



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.

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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, & Piiironen, 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 <i>P. longimembris</i> ² (TMRCA)	Diet overlap with <i>P. longimembris</i> ³	Habitat overlap with <i>P. longimembris</i> ³
Family: Heteromyidae					
	<i>P. longimembris</i> Pacific pocket mouse (<i>P. l. pacificus</i>) Los Angeles pocket mouse (<i>P. l. brevinasus</i>)	Weight: 6–9 g Body length: 50–70 mm Tail length: 60–85 mm	—	—	—
	<i>Chaetodipus fallax</i> San Diego pocket mouse	Weight: 14–26 g Body length: 70–91 mm Tail length: 105–120 mm	26.5	*	*
	<i>Dipodomys simulans</i> 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					
	<i>Peromyscus maniculatus</i> Deer mouse	Weight: 15–29 g Body length: 80–109 mm Tail length: 77–106 mm	65.3	33%	Horizontal: 10–35% Vertical: 95%
	<i>Reithrodontomys megalotis</i> 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).

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