

## COMPETITIVE INTERACTIONS BETWEEN TIPTON AND HEERMANN'S KANGAROO RATS IN THE SAN JOAQUIN VALLEY, CALIFORNIA

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**ABSTRACT**—We studied competition between the federally endangered Tipton kangaroo rat (*Dipodomys nitratoides nitratoides*) and the larger Heermann's kangaroo rat (*D. heermanni*) at a site in the San Joaquin Valley, California, where *D. n. nitratoides* had been translocated 4 years earlier. We found that five *D. heermanni* had smaller home ranges than did four *D. n. nitratoides* inside a fenced area of exclusion. Behavioral observations suggested that *D. n. nitratoides* avoided *D. heermanni*. After we removed *D. heermanni* from the area of exclusion, numbers of *D. n. nitratoides* increased 500% in 12 months, whereas numbers at a control site with *D. heermanni* were low and trending downward. We suggest that if translocations continue to be used to conserve *D. n. nitratoides*, it may be important to limit numbers of *D. heermanni* until *D. n. nitratoides* are well established.

**RESUMEN**—Estudiamos la competencia entre la rata canguro de Tipton (*Dipodomys nitratoides nitratoides*), amenazada al nivel nacional, y la más grande rata canguro de Heermann (*D. heermanni*) en un sitio en el valle de San Joaquín, California, donde *D. n. nitratoides* había sido trasladado hace cuatro años. Encontramos que cinco *D. heermanni* tuvieron rangos de hogar más pequeños que los de cuatro *D. n. nitratoides* dentro de un área cercada de exclusión. Observaciones sobre el comportamiento mostraron que *D. n. nitratoides* evitó a *D. heermanni*. Después de sacar *D. heermanni* de la exclusión, los números de *D. n. nitratoides* incrementaron en un 500% en 12 meses, mientras que los números en un sitio control con *D. heermanni* fueron bajos y tendiendo a disminuir. Sugerimos que si siguen las translocaciones para conservar *D. n. nitratoides*, puede ser importante limitar los números de *D. heermanni* hasta que *D. n. nitratoides* esté bien establecida.

Competition plays an important role in the structure and function of populations in an ecological community. Communities dominated by granivorous rodents in southwestern North America have provided a model for studying structure and competition in a community (see reviews by Brown and Harney, 1993; Randall, 1993; Kelt, 2011). One reason for this is that, in arid western North America, it is common to find many sympatric species utilizing similar resources. Much research has been done on how sympatric desert rodents experiencing interference competition partition for abiotic and biotic environmental factors. For example, differences in use of habitat types are well documented (Brown, 1975; Price, 1978; Price and Brown, 1983) especially among quadrupedal species, which typically prefer rocky or dense shrub-dominated areas, and bipedal species, which prefer open areas (Rosenzweig and Winakur, 1969; Price, 1986; Reichman and Price, 1993).

Interspecific interference competition, which is defined as competition through direct interaction, such as aggressive encounters between competitors (Pianka,

1978), is an important biotic factor that affects the structure of populations in communities of desert rodents (Munger and Brown, 1981; Brown and Munger, 1985; Heske et al., 1994). A well-known study excluding kangaroo rats from long-term monitoring plots in southeastern Arizona has demonstrated that small, quadrupedal heteromyid and murid species increased in the absence of larger bipedal competitors, while, at the same time, insectivores (*Onychomys torridus* and *O. leucogaster*) remained unchanged (Munger and Brown, 1981; Brown and Munger, 1985; Heske et al., 1994). Also, research has shown that species will shift their use of microhabitat, often using a greater variety of microhabitats, when other sympatric species are added or removed (Price, 1978; Larsen, 1986). Most previous studies have addressed competition between different functional groups (bipedal heteromyid and quadrupedal heteromyid or quadrupedal murid); competitive effects between species in the same functional group should be more pronounced (Brown and Harney, 1993).

