Note

Cache Pilfering in a Granivore Guild: Implications for Reintroduction Management

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ABSTRACT Reintroduction programs that release endangered species back into areas from which they have been extirpated 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 granivorous species in this foraging guild compete for seeds exploitatively and through direct interference interactions, and pocket mice are 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 post-release 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. The presence of other members of the seed-foraging guild, however, could have a net benefit for pocket mice, if the pocket mice pilfer from the other species' seed caches more than the other species pilfer from their caches. To test the frequency of cache pilfering between species, we conducted a field experiment with fluorescent dyed seeds. Two of 10 pocket mice pilfered from heterospecifics, but only 1 of 33 heterospecifics pilfered from pocket mice. In a field-enclosure experiment, we could not conclude that any of the 4 species tested used heterospecific scent to find (or avoid) seed caches, and pocket mice were less efficient in pilfering from artificial caches, recovering fewer seeds than the larger species. We did not find strong evidence that Pacific pocket mice benefit from living in sympatry with larger, dominant species. Although further research is needed to elucidate the relationship between heterospecific density and the prevalence of cache pilfering, a conservative reintroduction approach would be to select receiver sites with low densities of known competitors to benefit pocket mice during the critical post-release establishment phase. © 2019 The Wildlife Society.

KEY WORDS cache pilfering, interspecific competition, *Perognathus longimembris*, pocket mouse, reintroduction biology.

Reintroductions and translocations, the human-mediated movement of captive-born or wild animals to areas from which they have been extirpated, 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 and Swaisgood 2007), with success often measured by individual survival and reproduction in the months to years

following reintroduction (Griffith et al. 1989, Fischer and Lindenmayer 2000, Brichieri-Colombi and Moehrenschlager 2016). 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, Moehrenschlager 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 residents and reintroduced individuals have been documented to favor residents (Burns 2005).

Interventions to mitigate the negative effects of interspecific competition include temporarily reducing the density of competitors or selecting release sites with low densities of competitors (Moseby et al. 2011, Linklater et al. 2012, Shier et al. 2016). 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 (Stamps 1988, Reed and Dobson 1993, Parejo and Danchin 2004, Goodale et al. 2010) and the presence of other individuals (or their cues) at release sites can promote settlement, even in asocial species (Stamps and Swaisgood 2007, Shier and Swaisgood 2012). Another, untested, potential benefit of preserving community diversity is that introduced animals might benefit from the food caches of resident species at reintroduction sites (Price et al. 2000, 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 may be 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), it is possible that highly efficient primary foragers with large home ranges 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). It is unknown whether scent cues that are important for intra- and inter-specific communication (Randall 1987, Dempster and Perrin 1990, Arakawa et al. 2008) are also used in the discovery or decision making related to pilfering caches from other animals' territories.

We studied the natural caching and 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 and Wildlife Service [USFWS] 1998) at Dana Point Headlands and 3 sites within Marine Corps Base Camp Pendleton in Southern California, USA. No additional populations have been discovered since 1995 despite extensive surveys throughout the species' range (USFWS 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 (USFWS 1998).

