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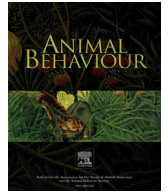## Authors

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Publication Date

DOI

Peer reviewed

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

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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.

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).

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

*Chaetodipus fallax were infrequently found in Meserve's study area and were not included in these comparisons.
[1] Average body size measures taken from Reid (2006).
[2] Time since most recent common ancestor (TMRCA) shared with P. longimembris in millions of years.
[3] 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 nonnative 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 eartags 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* × *C. fallax*; $N = 48$ *P. l. brevinasus* × *D. simulans*; $N = 48$ *P. l. brevinasus* × *P. maniculatus*; $N = 2$ *P. l. brevinasus* × *R. megalotis*; $N = 24$ *P. l. pacificus* × *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 × 61 × 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' (thrusted 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 (ΔAIC) 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 overdispersed 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 (ΔAIC) 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
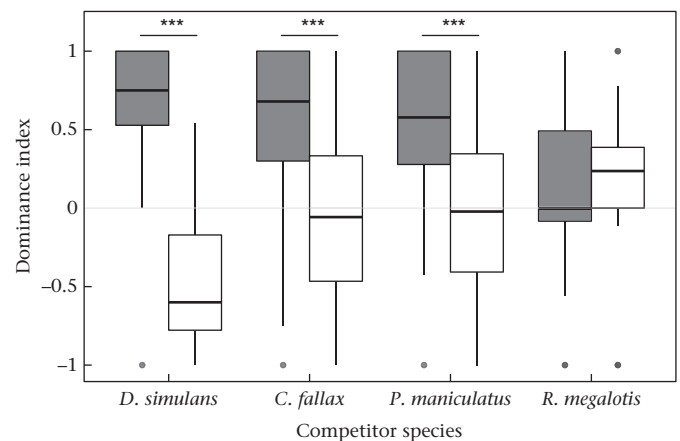

Figure 1. Dominance indices for little pocket mice (*P. longimembris*) and the four competitor species with which they were paired in dyadic encounters. Competitor species are grouped by family and ordered by body size (larger to smaller). The dominance index ranges from 1 (most dominant) to −1 (most 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
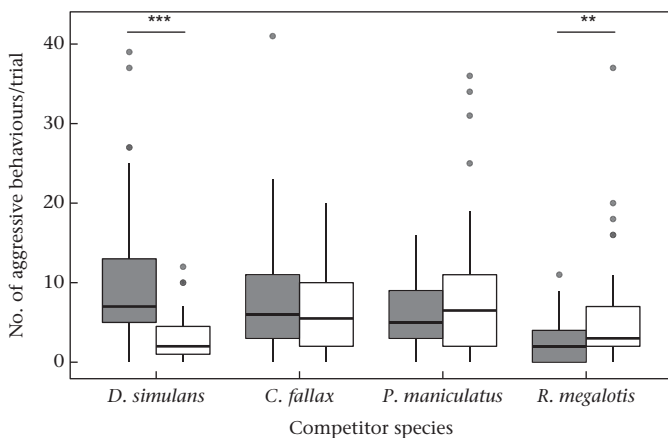

Figure 2. Aggression rates of little pocket mice (*P. longimembris;* open bars) and the four competitor species with which they were paired in 5 min dyadic encounters (grey bars). Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box plot definition.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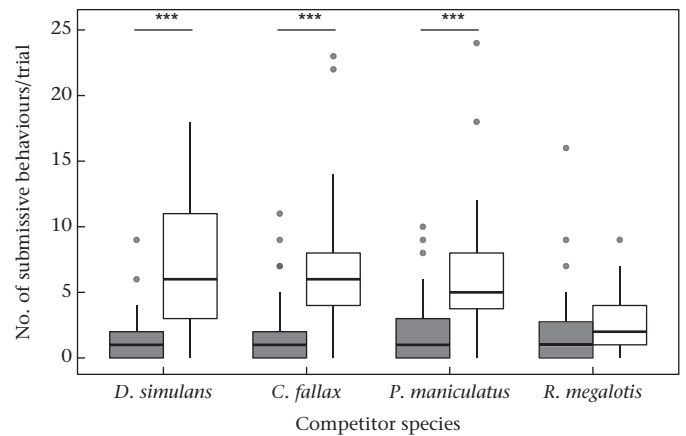

Figure 3. Submission rates of little pocket mice (*P. longimembris;* open bars) and the four competitor species with which they were paired in 5 min dyadic encounters (grey bars). Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box plot definition.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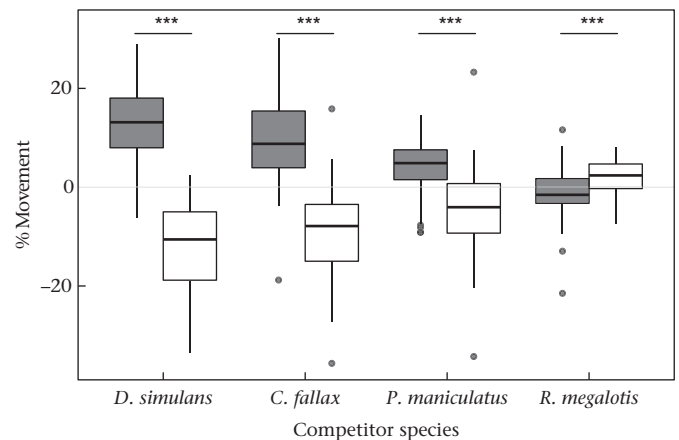

Figure 4. Average distance that each animal moved towards or away from its opponent, as a percentage of total movement. Positive values indicate pursuit while negative values indicate avoidance. Competitor species are grouped by family and ordered by body size (larger to smaller). See Fig. 1 for box 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	*P. longimembris*	**Weight difference**	**−0.010**	**0.002**	**−4.689**	**6.06e−6**	**<0.001**
		PELO sex	0.146	0.083	1.753	0.082	0.184
		Opponent sex	−0.131	0.084	−1.569	0.119	0.206
		PELO resident status	−0.044	0.083	−0.528	0.598	0.676
	Competitors	**Weight difference**	**0.006**	**0.002**	**2.875**	**0.005**	**0.024**
		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
Aggressive behaviour	*P. longimembris*	**Weight difference**	**−0.020**	**0.004**	**−4.612**	**3.98e−6**	**<0.001**
		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
		TMRCA	**−0.014**	**0.005**	**−2.921**	**0.003**	**0.024**
		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
Submissive behaviour	*P. longimembris*	Weight difference	0.002	0.003	0.446	0.655	0.710
		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
		PELO resident status	−0.068	0.121	−0.559	0.576	0.676
	Competitors	Weight difference	−0.011	0.005	−2.195	0.028	0.105
		PELO sex	**0.568**	**0.199**	**2.853**	**0.004**	**0.024**
		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 ΔAIC, 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 territorially 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

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.

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