Behaviorally, interspecific and intraspecific competi-

tion affect social structure and spacing of individuals in communities of desert rodents (Randall, 1993). Research on behavioral interactions between species has shown that species of larger heteromyids typically dominate species of smaller size through interference competition (Blaustein and Risser, 1976; Frye, 1983; Basset, 1995; Perri and Randall, 1999). Yet, at the same time, aggression is costly and avoidance may allow for coexistence of sympatric species (Perri and Randall, 1999).

We studied competitive interactions between Tipton (*Dipodomys nitratooides nitratooides*) and Heermann's kangaroo rats (*D. heermanni*), two species that often occur together in the San Joaquin Valley, California. *Dipodomys n. nitratooides*, a state and federally listed endangered species (United States Fish and Wildlife Service, 1988; California Department of Fish and Game, in litt.), is one of the smallest kangaroo rats (ca. 35 g) and is limited to relatively flat lands within the Tulare Basin (Williams and Kilburn, 1992). Although a protected species, current populations continue to decline or are unstable (Uptain et al., 1999; United States Fish and Wildlife Service, in litt.), and projects that eliminate sites occupied by *D. n. nitratooides* continue to be permitted. As a means of mitigating loss, translocations to other areas have been permitted to save some individuals, and this included a translocation in 2006 to the Allensworth Ecological Reserve (Germano et al., 2013). Offspring from the translocated population at Allensworth were studied in our analysis.

Also occupying the study site was *D. heermanni*, a medium-sized rodent (ca. 70 g) that ranges widely throughout central California in a variety of habitats (Williams and Kilburn, 1992). The subspecies in the San Joaquin Valley, *D. heermanni tularensis*, is widespread and relatively abundant in all but the wetter habitats in southern San Joaquin Valley and is not listed as a protected species. Because we thought that the larger *D. heermanni* could be negatively affecting the population of *D. n. nitratooides* on the reserve and because little is known about interactions between these two species, we initiated a case study that would investigate spacial patterns for each species and behavioral interactions occurring between the species and compare abundance and population trends of *D. n. nitratooides* between areas with and without *D. heermanni*. Because this study lacked replication and had small sample sizes, the scope of inferences based on these results are limited. However, results have important implications for the conservation of *D. n. nitratooides*.

Allensworth Ecological Reserve is in southern Tulare County, ca. 60 km north of Bakersfield, California (35°84'55"N, 119°34'88"W). The reserve is owned and managed by the California Department of Fish and Wildlife and consists of a patchwork of large and small parcels that are intermixed with conservation, agricultural, and grazing lands in private ownership (California

Department of Fish and Wildlife, in litt.). Common vegetational alliances at the reserve include *Suaeda moquinii* Shrubland Alliance (bush seepweed scrub), *Allenrolfia occidentalis* Shrubland Alliance (iodine bush scrub), *Centromadia* (pungens) Herbaceous Alliance (tar plant fields), *Amsinckia* (*menziesii*, *tessellata*) Herbaceous Alliance (fiddleneck fields), and *Bromus rubens*-*Schismus* (*arabicus*, *barbatus*) Semi-Natural Herbaceous Stands (red brome or Mediterranean grasslands; Sawyer et al., 2009). The area has a Mediterranean climate with hot, dry summers and cool, wet winters (National Oceanic and Atmospheric Administration, 2005). In the summer, daytime temperatures can exceed 37°C and, in the winter, the mean minimum is 1°C (National Oceanic and Atmospheric Administration, 2005). Virtually all rainfall occurs in the winter months from November–April and averages 18.6 cm/year (National Oceanic and Atmospheric Administration, 2005).

We conducted a case study and used only one control and one experimental study plot. On our experimental plot, we constructed a 1.5-ha exclusion-area on the north side of a periodically wet canal. The south side of the canal served as our control plot. We used 6.4-mm hardware cloth that was 1.23 m tall to construct an exclusion area 122-m by 122-m square. We used a self-propelled trencher to create a trench in which we buried the hardware cloth 30–50 cm deep, leaving 73–93 cm as an above-ground barrier. We used t-posts and rebar in corners and approximately every 9–15 m for structural support.