Extant populations of Pacific pocket mice co-occur with deer mice (*Peromyscus maniculatus*) and California pocket mice (*Chaetodipus californicus*). Dulzura kangaroo rats (*Dipodomys simulans*) are present within the historical range of the Pacific pocket mouse, including potential reintroduction sites, and currently coexist with the Los Angeles pocket mouse (*P. l. brevinasus*), the sister subspecies of the Pacific pocket mouse. The 2 subspecies are geographically and phylogenetically close (McKnight 2005), are both the smallest rodents in their communities, and have similar behavioral interactions with sympatric species (Chock et al. 2018). Although not yet listed as endangered, the Los Angeles pocket mouse is a species of special concern in California, and translocations are being used as mitigation for development of their remaining habitat. Los Angeles pocket mice co-occur with deer mice, Dulzura kangaroo rats, San Diego pocket mice (*Chaetodipus fallax*), and western harvest mice (*Reithrodontomys megalotis*). All of these species are nocturnal, solitary, occupy the same areas (Meserve 1976*a*, *b*), have high dietary overlap (Brown and Lieberman 1973, Meserve 1976*a*), and to varying extents store seasonally available seeds in caches either inside the burrow (larder hoards) or in shallow pits (scatter hoards) in their foraging ranges (Eisenberg 1962, Leaver and Daly 2001, Vander Wall et al. 2001; Table 1). Scatter-hoarded seeds are vulnerable to pilfering by any individual that comes across them. Larder-hoarded seeds are typically more defensible, but instances of individuals other than the resident leaving a burrow with pilfered seeds have been documented (Daly et al. 1992, Jenkins and Breck 1998). Because of their small burrow entrance size, little pocket mouse larder hoards are probably difficult for larger rodents to access (Jenkins and Breck 1998), but their scatter hoards would be susceptible to pilfering.

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 reported that little pocket mice of both subspecies are behaviorally subordinate to all larger species (Chock et al. 2018) and suggested that temporary competitor exclusion could be advantageous for reintroduced populations. These species, however, naturally coexist and positive effects from heterospecifics at a release site have not yet been considered.

Through a series of captive and field studies, we determined the susceptibility of Pacific pocket mice to heterospecific pilfering, compared rates of pilfering between species, and assessed whether the animals use heterospecific scent to find or avoid scatter hoards. Our primary study objective was to evaluate whether little pocket mice benefit from the presence of heterospecifics through an asymmetry in cache pilfering, which could affect management recommendations for future reintroductions and translocations of both subspecies.

Table 1. Descriptions of each species and their body size, home range size, and caching behavior. We included some values for closely related species, which are listed in the footnotes with references for all data. P. L. Meserve calculated overlap in diet and habitat between Pacific pocket mice and each other species using year-round trapping for a suite of species, including 4 of our focal species. Meserve ([1976b]) assessed diet overlap using fecal microscopy and we calculated the median overlap from his 9-month study. Meserve ([1976a]) measured horizontal habitat use with live-traps and vertical habitat use with smoked track cards, then quantified habitat overlap over 4 seasons in 1 year. California pocket mice were found infrequently in Meserve's study area and were not included in these comparisons.

	Body size[a]	Diet overlap with Pacific pocket mice (%)[b]	Habitat overlap with Pacific pocket mice (%)[c]	Home range size (ha)	Caching behavior
Family: Heteromyidae					
Pacific pocket mouse Los Angeles pocket mouse	Mass: 6–9 g Body length: 50–70 mm Tail length: 60–85 mm			0.018[d]	Larder hoard and scatter hoard[h]
San Diego pocket mouse California pocket mouse	Mass: 14–26 g Body length: 70–91 mm Tail length: 105–120 mm			0.55[e]	Primarily larder hoard, also scatter hoard[ii]
Dulzura kangaroo rat	Mass: 50–94 g Body length: 112–132 mm Tail length: 163–216 mm	93	Horizontal: 10–50 Vertical: 100	0.07[f]	Primarily scatter hoard, also larder hoard[ii]
Family: Cricetidae					
Deer mouse	Mass: 15–29 g Body length: 80–109 mm Tail length: 77–106 mm	33	Horizontal: 10–35 Vertical: 95	0.29[g]	Larder hoard and scatter hoard[j]

(Continued)

Table 1. (*Continued*)

	Body size[a]	Diet overlap with Pacific pocket mice (%)[b]	Habitat overlap with Pacific pocket mice (%)[c]	Home range size (ha)	Caching behavior
Western harvest mouse	Mass: 6–11 g Body length: 59–77 mm Tail length: 71–79 mm	45	Horizontal: 15–55 Vertical: 60–70	0.21[g]	May larder hoard[k] but minimal caching

