

CAPTIVE BREEDING AND ANTI-PREDATOR BEHAVIOR OF  
THE HEERMANN'S KANGAROO RAT  
(*DIPODOMYS HEERMANNI*)

FINAL REPORT  
Incorporating the  
ANNUAL REPORT FOR THE PERIOD  
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## Introduction

The Morro Bay kangaroo rat (*Dipodomys heermanni morroensis*) was added to the Federal Endangered Species List in 1970. Because loss of critical habitat since that date has ensured a precipitous population decline, recovery efforts have included captive breeding since 1984. Roberts and Rall (1992) provide comprehensive history of the captive breeding programs (antecedent to the Berkeley program) for *D.h. morroensis*, and its surrogate, *D.h. arenae*.

The captive breeding program was moved from the National Zoological Park to the University of California at Berkeley in May 1993. The new colony was established with 20 *D.h. arenae* taken from the wild. No wild *D. h. morroensis* are available, and the last captive individual died at the NZP in November 1993. The results of the first eight months of the Berkeley program are described in Yoerg (1994); the subsequent Annual reports are Yoerg (1995) and Yoerg (1996) and Yoerg (1997).

The present report describes work completed during the last 2 years of the project during the 1997 and 1998 calendar years. Because of the program's success in developing methods for breeding *D. heermanni* in captivity, the primary focus has shifted toward the study of social behavior, communication and the development of adaptive skills. This information can be used to design optimal reintroduction protocols, as well as to guide further captive breeding efforts.

General research methods and husbandry procedures are described in detail in the previous Annual Reports.

## **Breeding**

Forty-three estrous pairings were conducted during 1997 and 1998. The pairs were comprised of six females and fourteen males. Thirty-five of the pairings occurred in the standard introduction arena (Yoerg 1994). These pairings featured four captive-born females and two wild-caught females. No copulations resulted.

Eight estrous pairings involved pairs that were housed in adjacent private rooms (Yoerg 1996). When the female is in estrous, the tube connecting the rooms is opened and the rats interact uninhibited during the night. This procedure resulted in the only copulation during the two years. The female (91) was wild-caught and had not been pregnant in captivity prior to this time. She gave birth to two pups, which she neglected. The pups died in the first day.

Because the project was coming to an end and we needed to find homes for rats currently in the colony, breeding attempts were minimal during the last year.





FATHER: 40      Wild Captive-born    Age: juv May 93

DATE CONCEIVED: 22 June 93    PLACE CONCEIVED: long box  
GESTATION HOUSING: private room

DATE BORN: 22 July 93            NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (#64) male  
transferred to Jacob's lab 2 Feb 94  
PUP B: (#65) male  
transferred to Jacob's lab 2 Feb 94  
PUP C: (#66) male  
transferred to Jacob's lab 2 Feb 94  
PUP D: (#none) female  
died 23 Aug 93, 1 mo + 1 day old  
broken femur, euthanized

---

MOTHER: 85      Wild Captive-born    Age: 1+ yr  
FATHER: 86      Wild Captive-born    Age: 1+ yr

DATE CONCEIVED: 21 Sept 93    PLACE CONCEIVED: long box  
GESTATION HOUSING: social cage

DATE BORN: 21 Oct 93            NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (#67) male  
died 1 Oct 97, 3 years, 11 months, 11 days old  
PUP B: (#68) died 26 Dec 93 2 mo + 5 days old  
presumably killed by sib or mom  
PUP C: (#none) died 10 Nov 93, 20 days old  
cause unknown  
PUP D: (#none) died 13 Nov 93, 23 days old  
cause unknown

---

MOTHER: 48      Wild Captive-born    Age: approx. 1 yr.  
FATHER: 87      Wild Captive-born    Age: 2+ yr

DATE CONCEIVED: 9 Jan 94 PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 8 Feb 94 NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (# ) found dead in burrow, 19 days of age  
cause unknown; appeared healthy 2 days before  
PUP B: (# ) ditto  
PUP C: (# ) ditto

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MOTHER: 37 Wild Captive-born Age: 1+ yrs  
FATHER: 89 Wild Captive-born Age: 1 year

DATE CONCEIVED: 12 Mar 94 PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 11 Apr 94 NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (#69) male  
died 3 Jan 95 at 8 months, 23 days old  
necropsy showed ulcerated stomach.  
PUP B: (#70) male  
died 3 Sep 96, 2 years, 4 months, 23 days old  
PUP C: (#71) male  
died 18 Aug 95, 1 year, 4 months, 7 days old  
bacterial infection?

---

MOTHER: 85 Wild Captive-born Age: 1+ yr  
FATHER: 34 Wild Captive-born Age: 1+ yr

DATE CONCEIVED: 15 Mar 94 PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 15 Apr 94 NUMBER BORN: 2

DISPOSITION OF PUPS:

PUP A: (#72) male  
  
PUP B: (# ) found dead in burrow 8 May (approx. 22 days old)

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MOTHER: 48 Wild Captive-born Age: 1 year  
FATHER: 89 Wild Captive-born Age: 1+ years

DATE CONCEIVED: 11 Apr 94 PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 11 May 94 NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (# ) found dead in burrow 22 days of age (3 days dead)  
PUP B: (# ) found dead in burrow 22 days of age (3 days dead)  
PUP C: (# ) failing at 22 days of age  
          euthanized; autopsy

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MOTHER: 52 Wild Captive-born Age: 1 year  
FATHER: 43 Wild Captive-born Age: 1 + years

DATE CONCEIVED: 10 May 94 PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 11 June 94  
NUMBER BORN: 2 stillborn

DISPOSITION OF PUPS:

PUP A: (# ) found dead on day of birth; fluid sac at neck,  
          otherwise healthy looking; mom over pups  
PUP B: (# ) found dead on day of birth; healthy looking

---

MOTHER: 33 Wild Captive-born Age: 2+ yr  
FATHER: 87 Wild Captive-born Age: 2+ yr

DATE CONCEIVED: 13 Aug 94 PLACE CONCEIVED: long box  
unfamiliar pair GESTATION HOUSING: private room  
DATE BORN: 13 Sept 94 NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (#73) male

PUP B: (#74) male

PUP C: (#75) female  
          died 13 Sept 95 at 1 year old  
          bacterial infection

PUP D: (#76) female  
          died 9 Nov 97 at 3 years, 1 month, 26 days old

---

MOTHER: 52 Wild Captive-born  
FATHER: 53 Wild Captive-born

DATE CONCEIVED: 23 Sept 94 PLACE CONCEIVED: long box

DATE BORN: 24 October 94?      GESTATION HOUSING: private room  
NUMBER BORN: 1?

DISPOSITION OF PUPS:

PUP A: (# ) found dead in burrow 3 days after expected birth  
adequate size, not decomposed

---

MOTHER: 37      Wild Captive-born  
FATHER: 84      Wild Captive-born

DATE CONCEIVED: 8 Feb 1995      PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 11 Mar 95      NUMBER BORN: 1

DISPOSITION OF PUPS:

PUP A: (#77) male  
died 12 Sept 95 at 6 months, 1 day old  
bacterial infection?

---

MOTHER: 52      Wild Captive-born  
FATHER: 87      Wild Captive-born

DATE CONCEIVED: 14 Mar 95      PLACE CONCEIVED: long box  
GESTATION HOUSING: private room  
DATE BORN: 14 Apr 95      NUMBER BORN: 1

DISPOSITION OF PUPS:

PUP A: (# ) stillborn, found half-eaten

---

MOTHER: 75      Wild Captive-born      Age: 1 yr.  
FATHER: 72      Wild Captive-born

DATE CONCEIVED: 4 May 95      PLACE CONCEIVED: connected priv. rooms  
GESTATION HOUSING: private room

DATE BORN: 4 June 95  
NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (# 1) male

PUP B: (# 2) female

died 6 Dec 95 at 6 months, 2 days old  
bacterial infection, necropsy

PUP C: (# 3) female

died 18 Aug 95 at 2 months, 14 days old  
bacterial infection, necropsy

PUP D: (# 4) female

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MOTHER: 33      Wild Captive-born

FATHER: 43      Wild Captive-born

DATE CONCEIVED: 18 May 95      PLACE CONCEIVED: long box  
GESTATION HOUSING: private room

DATE BORN: 18 June 95      NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (# ) stillborn, found half-eaten on DOB

PUP B: (# ) stillborn, found half-eaten on DOB

PUP C: (# ) alive on DOB, but small and failing;  
dead 2 days later

PUP D: (# ) alive on DOB, but small and failing;  
dead 2 days later

---

MOTHER: 85      Wild Captive-born

FATHER: 74      Wild Captive-born

DATE CONCEIVED: 18 May 95      PLACE CONCEIVED: long box  
GESTATION HOUSING: private room

DATE BORN: 18 Jun 95      NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (# 5) male

died 9 Sept 95 at 2 months, 21 days old  
bacterial infection?

PUP B: (# 6) female

died 24 June 97 at 2 years, 1 month, 6 days old

PUP C: (# 7) male

died 13 Oct 95 at 4 months, 26 days old  
priv. rm pairing w/ f85

PUP D: (# 8) male

died 28 Aug 95 at 2 months, 10 days old  
bacterial infection?

---

MOTHER: 76      Wild Captive-born  
FATHER: 71      Wild Captive-born

DATE CONCEIVED: 16 Jul 95      PLACE CONCEIVED: connected priv. rooms  
GESTATION HOUSING: private room  
DATE BORN: 17 Aug 95      NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (# 9) male

PUP B: (# ) died 9 Sep 95  
bacterial infection?