We trapped *D. n. nitratooides* and *D. heermanni* using Sherman live traps baited with bird seed dominated by millet and containing wadded paper towels as bedding material. We opened and baited traps in the late afternoon and checked traps at first light the following morning unless temperatures were predicted to be <10°C, in which case we checked traps approximately 4 h after opening them. If conditions were predicted to be very cold, we used a small, palm-sized ball of polyester batting in traps instead of paper towel.

We marked kangaroo rats captured inside the area of exclusion and *D. n. nitratooides* captured at the control site with Passive-Integrated-Transponder (PIT) tags under the skin dorsally towards the neck (Williams et al., 1997). Any *D. n. nitratooides* that we caught around the perimeter just outside the area of exclusion at the start of the project in fall 2009 were placed inside the area of exclusion to supplement the small number of *D. n. nitratooides* caught within the area of exclusion.

To document the spacial patterns for each species and determine behavioral interactions between the two species, we attached radio-transmitters, tracked individual kangaroo rats, compiled and quantified behavioral observations, and calculated mean home-range size for both species. At the end of August 2009, we captured five *D. n. nitratooides* and paired them with five *D. heermanni*

that were caught in adjacent traps inside or just outside the exclusion-area. To these 10 individuals, we attached custom-fitted, 2-g radio transmitters (Model BD-2, Holohil Systems, Ltd., Carp, Ontario, Canada) using aluminum beaded chain that was fitted around the neck of individuals (Harker et al., 1999). We then released these kangaroo rats inside the area of exclusion.

We tracked kangaroo rats using a three-element Yagi antenna and Communications Specialist R-1000 receiver (Communications Specialists, Inc, Orange, California) for 19 days from 21 August–25 September 2009. The majority of monitoring took place from sunset (ca. 1930 h) until 2330–0130 h. However, we also tracked kangaroo rats from 0400–0600 h on 3 days. A day of monitoring included location of the burrow used during the day followed by 2–6 h of monitoring at night. We used a night-vision scope or the indirect light of a headlamp to locate individuals at night. If the individual was underground, we located its burrow. We recorded locations of burrows and individuals with a handheld computer equipped with Global Positioning System (Juno ST Trimble, Trimble Navigation, Ltd, Westminster, Colorado).

We used a night-vision scope and a handheld, digital sound-recorder to observe and vocally record behaviors of kangaroo rats at night. During each night of monitoring, we began by targeting one individual and intensively following it for 1 h, until it disappeared (we lost track of the individual), or until it went into a burrow. Depending on the length of the first observation, we located and followed other individuals the same night using the same methods. Typically, we located all individuals two–five times during a day of monitoring.

As we intensively followed an individual, we sequentially recorded behavior. We recorded an interaction between kangaroo rats if they were within 15 m of each other and there was an acknowledgement of the presence of another individual. Acknowledgment occurred when kangaroo rats stopped movement or foraging behavior and slightly raised their head to scan the area, which we believe indicated that kangaroo rats took note of the presence of other neighboring individuals. We recorded mutual tolerance between individuals if acknowledgment occurred between the individuals but no aggressive behavior was observed. When we recorded a chase between individuals, the chase was considered an interaction no matter how far apart individuals were or if there was acknowledgment before the chase began.

Using the Hawth's Tools Extension for ArcView 9.2 (Spatial Ecology, LLC, Toronto, Canada; <http://www.spatial-ecology.com/htools>), we calculated home ranges for *D. n. nitratoides* and *D. heermanni* from the total number of Global-Positioning-System-data points for each individual. We determined size of home ranges using 95%-minimum-convex-polygons. We used a minimum of 29 locations for each individual based on the stabilization of the home-range size that we found for both species

with this many locations. For one of the five *D. n. nitratoides* monitored, we had only 18 locations recorded before it went missing and, thus, we excluded this individual from the final statistical analysis. We used the Mann-Whitney rank test ( $\alpha = 0.05$ ) in the program MINITAB to compare the size of home ranges for *D. n. nitratoides* and *D. heermanni*.