[a] Reid (2006).
[b] Meserve ([1976*b*]).
[c] Meserve ([1976*a*]).
[d] Pacific pocket mouse range size, Shier ([2008]).
[e] Range size for long-tailed pocket mouse (*Chaetodipus formosus*), Maza et al. ([1973]).
[f] Range size for Stephens' kangaroo rat (*Dipodomys stephensi*), Price et al. ([1994]).
[g] Mcnab (1963).
[h] Pacific pocket mouse caching, this study.
[i] San Diego pocket mouse and Merriam's kangaroo rat (*Dipodomys merriami*) caching, Leaver and Daly ([2001]).
[j] Eisenberg (1962).
[k] Nowak (1999).

STUDY AREA

We studied caching behavior in captivity in the Pacific pocket mouse conservation breeding facility at the San Diego Zoo Safari Park in Escondido, California, USA, September 2016. We conducted field experiments using dyed seeds with Pacific pocket mice at Marine Corps Base Camp Pendleton (86 ha, 33.25° N, 117.39° W) May–August 2013 and Los Angeles pocket mice at the San Felipe Valley Wildlife Area (70 ha, 33.10° N, 116.53° W) April–September 2014. We conducted tests of scent use in cache pilfering with Los Angeles pocket mice at the San Jacinto Wildlife Area (244 ha, 33.13° N, 116.54° W) May–July 2015. All sites were in the Southern California/Northern Baja Coast ecoregion (Griffith et al. 2016) below 600 m elevation with essentially flat topographies. The vegetation community at all sites was primarily Coastal or Riversidean sage scrub and included fallow agricultural areas dominated by non-native grasses. Although wildlife areas were accessible to the public, the locations where we conducted our research were rarely visited. We conducted our field studies at night during spring, summer, and fall to coincide with peak rodent activity.

METHODS

Larder versus Scatter Hoarding

We quantified the relative larder- and scatter-hoarding behavior of Pacific pocket mice in captivity to assess the risk of pilfering by heterospecifics in the field. We maintained captive animals in a breeding facility in individual cages ($61 \times 28 \times 30$-cm plexiglass tanks) with 5 cm of sand substrate, a glass nest jar housed inside an opaque cup, and bedding material. Skylights provided natural light:dark cycles, and we used red lights 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 adult Pacific pocket mice (15 males, 5 females). At the start of the experiment, we removed all sand from the animals' cages, 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 commercial finch seed mix (white and red millet, canary, nyger, oat groats, rape, and flax seeds) for each animal, to be distributed over a 7-day period. Each night, we added approximately 3.1 g of seed mix to a petri dish in the front corner of each cage. We provided lettuce (5×5 cm every other night) to meet water needs. On the eighth day, we sifted the sand to recover seeds. We calculated the percent of seeds left in the feeding dish, on the surface of the sand, buried in the sand (scatter hoards), stored in the nest jar (larder hoards), or eaten (mass of the seeds recovered subtracted from initial mass of seeds provisioned). To test whether Pacific pocket mice use 1 caching strategy more than another, we used a Wilcoxon signed rank test to compare percentages of seeds stored in scatter hoards versus larder hoards. We conducted this analysis in R 3.5.1 (R Development Core Team 2018).

Frequency of Pilfering by Sympatric Species in the Field

We conducted field experiments to measure the frequency and direction of cache pilfering in the wild. We used Sherman live-traps (H.B. Sherman Traps, Tallahassee, FL, USA) with modified shortened doors to avoid tail injury. We placed traps across non-contiguous sites (50–100 traps/site, 8–20 sites/year). We opened traps and baited them with millet seed (microwaved for 5 min to prevent germination) between 1800 and 2000 and checked traps twice during the night at approximately 2200 and 0200. We closed traps during the 0200 check. We tagged all animals for identification. We used uniquely numbered ear tags for Dulzura kangaroo rats and deer mice (Monel 1005-1, National Band and Tag Co., Newport, KY, USA). For species with small ears (i.e., Pacific pocket mice, Los Angeles pocket mice, California pocket mice, San Diego pocket mice, western harvest mice) we injected visible implant elastomer (Northwest Marine Technology, Shaw Island, WA, USA) 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, mass, reproductive condition, and trap location.