PUP C: (# ) died 10 Sep 95  
bacterial infection, necropsy

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MOTHER: 76      Wild Captive-born  
FATHER: 51      Wild Captive-born

DATE CONCEIVED: 23 Oct 95      PLACE CONCEIVED: connected priv. rooms  
GESTATION HOUSING: private room  
DATE BORN: 23 Nov 95      NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (# 10 ) female

PUP B: (# 12) female  
died 7 Apr 97 at 1 year, 4 months, 14 days old

PUP C: (# ) died 16 Dec 95 at 1 month, 24 days old

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MOTHER: 37      Wild Captive-born  
FATHER: 89      Wild Captive-born

DATE CONCEIVED: 6 Nov 95      PLACE CONCEIVED: connected priv. rooms  
GESTATION HOUSING: private room  
DATE BORN: 6 Dec 95      NUMBER BORN: 4

DISPOSITION OF PUPS:

PUP A: (# 14) male

PUP B: (# 15) male

died 24 Aug 96 at 8 months, 18 days old

PUP C: (# 16) female

PUP D: (# ) died 10 Feb 96

accidental injury

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MOTHER: 46      Wild Captive-born

FATHER: 86      Wild Captive-born

DATE CONCEIVED: 26 Apr 96      PLACE CONCEIVED: private room

GESTATION HOUSING: private room

DATE BORN: 27 May 96      NUMBER BORN: 1

DISPOSITION OF PUPS:

PUP A: (# ) stillborn

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MOTHER: 861      Wild Captive-born

FATHER: ?      Wild Captive-born

DATE CONCEIVED: ?      PLACE CONCEIVED: wild

GESTATION HOUSING: private room

DATE BORN: 3 Jul 96      NUMBER BORN: 2

DISPOSITION OF PUPS:

PUP A: (# 17 ) female

PUP B: (# 18) male

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MOTHER: y/w      Wild Captive-born

FATHER: ?      Wild Captive-born

DATE CONCEIVED:      PLACE CONCEIVED: wild

GESTATION HOUSING: private room

DATE BORN: 3 Jul 96      NUMBER BORN: 3

DISPOSITION OF PUPS:

PUP A: (# 20 ) male

PUP B: (# 21 ) male

PUP C: (# 22 ) female

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MOTHER: 91      Wild Captive-born

FATHER: 98      Wild Captive-born

DATE CONCEIVED: 8 Feb 98

PLACE CONCEIVED: private room

GESTATION HOUSING: private room

DATE BORN: 9 Mar 98

NUMBER BORN: 2

DISPOSITION OF PUPS:

PUP A: (# ) stillborn?

PUP B: (#) stillborn?

## Colony Status

### Founding Members

Number	Sex	Litters	Offspring	Date Dead	Cause
33	F	3	7	9 Nov 97	old
36	F	0	0	2 Jan 95	?
37	F	3	7	4 Dec 96	old
38	F	0	0	1 Jun 96	?
39	F	1	3	11 Jul 96	homicide
45	F	0	0	31 July 97	old
46	F	2	2	25 Oct 96	old
48	F	3	3	17 Nov 97	old
85	F	4	7	25 Nov 96	old
90	F	1	3	12 Jul 93	homicide
34	M	1	1	29 Aug 97	old
40	M	2	5	20 Dec 95	old
43	M	3	3	28 May 96	old
44	M	0	0	18 Jan 96	accidental
49	M	0	0	14 Jan 97	old
83	M	0	0	11 Oct 97	old
84	M	2	4	20 Sept 98	old
86	M	2	2	20 Feb 98	old
87	M	3	4	28 Sept 97	broken leg
89	M	3	6	12 July 98	Old

### New Wild-caught members

Number	Sex	Date Acquired	Date Dead	Cause
y-wh-o	F	8 Jun 96	4 Dec 96	?
rd-wh	F	8 Jun 96	20 Jun 96	?
861	F	8 Jun 96	Transferred	
rd-bl	M	8 Jun 96	Transferred	
or-wh	M	8 Jun 96	Transferred	
91	F	18 Aug 96	Transferred	
92	F	18 Aug 96	19 Oct 97	?
93	F	18 Aug 96	Transferred	
94	F	18 Aug 96	Transferred	
95	M	18 Aug 96	27 July 97	Injuries
96	M	18 Aug 96	Transferred	
97	F	18 Aug 96	Transferred	
98	M	18 Aug 96	Transferred	

### Captive-born Members

Number	Sex	Bred?	Date Born	Date Dead	Cause
51	M	Y	16 May 93	21 Apr 96	?
52	F	Y/N	16 May 93	15 Mar 98	old
53	M	Y/N	16 May 93	19 Oct 95	infection
54	F	N	25 May 93	23 Oct 93	?
55	F	N	25 May 93	23 July 97	?
56	M	N	11 Jul 93	Transferred	
57	M	N	11 Jul 93	Transferred	
58	F	N	11 Jul 93	16 Feb 94	accidental
59	M	N	1 Jul 93	Transferred	
60	M	N	1 Jul 93	Transferred	
61	M	N	11 Jul 93	Transferred	
62	F	N	11 Jul 93	14 Sept 98	Old
63	F	N	11 Jul 93	29 July 98	Old
64	M	N	22 Jul 93	Transferred	
65	M	N	22 Jul 93	Transferred	
66	M	N	22 Jul 93	Transferred	
67	M	N	21 Oct 93	1 Oct 97	?
68	F	N	21 Oct 93	26 Dec 93	Accidental
69	M	N	11 Apr 94	3 Jan 95	?
70	M	N	11 Apr 94	3 Sep 96	?
71	M	Y	11 Apr 94	18 Aug 95	Infection
72	M	Y	15 Apr 94	Transferred	
73	M	N	13 Sep 94	Transferred	
74	M	Y	13 Sep 94	Transferred	
75	F	Y	13 Sep 94	13 Sep 95	Infection
76	F	Y	13 Sep 94	9 Nov 97	?
77	M	N	11 Mar 95	12 Sep 95	Infection
1	M	N	4 Jun 95	7 Mar 97	?
2	F	N	4 Jun 95	5 Dec 95	Infection
3	F	N	4 Jun 95	18 Aug 95	Infection
4	F	N	4 Jun 95	11 Nov 98	?
5	M	N	18 Jun 95	9 Sep 95	Infection
6	F	N	18 Jun 95	24 Jun 97	?
7	M	N	18 Jun 95	13 Oct 95	Infection
8	M	N	18 Jun 95	28 Aug 95	Infection
9	M	N	17 Aug 95	12 May 97	?
10	F	N	23 Nov 95	Transferred	
12	F	N	23 Nov 95	7 April 97	?
14	M	N	7 Dec 95	Transferred	
15	M	N	7 Dec 95	24 Aug 96	?
16	F	N	7 Dec 95	Transferred	
17	M	N	20 Jun 96	Transferred	
18	F	N	20 Jun 96	Transferred	
20	M	N	20 Jun 96	Transferred	
21	M	N	20 Jun 96	Transferred	
22	F	N	20 Jun 96	Transferred	

### Copulatory Behavior

The copulatory behavior of Heermann's kangaroo rat has never been formally described and published accounts of copulatory patterns in kangaroo rats in general are scarce. Eisenberg and Isaac (1963) report that mounts in *D. nitratoides*, *D. panamintinus* and *D. merriami* last from 1-7 minutes. These species appear to achieve multiple mounts, although it is not clear that each such mount was accompanied by intromission. Randall (1987) confirms that *D. merriami* engages in multiple mounts, but the two females she observed were mounted for only 20 secs at a time. Behrends (1981) reported that *D. ordii* shows a single mount pattern, although 8 of 12 of the copulatory sequences he observed involved 2 mounts. Other, mostly larger, kangaroo rat species may engage only in single mount sequences: A *D. microps* male mounted once for 45 seconds (Kenagy 1976), *D. deserti* engaged in single mounts lasting one to several minutes (Butterworth 1961), and a *D. spectabilis* male mounted once for 150 seconds (Randall 1987).

Few of these reports offer detailed accounts of copulatory sequences. I present such accounts below for 13 matings occurring in the breeding colony.

## Methods

The most important criteria for selecting potential mates for estrous females was the history of mating in the colony: males that had not yet participated in mating were preferred as potential mates in order to maintain the genetic diversity of the captive population. Males that had not mated with a particular female were also preferred. However, estrous females did not usually agree with my choices and often as many as 3 different males were paired in succession with an estrous female during a single night, usually without success.

Between May 1993 and May 1995, 118 estrous pairings were conducted in the testing arena using 14 females (8 wild-caught and 6 captive-born) and 16 males (9 wild-caught and 7 captive-born). Copulation data are presented from 13 matings that occurred between 6 females (5 wild-caught and one captive-born) and 9 males (7 wild-caught and 2 captive-born). No male-female pair copulated more than once, although one female (#48) and one male (#87) each mated 3 times.

## Results

Copulations— The 13 encounters between males and estrous females that resulted in copulation shared many features but also differed markedly. Courtship always preceded copulation, and conformed to the pattern described for other *Dipodomys* species (notably Eisenberg, 1963; Eisenberg & Isaac, 1963). All pairs engaged in circling (mutual naso-anal contact), crawling over and under, and the follow-hesitate behavior pattern, a direct precursor to mounting in which the male approaches the female from behind and she hesitates, perhaps allowing contact, before moving forward. Courtship was sometimes initiated immediately but often not until several minutes had passed (mean = 241 s, SD = 384, range 1-1170 s). Pre-courtship behavior was typically friendly, although in two cases brief fights occurred before courtship.

