relatedness or residency status. Repeated aggressive interactions from resident heterospecifics could lower the chances of



reintroduced pocket mice establishing burrows during the critical settlement period. As such, temporarily reducing the density of competing species might be an advisable reintroduction strategy, in combination with other interventions, such as predator exclusion. However, the presence of other members of the seed-foraging guild could have a net benefit for *P.*

*longimembris*, if pocket mice pilfer from the other species' seed caches more frequently than the other species pilfer from their caches. In a field experiment with dyed seeds I found that cache pilfering occurred infrequently, and a field-enclosure experiment revealed that none of the species use heterospecific scent to find (or avoid) seed caches. A year-long trapping study showed that species utilize spatial niche partitioning, but aggregate the timing of their activity, in areas with high levels of rodent activity. Species differed in the microhabitat they utilized, and although it is not clear if patterns of spatial niche partitioning are due to interspecific interactions or differences in habitat preferences, this study provided clear guidance for habitat management and release site selection for *P. longimembris*. Collectively, this research suggests that during the initial phases of reintroduction when Pacific pocket mice are establishing their burrows and foraging areas, they will benefit from a reduction of heterospecific competitors, who may displace them from optimal sites. However, during the later growth and regulation phases of a reintroduction, *P. longimembris* are expected to be able to persist without ongoing management of competitor species.

The dissertation of Rachel Yi-Ling Chock is approved.

Daniel T. Blumstein

Catherine Ann Sugar

Howard Bradley Shaffer

Debra Marie Grether Shier, Committee Co-Chair

Gregory F. Grether, Committee Co-Chair

University of California, Los Angeles

2018

## TABLE OF CONTENTS

|   |            |
|---|------------|
| <b>List of Figures and Tables.....</b>  | <b>vi</b>  |
| <b>Acknowledgments.....</b>   | <b>vii</b> |
| <b>Vita.....</b>  | <b>x</b>   |
| <b>Chapter 1: Body size, not phylogenetic relationship or residency, drives interspecific dominance in a little pocket mouse community.....</b> | <b>1</b>   |
| Abstract.....   | 1          |
| Introduction.....   | 1          |
| Methods.....  | 4          |
| Results.....  | 5          |
| Discussion.....   | 6          |
| References.....   | 8          |
| Supplemental Results.....   | 10         |
| <b>Chapter 2: No evidence that cache pilfering offsets costs of interspecific competition in a pocket mouse community.....</b>                  | <b>16</b>  |
| Abstract.....   | 17         |
| Introduction.....   | 18         |
| Materials and Methods.....  | 23         |
| Results.....  | 28         |
| Discussion.....   | 32         |
| Supplemental Results.....   | 36         |
| References.....   | 39         |
| <b>Chapter 3: Spatial niche partitioning, temporal aggregation, and differing habitat selection shape a rodent community.....</b>               | <b>46</b>  |
| Abstract.....   | 47         |
| Introduction.....   | 48         |
| Methods.....  | 53         |
| Results.....  | 62         |
| Discussion.....   | 71         |
| Supplementary Material.....   | 77         |
| References.....   | 79         |

## LIST OF FIGURES AND TABLES

|                 |    |
|-----------------|----|
| Figure 1-1..... | 5  |
| Figure 1-2..... | 6  |
| Figure 1-3..... | 6  |
| Figure 1-4..... | 6  |
| <br>            |    |
| Figure 2-1..... | 28 |
| Figure 2-2..... | 31 |
| <br>            |    |
| Figure 3-1..... | 63 |
| Figure 3-2..... | 68 |
| <br>            |    |
| Table 1-1.....  | 3  |
| Table 1-2.....  | 7  |
| Table 1-S1..... | 10 |
| Table 1-S2..... | 12 |
| Table 1-S3..... | 13 |
| Table 1-S4..... | 14 |
| <br>            |    |
| Table 2-1.....  | 21 |
| Table 2-2.....  | 29 |
| Table 2-S1..... | 36 |
| Table 2-S2..... | 37 |
| Table 2-S3..... | 38 |
| <br>            |    |
| Table 3-1.....  | 51 |
| Table 3-2.....  | 64 |
| Table 3-3.....  | 65 |
| Table 3-4.....  | 66 |
| Table 3-5.....  | 69 |
| Table 3-6.....  | 70 |
| Table 3-7.....  | 71 |
| Table 3-S1..... | 77 |
| Table 3-S2..... | 78 |

## ACKNOWLEDGMENTS

This dissertation would not have been possible without the mentorship, collaboration, support, and encouragement of a great many people. First and foremost, I thank my advisors Greg Grether and Debra Shier. Greg provided a home in his lab group, an open door to his time and advice, and a high bar for rigorous science. Debra took a chance on me and provided invaluable training and mentorship as a conservation biologist and the opportunity to study species few people have access to. My advisors both supported and challenged me, and I am incredibly grateful to them. I thank my committee members: Dan Blumstein, who always had time for my questions and suggestions for new directions; Catherine Sugar, who provided valuable and encouraging feedback; and Brad Shaffer for challenging me.

I am grateful to Will Miller at US Fish and Wildlife Services and Nancy Frost from California Department of Fish and Wildlife who approved my research proposals and allowed me to conduct this work. Sherri Sullivan at US Marine Corps Base Camp Pendleton, Randy Botta at San Felipe Valley Wildlife Area, and Scott Sewell at San Jacinto Wildlife Area approved this work and provided site access. Cheryl Brehme from US Geological Survey kindly provided guidance for vegetation surveys, track tube methodology, and feedback on analyses during annual meetings. Scott Tremor at San Diego Natural History Museum helped identify and facilitate access to suitable field sites with Los Angeles pocket mice. John and Nalani Webster gave me a home away from home while I conducted work on Camp Pendleton. Gil and Lynn Savage let me turn The Little Nest into a temporary field station, and Joseph Messin and Ken Halama let me turn the field station at UC Reserve Motte Rimrock into a temporary home.

I am indebted to all my field assistants who worked tirelessly with me: Daniel Disbrow, Emily Gray, Kimberly Horrell, Cassie Kovarik, Anna Kowalczyk, Matthew Lucero, Aliya McCarthy, Elizabeth Max, Julianne Pekny, Dalia Ruiz, Andrea Sork, and Laura Wade. For assistance with video analyses, sifting seeds, and entering data at UCLA I thank Jaspal Bassi, Jewel Fisher, Ashley Kranz, Courtney Lee, Kevin Neumann, Jake Nusynowitz, and Brianna Rodriguez. The immensely talented Joann Shih provided the illustrations.

My colleagues at the San Diego Zoo Institute for Conservation Research provided much needed moral and technical support. Maryke Swartz taught me to trap and handle pocket mice, and I could not have asked for a better introduction to nocturnal field work. Thea Wang, my doppelganger, has been a mentor in all aspects of field, school and life. Susanne Marczak and Emily Gray were the force behind my year-round trapping effort, and I am so grateful for their skill, speed, and humor. I know they did it for the burritos, but I appreciate it nonetheless. Shauna King and Samantha Leivers helped me with field and captive studies. Amaranta Kozuch inspired me with her dedication and compassion, and I miss her every day.

The members of the Grether Lab have offered valuable feedback, motivation, and inspiration through these years. Thanks to Adrea Gonzalez-Karlsson, Kathryn Peiman, Robert Cooper, Shawn McEachin, María Beatriz Cabezas Castillo, Madeline Cowen, Brigit Harvey and Elizabeth Reid-Wainscoat. I am particularly grateful to Jonathan Drury for being my go-to person for stats advice, career advice, writing advice, travel advice and life advice.

Thanks to UCLA Statistical Consulting, particularly Andy Lin, for their unfailing patience with my many questions and for taking the time to understand the nuances of my rodent battles. Jocelyn Yamadera and Tessa Villaseñor were instrumental in helping me navigate funding, contracts, and deadlines, and I am so appreciative of their kindness through it all.

My friends and classmates, especially Tiffany Armenta, Zac Shakner, Mairin Balisi, and Janet Buckner were a constant source of support and inspiration. Tina Wey has been a mentor and role-model from my application to my first publication, and helped me hone my skills of writing in coffee shops. Jenna Kruger, Tiffany Ong, Annie Bedigian, and Caitlin Neelon have stuck with me through the ups and the downs and are here to see me come out the other side. I thank my family- Roberta, Paul, and Caitlin Chock, for their unfailing support and encouragement. And to David Aveline, who has been my biggest champion, I couldn't have done this without you.

I am grateful for the funding which made this work possible. I received a U.S. Department of Education GAANN Fellowship, a UCLA Edwin W. Pauley Fellowship, a UCLA Chancellor's Prize, and funding from the Animal Behavior Society, La Kretz Center for California Conservation Science, Sea and Sage Audubon, Santa Monica Bay Audubon, UCLA Graduate Division and the UCLA Department of Ecology and Evolutionary Biology.

Chapter 1 is a reprint of a published paper- Chock, RY, Shier, DM, & Grether, GF. 2018. Body size, not phylogenetic relationship or residency, drives interspecific dominance in a little pocket mouse community. *Animal Behaviour*. 137: 197-204. The reprint is used here with the permission of Elsevier.

## VITA

### RACHEL YI-LING CHOCK

#### EDUCATION

MA, Biology and Conservation Biology, Clark University, Worcester, MA, 2008

BA, Environmental Science and Conservation Biology, Clark University, Worcester, MA, 2007

#### FELLOWSHIPS AND AWARDS

##### Fellowships

Edwin W. Pauley Fellowship, 2011 & 2014, Total \$30,000

UCLA EEB Departmental Fellowship, 2012, 2013 & 2014, Total \$27,000

US Department of Education GAANN Fellowship, 2012 & 2013, Total \$44,000

UCLA Chancellor's Prize Summer Mentorship Award, 2012 & 2013, Total \$10,000

##### Research Awards

Dean's Summer Scholar Award, 2017, Total \$10,500

La Kretz Center for CA Conservation Science Grant, 2013, 2014, 2015 & 2016, Total \$4,800

Sea & Sage Audubon Bloom-Hays Ecological Research Grant, 2014 & 2015, Total \$4,000

UCLA EEB Summer Research Award, 2012, 2013, 2014, 2015 & 2016, Total \$5,900

Animal Behavior Society E. O. Wilson Conservation Award, 2014, Total \$2,000

Santa Monica Bay Audubon Society Student Grant, 2014, Total \$550

##### Travel Awards

The Wildlife Society Southern California Chapter Travel Award, 2018, Total \$1,000

UCLA Graduate Division Research Travel Grant, 2014 & 2015, Total \$1,000

Animal Behavior Society- NSF Travel Award, 2012, Total \$2,000



## **PUBLICATIONS**

- Chock, R.Y., D.M. Shier, G.F. Grether. 2018. Body size, not phylogenetic relationship or residency status, drives interspecific dominance interactions in the little pocket mouse (*Perognathus longimembris*) community. *Animal Behaviour*. 137 (197-204).
- Chock, R.Y., T.W. Wey, L.A. Ebensperger, L.D. Hayes. 2017. Evidence for a behavioural syndrome and negative social assortment by exploratory personality in the communally nesting rodent, *Octodon degus*. *Behaviour* 154 (541-562).
- Baker, J.A., M.A. Wund, R.Y. Chock, L. Ackein, R. Elsemore, S.A. Foster. 2010. Predation history and vulnerability: conservation of the stickleback adaptive radiation. *Biological Conservation* 143 (1184-1192).

## **ORAL PRESENTATIONS**

- Chock, R.Y., D.M. Shier, G.F. Grether. Drivers of interspecific dominance in a little pocket mouse community. Southern California Animal Behavior Meeting, February 2018.
- Chock, R.Y., D.M. Shier, G.F. Grether. Little pocket mice: interspecific competition and coexistence in a rodent community. Animal Behavior Society Meeting, June 2015.
- Chock, R.Y. Interspecific competition and reintroduction of the endangered Pacific pocket mouse. UCLA EcoEvoPub Lecture Series, February 2014.
- Chock, R.Y. Ancestral plasticity and loss of a rare behavioral phenotype in threespine stickleback. UCLA EcoEvoPub Lecture Series, October 2011.
- Chock, R.Y. and S.A. Foster. Re-emergence of ancestral plasticity and the loss of a rare phenotype in threespine stickleback. Animal Behavior Society Meeting, August 2008.

**CHAPTER 1:**  
**BODY SIZE, NOT PHYLOGENETIC RELATIONSHIP OR RESIDENCY, DRIVES**  
**INTERSPECIFIC DOMINANCE IN A LITTLE POCKET MOUSE COMMUNITY**



Contents lists available at ScienceDirect

## Animal Behaviour

journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)

# Body size, not phylogenetic relationship or residency, drives interspecific dominance in a little pocket mouse community

Rachel Y. Chock<sup>a,\*</sup>, Debra M. Shier<sup>a,b</sup>, Gregory F. Grether<sup>a</sup>

<sup>a</sup> Department of Ecology & Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.

<sup>b</sup> Recovery Ecology, San Diego Zoo Institute for Conservation Research, Escondido, CA, U.S.A.

## ARTICLE INFO

### Article history:

Received 6 September 2017

Initial acceptance 6 November 2017

Final acceptance 1 December 2017

MS. number: A17-00719

### Keywords:

aggression

dominance

interference competition

*Perognathus longimembris*

pocket mouse

reintroduction biology

The role of interspecific aggression in structuring ecological communities can be important to consider when reintroducing endangered species to areas of their historic range that are occupied by competitors. We sought to determine which species is the most serious interference competitor of the endangered Pacific pocket mouse, *Perognathus longimembris pacificus*, and more generally, whether interspecific aggression in rodents is predicted by body size, residency status or phylogenetic relatedness. We carried out simulated territory intrusion experiments between *P. longimembris* and four sympatric species of rodents (*Chaetodipus fallax*, *Dipodomys simulans*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*) in a field enclosure in southern California sage scrub habitat. We found that body size asymmetries strongly predicted dominance, regardless of phylogenetic relatedness or the residency status of the individuals. The largest species, *D. simulans*, was the most dominant while the smallest species, *R. megalotis*, was the least dominant to *P. longimembris*. Furthermore, *P. longimembris* actively avoided encounters with all species, except *R. megalotis*. One management recommendation that follows from these results is that *P. longimembris* should not be reintroduced to areas with high densities of *D. simulans* until further research is carried out to assess the fitness consequences of the interactions. Our finding that the species least similar in body size is the most serious interference competitor of *P. longimembris* highlights an important distinction between interference and exploitative competition in rodent communities.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Understanding how similar species coexist in complex communities has puzzled ecologists for decades. Competition over shared resources may be reduced by niche partitioning in areas where species overlap (Hutchinson, 1959; Schoener, 1974). While it is well known that niche shifts can be driven purely by exploitative, or indirect, competition (i.e. resource depletion; Schluter, 2000), interference competition, in the form of interspecific aggression, also has the potential to drive niche shifts and structure ecological communities (Eccard & Ylonen, 2003; Grether, Losin, Anderson, & Okamoto, 2009; Grether, Peiman, Tobias, & Robinson, 2017; Grether et al., 2013; Peiman & Robinson, 2010; Robinson & Terborgh, 1995). Just as aggression between conspecifics can influence fitness through its effects on resource acquisition, reproduction and survival (Lahti, Laurila, Enberg, & Piironen, 2001), so can aggression between individuals of different species.

Interspecific aggression is widespread and often just as intense as intraspecific aggression (Ord & Stamps, 2009; Peiman & Robinson, 2010).

Aggression and other forms of interference competition are generally expected to reduce the probability of species coexisting (Amarasekare, 2002). Under some circumstances, however, interspecific aggression and avoidance can foster coexistence and stabilize communities (Grether et al., 2013; Robinson & Terborgh, 1995). Interspecific territoriality (site-specific aggression) is most likely to evolve when neither species consistently dominates the other in aggressive encounters (Maher & Lott, 2000; Peiman & Robinson, 2010), and can result in spatial niche partitioning that reduces exploitative resource competition between species and thereby promotes coexistence (Kaufmann, 1983; Robinson & Terborgh, 1995). When one species consistently dominates the other, avoidance of the dominant species by the subordinate species could also stabilize coexistence by causing spatial or temporal resource partitioning (Grether et al., 2017; Kaufmann, 1983; López-Bao, Mattisson, Persson, Aronsson, & Andrén, 2016; Perri & Randall, 1999; Rychlik & Zwolak, 2005).

\* Correspondence: R. Y. Chock, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 612 Charles E. Young Dr. East, Los Angeles, CA, 90095-7246, U.S.A.

E-mail address: [rchock@ucla.edu](mailto:rchock@ucla.edu) (R. Y. Chock).

<https://doi.org/10.1016/j.anbehav.2018.01.015>

0003-3472/© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Understanding how species interact in intact ecosystems is of critical importance to conservation, particularly when the goal is to reintroduce an endangered species back into a community. Reintroductions historically have low rates of success, as measured through survival and reproduction of individuals at the release site (Armstrong & Seddon, 2008). Success rates have been slowly improving as greater attention has been paid to factors such as habitat type, food availability, dispersal and predation risk (Seddon, Armstrong, & Maloney, 2007). Theory predicts that persistence of a reintroduced population would be more likely when competition is low, particularly for a small species at low initial abundance (Amarasekare, 2002; Grant, 1972); however, competitive relationships are rarely considered when planning reintroductions (Linnell & Strand, 2000; Seddon et al., 2007).

The Pacific pocket mouse, *Perognathus longimembris pacificus*, once thought to be extinct, was rediscovered in 1993 at the Dana Point Headlands and three different sites within Marine Corps Base Camp Pendleton in southern California (U.S. Fish & Wildlife Service, 1998). Since then, one of the Camp Pendleton populations has probably been lost (Brehme & Fisher, 2008), and no new populations have been discovered despite extensive surveys throughout the species' range (U.S. Fish & Wildlife Service, 2015). Captive breeding and reintroduction efforts are underway to establish additional wild populations, per the species Recovery Plan (U.S. Fish & Wildlife Service, 1998).






We sought to determine which ecologically similar species are the most important interference competitors of *P. l. pacificus*, to assist with the reintroduction programme and help wildlife managers select and manage release sites. Four other species of native rodent commonly occur in the same habitat (Coastal Sage Scrub; Meserve, 1976a, 1976b; Table 1) and have diets (Brown &

Lieberman, 1973; Meserve, 1976a) and seed-caching behaviour similar to *P. l. pacificus* (Eisenberg, 1962; Leaver & Daly, 2001; Vander Wall, Thayer, Hodge, Beck, & Roth, 2001). This includes two other species in the family Heteromyidae, the San Diego pocket mouse, *Chaetodipus fallax*, and the Dulzura kangaroo rat, *Dipodomys simulans*, and two species in the family Cricetidae, the deer mouse, *Peromyscus maniculatus*, and the western harvest mouse, *Reithrodontomys megalotis*. To study dominance interactions, we carried out simulated territory intrusion experiments in field enclosures. Because *P. l. pacificus* does not currently coexist with *D. simulans*, but *D. simulans* occurs within the historic range of *P. l. pacificus* and is present at potential reintroduction sites, some territory intrusion experiments were carried out using the sister subspecies *P. l. brevinasus* (Los Angeles pocket mouse; McKnight, 2005).

Our study also addresses a general question about interference competition in small mammal communities: do species differences in body size or phylogenetic distance (time since the most recent common ancestor), predict species-level dominance relationships? The answer to this question may enable our results to be extrapolated to other communities and be useful in conservation of other endangered small mammals. Body size is expected to be important in determining dominance (Blaustein & Risser, 1976; Grant, 1972; Peiman & Robinson, 2010; Persson, 1985; Robinson & Terborgh, 1995; Schoener, 1983; Shulman, 1985), with larger individuals dominating smaller ones (reviewed in Shelley, Tanaka, Ratnathicam, & Blumstein, 2004). Based on body size asymmetries alone, we predicted that the largest species, *D. simulans*, would be the most dominant to *P. longimembris*, that the medium-size species, *C. fallax* and *P. maniculatus*, would be of intermediate dominance, and that the smallest species, *R. megalotis*, would be

Table 1

Descriptions of each species and their similarity in size, diet, habitat and relatedness to the little pocket mouse, *Perognathus longimembris*

|   |   | Body size <sup>1</sup>  | Relatedness to <i>P. longimembris</i> <sup>2</sup> (TMRCAs) | Diet overlap with <i>P. longimembris</i> <sup>3</sup> | Habitat overlap with <i>P. longimembris</i> <sup>3</sup> |
|---|---|---|---|---|--|
| <b>Family: Heteromyidae</b>   |   |   |   |   |  |
|  | <i>P. longimembris</i><br>Pacific pocket mouse ( <i>P. l. pacificus</i> )<br>Los Angeles pocket mouse ( <i>P. l. brevinasus</i> ) | Weight: 6–9 g<br>Body length: 50–70 mm<br>Tail length: 60–85 mm       | —   | —   | —  |
|  | <i>Chaetodipus fallax</i><br>San Diego pocket mouse   | Weight: 14–26 g<br>Body length: 70–91 mm<br>Tail length: 105–120 mm   | 26.5  | *   | *  |
|  | <i>Dipodomys simulans</i><br>Dulzura kangaroo rat   | Weight: 50–94 g<br>Body length: 112–132 mm<br>Tail length: 163–216 mm | 28.9  | 93%   | Horizontal: 10–50%<br>Vertical: 100%                     |
| <b>Family: Cricetidae</b>   |   |   |   |   |  |
|  | <i>Peromyscus maniculatus</i><br>Deer mouse   | Weight: 15–29 g<br>Body length: 80–109 mm<br>Tail length: 77–106 mm   | 65.3  | 33%   | Horizontal: 10–35%<br>Vertical: 95%                      |
|  | <i>Reithrodontomys megalotis</i><br>Western harvest mouse   | Weight: 6–11 g<br>Body length: 59–77 mm<br>Tail length: 71–79 mm      | 65.3  | 45%   | Horizontal: 15–55%<br>Vertical: 60–70%                   |

\**Chaetodipus fallax* were infrequently found in Meserve's study area and were not included in these comparisons.

<sup>1</sup> Average body size measures taken from Reid (2006).

<sup>2</sup> Time since most recent common ancestor (TMRCAs) shared with *P. longimembris* in millions of years.

<sup>3</sup> Diet and habitat overlap from Meserve (1976b) using year-round trapping for a suite of species, including four of our focal species. Meserve assessed diet overlap using faecal microscopy, and we calculated the median overlap from his 9-month study. Horizontal habitat use was assessed using live-traps, while vertical habitat use was studied with smoked track cards. Habitat overlap was quantified over four seasons in one year (Meserve, 1976b).

most closely matched to *P. longimembris*. However, overlap in resource use is expected to affect the benefits of interspecific aggression for the dominant species (Houle, 1997; Myrberg & Thresher, 1974; Orians & Willson, 1964; Peiman & Robinson, 2010), and *P. longimembris* is more similar to the other heteromyids than to the cricetids in resource use (Meserve, 1976a, 1976b; Table 1). Based on this hypothesis, we predicted higher levels of aggression between *P. longimembris* and *C. fallax*, the closest relatives, than between *P. longimembris* and either *P. maniculatus* or *R. megalotis* (Meserve, 1976a, 1976b). Considering both phylogenetic relatedness and body size, we predicted that *D. simulans* (a heteromyid and the largest species in the community) would be the most important interference competitor of *P. longimembris*.

We also investigated factors that may override dominance relationships based on body size or relatedness. Observations of intraspecific territoriality by some heteromyids (Randall, 1984) and cricetids (Wolff, Freeberg, & Dueser, 1983), in addition to overlap between our focal species in diet, burrowing sites and defensibility of food cached in burrows suggest that these species might be interspecifically territorial. If so, interspecific dominance might be site specific, such that individuals are more aggressive as residents than as intruders, regardless of opponent species. We also examined patterns of active avoidance behaviour to determine whether *P. longimembris* minimizes aggressive encounters by avoiding opponents. Although subordinate species may be able to coexist with dominant species, avoidance is costly in terms of time and energy and can prevent subordinates from utilizing preferred habitats (Berger & Gese, 2007). Understanding how *P. l. pacificus* are affected by larger species in the community could aid reintroduction efforts by identifying ways to reduce interspecific interference.

## METHODS

Experiments were conducted with *P. l. pacificus* and *R. megalotis* in June 2013 and July 2016 at U.S. Marine Corps Base Camp Pendleton (33.39°N, 117.57°W). To increase sample sizes and include *D. simulans*, which is not currently sympatric with extant *P. l. pacificus* populations, we conducted experiments with a sister subspecies, *P. l. brevinasus* (Los Angeles pocket mice) and *D. simulans*, *R. megalotis*, *C. fallax* and *P. maniculatus* during April–September 2014 at the San Felipe Valley Wildlife Area (33.10°N, 116.53°W), and May–July 2015 at the San Jacinto Wildlife Area (33.13°N, 116.54°W). Our study was conducted when *P. longimembris* were above ground and active (Kenagy, 1973). All sites were characterized by coastal or Riversidean sage scrub, and included fallow agricultural areas that were dominated by non-native grasses (*Avena* and *Bromus* spp.).

### Testing Procedure

We used Sherman live-traps (H.B. Sherman Traps, Inc., Tallahassee, FL, U.S.A.) with modified shortened doors to avoid tail injury. In each year, traps were spread across noncontiguous sites (25–50 traps per site, between 8 and 20 sites per year). Traps were opened and baited with millet seed (microwaved for 5 min to prevent germination) between 1800 and 2000 hours and checked twice during the night at 2200 and 0200 hours. Traps were closed during the check at 0200 hours to ensure all behavioural experiments were conducted before dawn. All animals were individually tagged for identification. We used uniquely numbered ear tags for *D. simulans* and *P. maniculatus* (Monel 1005-1, National Band and Tag Co., Newport, KY, U.S.A.). For species with small ears (*P. l. pacificus*, *P. l. brevinasus*, *C. fallax*, *R. megalotis*), we injected visible implant elastomer (VIE- Northwest Marine Technology, Inc., Shaw Island, WA, U.S.A.) in unique colour combinations just under the

skin along the side of the tail (Shier, 2008). These permanent marks were visible under a black light on subsequent captures. For each individual trapped we recorded species, unique identity, sex, weight, reproductive condition and trap location. Adult males and females of each species were used in simulated territorial intrusions.

We conducted a total of 170 dyadic encounters between *P. longimembris* spp. and opponent species ( $N = 48$  *P. l. brevinasus*  $\times$  *C. fallax*;  $N = 48$  *P. l. brevinasus*  $\times$  *D. simulans*;  $N = 48$  *P. l. brevinasus*  $\times$  *P. maniculatus*;  $N = 2$  *P. l. brevinasus*  $\times$  *R. megalotis*;  $N = 24$  *P. l. pacificus*  $\times$  *R. megalotis*). In pilot trials we found no difference in behaviour between *P. l. brevinasus* and *P. l. pacificus* when paired with *P. maniculatus* ( $N = 10$ ), thus we combined trials with the two subspecies and analysed them together as *P. longimembris*. All species are solitary, and individuals were paired with heterospecifics of the same or opposite sex since aggressive interactions can take place between members of either sex. We counted an individual as a resident if it was trapped in the same location at least three times (Shier & Swaisgood, 2012). Each trial was conducted at the location where the resident was trapped, and the intruder individual was brought from a trapping area at least 200 m away to ensure the individuals were not familiar with one another (Maza, French, & Aschwanden, 1973; McNab, 1963; Shier, 2008).