We selected adult focal individuals to provision with seeds after identifying them as residents, as determined by trapping them a minimum of 3 nights in the same location (Shier and Swaisgood 2012). When we trapped a focal individual, we emptied its cheek pouches of previously collected seeds and placed it inside a clear plexiglass open-bottomed arena (61 × 61 × 61 cm) with 5 g of hulled millet in a tray. The millet was marked by shaking it with 0.5-g non-toxic fluorescent pigment (i.e., green, pink, blue ECO Pigment; DayGlo Color, Cleveland, OH, USA) that is frequently used in rodent studies (Lemen and Freeman 1985). The pigments persist in the environment for substantial periods of time and can be detected in cache sites for several weeks (Longland and Clements 1995). When consumed, these pigments pass through an animals' digestive tract and are visible in feces (Stapp et al. 1994, Longland and Clements 1995). Murray et al. (2006) verified that specific pigment colors are identifiable in the feces of multiple species of pocket mice and kangaroo rats for ≥72 hours after ingesting ≤0.5 g of fluorescently labeled millet seed. Millet does not grow naturally in the study areas but is an attractive bait food for all species in this rodent community. The purpose of the plexiglass arena was to detain the animal long enough for it to find the seed tray. The animals filled their cheek pouches from the seed tray before leaving the arena by digging under the arena sides. They could then bury the seeds in scatter hoards or return to their burrow to larder hoard. The animals could return to the seed tray by reentering under the edge of the arena and often made multiple trips back and forth to remove seeds from the tray. While the focal animal cached seeds, a seated observer (RYC) watched from a minimum of 5 m away through night vision goggles, which allowed for observation of foraging behavior while minimizing disturbance (Leaver

and Daly 2001, Murray et al. 2006). It took between 15 minutes and 3 hours for an individual to remove all seeds from the tray, with the average trial lasting 1 hour. We terminated trials and removed the seed tray if an animal did not return after 45 minutes. If only some of the seed was taken, we allowed the focal cacher an opportunity to take the remainder of the seeds the following night. If an individual did not take all the dyed seeds over 2 nights, we did not include it in the study and did not conduct another pilfering trial within 50 m. We did not try to control or identify the location of cached seeds. Focal cachers included 9 Pacific pocket mice, 9 Los Angeles pocket mice, 9 Dulzura kangaroo rats, and 5 San Diego pocket mice.

After provisioning each animal with dyed seeds, we set a 16-trap grid (4 × 4 traps, 4-m spacing) centered on the focal animals' burrow and trapped for 10 consecutive nights. We assumed all individuals trapped on the grid were close enough to the focal animal's caches (within 8.5 m) to have the opportunity to pilfer. We provided focal individuals within 50 m of one another different colored dyed seeds, which we could clearly distinguish from each other, allowing us to identify the caching individual that had been pilfered. Trials using the same colored seeds were separated by a minimum of 200 m to minimize the possibility a pilferer would have access to both caches (McNab 1963, Maza et al. 1973, Shier 2008). 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).

We calculated the average number of individuals of each species found within 8.5 m of each focal caching species, and the number that pilfered the caches of the focal species. We grouped trials of Pacific pocket mice and Los Angeles pocket mice in our analysis. Because of the small sample size of pilfering events, we did not analyze these data statistically.