To compare abundance of *D. n. nitratoides* and population trends in areas with and without *D. heermanni*, we removed *D. heermanni* from the area of exclusion by trapping five nights at the end of September 2009. Because three of the five *D. n. nitratoides* that we radio-tracked either were predated or went missing during the behavioral study, we again trapped outside the area of exclusion and moved two *D. n. nitratoides* captured to the inside of the area of exclusion to supplement the small population of *D. n. nitratoides* ( $n = 4$ ). We also trapped for one night in November 2009 at the remaining marginal habitat on the original translocation salvage site in Lamont, California and caught nine *D. n. nitratoides*. We released these animals at dusk into inactive burrows inside the area of exclusion, increasing the population of known *D. n. nitratoides* inside the area to 13 individuals.

To measure abundance of *D. n. nitratoides*, we trapped the exclusion-area and the control site every 2–3 months for a total of four times from February–November 2010. During each trapping session, we trapped for three–four nights and avoided any adverse weather. Any *D. heermanni* we captured inside the exclusion-area during any of these trapping sessions were removed. We used regression analysis ( $\alpha = 0.05$ ) to compare the change in numbers of *D. n. nitratoides* inside the area of exclusion with that at the control site.

The mean number of Global-Positioning-System-data points recorded was  $42.0 \pm 4.0$  (range of 29–54) for *D. heermanni* and  $42.6 \pm 7.1$  (range of 18–60) for *D. n. nitratoides*. The average size of home ranges was  $602.2 \pm 334.1 \text{ m}^2$  (range of 58.6–1,898.8  $\text{m}^2$ ) for the five *D. heermanni* with radio-transmitters and  $1,606.1 \pm 926.1 \text{ m}^2$  (range of 321.5–5,269.0  $\text{m}^2$ ) for the five *D. n. nitratoides* in the area of exclusion. The average home range of *D. n. nitratoides* excluding the individual with only 18 locations was  $1,921.6 \pm 1,124.1 \text{ m}^2$ . Even though the size of the home range of *D. n. nitratoides* was three times larger than that of *D. heermanni*, size of home ranges did not differ significantly ( $W = 19.0$ ,  $P = 0.176$ ).

We recorded 1,627 min of focal-observation-time of kangaroo rats with radio-transmitters. During this time, we observed 23 interspecific interactions between species of kangaroo rats and one interspecific interaction between a *D. n. nitratoides* and a San Joaquin pocket mouse (*Perognathus inornatus*). We also recorded 18 intraspecific interactions among *D. heermanni* but no interaction among *D. n. nitratoides*. In encounters between *D. n. nitratoides* and *D. heermanni*, there were nine instances when a *D. n. nitratoides* was chased away from

TABLE 1—Total number of individual *Dipodomys nitratoides nitratoides*, *D. heermanni*, and *Perognathus inornatus* caught on exclusion and control areas at Allensworth Ecological Reserve, Tulare County, California, from August 2009–October 2010. *Dipodomys heermanni* were removed from the exclusion area in September 2009 ( $n = 29$ ). Also listed is the number of juvenile (weighed  $\leq 30$  g) *D. n. nitratoides* trapped on exclusion and control areas.