We conducted dyadic encounters immediately following trap checks at 2200 and 0200 hours. Individuals were not held longer than the 4 h interval between checks. We used the same individual in no more than two trials, separated by a minimum of 24 h, once as the intruder and once as the resident, but never with the same opponent. We tested pairs of individuals in an arena (61  $\times$  61  $\times$  61 cm) made of clear Plexiglas with an open bottom, to allow focal subjects to see their surroundings and remain on natural substrate. For each encounter, we carried the arena to the trap site of the resident individual. Millet seed was scattered throughout, and if no natural cover was available, we added twigs and vegetation to two corners of the arena to provide cover. A removable opaque plastic partition initially split the arena into halves, and individuals were placed on separate sides to acclimate, as indicated by commencement of foraging (0.5–2 min). We removed the barrier at the beginning of the trial and allowed individuals to interact for 5 min. At the end of the trial, we released animals at their location of capture. Trials were recorded with an infrared camcorder (Bell & Howell DNV16HDZ-BKFull) on a tripod, and later transcribed into JWatcher (Blumstein & Daniel, 2007), an event logging program used to code behaviours and interactions for analysis, and Tracker (Brown, 2006), a movement quantification program to track a focal subject's position relative to their opponent through space and time.

Rodents were studied under protocols approved by the Institutional Animal Care and Use Committee of San Diego Zoo Global (protocol number 15-002). One observer (R.Y.C.) monitored all staged encounters through night-vision goggles to ensure the safety of the animals. No locked battles occurred, and no injuries were sustained in any of the trials.

### Behavioural Dominance

For each focal individual we counted the number of aggressive behaviours, which included 'approach' (oriented head and body and moved towards the other individual), 'displace' (an approach that resulted in the other individual moving away), 'chase' (pursuit of a fleeing individual), 'lunge' (thrusting body towards other), 'attack' (initiated sparring, biting or locked battle) and 'sandbathe' (rubbed side or ventrum against sand, depositing scent; Randall, 1987). We also counted the number of submissive behaviours, which were 'retreat' (movement away from opponent after

initiating proximity), 'displaced' (moved away from approaching opponent), 'flee' (rapid movement away from other individual following engagement) and 'jump/avoid' (jumped upwards and back away from opponent). The agonistic behaviours we observed were almost instantaneous; thus, we recorded counts rather than duration.

We calculated a dominance index to represent an animal's relative display of dominance-typical behaviour to subordinate-typical behaviour (Blaustein & Risser, 1976; Dempster & Perrin, 1990; Kaufmann, 1983; Rychlik & Zwolak, 2006; Shier & Randall, 2007). To calculate an individual's position on the dominance index, we added all aggressive behaviours and subtracted all subordinate behaviours, and then divided by the total number of behaviours. The index ranged from  $-1$  (always submissive) to  $1$  (always aggressive). A score of zero indicated the same number of aggressive and submissive behaviours.

#### Avoidance and Pursuit

To detect and quantify avoidance and pursuit, we measured each animal's movements during the experimental trials. In Tracker (Brown, 2006) we overlaid  $x$  and  $y$  axes on the video recording and set a reference length based on the wall of the arena. We recorded the position ( $x,y$  coordinates) of both individuals once per second by stepping through the video and clicking on a point between the animals' eyes. From this, we measured the change in distance initiated by each individual (i.e. moving closer to or further from the opponent) and the distance moved in any direction in each time step. We then divided the average distance moved towards (positive values) or away (negative values) by the average distance moved in any direction and multiplied the quotient by 100 to obtain a normalized average measure of avoidance or pursuit for each individual.

#### Predictors of Dominance

We calculated the difference in body size between each pair of opponents by subtracting the weight of the *P. longimembris* from the weight of the opponent that we measured in the field. For each competitor species, we calculated the time since most recent common ancestor (TMRCA) shared with *P. longimembris* in millions of years. We used the maximum clade credibility tree that Rolland, Condamine, Jiguet, and Morlon (2014) calculated and re-dated using Meredith et al.'s (2011) dates on Kuhn et al.'s (2011) pseudo-posterior distribution of 100 trees, which itself was created from Fritz et al.'s (2009) mammalian phylogeny with 5020 tips.

#### Statistical Analyses

We used the Wilcoxon matched-pairs signed-ranks test to examine whether *P. longimembris* differed from each competitor species in dominance, aggressive or submissive behaviours. We used generalized linear models (GLM) to identify predictors of variation in agonistic behaviour and avoidance and pursuit behaviour. These models allowed us to assess behaviour from the point of view of both *P. longimembris* and the competitor species. We also examined how *P. longimembris* behaviour changed when paired with different opponent species, and how the competitor species differed in their responses to *P. longimembris*. We assessed behavioural dominance using dominance index scores, aggressive and submissive behaviour of *P. longimembris* and each of the four competitor species. Our full model for all behavioural dominance and avoidance/pursuit behaviours included opponent species, *P. longimembris* sex, opponent sex, residency status and residency status by opponent species interaction. We also calculated a

reduced model without the interaction term, and a third model without the interaction term or the main effect of opponent species. We used the change in Akaike information criterion ( $\Delta AIC$ ) between the three models to select the best fit for each behaviour of interest. Models were fitted in R 3.1.2 (R Development Core Team, 2014). The aggressive and submissive count variables were over-dispersed relative to a Poisson distribution, so we used negative binomial regression ('glm.nb' function in the package MASS; Venables & Ripley, 2002). We determined that the dominance index followed a Gaussian distribution (based on visual inspection of residuals), which allowed us to use the 'glm' function even though the data were bounded at  $-1,1$ .

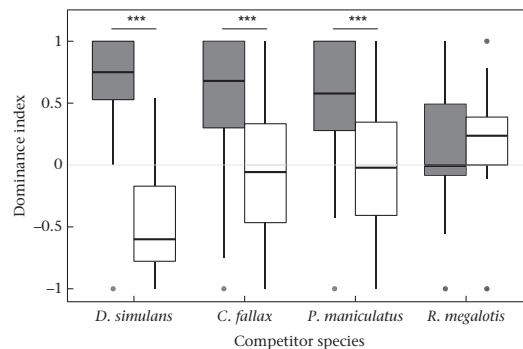
To test whether both body size and most recent common ancestor predicted dominance interactions, we used the change in Akaike information criterion ( $\Delta AIC$ ) to select the best model. The four models we compared were a basic model that included *P. longimembris* sex, residency status and opponent sex; the same basic model with difference in body weight between opponents added; the basic model with time since most recent common ancestor (TMRCA) added; or the basic model with both difference in weight and TMRCA added.

## RESULTS

#### Behavioural Dominance

All competitor species had higher dominance indices than *P. longimembris*, except for *R. megalotis*, which did not differ from *P. longimembris* (Fig. 1; Wilcoxon matched-pairs signed-ranks test: *D. simulans*:  $V = 1010$ ,  $P < 0.001$ ; *C. fallax*:  $V = 933.5$ ,  $P < 0.001$ ; *P. maniculatus*:  $V = 962$ ,  $P < 0.001$ ; *R. megalotis*:  $V = 86.5$ ,  $P = 0.7$ ).

The dominance index of *P. longimembris* was lower in trials with *D. simulans* than in trials with any other competitor species; otherwise, the dominance index of *P. longimembris* was not affected by competitor species identity (Fig. 1, Supplementary Table S1). The competitor species were similar to one another in their dominance indices in trials with *P. longimembris*, except for *R. megalotis*, which was lower on the dominance index than all other competitors (Fig. 1, Supplementary Table S1). There were no effects of residency status, sex of *P. longimembris* or sex of the competitor on the



**Figure 1.** Dominance indices for little pocket mice (*P. longimembris*) and the four competitor species with which they were paired in dyadic encounters. Competitor species are grouped by family and ordered by body size (larger to smaller). The dominance index ranges from 1 (most dominant) to  $-1$  (most subordinate). The distance between the competitor (grey bars) and *P. longimembris* (open bars) represents the asymmetry in dominance (\*\*\*)  $P < 0.001$ ). The box plots depict medians (horizontal lines) and interquartile ranges, IQR (boxes). Whiskers show spread of data (highest and lowest values within 1.5 IQR), and dots are outliers.

dominance index scores (Supplementary Table S1), and there was no interaction between residency status and opponent species (Supplementary Table S2).

Little pocket mice (*P. longimembris*) matched or exceeded their opponents in frequency of aggressive behaviour, except for *D. simulans*, which were more aggressive than *P. longimembris* (Fig. 2; Wilcoxon matched-pairs signed-ranks test: *D. simulans*:  $V = 913.5$ ,  $P < 0.001$ ; *C. fallax*:  $V = 591$ ,  $P = 0.41$ ; *P. maniculatus*:  $V = 481$ ,  $P = 0.38$ ; *R. megalotis*:  $V = 58$ ,  $P = 0.009$ ).

We found no effect of competitor species on *P. longimembris* aggressive behaviour (Fig. 2, Supplementary Table S1), but the competitor species differed from one another: *D. simulans* was the most aggressive, and *R. megalotis* was the least aggressive, towards *P. longimembris* (Fig. 2, Supplementary Table S1).

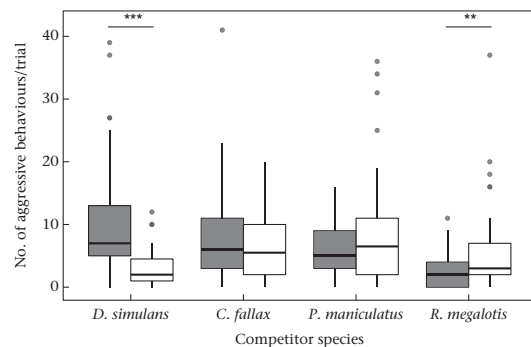
*P. longimembris* were more submissive than all species except *R. megalotis* (Fig. 3; Wilcoxon matched-pairs signed-ranks test: *D. simulans*:  $V = 17.5$ ,  $P < 0.001$ ; *C. fallax*:  $V = 53.5$ ,  $P < 0.001$ ; *P. maniculatus*:  $V = 69.5$ ,  $P < 0.001$ ; *R. megalotis*:  $V = 80.5$ ,  $P = 0.23$ ). *P. longimembris* exhibited fewer submissive behaviours towards *R. megalotis* than towards the other species, but otherwise was equally submissive towards the competitor species (Fig. 3, Supplementary Table S1). The competitor species did not differ from one another in frequency of submissive behaviours (Fig. 3, Supplementary Table S1).

#### Avoidance and Pursuit

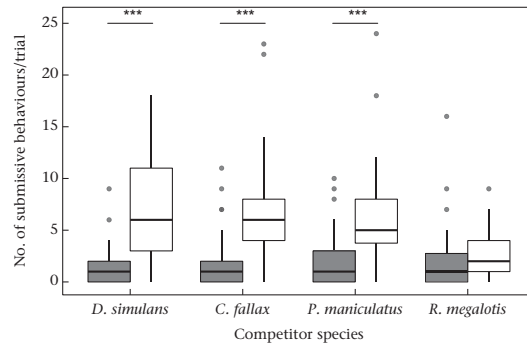
Most movement by *P. longimembris* increased the distance between the two individuals, indicating active avoidance. This was true for all opponent species except *R. megalotis*, which *P. longimembris* tended to move closer to rather than farther from (Fig. 4, Supplementary Table S3). Of the competitor species, *D. simulans* and *C. fallax* showed the highest percentage of movement pursuing *P. longimembris* (Fig. 4, Supplementary Table S3), and *P. longimembris* avoided these species more than the others. In all pairings, one species tended to pursue and the other avoided the opponent (Fig. 4; Wilcoxon matched-pairs signed-ranks tests: *D. simulans*:  $V = 1128$ ,  $P < 0.001$ ; *C. fallax*:  $V = 1176$ ,  $P < 0.001$ ; *P. maniculatus*:  $V = 1081$ ,  $P < 0.001$ ; *R. megalotis*:  $V = 12$ ,  $P < 0.001$ ).

#### Predictors of Dominance

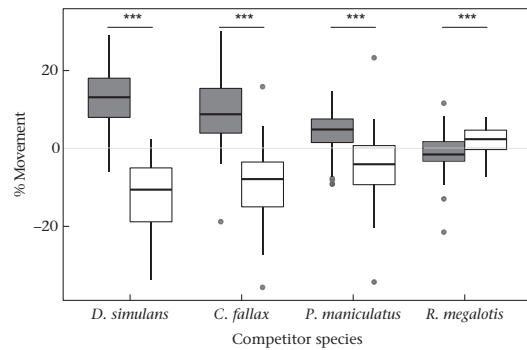
Differences in body weight between opponents improved the fit of all models and therefore helped account for variation in the



**Figure 2.** Aggression rates of little pocket mice (*P. longimembris*; open bars) and the four competitor species with which they were paired in 5 min dyadic encounters (grey bars). Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box plot definition. \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Figure 3.** Submission rates of little pocket mice (*P. longimembris*; open bars) and the four competitor species with which they were paired in 5 min dyadic encounters (grey bars). Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box plot definition. \*\*\* $P < 0.001$ .



**Figure 4.** Average distance that each animal moved towards or away from its opponent, as a percentage of total movement. Positive values indicate pursuit while negative values indicate avoidance. Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box plot definition. \*\*\* $P < 0.001$ .

behaviour of *P. longimembris* and the competitor species (Supplementary Table S4). A greater difference in weight corresponded to a greater difference in dominance (Table 2). Including time since the most recent common ancestor (TMRCA), in addition to difference in weight, improved the fit of models of competitor aggressive behaviour, *P. longimembris* subordinate behaviour, and pursuit and avoidance behaviour of both *P. longimembris* and competitor species (Supplementary Table S4). The direction of the TMRCA effect was that *P. longimembris* elicited fewer aggressive behaviours from, and directed fewer submissive behaviours towards, more distantly related competitor species (Table 2).

#### DISCUSSION

The greatest asymmetry in dominance was between *P. longimembris* and the largest species *D. simulans*. *P. longimembris* was also subordinate to *C. fallax* and *P. maniculatus*, but equal in dominance to *R. megalotis*, which is the most closely matched to *P. longimembris* in body size. Our findings are consistent with the prediction that larger species will dominate smaller species in one-on-one combat (Shelley et al., 2004), and our results support



**Table 2**

GLM results with dominance-related behaviours as the dependent variables and species weight difference and most recent common ancestor (TMRCA) as additional predictor variables

| Dependent variable   | Focal species          | Model term               | Estimate      | SE           | t             | P              | BH adjusted P    |
|----------------------|------------------------|--------------------------|---------------|--------------|---------------|----------------|------------------|
| Dominance index      | <i>P. longimembris</i> | <b>Weight difference</b> | <b>−0.010</b> | <b>0.002</b> | <b>−4.689</b> | <b>6.06e−6</b> | <b>&lt;0.001</b> |
|                      |                        | PELO sex                 | 0.146         | 0.083        | 1.753         | 0.082          | 0.184            |
|                      |                        | Opponent sex             | −0.131        | 0.084        | −1.569        | 0.119          | 0.206            |
|                      | Competitors            | PELO resident status     | −0.044        | 0.083        | −0.528        | 0.598          | 0.676            |
|                      |                        | <b>Weight difference</b> | <b>0.006</b>  | <b>0.002</b> | <b>2.875</b>  | <b>0.005</b>   | <b>0.024</b>     |
|                      |                        | PELO sex                 | −0.122        | 0.078        | −1.578        | 0.117          | 0.206            |
|                      |                        | Opponent sex             | −0.067        | 0.079        | −0.851        | 0.396          | 0.572            |
|                      |                        | PELO resident status     | −0.071        | 0.077        | −0.921        | 0.358          | 0.548            |
|                      |                        | <b>Weight difference</b> | <b>−0.020</b> | <b>0.004</b> | <b>−4.612</b> | <b>3.98e−6</b> | <b>&lt;0.001</b> |
| Aggressive behaviour | <i>P. longimembris</i> | PELO sex                 | 0.370         | 0.168        | 2.202         | 0.028          | 0.105            |
|                      |                        | Opponent sex             | −0.188        | 0.169        | −1.114        | 0.265          | 0.431            |
|                      |                        | PELO resident status     | −0.313        | 0.167        | −1.876        | 0.061          | 0.158            |
|                      | Competitors            | Weight difference        | 0.007         | 0.004        | 1.713         | 0.087          | 0.184            |
|                      |                        | <b>TMRCA</b>             | <b>−0.014</b> | <b>0.005</b> | <b>−2.921</b> | <b>0.003</b>   | <b>0.024</b>     |
|                      |                        | PELO sex                 | −0.088        | 0.146        | −0.603        | 0.547          | 0.676            |
|                      |                        | Opponent sex             | 0.021         | 0.148        | 0.142         | 0.887          | 0.923            |
|                      |                        | PELO resident status     | −0.113        | 0.145        | −0.776        | 0.438          | 0.599            |
|                      |                        | Weight difference        | 0.002         | 0.003        | 0.446         | 0.655          | 0.710            |
| Submissive behaviour | <i>P. longimembris</i> | TMRCA                    | −0.008        | 0.004        | −1.993        | 0.046          | 0.150            |
|                      |                        | PELO sex                 | 0.003         | 0.122        | 0.026         | 0.979          | 0.979            |
|                      |                        | Opponent sex             | 0.080         | 0.124        | 0.646         | 0.518          | 0.673            |
|                      | Competitors            | PELO resident status     | −0.068        | 0.121        | −0.559        | 0.576          | 0.676            |
|                      |                        | Weight difference        | −0.011        | 0.005        | −2.195        | 0.028          | 0.105            |
|                      |                        | <b>PELO sex</b>          | <b>0.568</b>  | <b>0.199</b> | <b>2.853</b>  | <b>0.004</b>   | <b>0.024</b>     |
|                      |                        | Opponent sex             | 0.388         | 0.200        | 1.942         | 0.052          | 0.151            |
|                      |                        | PELO resident status     | −0.329        | 0.195        | −1.686        | 0.092          | 0.184            |

PELO = *Perognathus longimembris*. Only the best models, based on  $\Delta AIC$ , are shown (see Supplementary Table S4 for model selection results). Benjamini–Hochberg adjusted P values control for false discovery rate (FDR). All significant terms are in bold.

previous findings that size differences predict the outcome of paired encounters (Brenner, Gaetano, Mauser, & Belowich, 1978; Grant, 1972; Langkilde & Shine, 2004; Schoener, 1983). However, we expected to see higher levels of aggression between *P. longimembris* and *R. megalotis* in our field enclosures, as equal competitors are more likely than asymmetric competitors to escalate conflicts (Maynard Smith & Parker, 1976; Meserve, 1976b). Instead, we found they were less aggressive towards one another than any of the other species pairs, suggesting they may not be in close competition for shared resources in the field.

While our findings of dominance fit our predictions based on differences in body size, the patterns of aggressive and submissive behaviours that make up the dominance scores were surprising. Based on the asymmetry in dominance, we had expected *P. longimembris* to always be less aggressive than its opponents, but this was only true with *D. simulans*. Instead, we found that the high frequency of submissive behaviours by *P. longimembris*, particularly towards fellow heteromyids, accounts for the species differences in dominance indices. Perhaps this should not be surprising, as Rowell (1966, 1974) and Kaufmann (1983) pointed out that subordinate behaviours are less conspicuous and often overlooked but are actually more important in maintaining dominance relationships than are aggressive behaviours. In her studies of dominance hierarchies in a group of captive baboons, Rowell (1966) found that the behaviour of the subordinate animal was closely correlated with social rank, whereas initiation of agonistic behaviour was much less well correlated with high rank. In these primate groups, it was the subordinate animals that maintained the hierarchy by giving way to the dominant animals, even when the dominant animals were not overtly aggressive or did not even acknowledge the other individuals (Rowell, 1974).

Avoidance of dominant individuals might reduce agonistic interactions while maintaining dominance hierarchies. We measured avoidance and pursuit in the experimental trials to determine whether subordinates actively avoided encounters with dominants,

which could have resulted in low frequencies of aggressive and submissive behaviours. We found instead that avoidance and pursuit behaviour were consistent with *P. longimembris* submissive behaviour and competitor aggressive behaviour, with the greatest asymmetry in avoidance and pursuit between *P. longimembris* and the larger and closely related heteromyid species.

Dominance relationships might not be consistent across all contexts if species are more aggressive while defending territories (Maher & Lott, 2000; Peiman & Robinson, 2010). The overlap in diet and burrowing sites, defensibility of resources and solitary nature of the species suggested that interspecific territoriality might occur in this community. If *P. longimembris* were interspecifically territorial, they would be more aggressive, and less submissive, as residents than as intruders, but this was not the case. Overall, we found no differences in behaviour of residents and intruders, indicating that dominance is not site specific. Although there is high overlap in resource use between our study species, if the cost of territorial defence is too high, interspecific territoriality might not be adaptive (Mikami & Kawata, 2004). The asymmetry in fighting ability likely overwhelms any residency advantages in direct encounters for *P. longimembris*. Nevertheless, the small size of *P. longimembris* may be advantageous. If larger species cannot fit in their burrow entrances, *P. longimembris* do not need to aggressively defend their seed larders against pilfering by other species (Jenkins & Breck, 1998). We did not test whether *P. longimembris* are territorial towards conspecifics, which would be able to pilfer the larders.

Our finding that *P. longimembris* were subordinate to all the larger species indicates that there may be fitness costs to living in sympatry. Research on captive rhesus monkeys, *Macaca mulatta*, revealed that subordinate individuals had over-reactive endocrine stress-response systems and were more likely to die of stress-related diseases than dominant animals (Sassenrath, 1970). Captive rodents housed in crowded conditions showed enlarged adrenal glands compared to wild-caught conspecifics, and low-ranking individuals had much greater enlargement than high-



ranking cage-mates (Barnett, 1963). The physiological response, like the behavioural response, appears to be stronger in subordinate, rather than dominant, individuals.

Although we did not assess fitness costs of dominance relationships, large-scale removal experiments in a similar community found that when all *Dipodomys* were excluded from fenced plots, the density of the smaller species, including *Perognathus*, significantly increased (Brown & Munger, 1985; Valone & Brown, 1995). Consistent with our dominance results, *Dipodomys* had a strong effect on the smaller competitors, suggesting these behavioural relationships might have fitness consequences and should be considered when designing reintroductions for endangered species.

#### Management Recommendations and Future Directions

Behavioural studies have been identified as a way to improve progress in applied conservation (Greggor et al., 2016), and the results from our study are already being used by wildlife managers reintroducing captive-bred populations of the endangered Pacific pocket mouse, *P. longimembris pacificus*. It is well known that the highest rates of mortality during reintroductions occur during the post-release settlement period (i.e. the first days to weeks following release) (Stamps & Swaisgood, 2007). Thus, to increase the probability of settlement and reintroduction success, it is critical that potential threats such as predators or competitors be minimized during this period. Our results show that *D. simulans* is the most dominant competitor of *P. longimembris*, suggesting it could exclude *P. l. pacificus* from preferred habitat and other limited resources during settlement. Additional research is needed to fully understand the long-term impacts *D. simulans* may have on *P. l. pacificus* and whether the little pocket mice are forced to occupy a smaller realized niche in sympatry (Ziv, Abramsky, Kotler, & Subach, 1993), or alternatively, if they experience any benefits from living in sympatry, such as advantages from pilfering caches of larger species (Price, Waser, & McDonald, 2000). Taken together, our results suggest a conservative reintroduction approach would be to select release sites for *P. l. pacificus* that do not contain *D. simulans*, or to avoid reintroducing *P. l. pacificus* into areas with medium to high density of *D. simulans*.

#### Acknowledgments

Illustrations by Joann Shih. We thank Daniel Disbrow, Emily Gray, Kimberly Horrell, Cassie Kovarik, Anna Kowalczyk, Matthew Lucero, Aliya McCarthy, Elizabeth Max, Julianne Pekny, Dalia Ruiz, Andrea Sork and Laura Wade for field assistance. For assistance with video analyses, we thank Jaspal Bassi, Jewel Fisher, Ashley Kranz, Courtney Lee, Kevin Neumann, Jake Nusynowitz and Brianna Rodriguez. We thank Jonathan P. Drury for calculating TMRCA for our species, and J. P. Drury, Daniel T. Blumstein, Michael H. Ferkin and two anonymous referees for helpful comments on the manuscript. Andy Lin at the University of California, Los Angeles (UCLA) Statistical Consulting provided statistical help. R. Y. Chock received a U.S. Department of Education GAANN Fellowship administered through UCLA, a UCLA Pauley Fellowship, a UCLA Chancellor's Prize, and funding from the Animal Behavior Society, La Kretz Center for California Conservation Science, Sea and Sage Audubon, Santa Monica Bay Audubon, UCLA Graduate Division and the Department of Ecology and Evolutionary Biology.

#### Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2018.01.015>.