Use of Conspecific or Heterospecific Scent to Find or Avoid Scatter Hoards

We tested whether Los Angeles pocket mice, San Diego pocket mice, Dulzura kangaroo rats, and deer mice use the scent of conspecifics or heterospecifics to find or avoid scatter hoards. Trapping and tagging procedures were identical to those described above, except we closed traps during the first check at 2200. To collect scented sand, we trapped animals in the field and placed 1 individual in a plexiglass tank (13 × 19 × 21 cm) on 340 g of clean, dry sand with millet seed *ad libitum*. We left animals undisturbed for 5 hours (Dempster and Perrin 1990, Ebensperger 2000) at which point we returned them to the location of capture. We sifted the sand to remove seeds and feces, and stored sand in clean glass jars with metal screw tops in a freezer for up to 5 nights before using it in the experiment (Randall 1987, Devenport et al. 1999).

The testing arena was an opaque plastic tub (89 × 51 × 48 cm) with 3 cm of clean, dry sand. We created artificial caches in plastic cups (59 ml) filled with sand and 2 g (±0.1 g) of millet buried at a depth of 1 cm, which should be detectable by all the

study species (Vander Wall et al. 2003). Sand in each of the artificial caches was unscented, conspecific-scented, or heterospecific-scented. Six cache cups, 2 of each scent treatment, were evenly spaced in the arena and placed into the sand. The tops 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).

We randomly selected focal individuals for this experiment from the available adult animals trapped each night. We balanced sex ratios for each focal species. We used individual Los Angeles pocket mice in up to 2 trials with different heterospecific scents, separated by a minimum of 24 hours because of logistical constraints of trapping enough unique individuals. We used individuals of the other species 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 hours. At the end of the trial, we released the focal animal and removed each artificial cache, sifted it, and weighed the remaining seeds. We calculated the difference between the amount initially provided (2 g) and the remainder as the mass of seeds taken. Caches that appeared undisturbed consistently had 2 g of seeds remaining; thus, time in sand did not alter the mass of the seeds.

We presented San Diego pocket mice, Dulzura kangaroo rats, and deer mice sand from Los Angeles pocket mice as the only heterospecific scent ($n = 20$ for each focal species). We presented Los Angeles pocket mice with heterospecific scent of San Diego pocket mice, Dulzura kangaroo rats, and deer mice ($n = 20$ for each), and western harvest mice ($n = 8$). We conducted 128 trials.

We used logistic regression to assess each species' ability to discover caches that were scented by heterospecifics, conspecifics, or unscented. We grouped all Los Angeles pocket mice together, regardless of heterospecific treatment, and included scent of the cache as a fixed effect and identity of the pilferer as a random effect. We ran the same test with discovered and undiscovered caches for each competitor species. We fitted logistic regression models in R 3.5.1 (R Development Core Team 2018) with the glmer function in the lme4 package (Bates et al. 2015), and we used the Anova function in the car package (Fox and Weisberg 2011) to conduct Wald chi-square tests on the overall effect of scent treatment. We also tested whether scent treatment affected the amount of seeds any of the species pilfered from discovered caches using linear regression. For each of the 4 species, mass of seeds taken was the outcome variable, scent of cache was a fixed effect and identity of pilferer was a random effect. When we found overall significance for scent (alpha of 0.05), we used paired comparisons to determine differences in pilfering by scent treatment. Finally, we compared the amount of seeds pilfered by each species, regardless of scent, using linear regression. We conducted all linear regressions in R 3.5.1 (R Development Core Team 2018) using the lmer function in the lme4 package (Bates et al. 2015). Protocols followed American Society of Mammalogists guidelines (Sikes and Animal Care and Use Committee 2016) and were approved by the Institutional Animal Care and Use Committee of San Diego Zoo Global (protocol number 15-002).

RESULTS

Over a 7-day period, captive Pacific pocket mice cached approximately 57% of the seeds provided. We did not detect a difference in the percent of seeds stored in larder hoards versus scatter hoards (Wilcoxon signed ranks test, $V = 102.5$, $P = 0.94$; Fig. 1).