The latency from initiation of courtship to the first mount was similarly variable (mean = 370 s, SD = 340, range = 50-875 s). Females assumed lordosis, arching the back and turning the tail to one side. During mounting the male grasped the female inguinally with the forepaws, and clasped her neck fur with his teeth. Mounts were characterized by pelvic thrusting sufficiently

vigorous to lift the female off the sand. Pairs sometimes, but not always, moved around the arena during a mount as the female allowed the thrusting to carry her and the male forward. The mean duration of a mount was 191.5 s (SD = 73.1, range = 13 - 545 s), and the male typically mounted the female 3.9 times (SD = 2.2, range = 2-8) during a mating session. The longest mount could occur either as the first (n = 2) or last mount (n = 3), or in between. The mean mount duration was inversely related to the mean number of mounts per encounter ( $r = -.773$ ,  $p < .05$ ), indicating that total mount duration was somewhat preserved (mean = 657.3 s, SD = 163.1, range = 325-887 s)

Ejaculation could not be determined reliably. Genital grooming by the male has been associated with completed ejaculation (Behrends, 1981; Butterworth, 1961; Engstrom & Dowler, 1981). Males groomed their genitals during 9 of the 13 copulatory sequences. In 5 of the 9 cases, grooming occurred after the final mount. However, 5 males also groomed in between mounts, either indicating that multiple ejaculations had occurred or that grooming can be dissociated from ejaculation.

Males always guarded females during copulatory sequences by grasping the neck fur and lying either over the female or off to one side. Males guarded females a mean of 3.6 times (SD = 1.6, range 1- 6) per mating session, with each guarding bout lasting a mean of 215.5 s (SD = 103.3). A mean total of 671.8 s (SD = 262.7) of guarding occurred during each copulatory sequence. In 11 of 13 copulations, a bout of guarding followed the last mount. The first guarding bout could follow the first mount (n = 3), the last mount (n = 2), or a mount in between. There was no correlation between the duration of mounting and the duration of guarding ( $r = 0.31$ , ns). However, as with mounting, the mean guard duration was inversely related to the mean number of guarding bouts per encounter ( $r = -.637$ ,  $p < .05$ ).

Some males, but no females, footdrummed during mating encounters. Footdrumming bouts, when they occurred, always followed the last mount (during 6 copulations by 4 different males). Post-copulatory footdrumming differed in several ways from footdrumming observed in this species in other contexts. First, post-copulatory footdrumming occurred outside the burrow; footdrumming has otherwise only been recorded from inside a natural or artificial burrow (Shier and Yoerg, 1999). Second, the males moved rapidly around the arena during post-copulatory footdrumming; drumming from within the burrow precludes this. Third, post-copulatory drumming bouts were typically longer than other drumming bouts, lasting up to 30 s.

Both sexes engaged in grooming during mating, but the behavior was more common in males. Some males groomed after the first mount, some after the last mount, some after intermediate mounts, and some males never groomed (n = 3). Given that copulatory sequences in which no grooming was observed could result in impregnation, grooming is not a reliable indicator of ejaculation in this species.

The entire courtship sequence lasted a mean of 36.1 min (2164.1 s, SD = 976.3 s, range 981-3165 s).

## **Discussion**

Copulation in Heermann's kangaroo rats differs in many respects from that reported for other kangaroo rat species. First, guarding has not been described elsewhere for kangaroo rats. Because it was a dominant feature of the copulatory sequences I observed, it is hard to believe that it might have been overlooked by the few other researchers who observed several matings of members of this genus. Mate guarding, and other mating features, such as copulatory plugs, suggests competitive mating and polygynous mating, which is consistent with other reports.

Second, mating sequences were longer than previously described for kangaroo rats. Individual mounts could last for several minutes, and the longer mount reported herein (over 9 minutes) sets a record for *Dipodomys* mating. The entire mating sequence lasted, on average, over 36 minutes from courtship through the last mounting-guarding bout. Such prolonged mating is surprising in a species that mates above ground exposed to so many predators.

Third, the footdrumming patterns displayed by some males at the end of the copulatory sequence has never been reported previously. This behavior differed markedly from that occurring in other contexts, and had a distinct celebratory flavor. It is possible that the function of this footdrumming is to advertise successful mating to other males in the vicinity.

# Effects of Rearing Condition on Sandbathing and Scent Preference

By Debra Shier

Sandbathing occurs in most Heteromyid species, including *Dipodomys heermanni* (Eisenberg 1963a). The behavior consists of digging in the substrate (typically sand), followed by rubbing the ventral or lateral portion of the body on the substrate, either once, or several times in rapid succession (For a more detailed description, see Methods).

Both the dorsal sebaceous gland and the perineal region contain scents or oils that are transferred to the substrate during sandbathing (Eisenberg 1963a). These oils not only contribute to maintaining a healthy pelage (Eisenberg 1963, Randall 1993), but are also used for olfactory communication (Eisenberg 1963ab, Randall 1991, 1994a). Female but not male, Merriam's kangaroo rats (*Dipodomys merriami*) respond to the dorsal gland secretions of males, and prefer secretions taken from familiar males to those taken from unfamiliar males (Randall, 1991). In the field, males of this species sandbathe near the burrows of estrous females; sandbathing sites may function to establish and maintain familiarity between potential mating partners (Randall, 1991).

Previous results from our colony (Yoerg, 1994, 1995, 1996) indicate that socialization reduces aggression among Heermann's kangaroo rats. Because aggression is a major impediment to successful mating, we need to understand the role of olfactory communication in regulating social interaction. A previous study has shown that captive-born males sandbathe significantly less than wild-caught males. The goal of this study is to determine how sandbathing behavior and scent are used by female kangaroo rats in managing social relationships in and out of estrus. A secondary goal is evaluating whether captivity modifies the expression of sandbathing in female kangaroo rats, and how those changes affect social interactions.

## Methods

**Subjects.** I tested eight wild-caught females and eight captive-born females. Four of the wild-caught females had been in captivity for 4 years and the others had been in captivity for 7 months, prior to this experiment. The captive-born females were born to wild-caught moms and raised in 3 x 4 m rooms until weaning.

**Housing.** All subjects were housed in either social cages or in standard 10-gallon aquaria and were maintained on the standard colony diet. Tests were conducted in March and April, 1997.

**Apparatus.** A standard 10-gallon aquarium served as the test arena. The aquarium was located in a 3 x 4 m private room with a sand-covered floor. A piece of tape placed vertically on the outside of the aquarium bisected the long side.

**Treatments.** There were three Substrate Conditions: 1) *Subject Scent*. One half of the aquarium contained only clean sand. The other half contained clean sand with 0.2 l of sand from the subject's home cage spread on top. 2) *Male Scent*. One half of the aquarium contained only clean sand. The other half contained clean sand with 0.2 l of sand from a wild caught male's home cage spread on top. 3) *Unscented*. Both halves of the aquarium were covered with clean sand only. In all conditions, substrate depth was approximately 3 cm.

Estrous assessment. A female was considered in estrus when her vagina opening is swollen to at least a “3” and perforate. Swelling was rated on a 5 point scale. Refer to Roest (1991), Thompson et. al. (1995), and Yoerg (1994). Once the female had a vaginal cast, she was considered anestrus.

Testing. Tests were 5 minutes in duration and were counterbalanced for conditions, state of estrus, and position and each rat was tested in each of the three conditions on the same night with a inter-test interval of at least 30 minutes. During tests, I sat 2 m from the testing arena, announcing behaviors into a hand-held tape recorder. Behaviors that were recorded were location in right or left side of the aquarium (i.e. scented vs. clean side in *Subject Scent* and *Male Scent* conditions), frequency and duration of sandbathing behaviors (see below), and time spent digging (moving sand with the forepaws).

Sandbathing. Two distinct topographies of sandbathing behavior occur in *Dipodomys heermanni*. Both types begin with rapid digging in the substrate with the forepaws. During **lateral sandbathing**, the rat lowers the side of its face to the ground, then the ipsilateral shoulder and flank, pushing with the hind legs in a single motion. The rat then usually resuming a standing posture, but may immediately begin another cheek, shoulder, flank sequence. During **ventral sandbathing**, digging is followed by a belly-rub, leg extension and flexion, and then the resumption of a standing posture. Again, the rat may quickly lower the head to the ground again, or may end the sandbathing bout. Ventral and lateral sandbathing maneuvers may be intermixed during a single bout, but are easily distinguished.

Data Analysis. Data from audio tapes were transcribed onto paper in real time, using a stop watch. A 4-way ANOVA was performed with Estrous Condition (anestrus vs. estrus) and Substrate Condition, Sand Type (scented vs. clean), and side (left vs. right) as within-subject factors and Rearing Condition (wild-caught vs. captive-born) as a between-subject factor. Dependent measures were: total sandbathing frequency, ventral sandbathing frequency, and lateral sandbathing frequency, time spent digging, time spent on own scent, time spent of male scent, time spent on clean scent, and number of moves across center. A one-way ANOVA was performed to test the potential differences between long and short-term captive wild-caught females.

## **Results**

Effects of Rearing Condition. Wild-caught female kangaroo rats behaved differently compared with the captive-born females (Figure 1). Wild-caught females sandbathed more overall,  $F(1,16) = 7.13$ ,  $p < .01$ , and had higher rates of both lateral  $F(1,16) = 8.28$ ,  $p < .01$  and ventral  $F(1,16) = 9.03$ ,  $p < .009$  sandbathing. Comparison of time spent digging and activity level (number of crosses) did not differ between wild-caught and captive-born females (Fs).