#### References

- Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings of the Royal Society B: Biological Sciences*, 269(1509), 2541–2550. <https://doi.org/10.1098/rspb.2002.2181>.
- Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution*, 23(1), 20–25. <https://doi.org/10.1016/j.tree.2007.10.003>.
- Barnett, S. A. (1963). *The rat: A study in behaviour*. Chicago, IL: Aldine.
- Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, 76(6), 1075–1085. <https://doi.org/10.1111/j.1365-2656.2007.01287.x>.
- Blaustein, A. R., & Risser, A. C. (1976). Interspecific interactions between three sympatric species of kangaroo rats (*Dipodomys*). *Animal Behaviour*, 24, 381–385. [https://doi.org/10.1016/S0003-3472\(76\)80047-4](https://doi.org/10.1016/S0003-3472(76)80047-4).
- Blumstein, D. T., & Daniel, J. C. (2007). *Quantifying behavior the JWatcher way*. Sunderland, MA: Sinauer.
- Brehme, C. S., & Fisher, R. N. (2008). 2008 Survey results for the Pacific pocket mouse: North and south San Mateo, Marine Corps Base, Camp Pendleton; with additional analyses to inform long-term monitoring design. U. S. Geological Survey Report Prepared for AC/S Environmental Security, Marine Corps Base, Camp Pendleton. Unpublished report.
- Brenner, F. J., Gaetano, C. P., Mauser, S. W., & Belowich, D. L. (1978). Body weight and social interactions as factors in determining dominance in captive eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 26, 432–437. [https://doi.org/10.1016/0003-3472\(78\)90060-X](https://doi.org/10.1016/0003-3472(78)90060-X).
- Brown, D. (2006). *Tracker*. In *Open source physics: A user's guide with examples*. <https://www.compadre.org/osp/items/detail.cfm?ID=7379>.
- Brown, J. H., & Lieberman, G. A. (1973). Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology*, 54, 788–797. <https://doi.org/10.2307/1935673>.
- Brown, J. H., & Munger, J. C. (1985). Experimental manipulation of a desert rodent community: Food addition and species removal. *Ecology*, 66(5), 1545–1563. <https://doi.org/10.2307/1938017>.
- Dempster, E. R., & Perrin, M. R. (1990). Interspecific aggression in sympatric *Gerrbillus* species. *Zeitschrift für Säugetierkunde*, 55, 392–398.
- Eccard, J. A., & Ylonen, H. (2003). Interspecific competition in small rodents: From populations to individuals. *Evolutionary Ecology*, 17, 423–440. <https://doi.org/10.1023/A:1027305410005>.
- Eisenberg, J. F. (1962). Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parvulus*. *Behaviour*, 19, 177–207. <https://doi.org/10.1163/156853962X000014>.
- Fritz, S. A., Bininda-Emonds, O. R. P., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, 12(6), 538–549. <https://doi.org/10.1111/j.1461-0248.2009.01307.x>.
- Grant, P. R. (1972). Interspecific competition among rodents. *Annual Review of Ecology and Systematics*, 3, 79–106. <http://www.jstor.org/stable/2096843>.
- Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., et al. (2016). Research priorities from animal behaviour for maximising conservation progress. *Trends in Ecology & Evolution*, 31(12), 953–964. <https://doi.org/10.1016/j.tree.2016.09.001>.
- Grether, G. F., Anderson, C. N., Drury, J. P., Kirschel, A. N. G., Losin, N., Okamoto, K., et al. (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., Losin, N., Anderson, C. N., & Okamoto, K. (2009). The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews*, 84(4), 617–635. <https://doi.org/10.1111/j.1469-185X.2009.00089.x>.
- Grether, G. F., Peiman, K. S., Tobias, J. A., & Robinson, B. W. (2017). Causes and consequences of behavioral interference between species. *Trends in Ecology & Evolution*, 32(10), 760–772. <https://doi.org/10.1016/j.tree.2017.07.004>.
- Houle, A. (1997). The role of phylogeny and behavioral competition in the evolution of coexistence among primates. *Canadian Journal of Zoology*, 75(6), 827–846. <https://doi.org/10.1139/z97-106>.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia. *American Naturalist*, 93(870), 145–159. <https://doi.org/10.1086/282070>.
- Jenkins, S. H., & Breck, S. W. (1998). Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy*, 79(4), 1221–1233. <https://doi.org/10.2307/1383013>.
- Kaufmann, J. H. (1983). On the definitions and functions of dominance and territoriality. *Biological Reviews*, 58(1), 1–20. <https://doi.org/10.1111/j.1469-185X.1983.tb00379.x>.
- Kenagy, G. J. (1973). Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology*, 54(6), 1201–1219.
- Kuhn, T. S., Mooers, A., & Thomas, G. H. (2011). A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution*, 2(5), 427–436. <https://doi.org/10.1111/j.2041-210X.2011.00103.x>.
- Lahti, K., Laurila, A., Enberg, K., & Piironen, J. (2001). Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Animal Behaviour*, 62, 935–944. <https://doi.org/10.1006/anbe.2001.1821>.
- Langkilde, T., & Shine, R. (2004). Competing for crevices: Interspecific conflict influences retreat-site selection in montane lizards. *Behavioral Ecology*, 14(4), 684–691. <https://doi.org/10.1007/s00442-004-1640-1>.

- Leaver, L. A., & Daly, M. (2001). Food caching and differential cache pilferage: A field study of coexistence of sympatric kangaroo rats and pocket mice. *Oecologia*, 128, 577–584. <https://doi.org/10.1007/S004420100686>.
- Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, 6, 169–176. <https://doi.org/10.1046/j.1472-4642.2000.00069.x>.
- López-Bao, J. V., Mattisson, J., Persson, J., Aronsson, M., & Andrén, H. (2016). Tracking neighbours promotes the coexistence of large carnivores. *Scientific Reports*, 6, 23198. <https://doi.org/10.1038/srep23198>.
- Maher, C. R., & Lott, D. F. (2000). A Review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, 143, 1–29. [https://doi.org/10.1674/0003-0031\(2000\)143\[0001:AROEDJ\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2000)143[0001:AROEDJ]2.0.CO;2).
- Maynard Smith, J., & Parker, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24, 159–175. [https://doi.org/10.1016/S0003-3472\(76\)80110-8](https://doi.org/10.1016/S0003-3472(76)80110-8).
- Maza, B. G., French, N. R., & Aschwarden, A. P. (1973). Home range dynamics in a population of heteromyid rodents. *Journal of Mammalogy*, 54(2), 405–425.
- McKnight, M. L. (2005). Phylogeny of the *Perognathus longimembris* species group based on mitochondrial cytochrome-b: How many species? *Journal of Mammalogy*, 86(4), 826–832. [https://doi.org/10.1644/1545-1542\(2005\)086\[0826:POTPLS\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)086[0826:POTPLS]2.0.CO;2).
- McNab, B. K. (1963). Bioenergetics and the determination of home range size. *American Naturalist*, 97(894), 133–140.
- Meredith, R. W., Janecka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., et al. (2011). Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, 334(6055), 521–524. <https://doi.org/10.1126/science.1211028>.
- Meserve, P. L. (1976a). Food relationships of a rodent fauna in a California coastal sage scrub community. *Journal of Mammalogy*, 57(2), 300–319. <https://doi.org/10.2307/1379690>.
- Meserve, P. L. (1976b). Habitat and resource utilization by rodents of a California coastal sage scrub community. *Journal of Animal Ecology*, 45(3), 647–666. <https://doi.org/10.2307/3573>.
- Mikami, O. K., & Kawata, M. (2004). Does interspecific territoriality reflect the intensity of ecological interactions? A theoretical model for interspecific territoriality. *Evolutionary Ecology Research*, 6(5), 765–775.
- Myrberg, A. A., & Thresher, R. E. (1974). Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Integrative and Comparative Biology*, 14(1), 81–96. <https://doi.org/10.1093/icb/14.1.81>.
- Ord, T. J., & Stamps, J. A. (2009). Species identity cues in animal communication. *American Naturalist*, 174(4), 585–593. <https://doi.org/10.1086/605372>.
- Orians, G. H., & Willson, M. F. (1964). Interspecific territories of birds. *Ecology*, 45(4), 736–745. <https://doi.org/10.2307/1934921>.
- Peiman, K. S., & Robinson, B. W. (2010). Ecology and evolution of resource-related heterospecific aggression. *Quarterly Review of Biology*, 85(2), 133–158. <https://doi.org/10.1086/652374>.
- Perri, L. M., & Randall, J. A. (1999). Behavioral mechanisms of coexistence in sympatric species of desert rodents, *Dipodomys ordii* and *D. merriami*. *American Society of Mammalogists*, 80(4), 1297–1310. <https://doi.org/10.2307/1383180>.
- Persson, L. (1985). Asymmetrical competition: Are larger animals competitively superior? *American Naturalist*, 126(2), 261–266. <https://doi.org/10.1086/284413>.
- Price, M. V., Waser, N. M., & McDonald, S. (2000). Seed caching by heteromyid rodents from two communities: Implications for coexistence. *Journal of Mammalogy*, 81(1), 97–106. [https://doi.org/10.1644/1545-1542\(2000\)081\[0097:SCBHRF\]3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2000)081[0097:SCBHRF]3E2.0.CO;2).
- Randall, J. A. (1984). Territorial defense and advertisement by footdrumming in bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population densities. *Behavioral Ecology*, 16(1), 11–20. <https://doi.org/10.1007/BF00293099>.
- Randall, J. A. (1987). Sandbathing as a territorial scent-mark in the bannertail kangaroo rat, *Dipodomys spectabilis*. *Animal Behaviour*, 35, 426–434. [https://doi.org/10.1016/S0003-3472\(87\)80267-1](https://doi.org/10.1016/S0003-3472(87)80267-1).
- Reid, F. A. (2006). *Mammals of North America*. New York, NY: Houghton Mifflin.
- Robinson, S. K., & Terborgh, J. (1995). Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology*, 64(1), 1–11. <https://doi.org/10.2307/5822>.
- Rolland, J., Condamine, F. L., Jiguet, F., & Morlon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, 12(1). <https://doi.org/10.1371/journal.pbio.1001775>.
- Rowell, T. E. (1966). Hierarchy in the organization of a captive baboon group. *Animal Behaviour*, 14, 430–443. [https://doi.org/10.1016/S0003-3472\(66\)80042-8](https://doi.org/10.1016/S0003-3472(66)80042-8).
- Rowell, T. E. (1974). The concept of social dominance. *Behavioral Biology*, 11(2), 131–154. [https://doi.org/10.1016/S0091-6773\(74\)90289-2](https://doi.org/10.1016/S0091-6773(74)90289-2).
- Rychlik, L., & Zwolak, R. (2005). Behavioural mechanisms of conflict avoidance among shrews. *Acta Theriologica*, 50(3), 289–308. <https://doi.org/10.1007/BF03192627>.
- Rychlik, L., & Zwolak, R. (2006). Interspecific aggression and behavioural dominance among four sympatric species of shrews. *Canadian Journal of Zoology*, 84, 434–448. <https://doi.org/10.1139/Z06-017>.
- Sassenrath, E. N. (1970). Increased adrenal responsiveness related to social stress in rhesus monkeys. *Hormones and Behavior*, 1(4), 283–298. [https://doi.org/10.1016/0018-506X\(70\)90021-8](https://doi.org/10.1016/0018-506X(70)90021-8).
- Schluter, D. (2000). Ecological character displacement in adaptive radiation. *American Naturalist*, 156, S4–S16. <https://doi.org/10.1086/303412>.
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39. <https://doi.org/10.1126/science.185.4145.27>.
- Schoener, T. W. (1983). Field experiments on interspecific competition. *American Naturalist*, 122(2), 240–285. <https://doi.org/10.1086/284133>.
- Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, 21(2), 303–312. <https://doi.org/10.1111/j.1523-1739.2006.00627.x>.
- Shelley, E. L., Tanaka, M. Y. U., Ratnathicam, A. R., & Blumstein, D. T. (2004). Can Lancaster's Laws help explain interspecific dominance in birds? *Condor*, 106(2), 395–400. <https://doi.org/10.1650/7424>.
- Shier, D. M. (2008). *Behavioral ecology and translocation of the endangered Pacific pocket mouse (Perognathus longimembris pacificus) for the period January 2007 – December 2007*. Escondido, CA: Conservation and Research for Endangered Species, San Diego Zoo (Unpublished report).
- 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, 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>.
- Shulman, M. J. (1985). Coral reef fish assemblages: Intra- and interspecific competition for shelter sites. *Environmental Biology of Fishes*, 13(2), 81–92. <https://doi.org/10.1007/BF00002576>.
- Stamps, J. A., & Swaisgood, R. R. (2007). Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, 102(3–4), 392–409. <https://doi.org/10.1016/j.applanim.2006.05.038>.
- U.S. Fish & Wildlife Service. (1998). *Recovery plan for the Pacific pocket mouse (Perognathus longimembris pacificus)*. Portland, OR: U.S. Fish and Wildlife Service.
- U.S. Fish & Wildlife Service. (2015). *Species occurrences for Carlsbad Fish and Wildlife Office*. Carlsbad, CA: U.S. Fish and Wildlife Service, Carlsbad Field Office.
- Valone, T. J., & Brown, J. H. (1995). Effects of competition, colonization, and extinction on rodent species diversity. *Science*, 267(5199), 880–883.
- Vander Wall, S. B., Thayer, T. C., Hodge, J. S., Beck, M. J., & Roth, J. K. (2001). Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). *Western North American Naturalist*, 61(1), 109–113.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.
- 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.

## Supplemental Results

| Dependent variable  | Focal species          | Model term                                      | Estimate      | SE           | t             | p-value        | BH adjusted p-value |
|---------------------|------------------------|---|---------------|--------------|---------------|----------------|---------------------|
| Dominance Index     | <i>P. longimembris</i> | <i>P. longimembris</i> sex                      | 0.124         | 0.079        | 1.565         | 0.120          | 0.221               |
|                     |                        | <b>opponent sp. 1 vs. 2</b>                     | <b>-0.365</b> | <b>0.104</b> | <b>-3.503</b> | <b>0.001</b>   | <b>0.004</b>        |
|                     |                        | opponent sp. 1 vs. 3                            | 0.077         | 0.105        | 0.735         | 0.464          | 0.563               |
|                     |                        | opponent sp. 1 vs. 4                            | 0.244         | 0.124        | 1.961         | 0.052          | 0.119               |
|                     |                        | <b>opponent sp. 2 vs. 3</b>                     | <b>0.442</b>  | <b>0.105</b> | <b>4.200</b>  | <b>4.39e-5</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 2 vs. 4</b>                     | <b>0.609</b>  | <b>0.125</b> | <b>4.854</b>  | <b>2.83e-6</b> | <b>&lt;0.001</b>    |
|                     |                        | opponent sp. 3 vs. 4                            | 0.166         | 0.125        | 1.329         | 0.186          | 0.279               |
|                     |                        | opponent sp. sex                                | -0.080        | 0.080        | -0.997        | 0.320          | 0.424               |
|                     |                        | <i>P. longimembris</i> resident status          | -0.032        | 0.079        | -0.412        | 0.681          | 0.746               |
|                     | Competitors            | <i>P. longimembris</i> sex                      | -0.098        | 0.073        | -1.353        | 0.178          | 0.279               |
|                     |                        | opponent sp. 1 vs. 2                            | 0.124         | 0.095        | 1.299         | 0.196          | 0.279               |
|                     |                        | opponent sp. 1 vs. 3                            | -0.014        | 0.096        | -0.146        | 0.884          | 0.900               |
|                     |                        | <b>opponent sp. 1 vs. 4</b>                     | <b>-0.392</b> | <b>0.114</b> | <b>-3.451</b> | <b>0.001</b>   | <b>0.004</b>        |
|                     |                        | opponent sp. 2 vs. 3                            | -0.138        | 0.096        | -1.431        | 0.154          | 0.258               |
|                     |                        | <b>opponent sp. 2 vs. 4</b>                     | <b>-0.516</b> | <b>0.115</b> | <b>-4.497</b> | <b>1.31e-5</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 3 vs. 4</b>                     | <b>-0.378</b> | <b>0.115</b> | <b>-3.300</b> | <b>0.001</b>   | <b>0.004</b>        |
|                     |                        | opponent sp. sex                                | -0.111        | 0.074        | -1.508        | 0.133          | 0.230               |
|                     |                        | <i>P. longimembris</i> resident status          | -0.044        | 0.072        | -0.618        | 0.537          | 0.638               |
| Aggressive Behavior | <i>P. longimembris</i> | <i>P. longimembris</i> sex                      | 0.356         | 0.160        | 2.221         | 0.026          | 0.071               |
|                     |                        | <b>opponent sp. 1 vs. 2</b>                     | <b>-0.873</b> | <b>0.216</b> | <b>-4.036</b> | <b>5.43e-5</b> | <b>&lt;0.001</b>    |
|                     |                        | opponent sp. 1 vs. 3                            | 0.209         | 0.206        | 1.015         | 0.310          | 0.421               |
|                     |                        | opponent sp. 1 vs. 4                            | -0.119        | 0.246        | -0.485        | 0.627          | 0.715               |
|                     |                        | <b>opponent sp. 2 vs. 3</b>                     | <b>1.082</b>  | <b>0.217</b> | <b>4.983</b>  | <b>6.27e-7</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 2 vs. 4</b>                     | <b>0.754</b>  | <b>0.257</b> | <b>2.935</b>  | <b>0.003</b>   | <b>0.010</b>        |
|                     |                        | opponent sp. 3 vs. 4                            | -0.328        | 0.247        | -1.331        | 0.183          | 0.279               |
|                     |                        | opponent sp. sex                                | -0.096        | 0.162        | -0.594        | 0.553          | 0.643               |
|                     |                        | <i>P. longimembris</i> resident status          | -0.337        | 0.158        | -2.128        | 0.033          | 0.084               |
|                     | Competitors            | <i>P. longimembris</i> sex                      | -0.003        | 0.136        | -0.025        | 0.980          | 0.980               |
|                     |                        | opponent sp. 1 vs. 2                            | 0.262         | 0.173        | 1.516         | 0.130          | 0.230               |
|                     |                        | opponent sp. 1 vs. 3                            | -0.284        | 0.179        | -1.586        | 0.113          | 0.215               |
|                     |                        | <b>opponent sp. 1 vs. 4</b>                     | <b>-1.046</b> | <b>0.228</b> | <b>-4.580</b> | <b>4.65e-6</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 2 vs. 3</b>                     | <b>-0.546</b> | <b>0.177</b> | <b>-3.077</b> | <b>0.002</b>   | <b>0.008</b>        |
|                     |                        | <b>opponent sp. 2 vs. 4</b>                     | <b>-1.308</b> | <b>0.229</b> | <b>-5.713</b> | <b>1.11e-8</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 3 vs. 4</b>                     | <b>-0.763</b> | <b>0.232</b> | <b>-3.288</b> | <b>0.001</b>   | <b>0.004</b>        |
|                     |                        | opponent sp. sex                                | -0.039        | 0.138        | -0.283        | 0.777          | 0.807               |
|                     |                        | <i>P. longimembris</i> resident status          | -0.160        | 0.135        | -1.191        | 0.234          | 0.325               |
| Submissive Behavior | <i>P. longimembris</i> | <i>P. longimembris</i> sex                      | 0.046         | 0.109        | 0.427         | 0.669          | 0.746               |
|                     |                        | opponent sp. 1 vs. 2                            | 0.174         | 0.192        | 0.907         | 0.365          | 0.452               |
|                     |                        | opponent sp. 1 vs. 3                            | -0.273        | 0.197        | -1.387        | 0.165          | 0.269               |
|                     |                        | <b>opponent sp. 1 vs. 4</b>                     | <b>-1.332</b> | <b>0.285</b> | <b>-4.670</b> | <b>3.01e-6</b> | <b>&lt;0.001</b>    |
|                     |                        | opponent sp. 2 vs. 3                            | -0.447        | 0.196        | -2.283        | 0.022          | 0.063               |
|                     |                        | <b>opponent sp. 2 vs. 4</b>                     | <b>-1.505</b> | <b>0.284</b> | <b>-5.292</b> | <b>1.21e-7</b> | <b>&lt;0.001</b>    |
|                     |                        | <b>opponent sp. 3 vs. 4</b>                     | <b>-1.058</b> | <b>0.288</b> | <b>-3.680</b> | <b>2.33e-3</b> | <b>&lt;0.001</b>    |
|                     |                        | opponent sp. sex                                | 0.031         | 0.111        | 0.281         | 0.779          | 0.807               |
|                     |                        | 1 vs. <i>P. longimembris</i> resident           | -0.257        | 0.197        | -1.383        | 0.191          | 0.279               |
|                     |                        | 2 vs. <i>P. longimembris</i> resident           | -0.363        | 0.196        | -1.853        | 0.064          | 0.140               |
|                     | Competitors            | 3 vs. <i>P. longimembris</i> resident           | 0.190         | 0.197        | 0.964         | 0.335          | 0.429               |
|                     |                        | 4 vs. <i>P. longimembris</i> resident           | 0.557         | 0.330        | 1.691         | 0.091          | 0.185               |
|                     |                        | 1 vs. 2* <i>P. longimembris</i> resident        | -0.106        | 0.277        | -0.383        | 0.702          | 0.755               |
|                     |                        | 1 vs. 3* <i>P. longimembris</i> resident        | 0.447         | 0.278        | 1.607         | 0.108          | 0.212               |
|                     |                        | 1 vs. 4* <i>P. longimembris</i> resident        | 0.815         | 0.383        | 2.126         | 0.034          | 0.084               |
|                     |                        | 2 vs. 3* <i>P. longimembris</i> resident        | 0.554         | 0.279        | 1.987         | 0.047          | 0.112               |
|                     |                        | <b>2 vs. 4* <i>P. longimembris</i> resident</b> | <b>0.921</b>  | <b>0.382</b> | <b>2.412</b>  | <b>0.016</b>   | <b>0.048</b>        |
|                     |                        | 3 vs. 4* <i>P. longimembris</i> resident        | 0.367         | 0.384        | 0.955         | 0.339          | 0.429               |
|                     |                        | <i>P. longimembris</i> sex                      | <b>0.580</b>  | <b>0.195</b> | <b>2.972</b>  | <b>0.003</b>   | <b>0.010</b>        |
|                     |                        | <b>opponent sp. sex</b>                         | <b>0.513</b>  | <b>0.197</b> | <b>2.605</b>  | <b>0.009</b>   | <b>0.029</b>        |
|                     |                        | <i>P. longimembris</i> resident status          | -0.355        | 0.193        | -1.834        | 0.067          | 0.141               |

**Table S1.** GLM results with dominance-related behaviours as the dependent variables. Only the best models, based on  $\Delta AIC$ , are shown (see Supplementary Table S2 for model selection results). Contrasts shown in the table are between the responses of *P. longimembris* to two other species or between the responses of the other species to *P. longimembris*. For example, the second line in the table, labelled ‘Opponent sp. 1 vs 2’ tests for a difference in the dominance index of *P. longimembris* in trials with opponents of species 1 and 2. Opponent species codes: 1 = *Chaetodipus fallax*, 2 = *Dipodomys simulans*, 3 = *Peromyscus maniculatus*, 4 = *Reithrodontomys megalotis*. Full model (*P. longimembris* submissive behaviour) includes *P. longimembris* sex, *P. longimembris* residency status, opponent species, opponent sex, opponent species\**P. longimembris* residency status. Benjamini–Hochberg adjusted *P* values control for false discovery rate (FDR). All significant terms are in bold.

| Dependent variable                         | Model  | Resid. Df  | Resid. Dev      | dAIC     | Weight      |
|--|--|------------|-----------------|----------|-------------|
| <i>P. longimembris</i> dominance index     | Full model   | 159        | 41.08           | 3.8      | 0.13        |
|  | <b>Full model without interaction</b>                                | <b>162</b> | <b>41.62</b>    | <b>0</b> | <b>0.87</b> |
|  | Full model without interaction or main effect of Opponent Sp.        | 165        | 49.25           | 22.5     | 0           |
| <i>P. longimembris</i> aggressive behavior | Full model   | 159        | 190.13          | 0.8      | 0.4         |
|  | <b>Full model without interaction</b>                                | <b>162</b> | <b>190.57</b>   | <b>0</b> | <b>0.6</b>  |
|  | Full model without interaction or main effect of Opponent Sp.        | 165        | 191.99          | 17.8     | 0           |
| <i>P. longimembris</i> submissive behavior | <b>Full model</b>  | <b>159</b> | <b>185.10</b>   | <b>0</b> | <b>0.77</b> |
|  | Full model without interaction                                       | 162        | 185.93          | 2.4      | 0.23        |
|  | Full model without interaction or main effect of Opponent Sp.        | 165        | 187.21          | 22.6     | 0           |
| <i>P. longimembris</i> avoidance & pursuit | Full model   | 158        | 11503.96        | 4.2      | 0.11        |
|  | <b>Full model without interaction</b>                                | <b>161</b> | <b>11627.39</b> | <b>0</b> | <b>0.89</b> |
|  | Full model without interaction or main effect of Opponent Sp.        | 164        | 15278.58        | 39.9     | 0           |
| Competitor dominance index                 | Full model   | 159        | 34.60           | 4.8      | 0.08        |
|  | <b>Full model without interaction</b>                                | <b>162</b> | <b>34.85</b>    | <b>0</b> | <b>0.92</b> |
|  | Full model without interaction or main effect of Opponent Sp.        | 165        | 39.31           | 14.4     | 0           |
| Competitor aggressive behavior             | Full model   | 159        | 195.86          | 5.6      | 0.06        |
|  | <b>Full model without interaction</b>                                | <b>162</b> | <b>195.88</b>   | <b>0</b> | <b>0.94</b> |
|  | Full model without interaction or main effect of Opponent Sp.        | 165        | 195.76          | 24.1     | 0           |
| Competitor submissive behavior             | Full model   | 159        | 174.78          | 2.8      | 0.14        |
|  | Full model without interaction                                       | 162        | 175.32          | 1.4      | 0.28        |
|  | <b>Full model without interaction or main effect of Opponent Sp.</b> | <b>165</b> | <b>176.18</b>   | <b>0</b> | <b>0.57</b> |
| Competitor avoidance & pursuit             | Full model   | 158        | 9000.35         | 5.1      | 0.07        |
|  | <b>Full model without interaction</b>                                | <b>161</b> | <b>9048.86</b>  | <b>0</b> | <b>0.93</b> |
|  | Full model without interaction or main effect of Opponent Sp.        | 164        | 13060.98        | 55.7     | 0           |

**Table S2.** Model selection results for models with dominance-related behaviours and avoidance/pursuit as the dependent variables. Full models include *P. longimembris* sex, *P. longimembris* residency status, opponent species, opponent sex, opponent species\**P. longimembris* residency status. AIC comparisons were made between models with and without the interaction term and/or opponent species. If  $\Delta AIC$  was  $<2$ , we chose the simplest model. The best model for each dependent variable is identified with bold text.

| Focal species          | Model term                      | Estimate | SE    | t             | P-value         | BH adjusted p-value |
|------------------------|---------------------------------|----------|-------|---------------|-----------------|---------------------|
| <i>P. longimembris</i> | <i>P. longimembris</i> sex      | 2.592    | 1.335 | 1.941         | 0.054           | 0.083               |
|                        | opponent sp. 1 vs. 2            | -2.352   | 1.748 | -1.346        | 0.180           | 0.216               |
|                        | <b>opponent sp. 1 vs. 3</b>     | 5.583    | 1.776 | <b>3.144</b>  | <b>0.002</b>    | <b>0.004</b>        |
|                        | <b>opponent sp. 1 vs. 4</b>     | 11.031   | 2.082 | <b>5.298</b>  | <b>3.80e-7</b>  | <b>1.37e-7</b>      |
|                        | <b>opponent sp. 2 vs. 3</b>     | 7.935    | 1.778 | <b>4.464</b>  | <b>1.51E-05</b> | <b>4.53e-6</b>      |
|                        | <b>opponent sp. 2 vs. 4</b>     | 13.383   | 2.103 | <b>6.364</b>  | <b>1.95e-9</b>  | <b>1.76e-9</b>      |
|                        | <b>opponent sp. 3 vs. 4</b>     | 5.448    | 2.112 | <b>2.579</b>  | <b>0.011</b>    | <b>0.019</b>        |
|                        | opponent sp. sex                | -1.926   | 1.360 | -1.416        | 0.159           | 0.204               |
|                        | <i>P. longimembris</i> resident | -0.699   | 1.323 | -0.528        | 0.598           | 0.598               |
| Competitors            | <i>P. longimembris</i> sex      | -1.939   | 1.178 | -1.646        | 0.102           | 0.141               |
|                        | opponent sp. 1 vs. 2            | 2.973    | 1.542 | 1.929         | 0.056           | 0.083               |
|                        | <b>opponent sp. 1 vs. 3</b>     | -5.553   | 1.567 | <b>-3.545</b> | <b>0.001</b>    | <b>0.001</b>        |
|                        | <b>opponent sp. 1 vs. 4</b>     | -11.200  | 1.837 | <b>-6.097</b> | <b>7.71e-9</b>  | <b>4.63e-9</b>      |
|                        | <b>opponent sp. 2 vs. 3</b>     | -8.526   | 1.568 | <b>-5.437</b> | <b>1.98e-7</b>  | <b>8.91e-8</b>      |
|                        | <b>opponent sp. 2 vs. 4</b>     | -14.173  | 1.855 | <b>-7.640</b> | <b>1.83e-12</b> | <b>3.29e-12</b>     |
|                        | <b>opponent sp. 3 vs. 4</b>     | -5.647   | 1.863 | <b>-3.030</b> | <b>0.003</b>    | <b>0.006</b>        |
|                        | opponent sp. sex                | -1.161   | 1.200 | -0.968        | 0.335           | 0.354               |
|                        | <i>P. longimembris</i> resident | 1.476    | 1.167 | 1.265         | 0.208           | 0.234               |