Trapping period	Exclusion area				Control area			
	<i>D. n. nitratoides</i>		<i>D. heermanni</i>	<i>P. inornatus</i>	<i>D. n. nitratoides</i>		<i>D. heermanni</i>	<i>P. inornatus</i>
	Total	No. of juveniles	Total	Total	Total	No. of juveniles	Total	Total
August–September 2009	5	0	31	6	8	2	112	12
February 2010	11	4	1	0	5	0	67	0
May 2010	8	0	2	6	1	0	27	0
July 2010	14	1	0	12	2	0	45	1
October 2010	30	7	0	33	1	1	46	6

an area by a *D. heermanni*. In four encounters, a *D. heermanni* approached an area where a *D. n. nitratoides* was foraging and the *D. n. nitratoides* retreated from the area before a chase was initiated. In the remaining 10 interactions, there was mutual tolerance. In seven of these instances, the two species foraged  $<5$  m apart, and, in the remaining three interactions, they foraged  $<15$  m apart. In the one interaction observed between a *D. n. nitratoides* and *P. inornatus*, the *D. n. nitratoides* chased the *P. inornatus* away from the shrub where it was foraging and then proceeded to forage under that shrub. The majority of the intraspecific interactions among *D. heermanni* involved a chase between two individuals (17 instances). Typically, when another *D. heermanni* began foraging near the home-burrow or mound of a resident *D. heermanni*, the resident would chase the intruder. Because we knew the locations of home-burrows of individuals with radio-transmitters, we could determine that, typically, the resident *D. heermanni* was the individual with the radio-transmitter. There was one intraspecific interaction of *D. heermanni* where mutually tolerant foraging ( $<5$  m apart) occurred. No fighting behavior was observed within or between the species.

After we removed 29 *D. heermanni* from the area of exclusion in September 2009, we caught one or two inside the area of exclusion in February and March 2010, and these individuals also were removed (Table 1). By summer 2010, *D. heermanni* was no longer detected inside the area of exclusion and did not reappear throughout the remainder of the study. At the same time, the number of *D. heermanni* on the control site remained high, although their numbers in 2010 were about one third of what they were in mid-2009 (Table 1).

The number of *D. n. nitratoides* increased by 500% in the area of exclusion from February–October 2010. The number of *D. n. nitratoides* at the control site remained consistently low, with only one or two individuals captured from May–October 2010. The number of *D. n. nitratoides* increased exponentially since the start of the study in the area of exclusion ( $F_{1, 4} = 29.20$ ,  $P = 0.006$ ;  $R^2 = 0.88$ ) but

decreased significantly at the control site ( $F_{1, 3} = 11.99$ ,  $P = 0.041$ ;  $R^2 = 0.80$ ; Fig. 1). While the population of *P. inornatus* at the control site increased slightly, the population in the area of exclusion increased by 450% (Table 1), although this increase was not significant ( $F_{1, 2} = 2.45$ ,  $P = 0.258$ ).

This study demonstrates that interspecific interference competition between *D. n. nitratoides* and *D. heermanni* plays an important role in the community structure of heteromyid rodents at our study site. Spatial patterns for both species, reported as estimates of home range, were clearly limited by small sample size with only five *D. heermanni* and five *D. n. nitratoides* with radio-transmitters and only four *D. n. nitratoides* surviving long enough to provide enough data to assess home range. However, while not statistically significant, it did appear that *D. n. nitratoides* foraged over a larger area and *D. heermanni* tended to forage in the vicinity of their home-burrow.

This trend is consistent with data on other species of kangaroo rats, which suggests that size of home range and sociality are inversely related to body size (Randall, 1993; Shier and Yoerg, 1999). For example, males and females of one of the largest species of kangaroo rats, *D. spectabilis*, have nonoverlapping territories and defend one to several large mounds (Schroder, 1979; Randall, 1984; Randall et al., 2002). *Dipodomys ingens*, the largest kangaroo rat, has similar behaviors and defends individual territories, called precincts, which are similar in size to the mound of a *D. spectabilis* (Braun, 1985; Randall, 1997). Both species are larder hoarders and defend stored caches (Randall, 1997). In a study on the Carrizo Plain, *D. ingens* had small home ranges (60–350 m<sup>2</sup>) and were active for an average of only 20 min/night (Braun, 1985).