Effects of Estrus and Substrate Condition. Anestrous females spent approximately the same amount of time sandbathing in the sand with their own scent as they did in male scented sand. In contrast, estrous females spent more time sandbathing in male scented sand than in sand with their own scent (Figure 2). There is a significant interaction between the two,  $F(1,16) = 4.57$ ,  $p < .05$ . Again, each component of sandbathing (lateral and ventral) showed the same interaction effect,  $F(1,16) = 7.39$ ,  $p < .01$ , and  $F(1,16) = 5.01$ ,  $p < .013$ , respectfully.

Effects of Scented versus Unscented Sand. Females spent more time digging  $F(1,16) = 5.05$ ,  $p < .01$ , and sandbathed more in scented sand than in unscented or clean sand,  $F(1,16) = 4.64$ ,  $p < .01$  (Figure 3).

Six-month versus Four-year wild-caught females. A one-way ANOVA was performed to compare the behaviors of females housed in captivity for six months versus those housed for four years. There were no significant differences by age for any behavioral measure (Figure 4).

**Table 1** Scoring system for estrous condition (after Villablanca, unpublished)

Swelling of Genitals	Discharge
1 = Clitoris large, vulva not swollen	1 = none
2 = vulva slightly risen, diameter greater than clitoris	2 = dry white crust
3 = Vulva noticeably risen, longer than wide	3 = striated cast
4 = Vulva large, top flat, edges round	4 = plug (mucous, black, post-copulatory noted)
5 = Vulva taut, top flat, edges straight	5 = fresh or dried blood

\*As a female goes into estrus, the opening of her vulva is assessed. There are three categories: NP - Not Perforate, AP - Almost Perforate and P - Perforate. Behavioral estrus is correlated with a perforate condition. However, because estrous periods during each cycle can range from a few hours to a few days, females were considered in estrus when the swelling was at least a '3' and her vulva opening was almost perforate to perforate.

Figure 1 Mean frequency of total sandbathing, lateral sandbathing and ventral sandbathing by wild-caught female kangaroo rats (filled bars) and captive-born females (open bars).

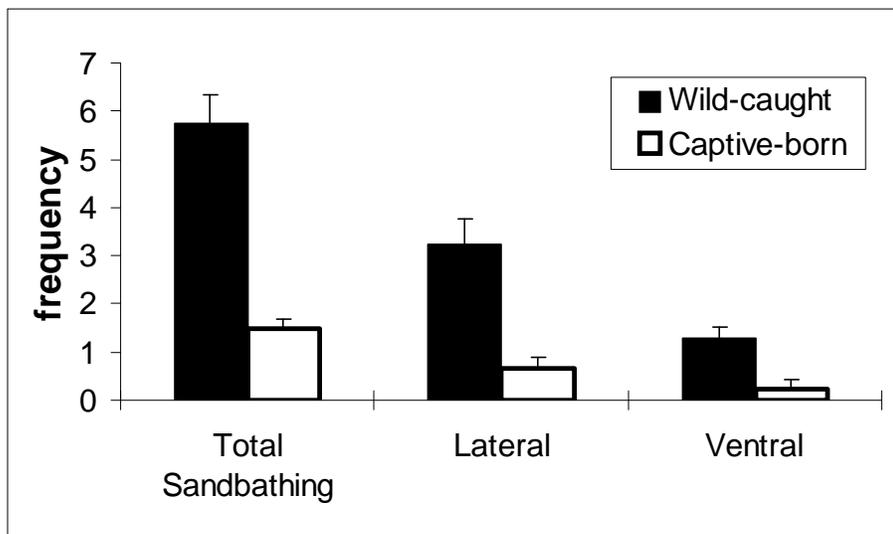


Figure 2 Mean frequency of total sandbathing by estrus (filled bars) and anestrus (open bars) females in sand containing their own scent and male scent.

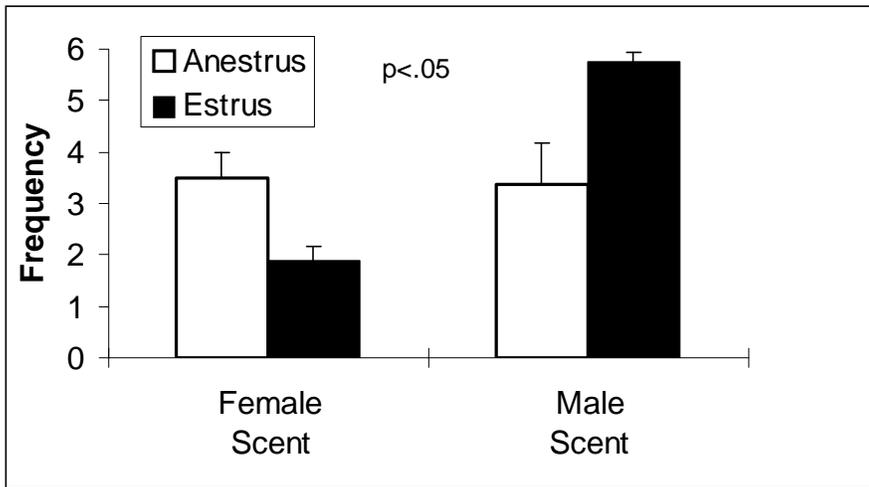


Figure 3 Mean frequency of sandbathing and duration digging in scented (filled bars) and unscented (open bars) sand.

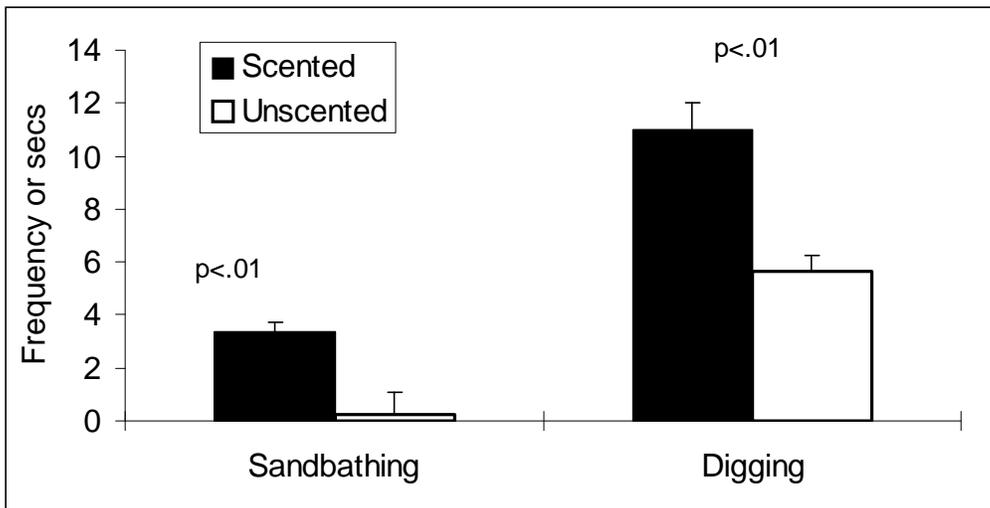
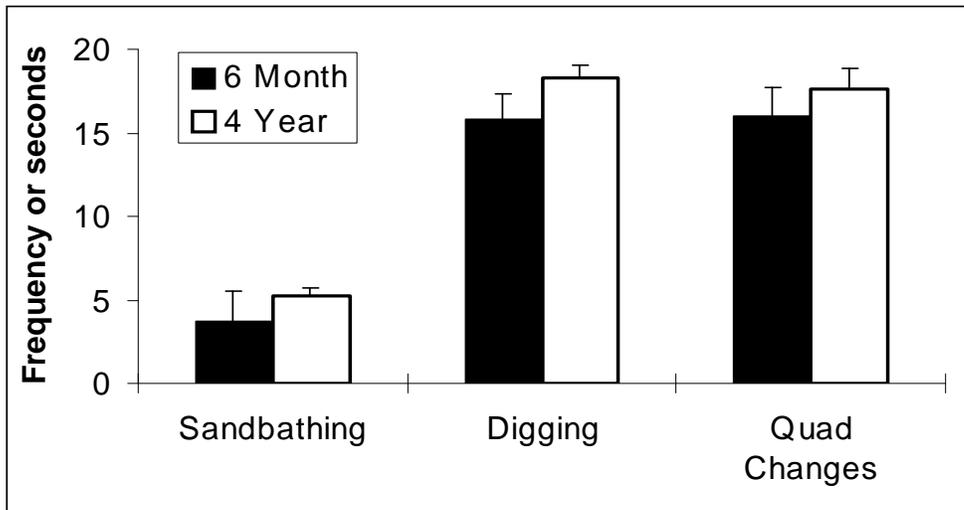


Figure 4 Mean frequency of sandbathing and quadrant changes, and duration of digging by 6 month (filled bars) and 4 year (open bars) wild-caught females.



## Discussion

The results showed that: 1) wild-caught females behaved different from captive-born females, 2) estrous females preferred to sandbathe more in male scented sand than in sand with their own scent while anestrous females had no preference, 3) females preferred scented sand to unscented sand, and 4) wild-caught females that had been in captivity for four years behaved the same as wild-caught females who were in captivity for only six months.

The wild-caught females spent more time sandbathing (lateral and ventral) than captive-born females. This behavior is more similar to sandbathing behavior of smaller kangaroo rat species and may function to communicate information in many contexts. In the wild, kangaroo rats live alone with their burrows diffusely spaced. Maintenance of their rudimentary social system may be imperative to their fitness. Because communication facilitates the maintenance of familiarity and socialization it would follow that their communication systems would be highly developed. This species uses footdrumming selectively; this indicates the potential importance of sandbathing activity as an alternative mode of communication.