**Table S3.** GLM results with avoidance (movement away from the opponent) or pursuit (movement toward the opponent) as the dependent variable. Only the best models, based on  $\Delta AIC$ , are shown (see Supplemental Table 2 for model selection results). Contrasts shown in the table are between the responses of *P. longimembris* to two other species or between the responses of the other species to *P. longimembris*. For example, the second line in the table, labeled “opponent sp. 1 vs 2”, tests for a difference in the movements of *P. longimembris* in trials with opponents of species 1 and 2. Opponent species codes: 1= *Chaetodipus fallax*, 2=*Dipodomys simulans*, 3= *Peromyscus maniculatus*, 4= *Reithrodontomys megalotis*. Benjamini-Hochberg adjusted p-values control for false discovery rate (FDR). All significant terms are in bold.

| Dependent variable                         | Model                      | Resid. Df  | Resid. Dev      | dAIC       | Weight      |
|--|----------------------------|------------|-----------------|------------|-------------|
| <i>P. longimembris</i> dominance index     | neither                    | 165        | 49.25           | 38.7       | 0           |
|  | <b>dWeight</b>             | <b>152</b> | <b>40.08</b>    | <b>0.6</b> | <b>0.43</b> |
|  | TMRCA                      | 164        | 45.54           | 27.4       | 0           |
|  | dWeight & TMRCA            | 151        | 39.42           | 0          | 0.57        |
| <i>P. longimembris</i> aggressive behavior | neither                    | 165        | 7617.57         | 238.2      | 0           |
|  | <b>dWeight</b>             | <b>152</b> | <b>177.69</b>   | <b>0</b>   | <b>0.69</b> |
|  | TMRCA                      | 164        | 192.09          | 80.4       | 0           |
|  | dWeight & TMRCA            | 151        | 177.72          | 1.6        | 0.31        |
| <i>P. longimembris</i> submissive behavior | neither                    | 165        | 187.21          | 70         | 0           |
|  | dWeight                    | 152        | 174.71          | 2          | 0.27        |
|  | TMRCA                      | 164        | 187.46          | 64.3       | 0           |
|  | <b>dWeight &amp; TMRCA</b> | <b>151</b> | <b>174.84</b>   | <b>0</b>   | <b>0.73</b> |
| <i>P. longimembris</i> avoidance & pursuit | neither                    | 164        | 15278.58        | 118.6      | 0           |
|  | dWeight                    | 151        | 12937.98        | 18         | 0           |
|  | TMRCA                      | 163        | 12299.01        | 84.1       | 0           |
|  | <b>dWeight &amp; TMRCA</b> | <b>150</b> | <b>11378.73</b> | <b>0</b>   | <b>1</b>    |
| Competitor dominance index                 | neither                    | 165        | 39.31           | 20.1       | 0           |
|  | <b>dWeight</b>             | <b>152</b> | <b>35.26</b>    | <b>0</b>   | <b>0.52</b> |
|  | TMRCA                      | 164        | 37.61           | 14.6       | 0           |
|  | dWeight & TMRCA            | 151        | 34.85           | 0.2        | 0.48        |
| Competitor aggressive behavior             | neither                    | 165        | 195.76          | 92.2       | 0           |
|  | dWeight                    | 152        | 181.71          | 6.5        | 0.04        |
|  | TMRCA                      | 164        | 196.37          | 76.9       | 0           |
|  | <b>dWeight &amp; TMRCA</b> | <b>151</b> | <b>182.01</b>   | <b>0</b>   | <b>0.96</b> |
| Competitor submissive behavior             | neither                    | 165        | 176.18          | 40.2       | 0           |
|  | <b>dWeight</b>             | <b>152</b> | <b>163.87</b>   | <b>0</b>   | <b>0.73</b> |
|  | TMRCA                      | 164        | 175.63          | 39.8       | 0           |
|  | dWeight & TMRCA            | 151        | 163.80          | 1.9        | 0.27        |
| Competitor avoidance & pursuit             | neither                    | 164        | 13060.98        | 125.5      | 0           |
|  | dWeight                    | 151        | 10758.67        | 22.5       | 0           |
|  | TMRCA                      | 163        | 9852.14         | 80.1       | 0           |
|  | <b>dWeight &amp; TMRCA</b> | <b>150</b> | <b>9196.49</b>  | <b>0</b>   | <b>1</b>    |

**Table S4.** Model selection results for models with dominance-related behaviors as the dependent variables and species weight difference (dWeight) and time since most recent common ancestor (TMRCA) as additional predictor variables. Full models include *P. longimembris* sex, residency

status, opponent sex, dWeight and TMRCA. AIC comparisons were made between models with and without dWeight and/or TMRCA. If  $\Delta AIC$  was  $<2$ , we chose the simplest model. The best model for each dependent variable is identified with bold text.



**CHAPTER 2:**  
**NO EVIDENCE THAT CACHE PILFERING OFFSETS COSTS OF INTERSPECIFIC**  
**COMPETITION IN A POCKET MOUSE COMMUNITY**

## ABSTRACT

Reintroduction programs for endangered species rarely take competitive interactions between species into account. The endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) is being reintroduced to parts of its former range where multiple species of native rodents have overlapping diets. The species in this foraging guild compete for seeds both exploitatively and through direct interference interactions, and *P. longimembris* is the smallest and least dominant species in the guild. Repeated aggressive interactions from resident heterospecifics could lower the chances of reintroduced pocket mice establishing burrows during the critical settlement period. As such, temporarily reducing the density of competing species through exclusionary fencing might be an advisable reintroduction strategy, in combination with other interventions, such as predator exclusion. However, the presence of other members of the seed-foraging guild could have a net benefit for *P. longimembris*, if pocket mice pilfer from the other species' seed caches more frequently than the other species pilfer from their caches. To test for cache pilfering, we conducted a field experiment with fluorescent dyed seeds. We also carried out a field-enclosure experiment to determine whether *P. longimembris* and three other species use conspecific or heterospecific scent to locate seed caches. The first experiment showed that cache pilfering occurred, but too infrequently for a meaningful comparison of species' pilfering rates. In the second experiment, none of the species appeared to use heterospecific scent to find (or avoid) seed caches. Our results therefore provide no evidence that Pacific pocket mice benefit sufficiently from the seed-caches of other species to offset the costs of interspecific competition.

## INTRODUCTION

Reintroductions and translocations are considered important conservation tools, but historically, they have low success rates (Armstrong and Seddon 2008). The highest rates of mortality occur in the post-release settlement period, the first days to weeks following relocation (Stamps & Swaisgood, 2007), but success is often measured by individual survival and reproduction in the months to years following reintroduction (Brichieri-Colombi & Moehrenschrager, 2016; Fischer & Lindenmayer, 2000; Griffith et al., 1989). Factors that influence both the immediate and long-term success of reintroduced individuals should be considered to improve reintroduction success (Seddon et al. 2007; Armstrong and Seddon 2008). Reducing predation pressure can improve survival rates of translocated animals (Short et al., 1992), but interactions with competitor species have rarely been considered, despite evidence that interspecific competition is an important part of community dynamics (Connell, 1983; Moehrenschrager et al., 2013). Interspecific aggression is widespread (Ord and Stamps 2009; Peiman and Robinson 2010) and can reduce fitness for subordinate species through its effects on resource acquisition, reproduction and survival (Lahti et al. 2001). In some cases, interactions between local residents and reintroduced individuals have been documented to favor residents (Burns 2005).

Interventions to mitigate the negative impacts of interspecific competition include temporarily reducing the density of competitors and/or selecting release sites with low densities of competitors (Linklater et al., 2012; Moseby et al., 2011; Shier et al., 2016). However, the possibility that reintroduced animals might benefit from the presence of competing species should also be considered. Some species rely on ‘public information’ to assess habitat quality (Goodale et al., 2010; Parejo & Danchin, 2004; Reed & Dobson, 1993; Stamps, 1988) and the presence of other individuals (or their cues) at release sites can promote settlement of new

animals, even in asocial species (Stamps and Swaisgood 2007; Shier and Swaisgood 2012). One, as yet untested, benefit of preserving community diversity at a reintroduction site is that resident food-caching species might facilitate access to shared resources, offsetting the costs of interspecific competition (Price and Mittler 2006).

Caching is a common strategy for ensuring access to food when supply is uneven (Vander Wall 1990). In food-caching systems, consumers harvest a primary resource, the spatial and temporal distribution of which is determined by patterns of initial production. Consumers then alter the spatial and temporal availability of food by concentrating it in storage areas that are accessible to other species through cache pilfering (Price and Mittler 2003). In this form of resource processing, in which resources are modified without being completely consumed (Heard, 1994; Mittler, 1997), highly efficient primary foragers with large home ranges can increase the availability of food to consumer species with smaller foraging ranges (Price and Mittler 2003).

Olfactory cues play an important role in finding food for nocturnal, granivorous rodents that forage for seeds in plant litter, vegetation, and soil (Howard and Cole 1967; Reichman and Oberstein 1977; Vander Wall 2000, 2003; Vander Wall et al. 2003). Sympatric desert rodents have also been found to use chemical cues to maintain temporal separation (Haim and Rozenfeld 1993; Johnston and Robinson 1993), and subordinate species can minimize aggressive encounters with dominant heterospecifics by avoiding them in space or time (Durant 2000). Scent cues that are important for intra- and inter-specific communication (Arakawa et al., 2008; Dempster & Perrin, 1990; Randall, 1987) might also be used in the discovery or decision making related to pilfering caches from other animals' territories (Vander Wall et al. 2003).






We studied the cache pilfering behavior of rodents in a coastal sage scrub community and

tested for both positive and negative effects of exploitative competition on the endangered Pacific pocket mouse, *Perognathus longimembris pacificus*. Once thought to be extinct, this subspecies of the little pocket mouse (*Perognathus longimembris*) was rediscovered in 1993 (U.S. Fish & Wildlife Service 1998) at Dana Point Headlands and three sites within Marine Corps Base Camp Pendleton in Southern California. No additional populations have been discovered since 1995 despite extensive surveys throughout the species' range (U.S. Fish & Wildlife Service 2015) and one of the rediscovered populations is now likely extinct (Brehme and Fisher 2008). Captive breeding and reintroduction efforts are underway to establish additional wild populations, per the species recovery plan (U.S. Fish & Wildlife Service 1998).

We conducted cache-pilfering trials in the field with native rodents that have similar diets and are present throughout the historic range of *P. l. pacificus*. We examined cache pilfering between *P. l. pacificus* and sympatric deer mice, *Peromyscus maniculatus*, and California pocket mice, *Chaetodipus californicus*. To expand the study to include kangaroo rats, *Dipodomys simulans*, which are not currently found in sympatry with extant *P. l. pacificus* populations but are present within the historic range, including potential reintroduction sites, we also studied interactions between putative competitors and a sister subspecies, *P. longimembris brevinasus* (Los Angeles pocket mouse), that is geographically and phylogenetically close to *P. l. pacificus* (McKnight 2005). *P. l. pacificus* and *P. l. brevinasus* are both the smallest members of their rodent communities. We examined cache pilfering between *P. l. brevinasus* and four native species: Dulzura kangaroo rats, *Dipodomys simulans*; San Diego pocket mice, *Chaetodipus fallax*; deer mice, *Peromyscus maniculatus*; and western harvest mice, *Reithrodontomys megalotis*. All of these species are solitary, occupy the same habitat (Meserve, 1976a, 1976b; Table 1), have high dietary overlap (Brown & Lieberman, 1973; Meserve, 1976a) and store

seasonally available seeds in caches either inside the burrow (larder hoards) or buried in small clumps (scatter hoards) in their foraging ranges (Table 1; Eisenberg, 1962; Leaver & Daly, 2001; Vander Wall et al., 2001).

**Table 1.** Descriptions of each species and their home range size, caching behavior, and similarity in size, diet, and habitat to the little pocket mouse, *Perognathus longimembris*.

|   |   | Body size <sup>1</sup> | Diet overlap with<br><i>P. longimembris</i> <sup>2</sup> | Habitat overlap with<br><i>P. longimembris</i> <sup>2</sup> | Home range size       | Caching behavior                                       |
|---|---|------------------------|--|---|-----------------------|--|
| Family: Heteromyidae  |   |                        |  |   |                       |  |
|    | <i>Perognathus longimembris</i>                     | Weight: 6-9g           | -  | -   | 0.018 ha <sup>3</sup> | Larder hoard & scatter hoard <sup>7</sup>              |
|   | Pacific pocket mouse ( <i>P.l. pacificus</i> )      | Body length: 50-70mm   |  |   |                       |  |
|   | Los Angeles pocket mouse ( <i>P.l. brevinasus</i> ) | Tail length: 60-85mm   |  |   |                       |  |
|    | <i>Chaetodipus</i> spp.                             | Weight: 14-26g         | *  | *   | 0.55 ha <sup>4</sup>  | Primarily larder hoard also scatter hoard <sup>8</sup> |
|   | San Diego pocket mouse ( <i>C. fallax</i> )         | Body length: 70-91mm   |  |   |                       |  |
|   | California pocket mouse ( <i>C. californicus</i> )  | Tail length: 105-120mm |  |   |                       |  |
|   | <i>Dipodomys simulans</i>                           | Weight: 50-94g         | 93%  | Horizontal: 10-50%  | 0.07 ha <sup>5</sup>  | Primarily scatter hoard also larder hoard <sup>8</sup> |
|   | Dulzura kangaroo rat                                | Body length: 112-132mm |  | Vertical: 100%  |                       |  |
|   |   | Tail length: 163-216mm |  |   |                       |  |
| Family: Cricetidae  |   |                        |  |   |                       |  |
|  | <i>Peromyscus maniculatus</i>                       | Weight: 15-29g         | 33%  | Horizontal: 10-35%  | 0.29 ha <sup>6</sup>  | Larder hoard & Scatter hoard <sup>9</sup>              |
|   | Deer mouse  | Body length: 80-109mm  |  | Vertical: 95%   |                       |  |
|   |   | Tail length: 77-106mm  |  |   |                       |  |
|  | <i>Reithrodontomys megalotis</i>                    | Weight: 6-11g          | 45%  | Horizontal: 15-55%  | 0.21 ha <sup>6</sup>  | Larder hoard <sup>10</sup>                             |
|   | Western harvest mouse                               | Body length: 59-77mm   |  | Vertical: 60-70%  |                       |  |
|   |   | Tail length: 71-79mm   |  |   |                       |  |

<sup>1</sup>Average body size measures taken from Reid (2006). <sup>2</sup>Diet and habitat overlap from Meserve (1976b) using year-round trapping for a suite of species, including four of our focal species. Meserve assessed diet overlap using fecal microscopy and we calculated the median overlap from his 9-month study. Meserve measured horizontal habitat use with live-traps and vertical habitat use with smoked track cards. Habitat overlap was quantified over four seasons in one year (Meserve 1976a). \**C. fallax* were infrequently found in Meserve's study area and were not included in these comparisons. <sup>3</sup>*P. l. pacificus* range size from Shier, 2008. <sup>4</sup>*Chaetodipus* spp. range size from Maza, French, & Aschwanden (1973) calculated for *C. formosus*. <sup>5</sup>*D. simulans*

range size from Price, Kelly, & Goldingay (1994) calculated for *D. stephensi*. <sup>6</sup>*P. maniculatus* and *R. megalotis* range size from McNab (1963). <sup>7</sup>*P. longimembris* caching behavior- this study. <sup>8</sup>*C. fallax* and kangaroo rat (*D. merriami*) caching behavior from Leaver & Daly (2001). <sup>9</sup>*P. maniculatus* caching behavior from Eisenberg (1962). <sup>10</sup>*R. megalotis* caching behavior from Nowak (1999).

Reintroduction programs might temporarily exclude members of the same foraging guild to minimize interspecific interactions, which can favor residents (Burns 2005) and reduce the chances of reintroduced individuals settling at the release site during the critical establishment phase. Previous research showed that *P. longimembris* is behaviorally subordinate to all larger species (Chock et al. 2018) and suggested that temporary competitor exclusion could be advantageous for reintroduced populations of Pacific pocket mice. However, these species naturally coexist and positive impacts from heterospecifics at a release site have not been considered. Our primary objective in this study was to evaluate whether *P. longimembris* benefit from the presence of heterospecifics by pilfering other species' caches more frequently than the other species pilfer from their caches. If that were shown to be the case, it would affect management recommendations for future reintroductions. We first examined *P. l. pacificus* caching behavior in captivity to determine their susceptibility to pilfering based on their tendency to scatter-hoard or larder-hoard provisioned seeds. In the field, we used dyed seeds to track pilfering between individuals and examined whether the animals use conspecific or heterospecific scent to find or avoid scatter hoards.

## MATERIALS AND METHODS

*Susceptibility of P. longimembris to heterospecific pilferers*---We quantified the larder- and scatter-hoarding behavior of *P. longimembris* in captivity to assess their susceptibility to heterospecific pilferers in the field. Captive *P. l. pacificus* were maintained in a breeding facility in individual cages (61 x 28 x 30 cm Plexiglas tanks) with 5 cm sand substrate, a glass nest jar housed inside an opaque PVC cup, and bedding material. Skylights provided natural light:dark cycles, and red lights were used at night to minimize disturbance. To study caching behavior and assess the proportion of seeds individuals cached in their nests (larder-hoarding) versus in the sand (scatter-hoarding), we observed 20 *P. l. pacificus* (15 males, 5 females). At the start of the experiment, we removed all sand from the animals' cages and replaced it with 5 cm of clean sand and removed seed caches from nest jars. We pre-weighed 22 g ( $\pm 0.1$  g) of the standard seed mix diet for each animal, to be distributed over a 7-day period. Each night, approximately 3.1 g of seed mix was added to a petri dish in the front corner of each cage. Individuals were given lettuce (5x5 cm every other night) to meet their water needs. On the eighth day we sifted the sand to recover seeds. We calculated the percent of seeds left (i) in the feeding dish, (ii) on the surface of the sand, (iii) buried in the sand (scatter hoards), (iv) stored in the nest jar (larder hoards), or (v) eaten (weight of the seeds recovered subtracted from initial weight of seeds provisioned). We used a pairwise Wilcoxon rank-sum test (WRST) to compare seed percentages between scatter hoards and larder hoards.

*Frequency of pilfering by sympatric species in the field*--- We tested the prevalence and direction of cache pilfering in the field at Marine Corps Base Camp Pendleton (33.25° N, 117.39° W) May-August 2013 with *P. l. pacificus* as the focal cacher (n=9), where *C.*



*californicus* and *P. maniculatus* were sympatric. We conducted additional trials at the San Felipe Valley Wildlife Area (33.10° N, 116.53° W) from April-September 2014 where the rodent community was comprised of *P. l. brevinasus*, *C. fallax*, *D. simulans* and *P. maniculatus*. We examined pilfering from focal cacher species *P. l. brevinasus* (n=9), *C. fallax* (n=5), and *D. simulans* (n=9) by all sympatric heterospecific species. *Reithrodontomys megalotis* was present at both sites but was never captured during these experiments. The habitat at these sites was primarily Coastal or Riversidean sage scrub, and some fallow agricultural areas that were dominated by non-native grasses (*Avena* and *Bromus* spp.).

We used Sherman live-traps (H.B. Sherman Traps, Inc., Tallahassee, FL, U.S.A.) with modified shortened doors to avoid tail injury. Traps were spread across non-contiguous sites (50-100 traps per site, between 8-20 sites per year). Traps were opened and baited with millet seed (microwaved for 5 min to prevent germination) between 1800-2000 and checked twice during the night at 2200 and 0200. Traps were closed during the 0200 check. All animals were individually tagged for identification. We used uniquely numbered ear tags for *D. simulans* and *P. maniculatus* (Monel 1005-1, National Band and Tag Co., Newport, KY). For species with small ears (*P. l. pacificus*, *P. l. brevinasus*, *C. fallax*, *R. megalotis*) we injected visible implant elastomer (VIE- Northwest Marine Technology, Inc., Shaw Island, WA) in unique color combinations just under the skin along the side of the tail (Shier 2008). These permanent marks were visible under a black light on subsequent captures. For each animal trapped, we recorded species, unique identity, sex, weight, reproductive condition, and trap location.

We selected focal individuals to provision with seeds after identifying them as residents, determined by trapping them a minimum of 3 nights in the same location (Shier and Swaisgood 2012). Once an appropriate focal animal was trapped, we emptied its cheek pouches of

previously collected seeds and placed it inside a clear Plexiglas open-bottomed arena (61 x 61 x 61 cm). We placed 5 g of hulled millet shaken with 0.5 g non-toxic fluorescent pigment (either green, pink, or blue ECO Pigment series, DayGlo Color Corp, Cleveland, OH) that passes through an animals' digestive tract and is visible in feces (Longland & Clements, 1995; Stapp et al., 1994) on a tray in the arena, and watched from a minimum of 5 m away through night vision goggles as the animal cached the seeds. The animal typically filled its cheek pouches and then dug under the edge of the arena to return to its burrow. It could return to the seed tray by reentering under the edge of the arena, and make as many trips back and forth as necessary to remove all seeds from the tray. The arena detained the animal long enough for it to identify the seed tray as a food source, and all individuals made multiple trips from the seed tray.

Fluorescence was always clearly visible in feces of the focal cacher on subsequent captures.

After provisioning an animal with dyed seeds, we trapped a 16-trap grid (4x4 traps, 4 m spacing) for 10 consecutive nights and collected fecal samples from all trapped individuals of any species. We wiped traps clean prior to opening each night and examined each animal and all feces under a black light for traces of fluorescent pigment, which would indicate cache pilfering, if it occurred (Daly et al. 1992; Murray et al. 2006). Trials with the same color fluorescent seeds were conducted at least 500 m apart so we could identify which caching individual was pilfered from.

*Use of conspecific or heterospecific scent to find or avoid scatter hoards---* We tested whether *P. longimembris*, *D. simulans*, *C. fallax* and *P. maniculatus* use scent of conspecifics or heterospecifics to either find or avoid scatter hoards. We conducted this study at the San Jacinto Wildlife Area (33.13° N, 116.54° W) from May-July 2015. Trapping and tagging procedures

were identical to those described above, except traps were closed during the first check at 2200. To collect scented sand, we trapped animals in the field and placed one individual in a Plexiglas tank (13 x 19 x 21 cm) on 340 g of clean, dry sand with millet seed ad libitum. Animals were left undisturbed for 5 hours (Dempster and Perrin 1990; Ebensperger 2000) at which point they were returned to their location of capture. This is likely more contact than an individual would have with the substrate surrounding a scatter hoard, but allowed us to test whether pilferers respond to species-specific scent at scatter hoards. Sand was sifted to remove seeds and feces, and stored in clean glass jars with metal screw tops in a freezer for up to 5 nights before being used in the experiment (Randall 1987; Devenport et al. 1999).

The testing arena was an opaque plastic tub (89 x 51 x 48 cm) with 3 cm of clean, dry sand. We created artificial caches in plastic cups (59 ml) filled with sand and 2 g ( $\pm 0.1$  g) of millet buried at a depth of 1 cm, which should be detectable by any of the species (Vander Wall et al. 2003). Sand in each of the artificial caches was either unscented, conspecific-scented, or heterospecific-scented. Six cache cups, two of each scent treatment, were evenly spaced in the arena and placed into the sand. The top of the artificial caches were flush with the sand in the arena, such that the plastic cups were not exposed but the treated sand was on the surface (Daly et al. 1992).

Focal cache pilferers of each species were randomly selected from the available adult animals trapped each night. We balanced sex ratios for each focal species. Individual *P. longimembris* were used in up to two trials with different heterospecific scents, separated by a minimum of 24 hr, due to logistical constraints of trapping enough unique individuals. The other species were used only once. We placed the focal individual in the testing arena close to the location of capture with the lid on to prevent escaping for 3 hr. At the end of the trial we released

the focal animal and removed each artificial cache, sifted it, and weighed the remaining seeds. The difference between the amount initially provided (2 g) and the remainder was calculated as the weight of seeds taken. Caches that appeared undisturbed consistently had 2 g of seeds remaining; thus, time in sand did not alter the weight of the seeds.

*Chaetodipus fallax*, *P. maniculatus*, and *D. simulans* were only exposed to *P. longimembris* as a heterospecific scent (n=20 for each focal species). *Perognathus longimembris* was presented with heterospecific scent of *C. fallax*, *P. maniculatus*, *D. simulans* (n=20 for each), and *R. megalotis* (n=8). We conducted 128 trials in total.

We compared *P. longimembris*' ability to discover caches scented by conspecifics, heterospecifics, or unscented using logistic regression (discovered/not discovered). We included scent of the cache as a fixed effect and identity of the pilferer as a random effect. We also tested whether the amount of seeds *P. longimembris* pilfered from discovered caches was affected by the scent of the cache, using linear regression. Weight of seeds taken was the outcome variable, scent of cache was a fixed effect and identity of pilferer was a random effect. We used similar tests to compare *C. fallax*, *P. maniculatus*, and *D. simulans* to one another in cache detection and amount pilfered from conspecific, unscented, and *P. longimembris*-scented caches. We also compared the total amount of seeds pilfered by each species, regardless of scent, using linear regression. All statistical analyses were conducted in R 3.3.2 (R Development Core Team, 2016).

Protocols followed American Society of Mammalogists guidelines (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016) and were approved by the Institutional Animal Care and Use Committee of San Diego Zoo Global (protocol number 15-002).

## RESULTS

*Susceptibility of P. longimembris to heterospecific pilferers*--- Pacific pocket mice (*P. l. pacificus*) did not differ in the percent of seeds they stored in larder hoards versus scatter hoards (Figure 1. WSRT  $V=102.5$ ,  $p=0.94$ ).