Out of 32 trials in which an individual cached fluorescent seed, we captured 137 unique individuals within 8.5 m of the focal animal's burrow, but we detected only 7 cases of pilfering (Table 2). Of the 7 pilferers we detected, 4 were instances of heterospecific pilfering (deer mice from little pocket mice, little pocket mice from San Diego pocket mice and Dulzura kangaroo rats, Dulzura kangaroo rats from San Diego pocket mice) and 3 had taken seeds from conspecifics (2 little pocket mice, 1 San Diego pocket mouse).

Of the little pocket mice that were trapped near focal little pocket mice, 2 of 23 pilfered from conspecific caches and 2 of 10 trapped near heterospecific focal individuals pilfered from caches of a different species (Table 2). We found fewer individual little pocket mice on the grids of heterospecific cachers (10 individuals over 14 trials) than on the grids of conspecific cachers (23 individuals over 18 trials). The deer mouse was the only species we caught that pilfered from little pocket mouse caches (1 of 23 individuals), and of the 33 heterospecifics trapped on grids where little pocket mice were the focal cachers, we observed only 1 individual pilfering.

For the Los Angeles pocket mouse and the 3 competitor species, we did not detect a difference in their discovery of caches based on scent treatment (Los Angeles pocket mouse Wald $\chi^2 = 2.25$, $P = 0.32$; Dulzura kangaroo rat Wald
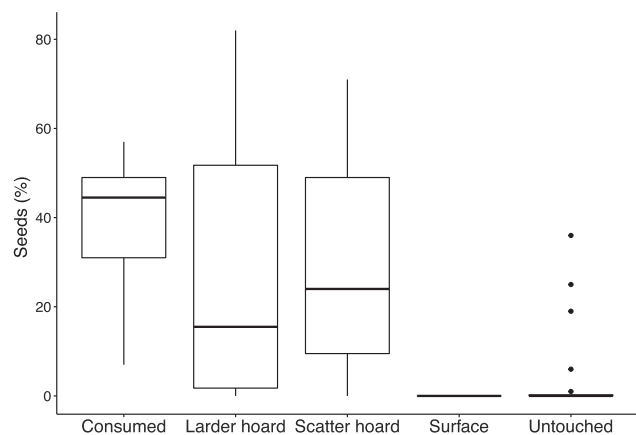

Figure 1. Seed placement by Pacific pocket mice during a 7-day captive caching study in Escondido, California, USA, September 2016. We calculated percent of seeds consumed from the difference between the mass of seeds given and the mass of seeds recovered in any location. We considered seeds stored in the nest to be larder hoarded and seeds buried anywhere in the substrate to be scatter hoarded. Surface refers to seeds that mice moved from the dish but left unburied, and untouched refers to seeds that mice did not remove from feeding dish. The boxplots depict medians (horizontal lines) and interquartile ranges (boxes). Whiskers show spread of data (highest and lowest values within 1.5 interquartile range), and dots are outliers.

Table 2. Species that cached fluorescent seeds and the potential and actual pilferers of each species in Southern California, USA, 2013 and 2014. Rows indicate the focal caching species and columns represents the number of unique individuals of each species that were trapped on the grids of each focal caching species, indicating they were close enough they had the opportunity to pilfer, and the number of individuals found to have pilfered (observed with fluorescence on their fur or in their feces). We report the mean per sampling grid for each species because of differences in sample size of focal caching species, in addition to the total number of potential and actual pilferers observed across all grids.