In contrast, captive-born females sandbathed at significantly lower rates than the wild-caught females. Because these females were adults at the time of testing, the low frequency of behavior may be attributed to lack of experience. Behavior that mediates social organization may be purely due to experience and learned from conspecifics in the natal burrow prior to dispersal. Yoerg and Shier (in press), found that juvenile kangaroo rats shadowed their mothers in the presence of a predator and may learn appropriate behaviors from her. Although little is known of mother-pup interactions in kangaroo rats, their close association in the burrow provides abundant opportunities for social learning. This intimate association may be important for the

development of behaviors that facilitate direct fitness both through predator related responses and through the maintenance of social organization which directly relates to reproductive potential. Philopatry has been established in *D. spectabilis* (Jones, Waser, Elliot, Link & Bush, 1988; Waser and Jones, 1989) and *D. merriami* (Jones, 1989), and is suspected in other *Dipodomys* species (Randall, 1993), including *D. heermanni* (Fitch, 1948). More information on social organization should illuminate questions about social learning of communication.

In addition, estrous females sandbathed more in male scented sand than in self-scented sand. This suggests that during estrus, females may be communicating reproductive condition to males through sandbathing. The reproductive condition of females may influence the communicative signals they produce as well as their own responses to signals of conspecifics. Estrous females often emit odors that are more attractive to males than those of females in anestrus (Johnston, 1979, 1983; Brown, 1985; Huck et. al. 1989; Ziegler et al. 1993). In a complementary fashion, other studies have shown that estrous females prefer male odors (Johnston 1983; Ferkin, 1995). Because sandbathing has both a functional role of maintaining pelage and a communicatory role, conveying estrus information through sandbathing would be adaptive by increasing potential reproductive output without increasing energy expenditure. Therefore, communication through sandbathing would be a particularly important during the mating season when the communication of individual identity to gain mates is most important.

By contrast, anestrus females did prefer to sandbathe more in either scent type (male scented vs. female scented sand). Because sandbathing was also present while females were anestrus, results suggest that sandbathing may function to communicate information of other contexts, such as, individual identity, and territorial spacing.

When tested with scented versus unscented sand, females preferred to spend more time digging and sandbathing in scented sand. In the wild, females of this species have smaller home ranges and may spend more time at home than males (Shier, unpublished data). Therefore, it would follow that females may not have as much opportunity to establish new sandbathing sites and, instead, would be sandbathing more to maintain spacing and conveying information in already marked areas. This coincides with Eisenberg (1963), which showed that kangaroo rats do sandbathe at established sandbathing sites more than in disturbed areas.

Finally, wild-caught females that had been in captivity for four years did not differ from those in captivity for only six months in their levels of sandbathing, digging, or quadrant changes. This suggests that while other behaviors may be degraded due to a captive environment, it is possible that females are able to maintain the ability to establish spacing and social organization while in captivity. This is a positive finding for captive breeding studies, which intend to reintroduce animals into the wild, and suggests that the difference in behavior by captive-born females is specific to experience.

Because the results demonstrate experience-related changes in behavior, the next step would be to design studies to understand which experience support the (presumably appropriate) wild-caught responses. Captive breeding programs that intend to reintroduce kangaroo rats into the natural environment should alter housing situations to be more conducive to the maintenance of individual burrow systems and social organization. Without appropriate experience during

development, captive-born individuals may never learn to convey information that maintains social organization and reproductive opportunities would be greatly hindered.

## What footdrumming signals in kangaroo rats

By Debra Shier and Sonja Yoerg

Communication is inherently social, functioning to define, regulate and maintain interactions and relationships. We know a great deal about the role of communication in species with complex social interactions (Blumstein & Armitage, 1997, Jarvis and Bennett, 1991), but understand less about how communication functions in solitary species. Even relatively asocial animals interact at territorial boundaries, at foraging areas, or, most obviously, during mating. Because asocial species are often solitary, territorial, and aggressive, communication is more likely to occur at a distance, but may nevertheless provide the foundation for the maintenance of social structure, however elementary. The present study examines 1) the information represented in a long-distance communication signal used by an asocial species and 2) the role of this signal in regulating social interaction.

Kangaroo rats (*Dipodomys* spp.) are nocturnal, burrowing, granivorous rodents, which occupy arid habitats in southwestern North America. This genus is useful for studying communication in simple social systems because it exhibits substantial interspecific variability in both sociality and communication. Although all adult kangaroo rats are solitary, living in burrows that are diffusely spaced, the amount and nature of the contact between individuals varies among species (Jones, 1993; Randall, 1994a). Larger species are usually aggressive and highly territorial: both male and female *D. spectabilis* defend exclusive territories (Randall, 1984), and *D. ingens* show no home range overlap with same-sex conspecifics (Braun, 1985). Smaller kangaroo rats, such as *D. merriami* and *D. ordii*, sometimes engage in non-agonistic contact and home ranges of males may overlap extensively with home ranges of both sexes (Behrends et al., 1986; Randall, 1989a). Intermediate-sized species, such as *D. heermanni*, appear territorial (Tappe, 1941; Shier, unpublished observations) and are aggressive during captive encounters (Roest, 1991; Thompson, Roberts & Rall, 1995; Yoerg, 1994, 1996), although social contact mitigates that aggression (Yoerg, in press).

The variability in sociality among kangaroo rats is matched by variability in the structure, function, and importance of one of the communication modes found in *Dipodomys*: footdrumming (Randall, 1994a). During footdrumming, the rat hits the hind feet on the ground to create mechanical vibrations. One thump on the ground is a footdrum; footdrums are grouped into short bursts called footrolls. Several footrolls can be combined to make a footdrumming sequence (Randall, 1989b). All of the larger, more aggressive species of kangaroo rat exhibit long or complex footdrumming patterns (Randall, 1997). *D. deserti* emits a simple pattern of single drums emitted at a slow rate, whereas the giant kangaroo rat (*D. ingens*) produces footdrums at a higher rate presented in a single footroll. By far the best-studied footdrummer is the banner-tailed kangaroo rat, *D. spectabilis*. This species produces complex footdrumming patterns during territorial interactions with conspecifics which may respond in kind (Randall, 1984, in press). Playback experiments have demonstrated that *D. spectabilis* can discriminate between the footdrumming signals of neighbors and non-neighbors (Randall 1994b). *D. spectabilis* is also the only kangaroo rat species known to use footdrumming during encounters with predators (Randall, Hatch & Hekkala, 1995; Randall & Stevens 1987, Randall & Matocq, 1997).

In the smaller, more social kangaroo rat species footdrumming is either completely absent or infrequent and incidental (Eisenberg 1963; Randall 1993). This observation, together with the data on footdrumming in larger species, suggests that signals emitted at a distance, such as footdrumming, may substitute for direct interaction. Indeed, in comparing three large kangaroo rat species, Randall (in press) found that *D. deserti* displayed both the lowest rates of footdrumming and the highest rates of territorial intrusion and direct contact with conspecifics. *D. deserti* is also the smallest of the three species. If body size is correlated with sociality, and increased sociality is correlated with a reduction in footdrumming, what, then, of the intermediate-sized species of kangaroo rats, such as *D. microps* and *D. heermanni*? Little is known. Kenagy (1976) observed two *D. microps* males footdrumming at different times on the same female's burrow mound; one male mounted her that night. Tappe (1941) provided the only published observations of footdrumming in wild *D. heermanni*. He heard drumming while he excavated mounds and occasionally before rats emerged from their burrows. In our captive breeding colony for the endangered Morro Bay kangaroo rat (*D. heermanni morroensis*), we use *D. h. arenae* as a surrogate. We regularly hear *D. h. arenae* footdrum during mixed-sex staged encounters and, very rarely, males footdrum after copulating (Yoerg, 1996).

The role of the footdrumming signal in regulating social dynamics in *D. heermanni* is a complete mystery. The aim of the present study was to begin to understand the function of footdrumming in this intermediate-sized, territorial, aggressive kangaroo rat, and to use that knowledge to build a more complete picture of how communication and social systems are integrated within and across *Dipodomys* species.

## Experiment 1

The goal of this experiment was to begin to reveal the information contained within the footdrumming signal. We staged encounters between mixed-sex pairs of kangaroo rats and compared the behavior of both rats before and after footdrumming episodes.

### Methods

**Subjects.** The subjects were 12 wild-caught adult *D. h. arenae* (6 males and 6 females). All had been in captivity for 18 months prior to testing and were at least one year old when trapped. The rats were trapped in Sherman live traps on 14 and 15 May 1993 at a site near Callender, California (San Luis Obispo County), and transferred to the captive breeding colony at the Field Station for Behavioral Research on the University of California Berkeley campus.

Previous studies with our captive colony have revealed that footdrumming occurs at a relatively low rate in *D. heermanni*, and that rates are generally higher in females (Yoerg, 1996).

Therefore, for this experiment we selected only females that footdrummed during previous encounters with males. Males were randomly assigned to females. Four of the six males had footdrummed during mixed-sex pairings staged for other purposes (Yoerg, 1996).

**Housing.** At the time of testing, all subjects lived either in standard individual glass aquaria (45 x 25 x 28 cm) with mesh lids or in clear acrylic cages of similar size. Rats in acrylic cages were separated from neighbors by a clear, perforated barrier that allowed limited interaction. The floors of the aquaria and cages were covered with 5 cm of sand mixed with 0.1 l of clay cat litter. We gave the animals seed mix (sunflower seed, millet, rolled oats, sesame and poppy seed) and

Purina mouse breeder blocks ad libitum, and lettuce and mealworms (*Tenebrio* larvae) twice per week. Natural photoperiod, humidity and temperatures prevailed.