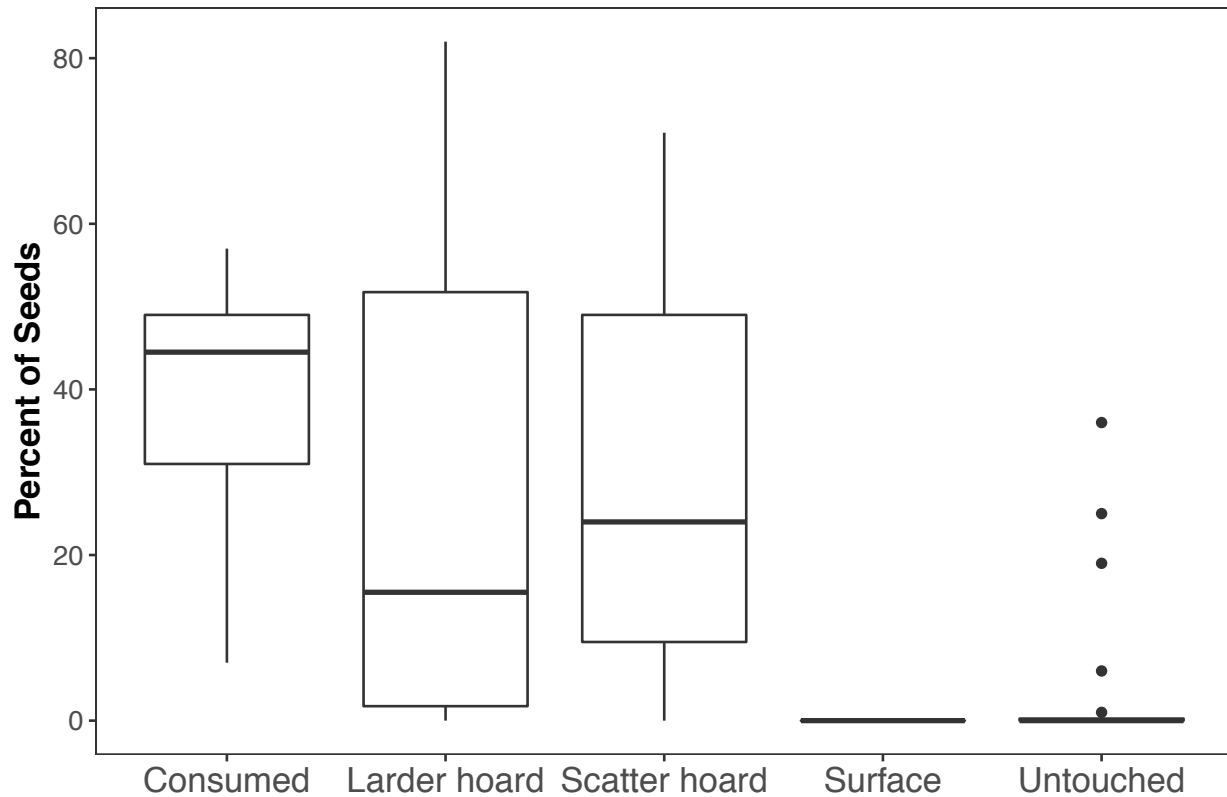


Figure 1. Seed placement by Pacific pocket mice during 7-day captive caching. Percent of seeds consumed was calculated from the difference between the weight of seeds given and the weight of seeds recovered in any location. Seeds stored in the nest were considered larder hoarded and seeds buried anywhere in the substrate were counted as scatter hoarded. "Surface" refers to seeds that were moved from the dish but left unburied, and "untouched" refers to seeds that were not removed from feeding dish.

*Frequency of pilfering by sympatric species in the field---* Out of 32 trials in which an individual cached fluorescent seed, only 7 cases of pilfering were identified although 137 unique individuals were captured in close proximity (10 m) to the caches and therefore had the opportunity to pilfer (Table 2). Of the 7 pilferers we detected, 3 had taken seeds from conspecifics (2 *P. longimembris*, 1 *C. fallax*).

Table 2. Species that cached fluorescent seeds and the actual and potential pilferers of each species surrounding them.

| Species of Focal Cacher          | Species Trapped to Check for Pilfering     |  |   |   |
|----------------------------------|--|--|---|---|
|                                  | <i>P. longimembris</i><br>#pilfer/#trapped | <i>D. simulans</i><br>#pilfer/#trapped | <i>Chaetodipus</i><br><i>spp.</i><br>#pilfer/#trapped | <i>P. maniculatus</i><br>#pilfer/#trapped |
| <i>P. longimembris</i><br>(n=18) | 2/23                                       | 0/8                                    | 0/2   | 1/23                                      |
| <i>D. simulans</i><br>(n=9)      | 1/9  | 0/20                                   | 0/7   | 0/0                                       |
| <i>C. fallax</i><br>(n=5)        | 1/1  | 1/6                                    | 1/38  | 0/0                                       |

Each column represents the number of unique individuals of each species that were trapped in a grid surrounding the focal caching individuals on 10 nights following seed provisioning. The top number is how many unique individuals of that species were found with fluorescence on their fur or in their feces, indicating they had pilfered caches. The bottom number is the total number of individuals of each species that were trapped within 10 m of caches and therefore had the opportunity to pilfer fluorescent seeds.

We found that *P. longimembris* pilfered from both conspecific and heterospecific caches. A higher proportion of *P. longimembris* pilfered seeds from heterospecific caches (2 of 10) than from conspecific caches (2 of 23), but there were too few pilfering events to justify statistical

analyses. *Peromyscus maniculatus* pilfered from *P. longimembris* (1 of 23), but no *D. simulans* or *C. fallax* pilfered from *P. longimembris*.

*Use of conspecific or heterospecific scent to find or avoid scatter hoards---* Pocket mice (*P. longimembris*) discovered fewer caches scented by *C. fallax* than by conspecifics (Supplementary Data S1;  $t=-2.1$ ,  $p=0.04$ ), but there were no differences in their discovery of caches scented by other species and conspecific-scented caches, or unscented caches (Supplementary Data S1). Of the caches they discovered, *P. longimembris* pilfered more seeds from conspecific compared to unscented caches (Figure 2; Supplementary Data S2;  $t=-2.69$ ,  $p=0.01$ ). There were no differences in the amount of seeds *P. longimembris* pilfered from any heterospecific scented caches compared the other scent treatments (Figure 2; Supplementary Data S2), and although they discovered more conspecific caches than *C. fallax* scented caches, there was no difference in the amount of seeds they took from these two scent treatments. The other species, *C. fallax*, *P. maniculatus*, and *D. simulans*, did not differ from each other in the discovery of conspecific, unscented, or *P. longimembris*-scented caches (Supplementary Data S1). Kangaroo rats (*D. simulans*) pilfered more seeds from conspecific scented caches than *P. longimembris* or unscented caches (Figure 2; Supplementary Data S2). Overall, *C. fallax* and *D. simulans* pilfered more seeds than either *P. maniculatus* or *P. longimembris* when all the scent treatments were combined (Figure 2; Supplementary Data S3).

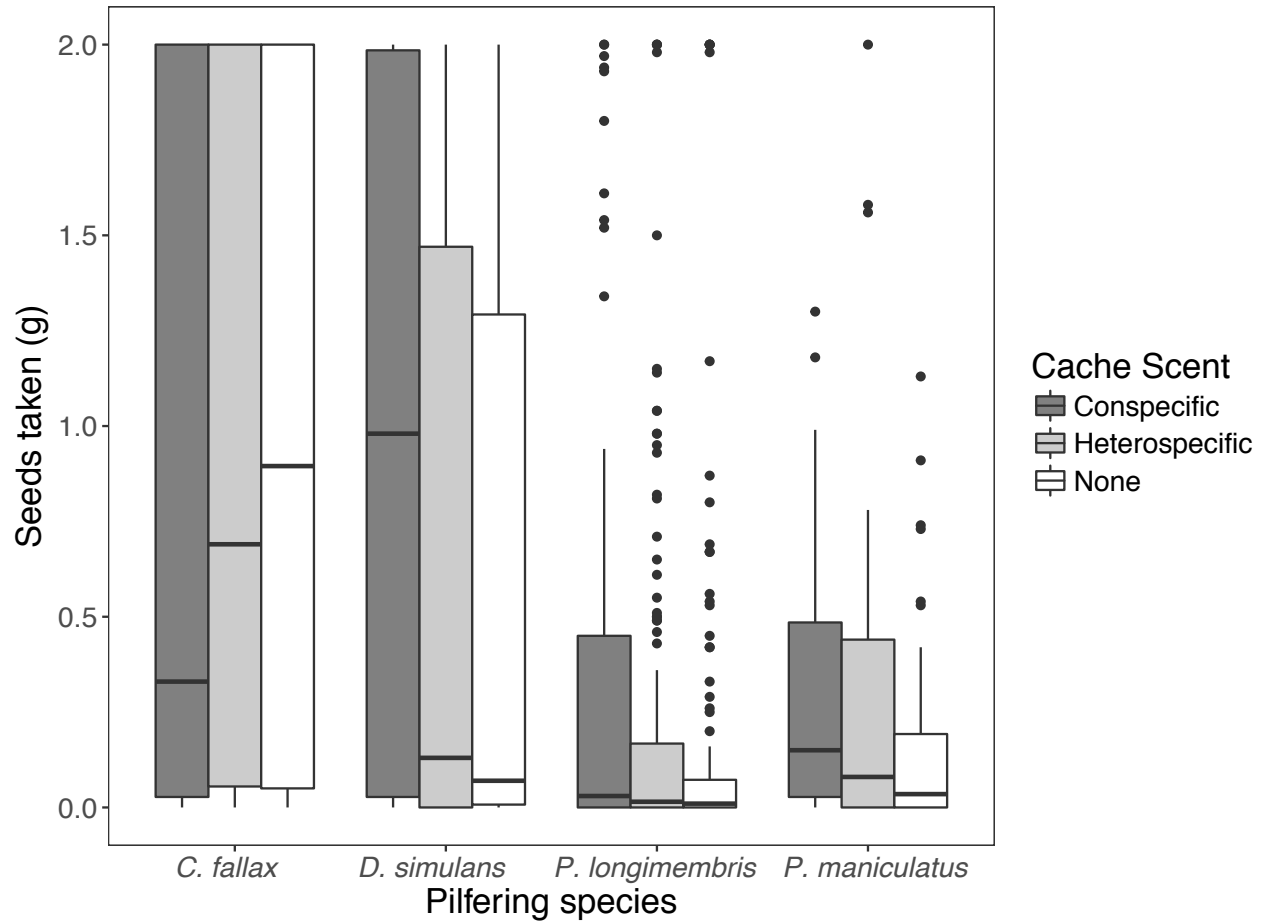


Figure 2. Weight of seeds taken from 2g artificial caches of each scent treatment (conspecific, heterospecific, or none) by each species during the 3 hr pilfering trials. The boxplots depict medians (horizontal lines) and interquartile ranges (boxes). Whiskers show spread of data (highest and lowest values within 1.5 IQR), and dots are outliers.



## DISCUSSION

We first quantified larder and scatter hoarding behavior of *P. longimembris* in captivity, to assess their susceptibility to heterospecific pilferers in the field, since previous studies reported conflicting results (Jenkins and Breck 1998; Price et al. 2000). The size difference between *P. longimembris* and most competitor species means that larger species likely cannot fit inside *P. longimembris* burrow entrances, effectively protecting larder hoards from heterospecific pilferers (Jenkins and Breck 1998). We found that *P. longimembris* in captivity scatter-hoarded the same proportion of seeds as they larder-hoarded, which indicates that a substantial proportion of their cached seeds could be susceptible to pilfering by heterospecifics in the field. We therefore studied pilfering both by and from *P. longimembris* in the field.

We found very low rates of cache pilfering in the field; only five percent of captured individuals had pilfered seeds from a dyed seed cache. This suggests that *P. longimembris* persistence is not facilitated by pilfering the caches of larger, dominant species. However, it is also unlikely that *P. longimembris* are negatively impacted by cache pilfering from other species, as only one instance of pilfering by a heterospecific was documented from the 33 individuals that had the opportunity.

The low rate of pilfering was surprising because similar studies have found much higher rates (Daly et al. 1992; Leaver and Daly 2001). Cache pilfering can vary seasonally (Vander Wall 2000), and might be lower during peak primary productivity, when more food is available (Leaver 2004). However, we ran experiments from April-September, which includes the late summer when seeds are less abundant and *P. longimembris* are caching in preparation for winter, when they remain in their burrows for 1-5 months and come out of torpor every few days to eat seeds from their larders (Bartholomew and Cade 1957; Kenagy 1973). Our baited traps provided

a flush of seeds in the area, which could have reduced the need for cache pilfering. Alternatively, although others have successfully tracked cache pilfering using dyed seeds (Daly et al. 1992; Leaver and Daly 2001; Murray et al. 2006), individuals that pilfered dyed seeds might have re-cached them, rather than consuming them, and groomed off traces of pigment from their fur. Consuming very small quantities of the dyed seeds could have made the dye impossible to detect in the feces and we could not verify the quantity of seeds pilfered or consumed from the fluorescent feces we did observe.

Due to the potential limitations of testing for cache pilfering in a natural system with dyed seeds, we also examined whether species in this rodent community use conspecific or heterospecific scent to find or avoid scatter hoards. Scent is an important cue for solitary species and can be used to advertise territory boundaries to both conspecifics and heterospecifics (Randall 1987; Dempster and Perrin 1990; Arakawa et al. 2008). One potential way for *P. longimembris* to benefit from the presence of larger seed-hoarding species would be to specialize on pilfering seeds from their caches, but we found no evidence of this. *P. longimembris* discovered fewer caches scented by *C. fallax* than with conspecific scent, but there were no differences in the amount of seeds they pilfered from conspecific and *C. fallax* scented caches. Of the caches they discovered, *P. longimembris* pilfered more from conspecific-scented caches compared to unscented caches. There were no differences in the amount of seeds *P. longimembris* pilfered from any heterospecific compared to other scent treatments. The other species did not differ in their discovery rate of any of the scent treatments. *Dipodomys simulans* pilfered more seeds from conspecific caches than either *P. longimembris* or unscented caches, while *C. fallax* and *P. maniculatus* pilfered equally from conspecific, *P. longimembris*, and

unscented caches. Our results suggest that none of these species uses heterospecific scent to find scatter hoards to pilfer.

Price and Mittler (2003) proposed that small, subordinate species could benefit from living sympatrically with species that travel greater distances while foraging and bring back seeds to cache, providing the smaller species a greater chance of encountering the processed resource (cached seeds) compared to the primary resource (seeds fallen from plants). However, this increased access to seeds would be most valuable when primary production of seeds is lowest and food is scarcest in the winter months. *P. longimembris* have an alternative strategy for dealing with extreme food scarcity, the reduction of metabolic activity through daily torpor and/or aestivation (Guppy and Withers 1999). Kenagy (1973) found that although there is some variation associated with annual levels of precipitation and individual differences, the majority of *P. longimembris* are inactive during the winter months, suggesting that they must cache enough seeds in the late summer and fall to fill their larders and survive winter. We found very low rates of *P. longimembris* pilfering in the late summer and early fall prior to aestivation. Furthermore, *P. longimembris* was less efficient in foraging on artificial scatter hoards, pilfering fewer seeds than either *D. simulans* or *C. fallax*, both species that are behaviorally dominant (Chock et al. 2018). It is therefore unlikely that *P. longimembris* significantly benefits from pilfering other species' caches.

Our findings suggest that *P. longimembris* does not benefit significantly from the presence of competitor species through cache pilfering. There may be other benefits from heterospecifics mediated through predation, and further studies are needed to understand the mechanisms, such as spatial or temporal niche partitioning, that allow *P. longimembris* to persist in these communities. Although these species can coexist in established communities,

reintroduced populations should be given every competitive advantage during the establishment phase following release. Previous studies of aggressive interference found that all larger species are behaviorally dominant to *P. longimembris* and recommended that managers should avoid release sites with medium or high densities of the larger heteromyids, or reduce densities of these larger heteromyids within release sites in order to minimize aggressive interference from residents during the critical establishment period following release (Chock et al. 2018). Rather than indicating that cache-pilfering offsets the costs of interference competition, our current results provide no evidence that Pacific pocket mice benefit sufficiently from the seed-caches of other species to offset the costs of interspecific competition. These results provide support for our previous recommendations of temporarily managing densities of known competitors during post-release establishment.

## SUPPLEMENTARY RESULTS

| Focal species          | Model term                       | Estimate      | SE           | t             | P-value      |
|------------------------|----------------------------------|---------------|--------------|---------------|--------------|
| <i>P. longimembris</i> | <b>Conspecific vs 1</b>          | <b>-0.840</b> | <b>0.402</b> | <b>-2.098</b> | <b>0.036</b> |
|                        | Conspecific vs 2                 | 0.068         | 0.399        | 0.171         | 0.864        |
|                        | Conspecific vs 3                 | 0.123         | 0.398        | 0.309         | 0.757        |
|                        | Conspecific vs 4                 | -0.906        | 0.574        | -1.577        | 0.115        |
|                        | Conspecific vs Unscented         | -0.370        | 0.260        | -1.424        | 0.154        |
|                        | Unscented vs 1                   | -0.472        | 0.397        | -1.191        | 0.234        |
|                        | Unscented vs 2                   | 0.438         | 0.398        | 1.102         | 0.270        |
|                        | Unscented vs 3                   | 0.493         | 0.398        | 1.240         | 0.215        |
|                        | Unscented vs 4                   | -0.534        | 0.572        | -0.936        | 0.349        |
| Competitors            | <i>P. longimembris</i> vs 1      | 0.039         | 0.510        | 0.076         | 0.939        |
|                        | <i>P. longimembris</i> vs 2      | 0.430         | 0.492        | 0.874         | 0.382        |
|                        | <i>P. longimembris</i> vs 3      | 0.798         | 0.520        | 1.536         | 0.124        |
|                        | <i>P. longimembris</i> vs Unscen | 0.319         | 0.328        | 0.975         | 0.33         |
|                        | Unscented vs 1                   | -0.281        | 0.519        | -0.541        | 0.589        |
|                        | Unscented vs 2                   | 0.110         | 0.497        | 0.222         | 0.824        |
|                        | Unscented vs 3                   | 0.479         | 0.522        | 0.918         | 0.359        |

**Table S1.**--- Logistic regression results with artificial caches that were discovered/not discovered as the outcome variable. Scent of cache (conspecific, heterospecific, unscented) was included as a fixed effect and identity of the pilferer as a random effect. Contrasts shown in the table are between the responses of *P. longimembris* to four heterospecific species-scented sand or between the responses of the other species to *P. longimembris* scented sand. For example, the first line in the table, labeled “Conspecific vs 1” tests for a difference in *P. longimembris* discovering caches with conspecific scent or species 1 scent. Opponent species codes: 1= *Chaetodipus fallax*, 2=*Dipodomys simulans*, 3= *Peromyscus maniculatus*, 4= *Reithrodontomys megalotis*. All significant terms are in bold.

| Focal species          | Model term                         | Estimate      | SE           | t             | P-value       |
|------------------------|------------------------------------|---------------|--------------|---------------|---------------|
| <i>P. longimembris</i> | Conspecific vs 1                   | 0.033         | 0.118        | 0.283         | 0.778         |
|                        | Conspecific vs 2                   | -0.190        | 0.103        | -1.841        | 0.067         |
|                        | Conspecific vs 3                   | -0.014        | 0.103        | -0.132        | 0.895         |
|                        | Conspecific vs 4                   | -0.039        | 0.176        | -0.222        | 0.825         |
|                        | <b>Conspecific vs Unscented</b>    | <b>-0.188</b> | <b>0.070</b> | <b>-2.692</b> | <b>0.008</b>  |
|                        | Unscented vs 1                     | 0.221         | 0.119        | 1.865         | 0.064         |
|                        | Unscented vs 2                     | -0.003        | 0.106        | -0.024        | 0.981         |
|                        | Unscented vs 3                     | 0.174         | 0.104        | 1.670         | 0.097         |
|                        | Unscented vs 4                     | 0.149         | 0.175        | 0.849         | 0.397         |
| Competitors            | <i>P. longimembris</i> vs 1        | -0.037        | 0.133        | -0.277        | 0.782         |
|                        | <b><i>P. longimembris</i> vs 2</b> | <b>0.439</b>  | <b>0.136</b> | <b>3.230</b>  | <b>0.001</b>  |
|                        | <i>P. longimembris</i> vs 3        | -0.148        | 0.135        | -1.099        | 0.273         |
|                        | <i>P. longimembris</i> vs Unscen   | -0.075        | 0.089        | -0.844        | 0.399         |
|                        | Unscented vs 1                     | 0.038         | 0.131        | 0.292         | 0.77          |
|                        | <b>Unscented vs 2</b>              | <b>0.514</b>  | <b>0.135</b> | <b>3.801</b>  | <b>0.0002</b> |
|                        | Unscented vs 3                     | -0.073        | 0.136        | -0.540        | 0.590         |

**Table S2.**--- Linear regression results with the weight of seeds taken from artificial caches that were discovered as the outcome variable. Scent of cache (conspecific, heterospecific, unscented) was included as a fixed effect and identity of the pilferer as a random effect. Contrasts shown in the table are between the responses of *P. longimembris* to four heterospecific species-scented sand or between the responses of the other species to *P. longimembris* scented sand. For example, the first line in the table, labeled “Conspecific vs 1” tests for a difference in the weight of seeds *P. longimembris* took from caches with conspecific scent or species 1 scent. Opponent species codes: 1= *Chaetodipus fallax*, 2=*Dipodomys simulans*, 3= *Peromyscus maniculatus*, 4= *Reithrodontomys megalotis*. All significant terms are in bold.

| Model term                         | Estimate      | SE           | t             | P-value                   |
|------------------------------------|---------------|--------------|---------------|---------------------------|
| <b><i>P. longimembris</i> vs 1</b> | <b>0.673</b>  | <b>0.122</b> | <b>5.491</b>  | <b>3.70e<sup>-7</sup></b> |
| <b><i>P. longimembris</i> vs 2</b> | <b>0.528</b>  | <b>0.116</b> | <b>4.535</b>  | <b>1.74e<sup>-5</sup></b> |
| <i>P. longimembris</i> vs 3        | 0.024         | 0.120        | 0.203         | 0.840                     |
| 1 vs 2                             | -0.145        | 0.142        | -1.021        | 0.31                      |
| <b>1 vs 3</b>                      | <b>-0.648</b> | <b>0.145</b> | <b>-4.468</b> | <b>2.24e<sup>-5</sup></b> |
| <b>2 vs 3</b>                      | <b>-0.503</b> | <b>0.140</b> | <b>-3.597</b> | <b>0.0005</b>             |

**Table S3.**--- Linear regression results with the weight of seeds taken from artificial caches regardless of scent. Species was included as a fixed effect and identity of the pilferer as a random effect. Contrasts shown in the table are between the responses of each species pair. For example, the first line in the table, labeled “*P. longimembris* vs 1” tests for a difference in the weight of seeds *P. longimembris* took from all caches with the weight of seeds species 1 took from all caches. Opponent species codes: 1= *Chaetodipus fallax*, 2=*Dipodomys simulans*, 3= *Peromyscus maniculatus*. All significant terms are in bold.

## REFERENCES

- Arakawa, H., D. C. Blanchard, K. Arakawa, C. Dunlap and R. J. Blanchard. 2008. Scent marking behavior as an odorant communication in mice. *Neuroscience and Biobehavioral Reviews* 32:1236–1248.
- Armstrong, D. P. and P. J. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution* 23:20–5.
- Bartholomew, G. A. and T. J. Cade. 1957. Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. *Journal of Mammalogy* 38:60–72.
- Brehme, C. S. and R. N. Fisher. 2008. 2008 Survey results for the Pacific pocket mouse: North and South San Mateo, Marine Corps Base, Camp Pendleton; with additional analyses to inform long-term monitoring design. U. S. Geological Survey Report Prepared for AC/S Environmental Security, Marine Corps Base, Camp Pendleton (2008). Unpublished report.
- Brichieri-Colombi, T. A. and A. Moehrensclager. 2016. Alignment of threat, effort, and perceived success in North American conservation translocations. *Conservation Biology* 30:1159–1172.
- Brown, J. H. and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* 54:788–797.
- Burns, C. E. 2005. Behavioral ecology of disturbed landscapes: the response of territorial animals to relocation. *Behavioral Ecology* 16:898–905.
- Chock, R. Y., D. M. Shier and G. F. Grether. 2018. Body size, not phylogenetic relationship or residency, drives interspecific dominance in a little pocket mouse community. *Animal Behaviour* 137:197–204.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition:



- Evidence from field experiments. *The American Naturalist* 122:661–696.
- Daly, M., L. F. Jacobs, M. I. Wilson and P. R. Behrends. 1992. Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behavioral Ecology* 3:102–111.
- Dempster, E. R. and M. R. Perrin. 1990. Interspecific odour discrimination in four Gerbillurus species. *Zeitschrift für Säugetierkunde* 55:321.
- Devenport, L., J. Devenport and C. Kokes. 1999. The role of urine marking in the foraging behaviour of least chipmunks. *Animal Behaviour* 57:557–563.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* 11:624–632.
- Ebensperger, L. A. 2000. Dustbathing and intra-sexual communication of social degus, *Octodon degus* (Rodentia: Octodontidae). *Revista Chilena de Historia Natural* 73:359–365.
- Eisenberg, J. F. [online]. 1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus*. *Behaviour* 19:177–207.
- Fischer, J. and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11.
- Goodale, E., G. Beauchamp, R. D. Magrath, J. C. Nieh and G. D. Ruxton. 2010. Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution* 25:354–361.
- Griffith, B., M. J. Scott, J. W. Carpenter and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–479.
- Guppy, M. and P. Withers. 1999. Metabolic depression in animals: physiological perspectives and biochemical generalizations. *Biological Reviews* 74:1–40.
- Haim, A. and F. M. Rozenfeld. 1993. Temporal segregation in coexisting *Acomys* species: the

- role of odour. *Physiology and Behavior* 54:1159–1161.
- Heard, S. B. 1994. Processing chain ecology: resource condition and interspecific interactions. *Journal of Animal Ecology* 63:451–464.
- Howard, W. E. and R. E. Cole. 1967. Olfaction in seed detection by deer mice. *Journal of Mammalogy* 48:147–150.
- Jenkins, S. H. and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy* 79:1221–1233.
- Johnston, R. E. and T. A. Robinson. 1993. Cross-species discrimination of individual odors by hamsters (Muridae: *Mesocricetus auratus*, *Phodopus campbelli*). *Ethology* 94:317–325.
- Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* 54:1201–1219.
- Lahti, K., A. Laurila, K. Enberg and J. Piironen. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Animal Behaviour* 62:935–944.
- Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. *Behavioral Ecology* 15:729–734.
- Leaver, L. A. and M. Daly. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. *Oecologia* 128:577–584.
- Linklater, W. L., J. V. Gedir, P. R. Law, R. R. Swaisgood, K. Adcock, P. du Preez, et al. 2012. Translocations as experiments in the ecological resilience of an asocial mega-herbivore. *PLoS ONE* 7:e30664.
- Longland, W. S. and C. Clements. 1995. Use of fluorescent pigments in studies of seed caching by rodents. *Journal of Mammalogy* 76:1260–1266.

- Maza, B. G., N. R. French and A. P. Aschwanden. 1973. Home range dynamics in a population of heteromyid rodents. *Journal of Mammalogy* 54:405–425.
- McKnight, M. L. 2005. Phylogeny of the *Perognathus longimembris* species group based on mitochondrial cytochrome-b: how many species? *Journal of Mammalogy* 86:826–832.
- McNab, B. K. 1963. Bioenergetics and the determination of home range size. *The American Naturalist* 97:133–140.
- Meserve, P. L. 1976a. Habitat and resource utilization by rodents of a California coastal sage scrub community. *Journal of Animal Ecology* 45:647–666.
- Meserve, P. L. 1976b. Food relationships of a rodent fauna in a California coastal sage scrub community. *Journal of Mammalogy* 57:300–319.
- Mittler, J. 1997. What happens when predators do not completely consume their prey? *Theoretical Population Biology* 51:238–251.
- Moehrensclager, A., D. M. Shier, T. P. Moorhouse, M. R. S. Price and J. H. Schaar. 2013. Righting past wrongs and ensuring the future: challenges and opportunities for effective reintroductions amidst a biodiversity crisis. P. in *Key Topics in Conservation Biology 2* (D. W. Macdonald & K. J. Willis, eds.). John Wiley & Sons, Oxford.
- Moseby, K. E., J. L. Read, D. C. Paton, P. Copley, B. M. Hill and H. A. Crisp. 2011. Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation* 144:2863–2872.
- Murray, A. L., A. M. Barber, S. H. Jenkins and W. S. Longland. 2006. Competitive environment affects food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys Merriami*). *Journal of Mammalogy* 87:571–578.
- Nowak. 1999. Walker's Mammals of the World. P. in. The Johns Hopkins University Press,

Baltimore and London.