Species of focal cacher		Little pocket mice trapped	Little pocket mouse pilferers	Dulzura kangaroo rats trapped	Dulzura kangaroo rat pilferers	San Diego pocket mice trapped	San Diego pocket mouse pilferers	Deer mice trapped	Deer mouse pilferers
Little pocket mice ($n = 18$)	$\bar{x}$	1.3	0.1	0.4	0	0.1	0	1.3	0.1
	Total	23	2	8	0	2	0	23	1
Dulzura kangaroo rats ($n = 9$)	$\bar{x}$	1	0.1	2.2	0	0.8	0	0	0
	Total	9	1	20	0	7	0	0	0
San Diego pocket mice ($n = 5$)	$\bar{x}$	0.2	0.2	1.2	0.2	7.6	0.2	0	0
	Total	1	1	6	1	38	1	0	0

$\chi^2 = 0.64$, $P = 0.73$; San Diego pocket mouse Wald $\chi^2 = 3.45$, $P = 0.18$; deer mouse Wald $\chi^2 = 3.04$, $P = 0.22$). Of the caches they discovered, Los Angeles pocket mice pilfered different amounts from the 3 scent treatments ($F_{2, 361} = 4.09$, $P = 0.02$). Specifically, they pilfered more seeds from conspecific compared to unscented caches ($t = -2.85$, $P = 0.01$), but we did not detect a difference in the amount of seeds pilfered from heterospecific-scented caches compared to conspecific-scented caches ($t = -1.62$, $P = 0.11$) or unscented caches ($t = 1.23$, $P = 0.22$; Fig. 2). For the 3 other species, we did not detect a difference in the amount of seeds pilfered from conspecific, unscented, or Los Angeles pocket mouse-scented caches (Dulzura kangaroo rat $F_{2, 98} = 2.66$, $P = 0.08$; San Diego pocket mouse $F_{2, 101} = 0.72$, $P = 0.49$; deer mouse $F_{2, 99} = 1.85$, $P = 0.16$; Fig. 2). The 4 species differed in the amount of seeds they pilfered during the 3-hour trials, regardless of scent treatment ($F_{3, 91} = 14.78$, $P \leq 0.001$). Overall, San Diego pocket mice and Dulzura kangaroo rats pilfered more seeds than either Los Angeles pocket mice or deer mice, when all the scent treatments were combined (Fig. 2; Table S1, available online in Supporting Information).

DISCUSSION

In captivity, we did not detect a difference between the proportion of seeds Pacific pocket mice scatter hoarded and the proportion they larder hoarded, which indicates that a substantial proportion of their cached seeds could be susceptible to pilfering by heterospecifics. Therefore, we studied pilfering by and from little pocket mice (Pacific and Los Angeles pocket mice) in the field.

Price and Mittler (2003) hypothesized 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). We found that more little pocket mice pilfered from heterospecifics (2 of 10) than other species pilfered from little pocket mice (1 of 33). Our results provide some support for Price and Mittler's (2003) hypothesis; little pocket mice pilfered more from larger species than they were pilfered from by heterospecifics. However, 8 of 10 little pocket mice captured close to caches of dyed seeds showed no evidence of pilfering from larger species, and in particular only 1 of 9 little pocket mice pilfered from Dulzura kangaroo rats, the largest and most behaviorally dominant species (Chock et al. 2018). It seems unlikely that little pocket mice are negatively affected by such a low level of cache pilfering by other species, but the low rates of pilfering provide only weak support for the hypothesis that little pocket mice benefit from sympatric heterospecifics through cache pilfering. Our small sample size (5–18 focal cachers/species) and length of observations (10 nights) may have limited our ability to observe pilfering events. Our results were, however, comparable to a similar study over a larger area and longer time frame that found 2–26% of individuals of each species had pilfered (Leaver and Daly 2001). This low rate of pilfering precluded the use of statistical tests, which limits the interpretation of our results but fits with the assessment that cache pilfering may not provide a large benefit to the smallest species in the community.