Apparatus. The testing arena was located in a 3 x 4 m room with three solid walls and one wall of floor-to-ceiling wire mesh covering louvered glass. Tests were conducted in a glass aquarium (30cm x 150cm x 50cm) fitted with an acrylic lid. The floor was covered with 5 cm of sand, which was sifted and thoroughly mixed, but not changed, between tests. A burrow consisting of a 30cm-long section of 5-cm ABS pipe joined to a T-section was located at either end of the box. Because kangaroo rats are nocturnal, all introductions were staged at least one hour after dark. A single 100-watt red light bulb illuminated the ceiling from above. All subjects had previously participated in mixed-sex encounters in this arena.

Procedure. The female was carried from her home cage to the testing room in her nest jar. The jar was then attached to the far end of one of the burrows. The procedure was then repeated with the male. Visual inspection of the vulva confirmed that females were anestrus at the time of testing.

An observer sat on the floor of the room 1 m from the test cage. Trials were 10 min in duration, during which time the following behaviors were continuously spoken into an audio cassette recorder: approach or leave (slow movement toward or away from the other rat), chase or flee (rapid movement toward or away from the other rat), in burrow (entire body within one of the ABS burrows), at burrow (head oriented toward burrow opening and within 3 cm while the burrow was occupied), fight (sparring, biting, or locked attack), sandbathing (rubbing side or ventrum against the sand), digging (movement of sand with forefeet, hindfeet, or both), and footdrumming (alternate striking of hindfeet on the ground). A stopwatch was used to measure the duration of the trial.

At the end of the trial, a barrier was inserted between the rats which were then encouraged to return to their nest jars. Tapes were later transcribed in real time, using a stopwatch, yielding a continuous record of behaviors of both animals to the nearest s. Trials were conducted every other day, with each pair tested three times over six days.

Data Analysis. Because females spent almost the entire 600-s trial in the burrow (mean = 587.0 ± 72.3 s) and rarely engaged in other behaviors, most data could not be normalized. When the values of a dependent variable for one sex did not vary (e.g. all females made zero approaches), mean values are reported and no statistics were conducted. Mann-Whitney *U* tests were applied to analyses of dependent measures with non-zero variance for both sexes. Repeated-measures analysis of variance was used to compare the behavior of males during the 10 s before and after footdrumming by females.

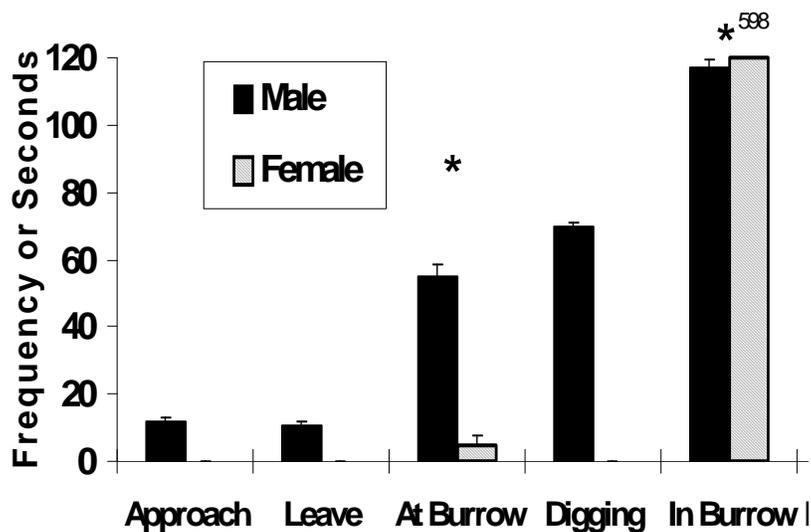
## **Results**

Kangaroo rats did not behave differently in the first, second or third trials: approach frequency,  $F(2,22) = 3.05$ ; leave frequency,  $F(2,22) = 2.28$ , duration in burrow,  $F < 1$ , duration at an occupied burrow,  $F(2,22) = 1.28$ ; duration digging,  $F < 1$ , all *ns*). For all the remaining analyses, then, we used the mean value of each of these behaviors across trials for each subject. Two pairs

each fought briefly once during one test and there was no chasing, fleeing or sandbathing during any test.

**Sex differences.** Figure 1 displays the substantial differences in the behavior of male and female kangaroo rats during the tests. Females spent approximately five times longer in a burrow than did males, Mann-Whitney  $U = 36, p < .01$ , and only females footdrummed, emitting a mean of  $6.8 \pm 3.8$  bouts of footdrumming per trial. Males approached females a mean of  $11.8 \pm 0.3$  times per trial, but females never approached males. Male rats spent more time at the entrance of the occupied burrow than did female rats and left the vicinity of females more than vice versa: at burrow,  $U = 36, p < .01$ ; leaving,  $U = 36, p < .01$ . Female kangaroo rats never dug in the sand during trials, but male rats spent a mean of  $69.8 \pm 30.0$  s digging per trial.

Figure 1 Mean responses (+ SEs) by male (filled bars) and female (striped bars) kangaroo rats during paired encounters. Mean in burrow duration for females is given above the bar. \* =  $p < .01$



**Comparison of male behavior before and after footdrumming.** Male kangaroo rats behaved differently before and after females footdrummed (Figure 2). Prior to the footdrumming signal, males more often approached the burrow occupied by the females,  $F(1,5) = 12.12, p < .02$ , spent more time at the burrow entrance of the female,  $F(1,5) = 27.71, p < .001$ , and spent more time digging than after the signal,  $F(1,5) = 9.67, p < 0.03$ . Following female footdrumming, males were more likely to move away from females,  $F(1,5) = 25.25, p < .001$ , and spend more time in their own burrow on the opposite side of the testing arena,  $F(1,5) = 7.09, p < .05$ , than they had prior to the female footdrumming. Male approach to the female burrow entrance was a reliable elicitor of footdrumming: a mean of 82.2% ( $\pm 23.1$ ) of approaches to the burrow entrance were followed within 5 s by footdrumming by the female. Although digging was more common before than after footdrumming, only a mean of 26.5% ( $\pm 19.1$ ) of digging bouts were followed by footdrumming. Digging while at the burrow entrance elicited footdrumming 55.6% ( $\pm 45.5$ ) of the time.

Figure 2 Mean frequency or duration (+ SEs) of behaviors by male kangaroo rats during the 10 s

before (open bars) and after (filled bars) a female footdrum. \* =  $p < .05$



## Discussion

All females footdrummed and did so only while in the nest jar or burrow. Male kangaroo rats never footdrummed during these interactions and behaved very differently immediately before and after female footdrumming. Before the footdrum signal, males were more likely to approach, dig, and stay near the females' burrow entrance. By contrast, after the footdrum signal, males were more likely to move away from the female and enter their own burrow. Approaching the entrance of the burrow occupied by the female almost always elicited footdrumming. This pattern of results suggests that 1) footdrumming in this species communicates unwillingness to interact, and 2) the effect of the footdrumming signal on the receiver is to cause retreat.

For this experiment we chose females with a history of footdrumming to ensure adequate data for analyses of male behaviors that occurred before and after the signal. Because males never footdrummed during Experiment 1, our findings can either be attributed to sex differences or to social status. In captive encounters, *D. heermanni* males are usually socially dominant to females: males approach, chase and initiate fights more often than do females (Yoerg, 1994, 1996). Because four of the six males tested in Experiment 1 had footdrummed during previous mixed-sex pairings, we favor the hypothesis that footdrumming depends on social status rather than sex. Nevertheless, although Experiment 1 clearly demonstrated the behavioral antecedents and consequences of footdrumming, sex differences and social status were confounded. The next experiment addresses this problem.

## Experiment 2

In this experiment, we constructed triads of kangaroo rats consisting of an adult male, an adult female and a juvenile male. Each possible dyad within the triad was then tested in a staged encounter as in Experiment 1. Juvenile males were selected as potentially subordinate individuals on the basis of field data suggesting that male mate competition is age-dependent, with older males enjoying greater success (Randall, 1991a). The goal of this experiment was to

determine how footdrumming and the antecedent and consequent behaviors are related to social status, and, if possible, to disentangle sex differences in behavior from these effects.

## Methods

The subjects were the 12 wild-caught adult *D. h. arenae* (6 male and 6 female) that were used in Experiment 1, and 6 captive-born juvenile males, 3-4 mos old. The captive-born rats had been housed with their mother and littermates in 3 x 4 m rooms from birth until about 5 weeks of age. At the time of testing all subjects lived in individual aquaria or social cages as described for Experiment 1. Subject weights were as follows: adult males, mean = 70.3, range = 58.0 - 76.9 g; juvenile males, mean = 68.9, range = 50.5 - 79.3 g; adult females, mean = 63.6, range = 60.0 - 66.8.

In order to systematically assign encounter partners, six triads consisting of one adult male, one adult female and one juvenile male were constructed. Adult male and female pairs were the same as in Experiment 1; juvenile males were randomly assigned to each pair form a triad. Within a triad, each possible dyad was tested once in random order at weekly intervals. Each subject was used in only one triad. Like the adult kangaroo rats, the juvenile males had previous experience in the testing arena, although no male-male encounters had ever been staged.

Tests were conducted using the same apparatus, procedures, dependent measures and data analysis as in Experiment 1. Analysis of variance was used to assess differences in female behavior during tests with adults and juvenile males. Pearson product-moment correlation  $r$  was used to relate body weight to footdrumming frequency.

## Results

As in Experiment 1, there were two distinct sets of behaviors exhibited in each of the dyadic encounters.