*Dipodomys heermanni*, which is intermediate in size among species of *Dipodomys*, appears to display territoriality and primarily larder hoards (Tappe, 1941; E. N. Tennant, pers. observ.). In a study of *D. h. arenae* in coastal dune scrub habitat, mean size of home range for females

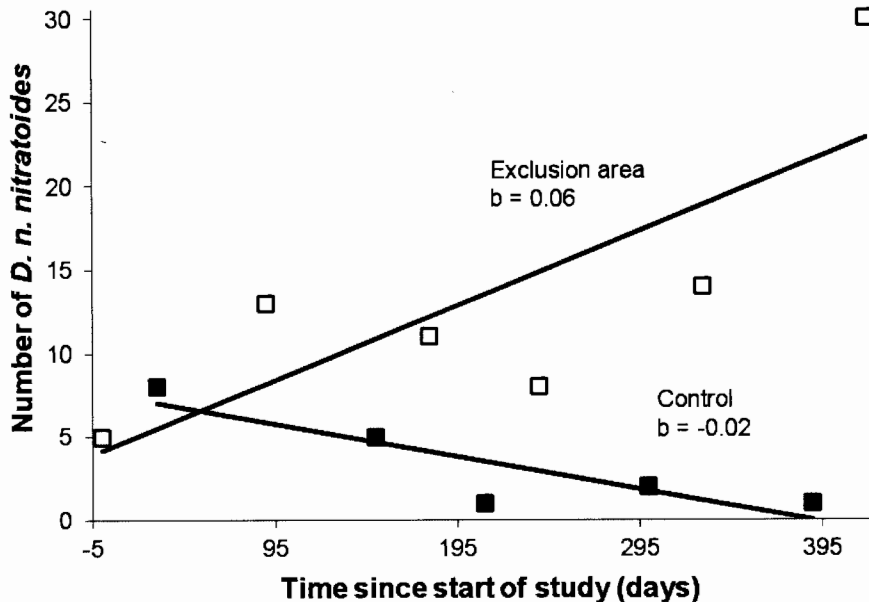


FIG. 1—Linear relationship between the number of *Dipodomys nitratooides nitratooides* caught in the area of exclusion (open squares) and on the control site (closed squares) and the length of study at Allensworth Ecological Reserve, Tulare County, California.

and males was 375 m<sup>2</sup> and 962 m<sup>2</sup>, respectively (Shier and Randall, 2004). While our study occurred in a different type of habitat and had smaller sample sizes, our mean home range for *D. heermanni* (602.2 ± 334.1 m<sup>2</sup>) was within the range of the size calculated by Shier and Randall (2004).

*Dipodomys merriami*, which is similar in size to *D. nitratooides* and occurs allopatrically in the southwestern deserts to the east, displays less territoriality, is less aggressive toward conspecifics, and tends to have overlapping home ranges between and among sexes (Randall, 1989, 1991, 1993). Mean size of home range for female and male *D. merriami* in Arizona was 705 m<sup>2</sup> and 1,671 m<sup>2</sup>, respectively (Perri and Randall, 1999). While our sample size was significantly smaller than that of Perri and Randall (1999), their values are near the size of the home range for *D. n. nitratooides* calculated in our study (1,921.6 ± 1,124.1 m<sup>2</sup>). Past studies also have suggested that smaller *Dipodomys* scatter-hoard and rely on memory to recover seeds rather than defense of larger hordes (Jacobs, 1992), which also explains the trend toward larger home ranges.