We found no evidence that any of these rodents use heterospecific scent to find or avoid scatter hoards. Scent
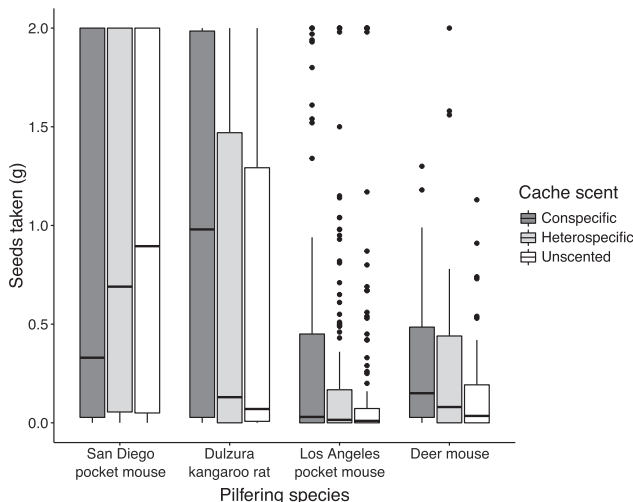

Figure 2. Mass of seeds taken from 2-g artificial caches of each scent treatment (conspecific, heterospecific, or unscented) by each species during 3-hour pilfering trials at the San Jacinto Wildlife Area, California, USA, 2015. The boxplots depict medians (horizontal lines) and interquartile ranges (boxes). Whiskers show spread of data (highest and lowest values within 1.5 interquartile range), and dots are outliers.

treatment (heterospecific, conspecific, or unscented) was not predictive of cache discovery by Los Angeles pocket mice, Dulzura kangaroo rats, San Diego pocket mice, or deer mice. Once discovered, Los Angeles pocket mice pilfered more seeds from conspecific caches compared to unscented caches, but we did not detect a difference in the amount of seeds they took from heterospecific caches compared to the other scent treatments. Cache scent did not affect the amount of seeds pilfered by competitor species. It is likely animals use the scent of seeds to locate scatter hoards (Vander Wall et al. 2003), and our results suggest heterospecific scent does not influence pilfering decisions. With all scent treatments combined, Los Angeles pocket mice were less efficient than other species in foraging from artificial caches, pilfering fewer seeds than either Dulzura kangaroo rats or San Diego pocket mice.

Increased access to seeds via pilfering would be most valuable when primary production of seeds is lowest and food is scarcest in the winter months. Little pocket mice have an alternative strategy for dealing with extreme food scarcity, the reduction of metabolic activity through daily torpor or estivation (Bartholomew and Cade 1957, Guppy and Withers 1999). Kenagy (1973) reported that although there is some variation in aboveground activity associated with annual levels of precipitation and individual differences, the majority of little pocket mice are inactive during the winter months, suggesting that they must cache enough seeds in the late summer and fall to fill their larders or emerge from their burrows only occasionally during this period to refill their cache and survive winter. We conducted experiments during the entire active season of little pocket mice (Apr–Sep), but future research could test the hypothesis that there are seasonal differences in pilfering, with little pocket mice pilfering more frequently in late summer when seeds are scarcer and they are preparing for and entering estivation. The density of animals in an area could also influence cache pilfering, and additional research is needed in these communities to distinguish between alternative hypotheses about the direction of this relationship. Higher densities might be associated with increased competition for resources and a greater likelihood of encountering a competitor's cache, increasing rates of pilfering at higher densities. Rodents can, however, change their caching patterns in response to conspecific pilfering to minimize cache loss (Clarke and Kramer 1994, Preston and Jacobs 2001, Murray et al. 2006), suggesting behavioral response to competitor cues can reduce pilfering. Although our trapping areas were too small to accurately estimate densities, future studies may be able to shed light on the relationship between heterospecific density and the prevalence of cache pilfering, which will aid in management recommendations for listed species.

MANAGEMENT IMPLICATIONS

Reintroduced populations of Pacific pocket mice should be given every competitive advantage during the establishment phase following release. In lieu of strong evidence that Pacific pocket mice gain an advantage from heterospecifics, we suggest that a conservative reintroduction approach would be to select receiver sites with low densities of heterospecifics or temporarily reduce densities of known competitors during the critical post-release establishment phase.

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