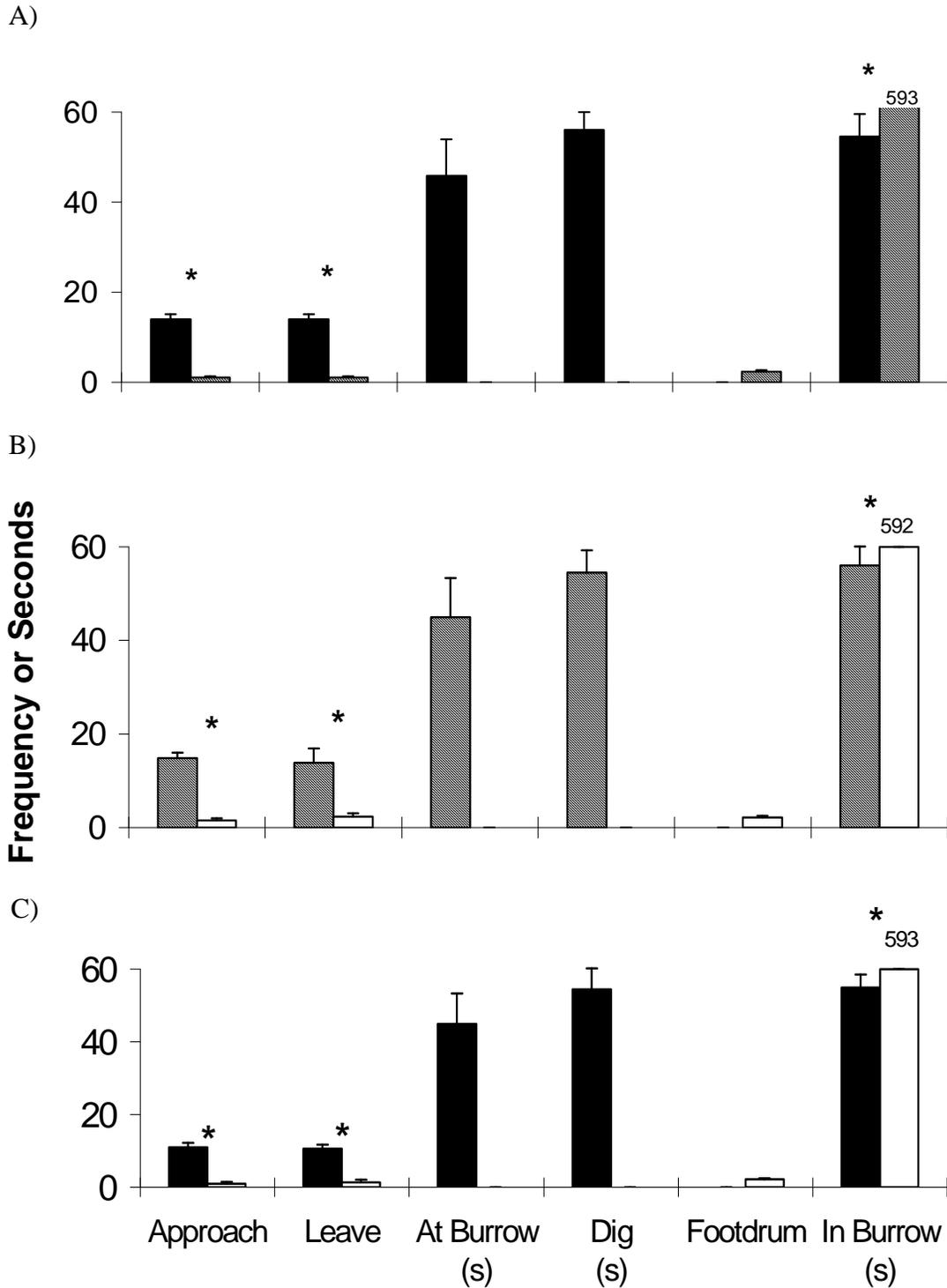
*Adult Male vs. Adult Female (Dyad 1).* When paired with adult females, adult males approached significantly more often than did the females,  $U= 36, p < .01$ . Only the males were observed digging (mean =  $78.2 \pm 24.3$  s) and at the entrance to the occupied burrow (mean =  $45.8 \pm 20.0$  s). In contrast, female kangaroo rats spent significantly more time in the burrow than did male rats,  $U= 36, p < .01$ , and only females footdrummed (Figure 4a). These results replicate those obtained in Experiment 1.

*Adult Female vs. Juvenile Male (Dyad 2).* Adult females changed their behavior in the presence of juvenile males, compared with encounters with adult males (Figure 4 b). Females approached significantly more often than did juvenile males,  $U= 36, p < .01$ , and female approach frequencies were higher during tests with juvenile males than with adult males,  $F(1,5) = 117.9, p < .0001$ . Only female kangaroo rats dug (mean =  $50.3 \pm 11.1$  s) and stayed at the entrance of the occupied burrow (mean =  $43.0 \pm 18.4$  s) during these interactions. In contrast, juvenile males spend significantly more time in the burrow than did the females,  $U= 36, p < .01$ . Female kangaroo rats stayed in the burrow longer during tests with adult males than during tests with juvenile males,  $F(1,5) = 2563.2, p < .0001$ , and only juvenile males footdrummed.

*Adult Male vs. Juvenile Male (Dyad 3).* Adult males behaved similarly during tests with females and with juvenile males (Figure 4c). Adult males approached more than did juvenile males,  $U=$

36,  $p < .01$ . Only the adult males dug (mean =  $54.4 \pm 14.1$  s) and stayed at the burrow (mean =  $45.0 \pm 20.5$  s). As in tests with adult females, juveniles spent significantly more time in the burrow than did adult males,  $U = 36$ ,  $p < .01$  and only the juveniles footdrummed.

Figure 3 Mean frequency or duration (+ SEs) during dyadic encounters by adult males (filled bars), adult females (striped bars), and juvenile males (open bars), adult males vs. adult females (dyad 1) (a), adult females vs. juvenile males (dyad 2) (b), and adult males vs. juvenile males (dyad3) (c). Mean in burrow duration for the subordinate rat is given above the bar. \* =  $p < .01$



Body size cannot account for these effects. For example, three of the six juvenile males were larger than the adult males with which they were paired. Across all subjects, footdrumming bouts per test was not correlated with body size ( $r = .120$ ,  $N = 18$ ).

*Elicitation of footdrumming.* For all three dyads, approaches to the entrance of the occupied burrow were usually followed within 5 s by footdrumming by the kangaroo rat inside, Dyad 1:  $71.4 \pm 29.4$  % of bouts at burrow; Dyad 2:  $75.3 \pm 20.8\%$ , Dyad 3:  $61.4 \pm 23.3$  %. About one-fifth of digging bouts elicited footdrumming from the rat in the burrow, Dyad 1:  $22.2 \pm .06$  % of digging bouts; Dyad 2:  $25.4 \pm 9.6\%$ , Dyad 3:  $20.4 \pm 7.4$  %. When kangaroo rats dug while at the entrance to the occupied burrow, footdrumming was likely to occur, Dyad 1:  $68.1 \pm 29.1$  % of digging bouts while at burrow; Dyad 2:  $50.0 \pm 10.5\%$ , Dyad 3:  $72.2 \pm 31.0$  %. For each of these measures, there was no effect of dyad type, at burrow:  $F < 1$ ; digging:  $F < 1$ ; at burrow while digging:  $F(2,15) = 1.31$ , *ns*.

*Latency to emerge.* Regardless of partner, adult male kangaroo rats emerged from the burrow earlier in the test than did either females,  $F(1, 10) = 1036.9$ ,  $p < .0001$ , or juvenile males,  $F(1,10) = 23.38$ ,  $p < .0001$ , Table 1. In addition, females behaved differently with adult males and juvenile males, emerging earlier in the presence of juvenile males than in the presence of adult males,  $F(1,10) = 649.13$ ,  $p < .0001$ . Juvenile males and adult males behaved similarly with different partners,  $F < 1$  for both.

Table 1. Latency to Emerge from the Burrow during Staged Encounters

Subject	Dyad Partner	Dyad	Mean latency to emerge (s) $\pm$ SD	Range
Adult Male	Adult Female	1	$20.3 \pm 14.6$	3 - 37
Adult Male	Juvenile Male	3	$25.5 \pm 9.0$	14 - 35
Adult Female	Juvenile Male	2	$98.0 \pm 47.9$	29 - 152
Juvenile Male	Adult Male	3	$413.0 \pm 268.0$	62 - 600
Juvenile Male	Adult Female	2	$497.5 \pm 214.2$	61 - 600
Adult Female	Adult Male	1	$593.0 \pm 4.1$	590 - 600

## Discussion

During paired encounters with adult male kangaroo rats, female rats behaved as they had in Experiment 1, staying in the burrow during most of the test and footdrumming in response to male approaches to the burrow entrance. After the female footdrummed, the male left the vicinity of her burrow. During tests with juvenile males, however, adult females adopted the behavior pattern displayed by adult males, while the juvenile males remained in the burrow and

footdrummed after female approaches. Juvenile male kangaroo rats responded similarly to the approach of adult male and female rats. Clearly, then, footdrumming is used by both sexes in this species in a similar way; the behavior is consistently evoked only in the more avoidant member of a pair and is followed by retreat of the other rat, regardless of sex.

### **General Footdrumming Discussion**

Footdrumming in kangaroo rats has been recorded reliably during territorial interactions and snake encounters (Randall, 1993). Playback experiments have shown that the larger species of kangaroo rat show a variety of responses to conspecific and heterospecific footdrumming patterns (Randall, 1994b, 1997; Ward & Randall, 1987). Our study, however, is the first systematic analysis of the sequence of behaviors surrounding bouts of spontaneous footdrumming in kangaroo rats. These detailed behavioral observations of both signaler and receiver are the necessary first step in decoding whatever information is present in the footdrumming signal (Hauser, 1996; Smith & Smith, 1996).