- Ord, T. J. and J. A. Stamps. 2009. Species identity cues in animal communication. *The American Naturalist* 174:585–93.
- Parejo, D. and E. Danchin. 2004. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behavioral Ecology* 16:96–105.
- Peiman, K. S. and B. W. Robinson. 2010. Ecology and evolution of resource-related heterospecific aggression. *The Quarterly Review of Biology* 85:133–158.
- Price, M. V, P. A. Kelly and R. L. Goldingay. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi* Merriam) and implications for conservation. *Journal of Mammalogy* 75:929–939.
- Price, M. V and J. E. Mittler. 2003. Seed-cache exchange promotes coexistence and coupled consumer oscillations: a model of desert rodents as resource processors. *Journal of Theoretical Biology* 223:215–231.
- Price, M. V and J. E. Mittler. 2006. Cachers, scavengers, and thieves: a novel mechanism for desert rodent coexistence. *The American Naturalist* 168:194–206.
- Price, M. V, N. M. Waser and S. McDonald. 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. *Journal of Mammalogy* 81:97–106.
- Randall, J. A. 1987. Sandbathing as a territorial scent-mark in the bannertail kangaroo rat, *Dipodomys spectabilis*. *Animal Behaviour* 35:426–434.
- Reed, J. M. and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* 8:253–256.
- Reichman, O. J. and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. *Ecology* 58:636–643.

- Reid, F. A. 2006. Mammals of North America. P. in. Houghton Mifflin Co., New York, NY.
- Seddon, P. J., D. P. Armstrong and R. F. Maloney. 2007. Developing the science of reintroduction biology. *Conservation Biology* 21:303–12.
- Shier, D. M. 2008. Behavioral ecology and translocation of the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) for the period January 2007 - December 2007. San Diego Zoo Report:1–57.
- Shier, D. M., S. Leivers, S. King, R. Y. Chock and J. P. Montagne. 2016. Captive breeding, anti-predator behavior and reintroduction of the Pacific pocket mouse (*Perognathus longimembris pacificus*) 2014-2016.
- Shier, D. M. and R. R. Swaisgood. 2012. Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology* 26:116–23.
- Short, J., S. D. Bradshaw, J. Giles, R. I. T. Prince and G. R. Wilson. 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia- a review. *Biological Conservation* 62:189–204.
- Sikes, R. S. and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *The American Naturalist* 131:329–347.
- Stamps, J. A. and R. R. Swaisgood. 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392–409.
- Stapp, P., J. K. Young, S. VandeWoude and B. Van Horne. 1994. An evaluation of the pathological effects of fluorescent powder on deer mice (*Peromyscus maniculatus*). *Journal*

- of Mammalogy 75:704–709.
- U.S. Fish & Wildlife Service. 1998. Recovery plan for the Pacific pocket mouse (*Perognathus longimembris pacificus*).
- U.S. Fish & Wildlife Service. 2015. Species occurrences for Carlsbad Fish and Wildlife Office: U.S. Fish and Wildlife Service, Carlsbad Field Office: Carlsbad, CA.
- Vander Wall, S. B. 1990. Food Hoarding in Animals. P. in. The University of Chicago Press, Chicago.
- Vander Wall, S. B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology 11:544–549.
- Vander Wall, S. B. 2003. How rodents smell buried seeds: a model based on the behavior of pesticides in soil. Journal of Mammalogy 84:1089–1099.
- Vander Wall, S. B., M. J. Beck, J. S. Briggs, J. K. Roth, T. C. Thayer, J. L. Hollander, et al. 2003. Interspecific variation in the olfactory abilities of granivorous rodents. Journal of Mammalogy 84:487–496.
- Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck and J. K. Roth. 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). Western North American Naturalist 61:109–113.

**CHAPTER 3**

**SPATIAL NICHE PARTITIONING, TEMPORAL AGGREGATION, AND DIFFERING**

**HABITAT SELECTION SHAPE A RODENT COMMUNITY**

## ABSTRACT

Translocations and reintroductions are often cited as important conservation tools, but typically have limited success. In California, 19 out of 31 species of heteromyids, a family of rodents which includes kangaroo rats, pocket mice, and kangaroo mice, are declining. Although many heteromyid translocations have been conducted, there are only two that have documented resulting viable populations that persist long-term. We conducted a year-round study of patterns of spatial and temporal niche partitioning in a community that included four heteromyids and three cricetids to determine suitable community compositions and heterospecific densities that could support translocated animals, particularly little pocket mice (*Perognathus longimembris*), the smallest species in the community. We found evidence for spatial niche partitioning between species, particularly Stephens' kangaroo rats (*Dipodomys stephensi*) and a suite of heterospecifics. These patterns that were associated with high levels of overall rodent activity and high *P. longimembris* activity. We also found that species aggregated their activity in similar times of the night in areas with high rodent activity, although there were no consistent species-pairs driving this overlap. Habitat surveys revealed the microhabitat features utilized by each species, and comparing the patterns of utilization between species could help managers assess the quality of a release site based on the presence of other species that have high overlap in microhabitat use with the focal species. These results also provide targets for habitat restoration and management plans. Our work suggests that little pocket mice will likely benefit from minimized interspecific competition during the early stages of translocation, but once established, their densities are not correlated with heterospecific densities, and they can likely persist without active management of competitor species.



## INTRODUCTION

It is still an open question how multiple rodent species that are similar in diet and habitat can persist in small mammal communities (Brown & Harney, 1993; Kelt, 2011; Price, Waser, & McDonald, 2000). Niche overlap and interspecific competition are expected to decline as sympatric species diverge in resource needs or behavior over time. In communities with species that maintain a high degree of resource overlap, it is often unclear how behaviorally subordinate species continue to persist with dominant species.

Spatial niche partitioning is predicted to occur when a subordinate species shifts to occupy a less-preferred habitat in sympatry with a dominant species. Subordinate prairie voles (*Microtus ochrogaster*) and dominant cotton rats (*Sigmodon hispidus*) both prefer areas with high density of vertical structures when they are alone. When placed together, breeding cotton rats use the same habitat as when they are alone, but prairie voles shift their habitat use and spend more time in areas with lower density of vertical structures, minimizing their spatial overlap with rats (Glass & Slade, 1980). Similarly, two species of desert gerbil prefer the same habitat (semistabilized sand dunes) in allopatry, but the subordinate *Gerbillus allenbyi* utilizes mainly the secondary habitat type (stabilized sand dunes) when in sympatry with dominant *G. pyramidum* (Ziv, Abramsky, Kotler, & Subach, 1993). Occupying a less preferred part of the habitat can allow the species to coexist, but the subordinate species that shifts its niche can suffer reduced fitness or lower population densities (Glass & Slade, 1980).

With or without spatial niche partitioning, species may partition their temporal niche, or the timing of their activity, in the presence of heterospecifics. These patterns can occur annually, with greater segregation of activity during seasons when resources are less abundant and competition is expected to be more intense (Llewellyn & Jenkins, 1987; Schoener, 1982).

Temporal niche partitioning can also occur on a diel scale, with species shifting their daily activity patterns to minimize overlapping in activity with another species (Carothers & Jakšić, 1984). An example of temporal partitioning occurs between two species of spiny mice that live in the arid deserts of the Middle East where the subordinate *Acomys russatus* is diurnally active when sympatric with the nocturnal *A. cahirinus*. When *A. cahirinus* is excluded, *A. russatus* is active during both the day and night (Gutman & Dayan, 2005). *A. russatus* maintains physiological and morphological features of a nocturnal species, suggesting interspecific competition has forced temporal shifts that may be costly in a hot, arid climate (Gutman & Dayan, 2005; Kronfeld-schor et al., 2001). The prairie voles that exhibit spatial niche partitioning in the presence of breeding cotton rats were found to co-occur with non-breeding cotton rats, but shifted their temporal activity patterns and concentrated their activity during the times of night the rats were least active (Glass & Slade, 1980). Shifts in activity patterns can minimize interspecific aggression, but may result in the subordinate species being excluded from the time of night resources are most abundant, forcing them to travel further or spend longer to obtain the same amount of resources. This can increase the energy costs of foraging unless the subordinate species is a superior exploitative competitor (Carothers & Jakšić, 1984; Ziv et al., 1993).







Heteromyids, a family of rodents that includes kangaroo rats, pocket mice, and kangaroo mice, often live in community assemblages of 1-15 different species of granivorous rodents, forming a seed-foraging guild (Brown & Harney, 1993). Through seed predation and soil disturbance resulting from foraging, burrowing, and caching, heteromyids can also function as keystone species, maintaining native shrubland and preventing its conversion to grassland (Brown & Heske, 1990; Heske, Brown, & Guo, 1993) and increasing soil hydrology and nutrient

cycling with their burrowing. Their burrows provide physical refuge and suitable microclimates for a variety of reptiles and invertebrates (Kay & Whitford, 1978), and the rodents are an important food source for many predators (Brown & Harney, 1993; Kotler, 1985). Of the 31 heteromyid species and subspecies present in California, 19 are listed by state or federal agencies as endangered, threatened, or species of special concern (CNDDDB, 2017). Habitat loss and fragmentation due to urban and agricultural development are the most pervasive threats to heteromyids in California (Goldingay, Kelly, & Williams, 1997), and can result in smaller population sizes, lower migration rates and genetic connectivity, and increased extinction risk (Vandergast, Bohonak, Weissman, & Fisher, 2007). Conservation strategies of translocation, or moving wild animals insitu from one site to another to create, reestablish, or augment wild populations (IUCN, 2013), and reintroductions, or release of animals, often captive-bred, to re-establish a population within the species' historic range (IUCN, 2013), are frequently used for populations of heteromyids to mitigate development. Although many translocations of heteromyids have been conducted (Germano, 2010; O'Farrell, 1999; Shier, Leivers, King, Chock, & Montagne, 2016; Wang & Shier, 2017; Williams, Germano, & Tordoff, 1993), very few have resulted in viable populations that persist over the long term (Germano, Saslaw, Smith, & Cypher, 2013; Shier & Swaisgood, 2012). Understanding the community dynamics and habitat requirements of each species can lead to more effective conservation measures (Seddon, Armstrong, & Maloney, 2007).

We studied niche partitioning and habitat selection in a community that included three declining heteromyids. The Los Angeles pocket mouse (*Perognathus longimembris brevinasus*) and San Diego pocket mouse (*Chaetodipus fallax*) are both California species of special concern, and Stephens' kangaroo rat (*Dipodomys stephensi*) is a federally endangered species. The

Dulzura kangaroo rat (*Dipodomys simulans*) and three species from the family cricetidae were also present: deer mouse (*Peromyscus maniculatus*), cactus mouse (*Peromyscus eremicus*), and western harvest mouse (*Reithrodontomys megalotis*). All species were trapped in the same areas and have high dietary overlap (Table 1; Meserve, 1976a, 1976b).

Table 1. Descriptions of each species and their similarity in size, diet and habitat to the little pocket mouse, *Perognathus longimembris*.

|   |   | Body size <sup>1</sup>  | Diet overlap with<br><i>P. longimembris</i> <sup>2</sup> | Habitat overlap with<br><i>P. longimembris</i> <sup>2</sup> |
|---|---|---|--|---|
| Family: Heteromyidae  |   |   |  |   |
|    | <i>Perognathus longimembris</i>                     | Weight: 6-9g  | -  | -   |
|   | Los Angeles pocket mouse ( <i>P.l. brevinasus</i> ) | Body length: 50-70mm  |  |   |
|   | Pacific pocket mouse ( <i>P.l. pacificus</i> )      | Tail length: 60-85mm  |  |   |
|   | <i>Chaetodipus fallax</i>                           | Weight: 14-26g  | *  | *   |
|   | San Diego pocket mouse                              | Body length: 70-91mm<br>Tail length: 105-120mm                    |  |   |
|  | <i>Dipodomys simulans</i>                           | Weight: 55-70g  | 93%  | Horizontal: 10-50%  |
|   | Dulzura kangaroo rat                                | Body length: 85-130mm   |  | Vertical: 100%  |
|   | <i>Dipodomys stephensi</i>                          | Tail length: 140-200mm  |  |   |
|   | Stephens' kangaroo rat                              | Weight: 45-73g<br>Body length: 98-129mm<br>Tail length: 146-188mm |  |   |
| Family: Cricetidae  |   |   |  |   |
|  | <i>Peromyscus maniculatus</i>                       | Weight: 15-29g  | 33%  | Horizontal: 10-35%  |
|   | Deer mouse  | Body length: 80-109mm   |  | Vertical: 95%   |
|   |   | Tail length: 77-106mm   |  |   |
|  | <i>Peromyscus eremicus</i>                          | Weight: 18-30g  |  |   |
|   | Cactus mouse  | Body length: 80-99mm  |  |   |
|   |   | Tail length: 83-113mm   |  |   |
|  | <i>Reithrodontomys megalotis</i>                    | Weight: 6-11g   | 45%  | Horizontal: 15-55%  |
|   | Western harvest mouse                               | Body length: 59-77mm  |  | Vertical: 60-70%  |
|   |   | Tail length: 71-79mm  |  |   |

<sup>1</sup>Average body size measures taken from Reid 2006. <sup>2</sup>Diet and habitat overlap from Meserve (1976b) using year-round trapping for a suite of species, including four of our focal species. Meserve assessed diet overlap using fecal microscopy and we calculated the median overlap

from his 9-month study. Horizontal habitat use was assessed using live-traps, while vertical habitat use was studied with smoked track cards. Habitat overlap was quantified over four seasons in one year (Meserve, 1976b). \**C. fallax* were infrequently found in Meserve's study area and were not included in these comparisons.

We were particularly interested in understanding how the Los Angeles pocket mouse, the smallest species in the community, persists with larger competitors. Pocket mice are behaviorally subordinate to larger species, and there is no indication that interspecific dominance is site-specific (i.e. they do not defend interspecific territories) (Chock, Shier, & Grether, 2018). Price and Mittler (2003) proposed that small, subordinate species could benefit from living sympatrically with species that travel greater distances while foraging and bring back seeds to cache, providing the smaller species a greater chance of encountering and pilfering the processed resource (cached seeds) compared to the primary resource (seeds fallen from plants). However, field studies show that *P. longimembris* pilfer from other species at very low rates, are not better able to find or deplete heterospecific scented caches compared to conspecific scented caches, and are less efficient at pilfering artificial caches than the larger species (Chock, Grether, & Shier, in review). Finding no evidence that advantages in exploitative competition outweigh negative effects of interference competition, we examined whether Los Angeles pocket mice reduce the intensity of interspecific competition through spatial or temporal niche partitioning.

Through a year-round trapping study we tested for patterns of spatial, annual, or diel niche partitioning between the six sympatric rodent species. If niche partitioning is utilized to minimize aggressive interactions, we predicted the highest degree of niche partitioning would occur between Los Angeles pocket mice (*Perognathus longimembris brevinasus*) and the larger,

behaviorally dominant species (Chock et al., 2018). We also determined the habitat features that were preferentially utilized by each species. The results elucidate co-occurrence and microhabitat use of these species in intact communities, and can help set targets for identifying suitable communities and habitat features for future translocations of any of these species. These findings will also be utilized for release site selection and management for ongoing reintroductions of endangered Pacific pocket mice (*Perognathus longimembris pacificus*), which is geographically, phylogenetically, and behaviorally close to its sister-subspecies *P. l. brevinasus* (Chock et al., 2018; McKnight, 2005).

## METHODS

### *Data collection*

This research was conducted at the San Jacinto Wildlife Area, Riverside County, California, USA (33.13° N, 116.54° W) August 2015-July 2016. Eight trapping grids were established a minimum of 200 m apart to minimize the possibility of the same individuals being trapped on different grids (Maza, French, & Aschwanden, 1973; McNab, 1963; Shier, 2008). Sets of 49 traps were arranged in 7 x 7 grids with 6.25 m spacing. We used Sherman live-traps (H.B. Sherman Traps, Inc., Tallahassee, FL, U.S.A.) with modified shortened doors to avoid tail injury. Traps were opened and baited with millet seed (microwaved for 5 min to prevent germination) before dusk and checked three times during the night to quantify early (within 2 hours of dusk), middle of the night, and late (within 2 hours of dawn) activity. The exact times of trap-checks varied seasonally as the length of night changed. Traps were closed during the late check to prevent animals from entering during the day. We conducted 3 consecutive nights of trapping

each month in the week surrounding the new moon to minimize variability in foraging activity related to the lunar cycle (Prugh & Golden, 2014).

All animals were individually tagged for identification. We used uniquely numbered ear tags for *Dipodomys simulans*, *Dipodomys stephensi*, *Peromyscus maniculatus* and *Peromyscus eremicus* (Monel 1005-1, National Band and Tag Co., Newport, KY). For species with small ears (*Perognathus longimembris brevinasus*, *Chaetodipus fallax*, *Reithrodontomys megalotis*) we injected visible implant elastomer (VIE- Northwest Marine Technology, Inc., Shaw Island, WA) in unique color combinations just under the skin along the side of the tail (Shier, 2008). These permanent marks were visible under a black light on subsequent captures. The first time each individual was trapped every month we recorded species, unique ID, sex, weight, reproductive condition, and trap location. For all recaptures within a month, we recorded ID and trap location. This work was carried out under protocols approved by the Institutional Animal Care and Use Committee of San Diego Zoo Global (protocol number 15-002).

We conducted habitat surveys at all of the trap locations May-June 2016 following protocol designed by USGS (Brehme, Clark, Burlaza, & Fisher, 2016) to determine whether species differ in their utilization of microhabitat features. Within a 6 x 6 m square centered on the trap location, we visually surveyed the ground layer (<10cm height) and estimated the percent cover of open ground (bare, exposed soil including sandy patches, duff/disarticulated forbs, dirt roads), woody debris/leaf litter (including dead shrubs where they touch the ground, fallen leaves, broken sticks of shrubs, but not disarticulated forbs), forbs (including both live and dead forbs attached to the ground) and non-native grass (no native grasses were present). We also surveyed the shrub layer and visually estimated the percent of the plot covered by shrubs at crown height.

We collected soil samples from 5 locations (at the centrally located trap, and the second trap in from each of the four corners) on each grid and conducted soil texture analyses. We scraped off the top layer of organic material, used a sharp hand trowel to cut down to 8 cm and collected 100 g of soil. We determined the percentage of sand, clay, and silt in each of our samples using the Bouyoucos Hydrometer Method (Gee & Bauder, 1986).

For each of the 44 trap locations (pixels) on a grid where we did not collect soil, we calculated the weighted distance from the center of each pixel (i) to each of the 5 soil sample points (j) using the equation

$$p_{ij} = \frac{(\frac{1}{d_{ij}})^2}{\sum_j (\frac{1}{d_{ij}})^2}$$

where  $d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$  and x and y represent coordinates of each pixel. The weighted distance was then multiplied by the measured value for sand, clay, and silt for each censused point, resulting in a composite value for each of the remaining 44 points on the grid.

## ***Data Analysis***

### **Spatial niche use**

To test whether species segregate or aggregate in space, we analyzed species co-occurrence patterns at trap locations on each of 8 survey grids over 4 seasons (Fall: August-October; Winter: November-January; Spring: February-April; Summer: May-July). We constructed presence-absence matrices with species ( $n = 3-6$ ) as rows and trap location ( $n = 49$ ) as columns. A total of 32 matrices of grid-seasons (8 grids x 4 seasons) were assessed. We evaluated species co-occurrence patterns using the C-score (Stone & Roberts, 1990), which



measures the number of ‘checkerboard units’ of all species pairs in an assemblage. A checkerboard unit is calculated for species pair AB by

$$C_{AB} = (r_A - S)(r_B - S)$$

where  $r_A$  is the row total for species A,  $r_B$  is the row total for species B, and S is the total number of ‘sites’ (e.g. trap locations) that contain both A and B. Species that always occur together (complete aggregation) will have a C-score of zero. The greater the segregation of species, the larger the C-score will be, to a maximum of  $r_A r_B$  (complete segregation). For each grid-season pairwise C-scores were calculated for each species pair and then averaged over all possible pairs of species in the assemblage to find a community C-score. Observed community C-scores were compared to average community C-scores generated from 5000 randomized matrices. Null assemblages were created in EcoSimR (Gotelli, Hart, & Ellison, 2015) using a fixed-fixed model (SIM9). This algorithm preserves the number of occurrences of each species (row totals) and the number of species in each sample (column totals) in the observed data for all the null (simulated) communities, and is robust to both type I and type II errors (Gotelli, 2000). If species are partitioning their spatial activity, then the observed community C-score should be larger than expected by chance (i.e. larger than the scores generated from the null assemblage). If species are aggregating their spatial activity, then the observed community C-score should be smaller than expected by chance (i.e. smaller than the scores generated from the null assemblage).

We could not directly compare the community C-score of grid-seasons to one another, as they differed in the number of species present, thus we calculated the standard effect size (SES) of each grid-seasons. The SES reports the number of standard deviations the observed community C-score index is above or below the mean of the randomized assemblage to allow for a between-assemblage comparison (Gotelli & McCabe, 2002; Gurevitch, Morrow, Wallace, &

Walsh, 1992; Wittman et al., 2010). The SES is calculated as  $(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$ , where  $I_{\text{obs}}$  corresponds to the index for the observed assemblage,  $I_{\text{sim}}$  corresponds to the index for the null assemblages, and  $S_{\text{sim}}$  is the standard deviation of the null assemblages.

We found 8 of 32 grid-seasons were significantly different from the null expectation, and all had community C-scores larger than expected by chance. We identified the species pair(s) that contributed the most to these patterns of spatial niche partitioning. The community C-score is an average of all pairwise C-scores, thus we considered species pairs with C-scores in the 95<sup>th</sup> percentile (largest 5%) of all the pairwise combinations for that community as contributing the most to the significance of the C-score test, following Arrington et al. (2005) and Pickles et al. (2012).

### **Temporal activity patterns**

We determined whether species segregate or aggregate their annual (monthly) activity or diel (nightly) activity using null model analyses to examine the temporal overlap of species. We constructed matrices with species ( $n = 3-6$ ) as rows and month ( $n=12$ ) or time of night ( $n = 3$ ) as columns for each grid. Matrix entries were the total number of occurrences of each species during each sampling period (3 checks/night x 3 nights/month for annual activity; 3 nights/month x 3 months for nightly activity within each season) in each grid.

We used the Czekanowski index (Feinsinger, Spears, & Poole, 1981), which quantifies the area of intersection of two resource utilization (e.g. time of night) histograms for a pair of species. It is a symmetrical index that ranges from 0 (no overlap, or complete segregation) to 1 (complete overlap, or aggregation) and is calculated for each species pair and then averaged over

all possible pairs of species in the assemblage. For species 1 and 2 the Czekanowski index is defined as

$$O_{12} = O_{21} = 1 - 0.5 \left( \sum_{i=1}^n |p_{i1} - p_{i2}| \right)$$

where  $p_{i1}$  is the proportion of occurrences of species 1 in a time interval (early, middle, or late) out of all times it was found during the sampling period.

The average pairwise niche overlap was then compared to the average calculated for randomized assemblages. Communities were randomized 1000 times using randomization algorithm 3 (RA3) in the niche overlap model in EcoSimR (Gotelli et al., 2015). RA3 retains the niche breadth of each species, or the relative degree of specialization, but randomly alters which particular resource categories (time of night) are used. Resource states were set as equiprobable, as time is assumed to be equally available to all species in the absence of species interactions. If species are partitioning the time of night in which they are active, then the niche overlap index should be smaller than expected by chance (i.e. smaller than the indices generated from the null assemblage). If species are aggregating their activity in a particular time of night, then the niche overlap index should be larger than expected by chance (i.e. larger than the indices generated from the null assemblage).

We calculated the standard effect size (SES) for each grid-season (see methods above) to allow for a between-assemblage comparison of nightly activity patterns.

In 7 of 32 grid-seasons, communities had index values that were significantly different and larger than the null expectation. We identified the species pair(s) that had index values in the 95<sup>th</sup> percentile (largest 5%) of all the pairwise combinations as strong contributors to the community-wide patterns of overlap in nightly activity.

## Factors that predict niche partitioning

To determine which factors predict spatial segregation patterns or nightly temporal aggregation, we used generalized linear models comparing the standard effect size (SES) of each grid-season. Large positive SES values indicate a high degree of spatial segregation or temporal aggregation, respectively. In our regression models for either spatial or temporal niche partitioning, SES was the dependent variable and grid, season, number of total captures of all species on a grid during each season, total number of *P. l. brevinasus* captures on each grid during each season, species richness (i.e. number of species present on a grid during each season), and a single species were included as fixed effects in full models. We calculated reduced models dropping out one at a time species, richness, *P. l. brevinasus* captures, or total captures, and used the change in Akaike information criterion ( $\Delta\text{AIC}$ ) to select the best fit model. If  $\Delta\text{AIC}$  was  $<2$ , we chose the simplest model. Models were fitted in R 3.3.2 (R Development Core Team 2016).

## Resource selection

We surveyed 5 habitat features and the soil texture of each pixel (see Data Collection) and used principal components analysis (PCA) to collapse the variables. This resulted in 2 principal components for habitat; habitat component 1 was correlated with increasing canopy cover and decreasing forb cover, and habitat component 2 correlated with increasing woody debris/leaf litter and decreasing open ground. Information about soil type was one-dimensional, so 1 component explained most of the variability in texture. Soil component 1 was correlated with increasing clay and silt and decreasing sand. We plotted habitat component 1 and habitat

component 2 for the locations where we trapped each species to compare the similarities and differences between habitat usage of each species.

We also analyzed the habitat features that were preferentially utilized (used relative to available) by each of the 6 species across our trapping grids during the summer (May-July) 2016. We considered each trapping grid as 49 non-overlapping pixels of habitat (3m x 3m) centered on the trap location. An animal captured in a trap was considered as using that pixel, and all 49 pixels were considered as available to each individual caught on a grid to minimize uncertainty due to sampling error (Benson, 2013). Although traps were baited, an animal would need to already be in the pixel in order to detect the bait, and traps were placed close together (6.25m spacing) to provide multiple options within the expected range of each individual. We could not determine if an animal visited another pixel but did not enter the trap, but this is similar to collared animals where locations are taken at set intervals with missing information on where the animal moves between those intervals, which is the most commonly used data for these analyses (Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010). We compared features of the used versus available pixels for each individual using a binomial generalized linear mixed model (GLMM). The dependent variable included the pixels used by each individual (n=1-26) and pixels available (n=49) to each individual.

Fixed effects included the ‘resource’ variables associated with each pixel- habitat PC1, habitat PC2, and soil PC1. Individual ID and grid number were included as a random effects. Models were fitted in R 3.3.2 (R Development Core Team 2016) with the ‘glmer’ function in the lme4 package (Bates et al., 2015).