Our behavioral observations, while not replicated, follow the pattern of larger heteromyids using aggressive interference to outcompete smaller species noted in previous assessments (Blaustein and Risser, 1976; Frye, 1983; Basset, 1995; Perri and Randall, 1999). Although laboratory experiments with paired individuals of either conspecifics or different species often result in agonistic behaviors (Blaustein and Risser, 1976; Bleich and Price, 1995; Perri and Randall, 1999), we did not observe any aggressive contact between heteromyids during behavioral observations at our site during fall 2009. Our limited observations of interactions

between and among *D. n. nitratooides* and *D. heermanni* are similar to findings by Perri and Randall (1999) and suggest that avoidance, rather than aggression, mediates most interactions and allows for some level of coexistence between species. In fact, we observed chase-behavior more often intraspecifically (among *D. heermanni*) than interspecifically (between *D. heermanni* and *D. n. nitratooides*). Again, this is similar to the results of Perri and Randall (1999), which showed that the slightly larger *D. ordii* displaced conspecifics significantly more often than it displaced the smaller *D. merriami*. Perri and Randall (1999) suggest that intraspecific competition between larger and more territorial species is likely a stronger force in these communities than interspecific competition, unless populations are dense and resources are limited.

The abundance and population trends of *D. n. nitratooides* between areas with and without *D. heermanni* at our site suggest that *D. heermanni* are competitively depressing this population of translocated *D. n. nitratooides*. The removal of *D. heermanni* from our area of exclusion coincided with an increase of 450–500% in numbers of *D. n. nitratooides* and *P. inornatus* in little more than 1 year. Although *D. n. nitratooides* continued to be present at the control site, we captured only one or two individuals from May–October 2010 and there was a significant decrease in abundance during the study.

Because our control site was not fenced, we trapped an area surrounding the site in November 2010 to be sure that *D. n. nitratooides* had not simply moved off the site. The results of this trapping effort were similar to our results from trapping at the control site (35 *D. heermanni* and one *D. n. nitratooides*); thus, we do not think that *D. n. nitratooides* dispersed from the control site. Also, the

adjacent property to the south and west was converted to irrigated orchard in 2008; thus, the available dispersal area for small mammals was limited.

The result of excluding the largest heteromyid at our study site is similar to that of previous studies, demonstrating that competition is a strong force in structure of heteromyid communities. Typically, in past experiments, the removal of one or more species in different functional groups leads to an increase in the remaining species that utilize similar resources (Munger and Brown, 1981; Brown and Munger, 1985; Heske et al., 1994). The increase of 450% in the number of *P. inornatus* in our area of exclusion is further evidence of competitive release between different functional groups. This type of competitive release also has been recorded during periods of decline of kangaroo rats in the San Joaquin Valley. The winter of 1994–1995 was the fifth wettest on record in the valley and led to a dramatic decline in kangaroo rats (Single et al., 1996). Subsequent, but not sustained, increases in *P. inornatus* during this time may have been caused by competitive release (Cypher, 2001).

Although competitive release between species within the same functional group is expected to be more pronounced (Brown and Harney, 1993), *D. n. nitratooides* and *P. inornatus* increased at similar rates in our area of exclusion. However, this may be because of the short duration of our study and that the area had unsaturated levels of each species. Based on evidence that larger heteromyids typically dominate smaller heteromyids through interference competition (Blaustein and Risser, 1976; Frye, 1983; Basset, 1995; Perri and Randall, 1999), we would expect that, over time, the larger *D. n. nitratooides* would dominate the smaller *P. inornatus*.

While we cannot generalize about the results of this study, we recommend that the competitive effects of larger, coexisting species be considered in the translocation and reintroduction of *D. n. nitratooides*. If sites with appropriate habitat for *D. n. nitratooides* and without competitors cannot be identified, it may be necessary to remove competitors for initial populations of *D. n. nitratooides* to become established. Patterns in the use of burrows during the day suggest that kangaroo rats may prefer to avoid the home ranges of other species (Perri and Randall, 1999). Thus, it may be possible that, once a population of *D. n. nitratooides* is established on a site, abundance and spacing mechanisms may allow them to better compete and coexist with *D. heermanni*.

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## FIRST RECORDS OF JAGUAR (*PANTHERA ONCA*) FROM THE STATE OF MICHOACÁN, MEXICO

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