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Kinship associations of a solitary rodent, *Dipodomys ingens*, at fluctuating population densities

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The formation of kin groups is an important step in the path to evolution of sociality in mammals. We used microsatellite DNA analyses, trapping and radiotelemetry data to investigate spatial and genetic associations of the solitary giant kangaroo rat, *Dipodomys ingens*. We predicted that, as population densities increase, dispersal distances should decrease to form kin groups. As predicted, females decreased dispersal distances as population densities increased to form female kin clusters of related neighbours. Males also decreased dispersal distances, but only at the highest density, and they did not form kin clusters. Males seemed to adjust their home ranges to overlap unrelated females as a possible strategy to avoid inbreeding. They were not highly related to the majority of females that they overlapped, and the nearest neighbour in most cases was an unrelated female. The significant decrease in distance between female neighbours and the formation of female kin groups at high population density represents a potential increase in social interactions among these solitary rodents. Further research is necessary to determine the extent to which *D. ingens* is able to discriminate between kin and other familiar animals and whether they interact preferentially to facilitate the success of closely related kin.

Because the evolution of sociality consists of many steps along a continuum from solitary to highly social (Michener 1983; Blumstein & Armitage 1997; Faulkes & Bennett 2007; Lacey & Ebensperger 2007), clues to the evolution of sociality can be found by studying the behaviour of less gregarious species. Kinship is a key factor essential to the expression and development of social behaviour (Hamilton 1963, 1964; Alexander 1974), and female philopatry, defined as retention of young in the natal territory, that results in female kin groups can be an important step on the path to the evolution of social behaviour in mammals (Armitage 1981, 1999; Waser & Jones 1983; Perrin & Lehmann 2001). Sociality is enhanced because kin show increased tolerance and higher rates of amicable interactions than nonkin (Waser & Jones 1983; Maher 2009a).

Female kin groups occur in mammals of variable social complexity (Reviewed in Silk 2007), and kin structures change in response to shifts in the relative costs and benefits of life history trade-offs, reproduction and dispersal strategies (Nutt 2008; Maher 2009b). In recent years, researchers have discovered that even some solitary mammals have a matrilineal, genetic structure similar to that of more social species (Kays et al. 2000; Kappeler et al. 2002; Fredsted et al. 2004; Cutrera et al. 2005; McEachern et al. 2007; Maher 2009a, b). Kin selection, therefore, could be an important driver of evolutionary adaptation in noncooperative as well as cooperative species (Hatchwell 2010).

Dipodomys ingens, the giant kangaroo rat, is a solitary, territorial rodent that lives and forages almost exclusively within a small burrow area of approximately 2–5 m in diameter, known as a 'precinct'. The kangaroo rats rarely create new burrows, preferring instead to take over, renovate or expand existing burrows. Only one animal usually resides within a single precinct; however, two or more animals, particularly at high densities, may sometimes occupy burrows that appear clustered within a single large precinct (Cooper & Randall 2007; J. Randall, unpublished data). Similar to many arid-adapted, small mammals, *D. ingens* is subject to fluctuations in population density through successive years (Williams 1992; Williams & Germano 1992). To date, no studies have investigated natal dispersal behaviour in *D. ingens*, but it is believed that individuals typically disperse over relatively short distances and have high lifetime site fidelity (Good et al. 1997), as is true of the closely related and ecologically similar banner-tailed kangaroo rat, *Dipodomys spectabilis* (Randall 1984; Jones 1988; Waser & Elliott 1991; Winters & Waser 2003).

Although *D. ingens* is considered a solitary species and individuals can be fiercely territorial in defending their precincts, they maintain a rudimentary social structure based on neighbour recognition

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(Murdock & Randall 2001; Randall et al. 2002). *Dipodomys ingens*' mating system has been described as promiscuous or polygynous, although reproductive tactics seem flexible and vary with changing environmental or demographic conditions, and in some cases a male and female seem to mate monogamously (Randall et al. 2002). Males expand their home ranges during the breeding season to overlap and monitor the reproductive state of potentially receptive females, while *D. ingens* females remain in their central territory (Cooper & Randall 2007).

To gain insight into the evolution of sociality we examined changes in genetic relationships and spatial associations of *D. ingens* as population densities changed from low to high densities. Because animals often have limited access to territories (precincts) at high densities, we predicted that dispersal distances of females would decrease and that philopatry would increase with increasing population density, resulting in the formation of neighbourhoods of female kin. We based this prediction on the habitat saturation hypothesis, within the ecological constraints model, which predicts that lack of suitable den sites or territories at high population densities may be a primary ecological constraint on dispersal (Emlen 1982; Solomon 2003; Schradin et al. 2010), and from prior observations that females sometimes remain close to their natal area and may live near female neighbours (Cooper & Randall 2007; J. Randall, unpublished data). We also tested the hypothesis that males avoid inbreeding with closely related females and, therefore, disperse further than females to find nonrelatives as mates (Dieckmann et al. 1999; Perrin & Mazalov 1999).