### **Density of *P. l. brevinasus***

We calculated the density of each species using likelihood-based spatially explicit capture-recapture (SECR) models (Efford, 2017). SECR models have advantages over traditional closed-population models in that they address the uncertain edge effects and spatially heterogeneous detection probability caused by movement in conventional animal trapping (Efford, 2011). Spatially explicit capture-recapture models incorporate movement by assuming each individual has an activity center, which remains constant over the survey, and that the capture probability is a monotonically decreasing function of the distance between the activity center and the trap (Borchers & Efford, 2008). Our traps captured one animal at a time, thus did not act independently because an animal captured in one trap could not be captured in another trap until it was released. Although there is no established general adjustment for the per-trap probability of single-catch traps, density estimates using the multi-catch likelihood for single-catch data appear only slightly biased (Efford, Borchers, & Byrom, 2009), and we used the ‘single’ detector type in our analyses. For each species, we included the spatial location of each trap (detector) and the detection history (trapping record) of every individual. We considered May, June, and July as separate sessions, or independent sampling blocks. We used multi-session models to estimate density of each species over the summer season. We limited density calculations to summer months so we could test for effects of habitat features, which were only recorded in the summer, on *P. l. brevinasus* density.

## RESULTS

### Spatial niche use

Spatial niche overlap was less than expected during 8 of 32 grid-season trapping bouts (Table S1; Grid 1 Summer; Grid 4 Fall, Winter, Spring, Summer; Grid 6 Fall, Winter, Summer), indicating spatial niche partitioning between species. We investigated the features of the grid-seasons that were associated with spatial activity patterns described below in “Factors that predict spatial segregation and temporal aggregation”. We determined which of the 72 total species pairs had the highest contribution to the C-score for each community to assess whether any particular pairs were consistently strong in their patterns of spatial avoidance. In the 8 grid-seasons that exhibited niche partitioning, we identified 9 species pairs comprised of 6 different species (Table 2) that had the highest contribution to the overall C-scores (pairwise scores in the top 5% of all possible species pair interactions in each community), with *D. stephensi* represented in 7 of 9 pairs (Table 2).

### Temporal activity patterns

#### Annual Overlap

With all grids and times of night combined, the observed index of annual temporal overlap was greater than expected from a null distribution (Observed Czekanowski Index=0.735, 95% CI=0.69-0.73, lower-tail  $p=0.99$ , upper-tail  $p=0.1$ ; Figure 1), signifying that species are more similar in their patterns of monthly activity levels than expected by chance. We investigated the features of the grid-seasons that were associated with temporal activity patterns below in “Factors that predict spatial segregation and temporal aggregation”.

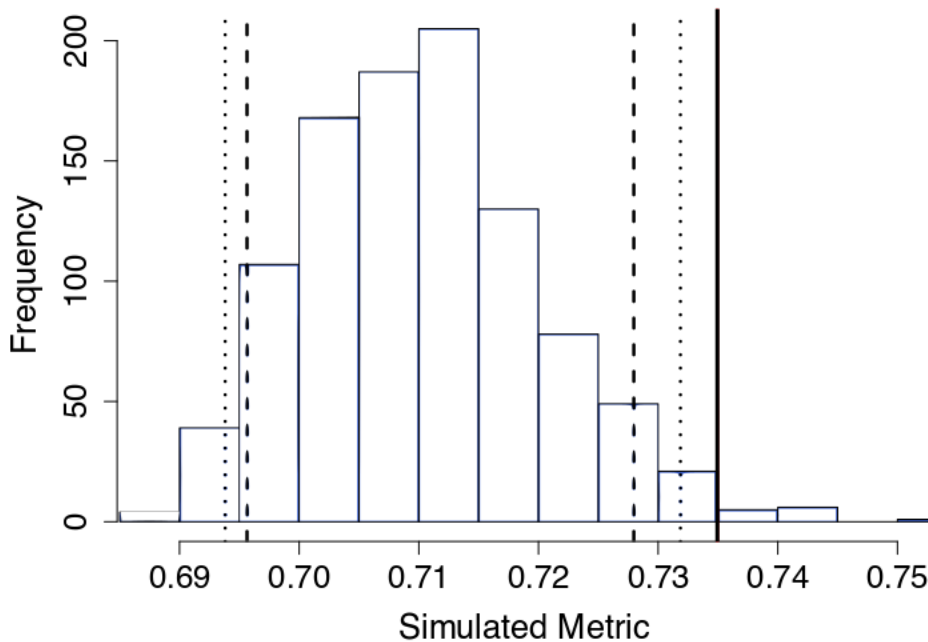


Figure 1. Histogram of 1000 simulated metric values of species' overlap in annual activity patterns. The solid vertical line indicates the observed metric for the field data. The pair of vertical long-dash lines indicate the 95% one-tailed cutpoints, and the short-dash lines indicate the 95% two-tailed cutpoints; the latter constitutes a proper 95% confidence interval for the null distribution.

### Nightly overlap

In 7 of 32 grid-season trapping bouts (Grid 1 Summer; Grid 2 Summer, Spring; Grid 4 Spring, Winter, Fall; Grid 6 Winter) the within-night temporal niche overlap was larger than expected (Table S2), indicating these species aggregated their activities throughout the night. There were no differences between the observed and expected measures of niche partitioning in the remaining trapping bouts. There were no consistent species pairs that drove the patterns of activity overlap. Out of 62 species pairs, 7 different combinations of 5 species contributed to the



highest pairwise scores (top 5% of all species pair interactions) in communities that demonstrated significant temporal aggregation (Table 2).

Table 2. Species pairs with the highest (95<sup>th</sup> percentile) contribution to overall community patterns of spatial partitioning (8 grid-seasons; 9 species pairs) or temporal aggregation (7 grid-seasons; 7 species pairs).

|                         | <i>D. stephensi</i> | <i>D. simulans</i> | <i>C. fallax</i> | <i>P. l. brevinasus</i> | <i>P. maniculatus</i> | <i>P. eremicus</i> |
|-------------------------|---------------------|--------------------|------------------|-------------------------|-----------------------|--------------------|
| <i>D. stephensi</i>     |                     | 2                  | 4                | 1                       |                       |                    |
| <i>D. simulans</i>      | 1                   |                    |                  |                         | 1                     |                    |
| <i>C. fallax</i>        | 1                   | 1                  |                  |                         |                       |                    |
| <i>P. l. brevinasus</i> |                     |                    | 1                |                         |                       | 1                  |
| <i>P. maniculatus</i>   | 1                   | 1                  | 1                |                         |                       |                    |
| <i>P. eremicus</i>      |                     |                    |                  |                         |                       |                    |

Spatial niche partitioning is shown above the diagonal and nightly temporal aggregation is shown below the diagonal. Values indicate the number of times a particular species pair had a pairwise C-score value (spatial niche partitioning) or Czekanowski Index score (temporal aggregation) in the 95<sup>th</sup> percentile of all pairwise combinations in each community (as per Arrington et al. 2005, Pickles et al. 2012).

### Factors that predict spatial segregation and temporal aggregation

The model that best fit the spatial segregation data included grid, season, total number of captures, total number of *P. l. brevinasus* captures, species richness, and *P. eremicus* (Table 3).

Spatial niche partitioning, indicated by large SES scores, was greatest in areas with high levels of

overall rodent activity and high levels of *P. l. brevinasus* activity (Table 4). Spatial niche partitioning was less likely to occur in areas where cactus mice, *P. eremicus*, were found (Table 4).

Temporal aggregation was best described by the model that included grid, season, total number of captures and total number of *P. l. brevinasus* captures (Table 3). Larger SES scores corresponded to temporal aggregation, and were positively associated with the total number of captures of all species (Table 4), indicating that increased rodent activity is associated with higher overlap of different species during similar times of night.

Table 3. Model selection results for spatial co-occurrence and temporal niche overlap.

| Dependent variable                | Model  | Resid. Df | Resid. Dev    | dAIC     | Weight      |
|-----------------------------------|--|-----------|---------------|----------|-------------|
| SES spatial co-occurrence scores  | Grid & season  | 27        | 697.57        | 15.2     | 0           |
|                                   | # total captures, grid & season  | 26        | 521.39        | 7.9      | 0.01        |
|                                   | # <i>P. l. brevinasus</i> captures, # total captures, grid & season  | 25        | 460.63        | 5.9      | 0.03        |
|                                   | Richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season                                | 24        | 455.48        | 7.6      | 0.01        |
|                                   | <i>P. l. brevinasus</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season      | 23        | 433.82        | 8        | 0.01        |
|                                   | <i>C. fallax</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season             | 23        | 429.38        | 7.7      | 0.01        |
|                                   | <i>D. simulans</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season           | 23        | 391.09        | 4.7      | 0.06        |
|                                   | <b><i>P. eremicus</i>, richness, # <i>P. l. brevinasus</i> captures, # total captures, grid &amp; season</b> | <b>23</b> | <b>337.73</b> | <b>0</b> | <b>0.6</b>  |
|                                   | <i>P. stephensi</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season          | 23        | 355.94        | 1.7      | 0.26        |
|                                   | <i>R. megalotis</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season          | 23        | 453.15        | 9.4      | 0.01        |
| SES temporal niche overlap scores | Grid & season  | 27        | 60.93         | 3.6      | 0.04        |
|                                   | # total captures, grid & season  | 26        | 55.47         | 2.6      | 0.07        |
|                                   | <b># <i>P. l. brevinasus</i> captures, # total captures, grid &amp; season</b>                               | <b>25</b> | <b>48.09</b>  | <b>0</b> | <b>0.26</b> |
|                                   | Richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season                                | 24        | 47.63         | 1.7      | 0.11        |
|                                   | <i>P. l. brevinasus</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season      | 23        | 46.60         | 3        | 0.06        |
|                                   | <i>C. fallax</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season             | 23        | 47.54         | 3.6      | 0.04        |
|                                   | <i>D. simulans</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season           | 23        | 46.02         | 2.6      | 0.07        |
|                                   | <i>P. eremicus</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season           | 23        | 43.02         | 0.4      | 0.21        |
|                                   | <i>D. stephensi</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season          | 23        | 45.99         | 2.6      | 0.07        |
|                                   | <i>R. megalotis</i> , richness, # <i>P. l. brevinasus</i> captures, # total captures, grid & season          | 23        | 46.59         | 3        | 0.06        |

SES (standard effect size) of spatial and temporal scores were used to allow for a between-assemblage comparison. Full models included grid, season, number of total captures of all species on a grid during each season, total number of *P. l. brevinasus* captures on each grid during each season, species richness (i.e. number of species present on a grid during each season), and a single species. AIC comparisons were made between models, and if  $\Delta AIC$  was

<2, we chose the simplest model. The best model for each dependent variable is identified with bold text.

Table 4. GLM results with standard effect size (SES) for spatial co-occurrence scores and temporal niche overlap scores as the dependent variables.

| Dependent variable                | Model term                                | Estimate      | SE           | t            | P-value      |
|-----------------------------------|---|---------------|--------------|--------------|--------------|
| SES spatial co-occurrence scores  | <b>Intercept</b>                          | <b>-15.56</b> | <b>5.20</b>  | <b>-2.99</b> | <b>0.01</b>  |
|                                   | Grid                                      | 0.84          | 0.42         | 2.02         | 0.06         |
|                                   | Season                                    | 1.08          | 2.03         | 0.53         | 0.60         |
|                                   | <b># <i>P. l. brevinasus</i> captures</b> | <b>-0.05</b>  | <b>0.02</b>  | <b>-2.18</b> | <b>0.04</b>  |
|                                   | <b># total captures</b>                   | <b>0.03</b>   | <b>0.01</b>  | <b>3.25</b>  | <b>0.004</b> |
|                                   | Richness                                  | 1.97          | 1.21         | 1.63         | 0.12         |
|                                   | <b><i>P. eremicus</i></b>                 | <b>-6.28</b>  | <b>2.22</b>  | <b>-2.83</b> | <b>0.01</b>  |
| SES temporal niche overlap scores | Intercept                                 | -0.94         | 1.26         | -0.75        | 0.46         |
|                                   | Grid                                      | 0.10          | 0.15         | 0.71         | 0.49         |
|                                   | Season                                    | 0.99          | 0.70         | 1.43         | 0.17         |
|                                   | # <i>P. l. brevinasus</i> captures        | -0.01         | 0.01         | -1.96        | 0.06         |
|                                   | <b># total captures</b>                   | <b>0.01</b>   | <b>0.003</b> | <b>2.26</b>  | <b>0.03</b>  |

Only the best models, based on  $\Delta AIC$ , are shown (see Table 2 for model selection results).

## Resource selection

We plotted each species' use of the habitat features represented in Habitat PC1 (increasing canopy cover and decreasing forb cover; Table 5) and Habitat PC2 (increasing leaf litter and decreasing open ground; Table 5) to compare the use of these features between species (Figure 2). Each point represents a trap location where that species was captured, and the values of Habitat PC1 and Habitat PC2 at that location. Ellipses indicate the 95% interval of use by each species, and are color-coded to match the points. Smaller ellipses show more restricted habitat use by some species (e.g. *D. stephensi* in purple and *D. simulans* in pink each have relatively small ellipses, and are more restricted in the habitat values of PC 1 that they use), while large

ellipses indicate usage of a wider variety of habitat features (e.g. *P. maniculatus* in orange spans a large range of values for PC1 and PC2). Overlap between the points/ellipses of different species indicate similar use of habitat features, and a lack of ellipse overlap highlights species that differ in the habitat features they utilize. *P. maniculatus* in orange overlaps with all the other species, as it has the least restricted usage of different habitat features. *D. stephensi* (purple) and *P. l. brevinasus* (green) have high overlap with one another, concentrating their activity in areas that are negative on PC 1, or have low shrub canopy cover and high forb cover. This also suggests that the presence of *D. stephensi* can indicate habitat that is highly suitable for translocated *P. l. brevinasus*, and vice versa for translocated *D. stephensi*. In areas with higher shrub cover (positive values of PC 1) three species cluster; *C. fallax* (grey), *D. simulans* (red), and *P. eremicus* (blue). Although *C. fallax* has slightly less restricted habitat usage (shown by a larger ellipse), these species may indicate high quality habitat for one another. Species that show no overlap, such as *D. stephensi* (purple) with either *D. simulans* (red) or *P. eremicus* (blue) differ the most in their habitat usage, with *D. stephensi* exclusively using areas with low shrub cover and the other two species utilizing areas of high shrub cover. This also suggests that the presence of *D. simulans* or *P. eremicus* would indicate low-quality areas to translocate *D. stephensi* into.

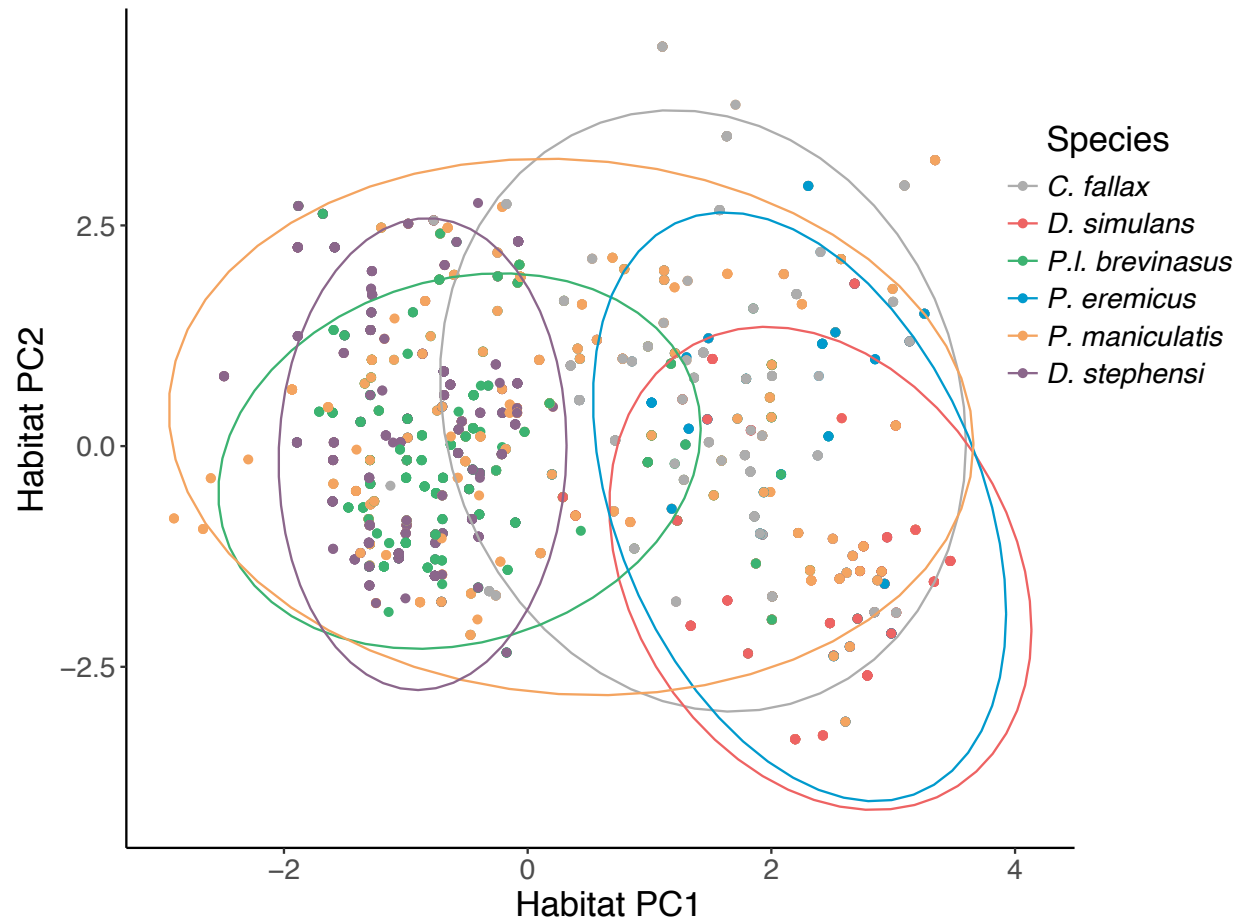


Figure 2. Values of Habitat PC1 and Habitat PC2 with 95% ellipses used by each species.

Positive values of Habitat PC1 indicate high shrub canopy cover relative to forb cover. Positive values of Habitat PC2 indicate high leaf litter/woody debris relative to open ground.

Table 5. Loadings of habitat features on the first two factors and loadings of soil features on the first factor and the total variance explained by the factors, from principal component analysis (bold indicates dominant loadings).

| Habitat feature     | Factor 1     | Factor 2     | Soil feature        | Factor 1     |
|---------------------|--------------|--------------|---------------------|--------------|
| Canopy cover        | <b>0.63</b>  | 0.03         | Sand                | <b>-0.60</b> |
| Forbs               | <b>-0.63</b> | -0.10        | Clay                | <b>0.56</b>  |
| Open ground         | 0.24         | <b>-0.67</b> | Silt                | <b>0.58</b>  |
| Leaf litter         | 0.25         | <b>0.67</b>  | Percent of variance | 92.38        |
| Grass               | -0.28        | 0.30         |                     |              |
| Percent of variance | 40.67        | 34.28        |                     |              |

Generalized linear mixed models (GLMM) of the used and available pixels for individuals of each species revealed which habitat features were not only used by each species (as presented in Figure 2), but utilized more or less relative to what was available to each species (Table 6). Here we include soil texture (Soil PC1; increases with increasing clay and silt and decreasing sand) in addition to Habitat PC1 and Habitat PC2. *P. l. brevinasus* used low canopy cover and higher forb cover (habitat component 1), and more leaf litter/woody debris than open ground (habitat component 2).

*C. fallax* and *D. simulans* utilized similar habitat- they showed a bias towards areas with high shrub canopy cover and low forb cover (habitat component 1), more open ground than woody debris/leaf litter (habitat component 2), and sandy soils with a low proportion of clay and silt (soil component 1) (Table 6).

*D. stephensi* preferentially utilized areas with low canopy cover and higher forb cover (habitat component 1), and more open ground than woody debris/leaf litter (habitat component 2) (Table 6).

*P. maniculatus* was found in habitat with more woody debris/leaf litter than open ground (habitat component 2) (Table 6). *P. eremicus* occurred in habitat pixels with high shrub canopy cover and low forb cover (habitat component 1) (Table 6).

Table 6. GLMM results for resource selection by each species.

| Species                 | Model term         | Estimate     | SE          | t            | P-value         |
|-------------------------|--------------------|--------------|-------------|--------------|-----------------|
| <i>P. l. brevinasus</i> | <b>Habitat PC1</b> | <b>-0.18</b> | <b>0.06</b> | <b>-3.09</b> | <b>0.002</b>    |
|                         | <b>Habitat PC2</b> | <b>0.12</b>  | <b>0.05</b> | <b>2.29</b>  | <b>0.02</b>     |
|                         | Soil PC1           | 0.03         | 0.06        | 0.53         | 0.59            |
| <i>C. fallax</i>        | <b>Habitat PC1</b> | <b>0.50</b>  | <b>0.06</b> | <b>8.37</b>  | <b>2e-16</b>    |
|                         | <b>Habitat PC2</b> | <b>-0.17</b> | <b>0.06</b> | <b>-2.90</b> | <b>0.004</b>    |
|                         | <b>Soil PC1</b>    | <b>-0.23</b> | <b>0.07</b> | <b>-3.29</b> | <b>0.001</b>    |
| <i>D. simulans</i>      | <b>Habitat PC1</b> | <b>0.52</b>  | <b>0.10</b> | <b>5.25</b>  | <b>1.54e-7</b>  |
|                         | <b>Habitat PC2</b> | <b>-0.26</b> | <b>0.09</b> | <b>-2.99</b> | <b>0.003</b>    |
|                         | <b>Soil PC1</b>    | <b>-0.18</b> | <b>0.08</b> | <b>-2.30</b> | <b>0.02</b>     |
| <i>D. stephensi</i>     | <b>Habitat PC1</b> | <b>-0.43</b> | <b>0.07</b> | <b>-6.21</b> | <b>5.43e-10</b> |
|                         | <b>Habitat PC2</b> | <b>-0.15</b> | <b>0.06</b> | <b>-2.49</b> | <b>0.01</b>     |
|                         | Soil PC1           | 0.01         | 0.08        | 0.06         | 0.95            |
| <i>P. maniculatus</i>   | Habitat PC1        | 0.00         | 0.04        | -0.10        | 0.92            |
|                         | <b>Habitat PC2</b> | <b>0.16</b>  | <b>0.05</b> | <b>3.29</b>  | <b>0.001</b>    |
|                         | Soil PC1           | 0.05         | 0.05        | 0.97         | 0.33            |
| <i>P. eremicus</i>      | <b>Habitat PC1</b> | <b>0.65</b>  | <b>0.10</b> | <b>6.45</b>  | <b>1.14e-10</b> |
|                         | Habitat PC2        | -0.18        | 0.10        | -1.81        | 0.07            |
|                         | Soil PC1           | 0.06         | 0.073       | 0.87         | 0.39            |

Habitat PC1 increases with increasing canopy cover and decreasing forb cover. Habitat PC2 increases with increasing leaf litter and decreasing open ground. Soil PC1 increases with increasing clay and silt and decreasing sand. Models also included random effects of grid and individual identity.

### Density of *P. l. brevinasus*

To help inform release site selection for the smallest and behaviorally subordinate species, we tested for a correlation between the density of *P. l. brevinasus* during the summer and any other species or any habitat features, but found no relationships (Table 7).

Table 7. GLM results for *P. l. brevinasus* density in relation to habitat features and heterospecifics

| Dependent variable              | Model term                    | Estimate | SE     | t     | P-value |
|---------------------------------|-------------------------------|----------|--------|-------|---------|
| <i>P. l. brevinasus</i> density | Intercept                     | -144.78  | 326.97 | -0.44 | 0.69    |
|                                 | Open ground                   | 4.93     | 5.10   | 0.97  | 0.41    |
|                                 | Woody debris/leaf litter      | 3.18     | 4.79   | 0.66  | 0.55    |
|                                 | Forb cover                    | -1.90    | -0.66  | 0.56  | 0.56    |
|                                 | Shrub canopy cover            | -3.99    | 2.80   | -1.43 | 0.25    |
| <i>P. l. brevinasus</i> density | Intercept                     | 32.90    | 29.44  | 1.12  | 0.38    |
|                                 | <i>C. fallax</i> density      | -1.12    | 3.62   | -0.31 | 0.79    |
|                                 | <i>D. simulans</i> density    | -0.55    | 2.10   | -0.26 | 0.82    |
|                                 | <i>D. stephensi</i> density   | 0.10     | 0.80   | 0.12  | 0.91    |
|                                 | <i>P. maniculatus</i> density | -0.78    | 1.64   | -0.48 | 0.68    |
|                                 | <i>P. eremicus</i> density    | 0.95     | 2.159  | 0.44  | 0.70    |

## DISCUSSION

We found evidence of spatial niche partitioning in a quarter of our grid-season trapping bouts. There was no clear seasonal pattern of spatial segregation, which was observed in all 4 seasons but on only 3 different grids. The factors that were associated with niche partitioning were the total number of captures of all species, the number of *P. l. brevinasus* captures, and either the absence of *P. eremicus* or the presence of *D. stephensi*, because the models containing each of these species had the lowest  $\Delta$ AIC scores that were within 2 of one another. *P. eremicus* and *D. stephensi* only co-occurred in 3 out of 32 grid-season trapping bouts during our study. Competition is more likely to occur at higher densities (Connell, 1983), thus it is not surprising that indices of spatial niche partitioning, which may function to minimize competitive interactions, are higher with an increasing number of captures, or greater activity in an area.

We identified nine species pairs that had the greatest contributions (identified as the 95<sup>th</sup> percentile of pairwise scores) to the overall patterns of niche partitioning in the 8 grid-seasons with significant spatial partitioning. *D. stephensi* was in 7 of these 9 pairs, suggesting this species



was an important contributor to observed patterns of spatial segregation. One possible explanation is that aggressive interactions between *D. stephensi* and the other species are driving these patterns of segregation. There is some evidence that *D. stephensi* is behaviorally dominant to *D. simulans* (Bleich & Price, 1995). The subordinate species might occupy less-preferred habitat when in sympatry with a dominant species (Glass & Slade, 1980), resulting in patterns of spatial niche partitioning. Alternatively, differences in habitat preferences, mediated through predation and/or foraging behavior, of sympatric species can result in the same patterns of spatial segregation in patchy habitat (Kotler, 1984; Thompson, 1982b). Our results show that *D. stephensi* occupy areas with low shrub cover relative to forb cover, and more open ground relative to woody debris and leaf litter. The three species that segregate their space use with *D. stephensi* have different patterns of microhabitat utilization. *C. fallax* and *D. simulans* both show a bias for high shrub cover relative to forb cover, and bare ground under the shrub canopy. *P. l. brevinasus* is similar to *D. stephensi* in its use of low shrub cover, but occupies areas with more woody debris and leaf litter relative to areas of bare ground. Similarly, *P. l. brevinasus* also exhibits spatial partitioning with *P. eremicus*, which differs in microhabitat use, inhabiting areas of higher shrub canopy cover. While observed patterns of spatial segregation could be due to differences in microhabitat preference rather than interference interactions, we cannot rule out that “preferences”, or patterns of utilization, have been influenced by the ghost of competition past (Connell, 1980), or that historic interference drove species to shift their habitat use to minimize niche overlap, subsequently adapting to this newer niche and appearing to “prefer” it. While we tried to vary the community composition, density, and habitat features between our 8 survey grids, a removal experiment would be the best way to determine whether interspecific interactions or differing habitat preferences drive spatial segregation between species.

There was greater aggregation in monthly activity patterns than expected by chance. This is consistent with research by O'Farrell (1974) who found that some species estivated while others did not, but there were no other clear patterns in seasonal activity. Although no *P. l. brevinasus* were trapped in January or February, when they were likely estivating (Bartholomew & Cade, 1957; Kenagy, 1973), other species also decreased activity in these months. Similarity in annual activity patterns may be due to similar thermal constraints (Albrecht & Gotelli, 2001; Daly, Behrends, Wilson, & Jacobs, 1992), or similar increase in activity and/or reproduction and higher densities in response to seasonal availability of shared food resources (Kelt, 1999; Meserve, 1976a; Reed, Kaufman, & Kaufman, 2006).

We found no evidence for temporal niche partitioning, and in 7 of 32 grid-season trapping bouts we observed patterns of temporal niche aggregation. There was no seasonal pattern of overlap in activity and no effect of grid or species richness. Total number of captures, a measure of higher activity levels, did correspond with increased nightly temporal overlap. These patterns are consistent with observations of ant communities, where species with similar thermal tolerances aggregated their activity patterns during the times of day that were not too hot or cold (Albrecht & Gotelli, 2001; Wittman et al., 2010), and there is some evidence of evolutionary constraints of temporal niche partitioning in rodents (Kronfeld-Schor & Dayan, 2003). An example of temporal niche partitioning between two species of desert gerbils (*Gerbillus allenbyi* and *G. pyramidum*) involves a subordinate species, *G. allenbyi*, that is a more efficient forager at low resource-densities shifting its activity to the later part of the night when in sympatry with the dominant *G. pyramidum*, who arrives at fallen seeds first and depletes the newly available resources (Ziv et al., 1993). There is little evidence that *P. longimembris* are more efficient foragers than larger, dominant species (Chock et al., in review; Reichman &

Oberstein, 1977), thus shifting foraging activity to a later part of the night after other species have depleted the seed resources may not be a viable strategy for coexistence.

There were no species-pairs that exhibited clear patterns of nightly temporal aggregation. *C. fallax* contributed strongly (95<sup>th</sup> percentile of pairwise overlap scores) in 4 of the 7 instances of temporal aggregation, but overlapped with 4 different species. Temporal aggregation could provide benefits through a dilution effect, where each individual has a lower probability of predation as the number of animals above ground and active (i.e. group size of all potential prey) increases (Foster & Treherne, 1981), which would be consistent with our observation that overlap in activity patterns was correlated with increasing activity of all species.

We expected to find the strongest patterns of spatial and/or temporal niche portioning between *P. l. brevinasus* and the species previously identified as behaviorally dominant and more efficient cache pilferers, *D. simulans* and *C. fallax* (Chock et al., 2018; Chock et al., in review). However, we found no evidence of spatial partitioning between these species, and on one grid-season *P. l. brevinasus* aggregated in nightly activity with *C. fallax*. Overall we found little evidence that spatial or temporal niche partitioning are mechanisms by which *P. longimembris* persists in communities with these dominant competitor species. *D. stephensi* and *P. eremicus*, the species that showed strong spatial niche partitioning with *P. longimembris*, were not included in our previous study of interspecific aggression (Chock et al., 2018), thus we cannot determine whether behavioral interactions or differences in habitat preference drive these patterns of spatial niche partitioning. We did find that each species varies in their preferentially utilized microhabitat characteristics of shrub cover, forb cover, open ground, woody debris/leaf litter, and to a lesser extent soil texture.

Interspecific aggression may result in reduced densities of a subordinate species, regardless of niche partitioning. Removal experiments in similar rodent communities found that when all *Dipodomys* were excluded from fenced plots, the density of the smaller species, including *Perognathus*, significantly increased (Brown & Munger, 1985; Valone & Brown, 1995). Here we found no relationship between *P. l. brevinasus* densities and heterospecific densities across our 8 grids during the summer months, although we acknowledge this is a small sample size as grids differed in their species richness and community composition.

Our findings elucidated habitat use in the presence of heterospecifics, but do not provide strong evidence that spatial or temporal niche partitioning cause a subordinate species to occupy a smaller realized niche in sympatry with dominant species. *D. stephensi* exhibited the strongest spatial niche partitioning of the six species, but as one of the largest, and therefore probably a dominant species, this is likely due to strong preferences of *D. stephensi* for low shrub cover, high forb cover, and more open ground relative to leaf litter/woody debris. This habitat utilization is consistent with previous observations (Bleich & Price, 1995; O'Farrell & Uptain, 1987; Price, Longland, & Goldingay, 1991), and provides clear habitat management strategies and criteria for translocation release-site selection. *C. fallax* disproportionately utilized habitat with high shrub canopy cover and low forb cover, more open ground than woody debris/leaf litter, and sandy soils with a low proportion of clay and silt. *P. l. brevinasus* used low canopy cover and higher forb cover, and more leaf litter/woody debris than open ground. These findings are not entirely consistent with generalizations that divergence in anti-predator behavior and foraging efficiency drives predictable differences between bipedal species (kangaroo rats; *Dipodomys*) and quadrupedal species (pocket mice; *Chaetodipus* and *Perognathus*) in utilization of shrub cover (Daly, Jacobs, Wilson, & Behrends, 1992; Kotler, 1984; Price, 1978; Thompson,

1982a). This highlights the need for translocations and reintroductions to consider the needs of the focal species within the community composition of the release site.

Taken together with previous findings that *P. longimembris* are behaviorally subordinate to larger species (Chock et al., 2018) and no evidence to suggest they offset costs of interspecific aggression through pilfering the caches of larger species (Chock et al., in review), these results can be informative for translocations and reintroductions of Los Angeles pocket mice (*P. l. brevinasus*) and Pacific pocket mice (*P. l. pacificus*). During the early survival and establishment phases of reintroduction, reducing densities of larger, dominant species through exclusionary fencing can benefit *P. longimembris* by minimizing aggressive interactions which may displace them from establishing optimal burrow and foraging sites. Our study of intact communities suggests that none of the heterospecifics has a negative effect on *P. longimembris* densities, and thus, during the later growth and regulation phases of a reintroduction, fencing can be removed as resident pocket mice will be able to persist without active management of competitor species. We recommend that managers select or modify reintroduction sites to contain the microhabitat features that are preferentially utilized by *P. longimembris*. These measures will help reestablish pocket mice into diverse rodent communities, similar to those they naturally occur in, while taking into account the unique challenges faced by small population of released animals during different stages of a translocation.

## SUPPLEMENTARY MATERIAL

| Grid | Season | Observed Index | Lower 95% CI | Upper 95% CI | Lower-tail P | Upper-tail P | SES          |
|------|--------|----------------|--------------|--------------|--------------|--------------|--------------|
| 1    | Summer | 93.70          | 82.30        | 90.80        | 0.99         | <b>0.00</b>  | <b>3.73</b>  |
| 1    | Spring | 92.20          | 89.60        | 97.80        | 0.44         | 0.58         | -0.31        |
| 1    | Winter | 57.50          | 54.00        | 63.00        | 0.20         | 0.84         | -0.65        |
| 1    | Fall   | 65.50          | 61.90        | 71.60        | 0.48         | 0.54         | -0.19        |
| 2    | Summer | 77.80          | 74.93        | 81.74        | 0.56         | 0.46         | 0.03         |
| 2    | Spring | 82.83          | 82.50        | 87.67        | 0.10         | 0.95         | -1.24        |
| 2    | Winter | 48.33          | 46.50        | 57.17        | 0.31         | 0.70         | -0.58        |
| 2    | Fall   | 96.00          | 95.10        | 100.10       | 0.21         | 0.82         | -0.88        |
| 3    | Summer | 43.00          | 40.33        | 51.00        | 0.73         | 0.39         | 0.18         |
| 3    | Spring | 64.67          | 64.00        | 76.00        | 0.38         | 0.89         | -0.89        |
| 3    | Winter | 19.67          | 19.67        | 29.67        | 0.70         | 1.00         | -0.42        |
| 3    | Fall   | 46.33          | 46.33        | 51.00        | 0.39         | 1.00         | -0.75        |
| 4    | Summer | 125.00         | 115.40       | 122.40       | 1.00         | <b>0.00</b>  | <b>3.62</b>  |
| 4    | Spring | 95.10          | 77.20        | 83.60        | 1.00         | <b>0.00</b>  | <b>9.42</b>  |
| 4    | Winter | 171.67         | 130.67       | 136.83       | 1.00         | <b>0.00</b>  | <b>23.13</b> |
| 4    | Fall   | 120.10         | 106.10       | 114.50       | 1.00         | <b>0.00</b>  | <b>4.81</b>  |
| 5    | Summer | 66.00          | 60.00        | 73.33        | 0.83         | 0.43         | 0.51         |
| 5    | Spring | 110.67         | 106.00       | 117.33       | 0.77         | 0.31         | 0.32         |
| 5    | Winter | 121.00         | 121.00       | 135.00       | 0.10         | 1.00         | -1.23        |
| 5    | Fall   | 67.83          | 66.83        | 75.00        | 0.16         | 0.84         | -0.80        |
| 6    | Summer | 129.10         | 121.80       | 128.20       | 0.99         | <b>0.01</b>  | <b>2.88</b>  |
| 6    | Spring | 103.83         | 100.50       | 109.67       | 0.58         | 0.46         | -0.01        |
| 6    | Winter | 142.00         | 122.67       | 128.00       | 1.00         | <b>0.00</b>  | <b>12.57</b> |
| 6    | Fall   | 80.07          | 74.13        | 78.20        | 1.00         | <b>0.00</b>  | <b>4.24</b>  |
| 7    | Summer | 108.00         | 106.67       | 118.67       | 0.20         | 0.89         | -0.79        |
| 7    | Spring | 60.33          | 59.00        | 68.00        | 0.48         | 0.81         | -0.66        |
| 7    | Winter | 41.33          | 39.00        | 44.67        | 0.83         | 0.33         | 0.91         |
| 7    | Fall   | 30.83          | 30.50        | 36.00        | 0.35         | 0.74         | -0.85        |
| 8    | Summer | 44.33          | 44.00        | 50.67        | 0.36         | 0.80         | -0.84        |
| 8    | Spring | 37.33          | 37.33        | 37.33        | 1.00         | 1.00         | 0.00         |
| 8    | Winter | 66.00          | 60.67        | 69.00        | 0.93         | 0.10         | 1.45         |
| 8    | Fall   | 18.00          | 18.00        | 23.33        | 0.57         | 1.00         | -0.72        |

Table S1. Spatial niche partitioning C-score results for all grid-seasons. Observed Index is the C-score value for the community present in each grid-season. Confidence intervals are the 95% two-tailed cutpoints for the null distribution generated from 5000 simulations. P-values indicate whether the observed index fell beyond the lower or upper confidence intervals. SES is the standard effect size, or the number of standard deviations the observed community C-score index is above or below the mean of the randomized distribution. Significant values are bolded.

| Grid | Season | Observed Index | Lower 95% CI | Upper 95% CI | Lower-tail P | Upper-tail P | SES         |
|------|--------|----------------|--------------|--------------|--------------|--------------|-------------|
| 1    | Summer | 0.96           | 0.89         | 0.94         | 1.00         | <b>0.00</b>  | <b>4.11</b> |
| 1    | Spring | 0.87           | 0.86         | 0.91         | 0.34         | 0.67         | -0.59       |
| 1    | Winter | 0.93           | 0.92         | 0.95         | 0.60         | 0.41         | 0.07        |
| 1    | Fall   | 0.83           | 0.82         | 0.87         | 0.24         | 0.77         | -0.87       |
| 2    | Summer | 0.92           | 0.86         | 0.91         | 1.00         | <b>0.00</b>  | <b>3.56</b> |
| 2    | Spring | 0.83           | 0.77         | 0.82         | 0.99         | <b>0.02</b>  | <b>2.95</b> |
| 2    | Winter | 0.95           | 0.93         | 0.96         | 0.94         | 0.07         | 1.81        |
| 2    | Fall   | 0.91           | 0.90         | 0.93         | 0.54         | 0.47         | -0.11       |
| 3    | Summer | 0.84           | 0.79         | 0.89         | 0.75         | 0.28         | 0.53        |
| 3    | Spring | 0.95           | 0.91         | 0.96         | 0.95         | 0.11         | 1.45        |
| 3    | Winter | 0.94           | 0.86         | 0.94         | 1.00         | 0.33         | 1.04        |
| 3    | Fall   | 0.91           | 0.90         | 0.92         | 0.45         | 0.61         | 0.16        |
| 4    | Summer | 0.87           | 0.83         | 0.89         | 0.89         | 0.12         | 1.26        |
| 4    | Spring | 0.90           | 0.81         | 0.88         | 1.00         | <b>0.00</b>  | <b>3.61</b> |
| 4    | Winter | 0.84           | 0.78         | 0.83         | 0.98         | <b>0.02</b>  | <b>1.80</b> |
| 4    | Fall   | 0.91           | 0.84         | 0.91         | 0.99         | <b>0.01</b>  | <b>2.93</b> |
| 5    | Summer | 0.62           | 0.62         | 0.70         | 0.35         | 1.00         | -1.25       |
| 5    | Spring | 0.92           | 0.72         | 0.92         | 1.00         | 0.06         | 2.40        |
| 5    | Winter | 0.93           | 0.88         | 0.94         | 0.90         | 0.14         | 1.24        |
| 5    | Fall   | 0.63           | 0.60         | 0.66         | 0.82         | 0.22         | 0.75        |
| 6    | Summer | 0.92           | 0.88         | 0.94         | 0.93         | 0.07         | 1.72        |
| 6    | Spring | 0.70           | 0.61         | 0.73         | 0.89         | 0.12         | 1.33        |
| 6    | Winter | 0.92           | 0.87         | 0.92         | 0.99         | <b>0.01</b>  | <b>2.64</b> |
| 6    | Fall   | 0.82           | 0.80         | 0.85         | 0.61         | 0.39         | -0.01       |
| 7    | Summer | 0.88           | 0.88         | 0.95         | 0.10         | 0.00         | -1.32       |
| 7    | Spring | 0.77           | 0.76         | 0.85         | 0.28         | 0.83         | -0.71       |
| 7    | Winter | 0.52           | 0.45         | 0.56         | 0.67         | 0.44         | 0.50        |
| 7    | Fall   | 0.58           | 0.51         | 0.65         | 0.75         | 0.27         | 0.47        |
| 8    | Summer | 0.79           | 0.75         | 0.87         | 0.90         | 0.13         | 1.37        |
| 8    | Spring | 0.57           | 0.48         | 0.57         | 1.00         | 0.06         | 1.73        |
| 8    | Winter | 0.84           | 0.84         | 0.89         | 0.68         | 1.00         | -0.69       |
| 8    | Fall   | 0.78           | 0.71         | 0.80         | 0.90         | 0.16         | 1.22        |

Table S2. Temporal niche partitioning Observed Index is the Czekanowski Index for the community present in each grid-season. Confidence intervals are the 95% two-tailed cutpoints for the null distribution generated from 1000 simulations. P-values indicate whether the observed index fell beyond the lower or upper confidence intervals. SES is the standard effect size, or the number of standard deviations the observed community C-score index is above or below the mean of the randomized distribution. Significant values are bolded.

## REFERENCES

- Albrecht, M., & Gotelli, N. J. (2001). Spatial and temporal niche partitioning in grassland ants. *Oecologia*, 126, 134–141. <https://doi.org/10.1007/s004420000494>
- Bartholomew, G. A., & Cade, T. J. (1957). Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. *Journal of Mammalogy*, 38(1), 60–72.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., ...  
Grothendieck, G. (2015). Package “lme4.”
- Benson, J. F. (2013). Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. *Methods in Ecology and Evolution*, 4(3), 244–251. <https://doi.org/10.1111/2041-210x.12006>
- 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.
- Borchers, A. D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64(2), 377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>
- Brehme, C. S., Clark, D. R., Burlaza, M. A., & Fisher, R. N. (2016). *Pacific Pocket Mouse Habitat Protocol*.
- Brown, J. H., & Harney, B. A. (1993). Population and community ecology of heteromyid rodents in temperate habitats. In H. H. Genoways & J. H. Brown (Eds.), *Biology of the Heteromyidae* (Special Pu, pp. 618–651). The American Society of Mammalogists.
- Brown, J. H., & Heske, E. J. (1990). Control of a desert-grassland transition by a keystone rodent



- guild. *Science*, 250(4988), 1705–1707. <https://doi.org/10.1126/science.250.4988.1705>
- Brown, J. H., & Munger, J. C. (1985). Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, 66(5), 1545–1563. Retrieved from doi:10.2307/1938017
- Carothers, J. H., & Jakšić, F. M. (1984). Time as a niche difference: the role of interference competition. *Oikos*, 42, 403–406.
- 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>
- Chock, R. Y., Grether, G. F., & Shier, D. M. (In review). No evidence that cache pilfering offsets costs of interspecific competition in a pocket mouse community.
- CNDDDB. (2017). *Special Animals List*.
- Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35(2), 131–138. <https://doi.org/10.2307/3544421>
- Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist*, 122(5), 661–696.
- Daly, M., Behrends, P. R., Wilson, M. I., & Jacobs, L. F. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour*, 44(1), 1–9. [https://doi.org/10.1016/S0003-3472\(05\)80748-1](https://doi.org/10.1016/S0003-3472(05)80748-1)
- Daly, M., Jacobs, L. F., Wilson, M. I., & Behrends, P. R. (1992). Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behavioral Ecology*, 3(2), 102–111.

- Efford, M. G., Borchers, D.L., & Byrom, A.E. (2009). Density estimation by spatially explicit capture – recapture: likelihood-based methods. In: D. L. Thompson, E. G. Cooch, & M. J. Conroy (eds) *Modeling Demographic Processes in Marked Populations* (pp. 255-269). Springer.
- Efford, M. G. (2011). Estimation of population density by spatially explicit capture – recapture analysis of data from area searches. *Ecology*, 92(12), 2202–2207.
- Efford, M. G. (2017). Package “ secr .”
- Feinsinger, P., Spears, E. E., & Poole, R. W. (1981). A simple measure of niche breadth. *Ecology*, 62(1), 27–32.
- Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S., & Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1550), 2233–44. <https://doi.org/10.1098/rstb.2010.0079>
- Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, 466–467.
- Gee, G. W., & Bauder, J. w. (1986). Particle size analysis. In A. Klute (Ed.), *Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods. Agronomy Monograph No. 9 (2ed)* (pp. 383–411). Madison, WI: American Society of Agronomy/Soil Science Society of America.
- Germano, D. J. (2010). *Survivorship of translocated kangaroo rats in the San Joaquin Valley, California* (Vol. 96).
- Germano, D. J., Saslaw, L. R., Smith, P. T., & Cypher, B. L. (2013). Survivorship and reproduction of translocated Tipton kangaroo rats in the San Joaquin Valley, California.

- Endangered Species Research*, 19, 265–276. <https://doi.org/10.3354/esr00470>
- 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(2), 358–370.
- Goldingay, R. L., Kelly, P. A., & Williams, D. F. (1997). The kangaroo rats of California: endemism and conservation of keystone species. *Pacific Conservation Biology*, 3(1), 47–60.
- Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81(9), 2606–2621.
- Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015). EcoSimR: Null model analysis for ecological data. <https://doi.org/10.5281/zenodo.16522>
- Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83(8), 2091–2096.
- Gurevitch, J., Morrow, L. L., Wallace, A., & Walsh, J. S. (1992). A Meta-Analysis of Competition in Field Experiments. *The American Naturalist*, 140(4), 539–572.
- Gutman, R., & Dayan, T. (2005). Temporal partitioning: an experiment with two species of spiny mice. *Ecology*, 86(1), 164–173.
- Heske, E. J., Brown, J. H., & Guo, Q. (1993). Effects of Kangaroo Rat Exclusion on Vegetation Structure and Plant Species Diversity in the Chihuahuan Desert. *Oecologia*, 95(4), 520–524.
- IUCN. (2013). *Guidelines for Reintroductions and Other Conservation Translocations*.
- Kay, F. R., & Whitford, W. G. (1978). The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in Southcentral New Mexico. *The American Midland Naturalist*, 99(2), 270–279.
- Kelt, D. A. (1999). Assemblage Structure and Quantitative Habitat Relations of Small Mammals along an ecological gradient in the Colorado Desert of southern California. *Oikos*, 22(6),

659–673.

Kelt, D. A. (2011). Comparative ecology of desert small mammals: a selective review of the past 30 years. *Journal of Mammalogy*, 92(6), 1158–1178. <https://doi.org/10.1644/10-MAMM-S-238.1>

Kenagy, G. J. (1973). Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology*, 54(6), 1201–1219.

Kotler, B. P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology*, 65(3), 689–701.

Kotler, B. P. (1985). Owl predation on desert rodents which differ in morphology and behavior. *Journal of Mammalogy*, 66(4), 824–828.

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, 34, 153–181.  
<https://doi.org/10.1146/132435>

Kronfeld-schor, N., Shargal, E., Haim, A., Dayan, T., Zisapel, N., & Heldmaier, G. (2001). Temporal partitioning among diurnally and nocturnally active desert spiny mice : energy and water turnover costs, 26, 139–142.

Llewellyn, J. B., & Jenkins, S. H. (1987). Patterns of niche shift in mice: Seasonal changes in microhabitat breadth and overlap. *The American Naturalist*, 129(3), 365–381.

Maza, B. G., French, N. R., & Aschwanden, A. P. (1973). Home range dynamics in a population of heteromyid rodents. *Journal of Mammalogy*, 54(2), 405–425.

McKnight, M. L. (2005). Phylogeny of the *Perognathus longimembris* species group based on mitochondrial cytochrome-b: how many species? *Journal of Mammalogy*, 86(4), 826–832.  
Retrieved from [https://doi.org/10.1644/1545-1542\(2005\)086\[0826:POTPLS\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)086[0826:POTPLS]2.0.CO;2)

- McNab, B. K. (1963). Bioenergetics and the determination of home range size. *The American Naturalist*, 97(894), 133–140.
- Meserve, P. L. (1976a). Food relationships of a rodent fauna in a California coastal sage scrub community. *Journal of Mammalogy*, 57(2), 300–319. Retrieved from <https://doi.org/10.2307/1379690>
- Meserve, P. L. (1976b). Habitat and resource utilization by rodents of a California coastal sage scrub community. *Journal of Animal Ecology*, 45(3), 647–666. Retrieved from doi: 10.2307/3573
- O’Farrell, M. J. (1974). Seasonal activity patterns of rodents in a sagebrush community. *Journal of Mammalogy*, 55(4), 809–823.
- O’Farrell, M. J. (1999). Translocation of the endangered San Bernardino kangaroo rat. *Transactions of the Western Section of the Wildlife Society*, 35, 10–14.
- O’Farrell, M. J., & Uptain, C. E. (1987). Distribution and aspects of the natural history of Stephens’ kangaroo rat *Dipodomys stephensi* on the Warner Ranch, San Diego Co., California. *The Wasmann Journal of Biology*, 45(1–2), 34–48.
- Price, M. V. (1978). The role of microhabitat in structuring desert rodent communities. *Ecology*, 59(5), 910–921.
- 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. *American Midland Naturalist*, 126(1), 172–186.
- Price, M. V, & Mittler, J. E. (2003). Seed-cache exchange promotes coexistence and coupled consumer oscillations: a model of desert rodents as resource processors. *Journal of Theoretical Biology*, 223(2), 215–231. [https://doi.org/10.1016/S0022-5193\(03\)00088-2](https://doi.org/10.1016/S0022-5193(03)00088-2)

- Price, M. V., Waser, N. M., & McDonald, S. (2000). Seed caching by heteromyid rodents from two communities: implications for coexistence. *Journal of Mammalogy*, 81(1), 97–106. Retrieved from [https://doi.org/10.1644/1545-1542\(2000\)081%3C0097:SCBHRF%3E2.0.CO;2%0A%0A](https://doi.org/10.1644/1545-1542(2000)081%3C0097:SCBHRF%3E2.0.CO;2%0A%0A)
- Prugh, L. R., & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, 83(2), 504–514. <https://doi.org/10.1111/1365-2656.12148>
- Reed, A. W., Kaufman, G. A., & Kaufman, D. W. (2006). Species richness-productivity relationship for small mammals along a desert-grassland continuum: differential responses of functional groups. *Journal of Mammalogy*, 87(4), 777–783.
- Reichman, O. J., & Oberstein, D. (1977). Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. *Ecology*, 58(3), 636–643.
- Reid, F. A. (2006). *Mammals of North America*. New York, NY: Houghton Mifflin Co.
- Schoener, T. W. (1982). The controversy over interspecific competition: despite spirited criticism, competition continues to occupy a major domain in ecological thought. *American Scientist*, 70(6), 586–595.
- Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, 21(2), 303–12. <https://doi.org/10.1111/j.1523-1739.2006.00627.x>
- Shier, D. M. (2008). Behavioral ecology and translocation of the endangered Pacific pocket mouse (*Perognathus longimembris pacificus*) for the period January 2007 - December 2007. *San Diego Zoo Report*, 1–57.
- Shier, D. M., Leivers, S., King, S., Chock, R. Y., & Montagne, J. P. (2016). *Captive breeding*,

- anti-predator behavior and reintroduction of the Pacific pocket mouse (Perognathus longimembris pacificus) 2014-2016.*
- Shier, D. M., & Swaisgood, R. R. (2012). Fitness costs of neighborhood disruption in translocations of a solitary mammal. *Conservation Biology*, 26(1), 116–23.  
<https://doi.org/10.1111/j.1523-1739.2011.01748.x>
- Stone, L., & Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia*, 85(1), 74–79.
- Thompson, S. D. (1982a). Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. *Ecology*, 63(5), 1303–1312.
- Thompson, S. D. (1982b). Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. *Ecology*, 63(5), 1313–1321.
- Valone, T. J., & Brown, J. H. (1995). Effects of competition, colonization, and extinction on rodent species diversity. *Science*, 267(5199), 880–883.
- Vandergast, A. G., Bohonak, A. J., Weissman, D. B., & Fisher, R. N. (2007). Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: Phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: Stenopelmatus). *Molecular Ecology*, 16(5), 977–992.  
<https://doi.org/10.1111/j.1365-294X.2006.03216.x>
- Wang, T., & Shier, D. (2017). *Translocation of the endangered San Bernardino kangaroo rat (Dipodomys merriami parvus) for the period January 2012-June 2017.*
- Williams, D. F., Germano, D. J., & Tordoff, W. I. (1993). *Population studies of endangered kangaroo rats and blunt-nosed leopard lizards in the Carrizo Plain Natural Area, California*. Sacramento, CA.

- Wittman, S. E., Sanders, N. J., Ellison, A. M., Jules, E. S., Ratchford, J. S., & Gotelli, N. J. (2010). Species interactions and thermal constraints on ant community structure. *Oikos*, 119, 551–559. <https://doi.org/10.1111/j.1600-0706.2009.17792.x>
- 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.