METHODS

Study Site and Animals

We conducted our research in 2004–2007 on a 115 × 190 m study site established in 1999 on the Carrizo Plain National Monument, San Luis Obispo County, California, U.S.A. The years 2005 and 2006 were characterized by higher than average rainfall and abundant vegetation, and population density increased in 2005 to a peak in May 2006 before declining rapidly to a low in May 2007 (Table 1). Such high densities of *D. ingens* had not been seen in the Carrizo Plain since 1995 (J. Randall, personal observation).

We knew positions of *D. ingens* precincts on the study site from prior studies (Randall et al. 2002; Cooper & Randall 2007). These sites remained relatively stable from year to year and commonly consisted of discrete territories of multiple burrows clustered together. We recorded the location of active precincts from the centre of burrow activity with a Garmin eTrex Legend GPS unit during each year of the study using the WGS 84 format. New coordinates were recorded when we observed large changes in activity centres.

All research was approved under permit number TE799486-4 from the U.S. Fish and Wildlife Service and a Memorandum of Understanding (MOU) from the Department of California Fish and Game to J. Randall. The San Francisco State University Animal Care and Use Committee approved all research.

Trapping, Marking and Observations

We trapped 196 individual kangaroo rats over 77 nights from 2004 to 2007 using established techniques (Randall et al. 2002; Table 1). We weighed kangaroo rats to the nearest 1 g and applied numbered eartags covered with reflectant, colour-coded tape for individual identification at night. We used night-vision goggles and infrared illumination to observe kangaroo rats to verify individual territories, home ranges, mother–offspring relationships and interactions between neighbours.

For DNA analysis we cut a small portion of the tip of one ear (about 1 × 3–4 mm). The tissue samples were placed in 95% ethanol and stored at 0 °C until transferred to the laboratory, where they were stored at −20 °C for up to 18 months before DNA extraction.

We examined the genitals of each animal for evidence of reproductive condition (Randall et al. 2002). Females were also inspected for evidence of lactation (swollen, bare or elongated nipples) or nonlactating condition (small, fur-covered nipples) and for the presence of a postcopulatory plug. We classified new, unmarked animals, with good pelage, that showed no signs of reproduction and weighed less than 120 g as juveniles (Randall et al. 2002).

Radiotracking

During the breeding season, 15 March–27 April 2006, we conducted a radiotracking study to determine the home ranges of 24 male *D. ingens*. We did not radiotrack females because prior studies showed that females remain in the core area of their territories during breeding, whereas males travel to female territories to mate (Randall et al. 2002; Cooper & Randall 2007). Following the radiotracking procedures used in Cooper & Randall (2007), we attached mouse-style transmitters (model MD-2C; Holohil Systems Ltd, Carp, ON, Canada) around the necks of kangaroo rats with stainless-steel chain-ball collars (Harker et al. 1999; Cooper & Randall 2007). Animals wore the collars for an average ± SE of 30 ± 0.93 days.

We radiotracked the kangaroo rats on a 110 × 150 m grid consisting of tall survey flags, placed 10 m apart, in the centre of the study site with handheld Yagi antennas and 12-channel receivers (AVM Instrument Co., Colfax, CA, U.S.A.). To minimize disturbance, we listened to the transmitter signal on headphones and viewed the kangaroo rats with Generation III night-vision goggles. We recorded the location of each male at 1 h intervals using a compass bearing from either a grid flag or a precinct marker on 26 nights, and took readings of day burrows 10 times. Because a kangaroo rat could easily traverse its home area in 5–10 min, we considered an interval of 1 h ample time for the animal to move to a new location, and thus we considered 1 h between telemetry readings independent.

We converted 67–86 (mean ± SE = 77.88 ± 1.29) compass locations per animal into GPS coordinates, mapped the locations on an Excel spreadsheet and estimated home ranges with the minimum-convex polygon (MCP) methods using the program Biotas (Ecological Software Solutions, LLC, http://www.ecostats.com). We calculated 95% and 100% MCP to allow for comparisons with previous

Table 1
Number and density of *D. ingens* on the study site during trapping intervals 2004–2007

Year	Dates	Adult females	Adult males	Juvenile females	Juvenile males	Total	Recaptures*	Density/ha
2004	12–19 July	37	37	1	1	76	5	35
2005	7–14 June	46	50	19	10	125	21	57
2006	23 Feb–15 May	51	72	17	14	154†	80	70
	24–30 Aug	46	59	5	5	115	105	52
2007	7–14 May	25	31	3	2	61	52	28

Individuals were assumed present during the interval between the date of first capture and the date of last capture.
* Recaptures: number of animals in the study site carried over from at least 1 year.
† Overestimate, 19 animals trapped only once.