Our results demonstrate that footdrumming in *D. heermanni* is contingent upon a particular social context. When pairs of kangaroo rats are placed in the introduction arena, both rats almost always enter separate burrows. One or both rats then emerge. How do rats decide when to emerge and seek interaction with the other rat, or whether to emerge at all? Consider Experiment 2. Adult males always emerged first, then approached the female or juvenile male's burrow. Female kangaroo rats remained in the burrow for at least 30 s. If no rat had approached during that time, the female emerged and approached the other burrow, typically eliciting footdrumming from the juvenile male within. If, on the other hand, a male had approached her burrow before she had emerged, she footdrummed in response to his approach, and he usually moved away in response to the footdrumming. Therefore, the likelihood that a rat will footdrum during a given encounter is a joint function of its latency to emerge from its burrow and of the approach tendencies of the other rat.

Our findings suggest that the role of footdrumming in regulating social interaction in this species may be somewhat different than that described for the other larger kangaroo rat species. In *D. heermanni*, the signal indicates that the drumming rat, who is already inside a burrow, is reluctant to interact with the approaching rat. Loosely speaking, the signal seems to mean: leave me alone. If footdrumming carries the same message in other kangaroo rat species, it should be emitted under similar circumstances and produce a similar behavioral effect in the receiver. The available data yield a mixed answer to this question. The banner-tailed kangaroo rat, *D. spectabilis*, footdrums both inside and outside the burrow (Randall, 1984, 1997), unlike our *D. heermanni* which never footdrummed from outside the burrow. Between 9 and 25% of footdrumming episodes in *D. spectabilis* occurred as footdrumming exchanges with conspecifics, and in both *D. spectabilis* and *D. deserti*, playbacks elicited footdrumming responses in most individuals (Randall, 1984, 1997). We never heard *D. heermanni* engage in footdrumming exchanges in these tests nor in any other circumstances during the 5 year tenure of our captive colony. Curiously, *D. deserti* approached the speaker during playbacks of conspecific footdrumming; this species is the most overtly aggressive of the three larger species and visits and enters neighboring burrows frequently (Randall, 1997).

Other behaviors associated with footdrumming appear more similar across species. First, upon hearing playbacks of footdrumming sequences, *D. spectabilis* usually retreats into a burrow

(Randall, 1994, 1997), a response akin to that observed in our experiments with *D. heermanni*. *D. ingens*, the Giant kangaroo rat, was also more likely to enter a burrow during playbacks than before (Randall, 1997). Second, in all three of the larger species, footdrumming while at another rat's burrow was rare (Randall, 1997), as one would expect if footdrumming communicates reluctance to interact. Finally, our juvenile male *D. heermanni* footdrummed during more tests than did either adult males or adult females. Randall (1984) found that juvenile male and female *D. spectabilis* also drummed far more frequently than adults of either sex. This effect was independent of population density and therefore was probably unrelated to increased encounters during territorial establishment. Rather, high rates of footdrumming in juvenile rats may reflect their subordinate social status. Field data suggest that older, established males that are able to chase younger males away from estrous females may enjoy greater mating success (Randall, 1991a). Juvenile kangaroo rats may therefore use footdrumming to indicate unwillingness to escalate such a contest (Maynard Smith & Parker, 1976).

In addition to social context, the location or structure of the encounter also appears to affect the probability of footdrumming. Footdrumming occurs infrequently during mixed-sex staged encounters in our laboratory (Yoerg, 1996), but was elicited in every test but one in Experiment 1 and 2. The only difference in protocol was that in the present experiments, nesting jars from the home cage were placed in the testing arena and attached to the artificial burrows; in the standard protocol, burrows, but no nest jars, are present. In the field, footdrumming in *D. heermanni* has been recorded during burrow excavation (Tappe, 1941) and when another rat is placed near the main burrow entrance (Shier, personal observation). Similarly, no footdrumming was observed during encounters between pairs of *D. spectabilis* that were staged on one rat's territory, but away from the main burrow mound (Randall, 1989c). This species, however, footdrums reliably in response to repeated, direct territorial challenges on the burrow mound (Randall, 1984), to scratching near the burrow entrance (Randall, 1989b), and, usually, after playbacks from speakers located on or near the mound (Randall, 1994b, 1997). Taken together, these data show that footdrumming is most commonly and easily elicited from rats in their territorial core. The signal meaning, in the context described here is, therefore, perhaps closer to "Get away from my home" than "Leave me alone".

This contextual analysis of footdrumming aids in understanding how this mode of communication functions across the *Dipodomys* genus. In the smaller, more social kangaroo rat species, home ranges overlap extensively and direct encounters between rats are more common and more easily tolerated. Smaller species probably use visual assessment during encounters to regulate social interaction, although olfactory cues are also important (Randall, 1991b). Long-distance communication, such as that afforded by footdrumming, is less necessary in species with relaxed territorial boundaries. The larger kangaroo rat species are decidedly more aggressive and more territorial and may therefore use long-distance communication to manage social interaction at a safe distance. Head-thumping in subterranean mole-rats (*Spalax ehrenbergi*) appears to have evolved for similar reasons (Heth, Frankenberg, Pratt & Nevo, 1991). These communication modes may function comparably to territorial bird song, allowing low-risk information dissemination to one or more receivers (McGregor, 1993). Further studies, both in the laboratory and in the field, are required to decode the footdrumming signals emitted by various kangaroo rat species and to relate that information to ecological and behavioral variables.

What accounts for interspecific variation in social behavior and communication in *Dipodomys*? One possibility is that territoriality and, hence, social and communication systems are determined by food caching strategies. Some kangaroo rat species store food predominantly in numerous surface caches near the food source or the burrow, while other species use the burrow system itself as a larder. The smaller, more social species of kangaroo rats, such as *D. merriami* and *D. venustus*, create mostly surface caches, while the larger species, *D. spectabilis* in particular, store large quantities of seed within the burrow mound (Reichman & Price, 1993; Vander Wall, 1990). By virtue of their size, larger kangaroo rats are presumably better able to assiduously defend stores of seeds. Smaller species also depend on stored food, but rely on memory for dispersed, inconspicuous caches sites to recover, rather than to defend it (Jacobs, 1992). Territoriality and social intolerance, then, should be associated with greater dependence on larder-hoarding: the available data support this hypothesis. *D. spectabilis* is highly territorial and an ardent larder-hoarder. *D. heermanni* also appears territorial and creates mostly larder caches (Tappe, 1941). Interestingly, of the three larger species of kangaroo rat, *D. ingens* was the most socially tolerant (Randall, 1997); this species uses both scatter-hoarding and larder-hoarding strategies (Shaw, 1934).

Different patterns of resource use may allow several species of *Dipodomys* and other Heteromyid rodents to coexist within the same ecological community (Reichman & Price, 1993). Thus, body size may affect the cost of different foraging and food storage patterns, which may determine the degree of territorial defense. Territoriality, in turn, shapes the nature of social interaction and the modes of communication that are best suited to regulate it.

## Effects of familiarity on Social Behavior

By Debra Shier

Previous experiments on the meaning of the footdrumming signal suggest that it is given by the subordinate individual to indicate an unwillingness to interact (Shier, unpublished data; Yoerg, 1996). Some field data (Randall, 1989ab) support the idea that familiarity reduces aggression. Our laboratory studies, however, have shown that regular exposure to conspecifics produces a general socializing effect that is not specific to particular pairs of familiarized rats: socially-housed rats are friendlier to all other rats, not just neighbors (Yoerg, 1995). Nevertheless, familiarity may affect social interaction in more subtle ways, and footdrumming, as a behavior designed for a social purpose, may be a sensitive indicator of changes in compatibility.

The evolution of social organization has long been of interest to ethologists who study gregarious mammals (Michener 1983; Hamilton, 1963; Maynard-Smith, 1965; Trivers, 1971). Group living can increase fitness through division of labor, acquisition of resources, and avoidance of predators which leads to an increased reproductive output (Alexander, 1974; Slobodchikoff, 1988). Traditionally it has been thought that once a group is established, social structure and social behaviors may increase the benefits of aggregation (Alexander, 1974). Thus behaviors such as alarm calling (Sherman, 1977), allogrooming (Hart and Hart, 1992), dominance relationships (Bernstein, 1981), food calling and sharing (Benz, 1993; Hauser 1996), helping (Brown, 1987), and individual recognition (Wrangham, 1983) can evolve once groups are formed.

With the many benefits of social living, why are only a small proportion of vertebrate species social? One reason may be because the fitness costs associated with sociality may outweigh the benefits. Social life clearly can create increased competition for resources such as food, mates, and nest sites (Alcock, 1993, Wrangham et. al., 1993). Group living can also be detrimental to an individual's reproductive success. Subordinate members of a group often experience decreased direct reproductive fitness through suppression of estrous cycling by the dominant female (Mech, 1970, Emlen, 1982), through infanticide by other group members (Hrady, 1977, Hoogland, 1995), or through a reduction in the annual number of offspring produced (Blumstein and Armitage, 1998). Another cost of sociality is increased vulnerability to brood parasitism. Brown and Brown (1989) found that female cliff swallows occasionally dump their eggs into the nests of neighboring females. Not only does this behavior induce the parasitized female to incubate an extra egg, but it also causes her to lay fewer eggs of her own. Increased risk of infection by contagious diseases and parasites has also been found to be positively correlated with increased group size (Brown and Brown, 1989, Mooring and Hart, 1992). Finally, larger groups attract more predators (Kruuk, 1964; Pienkowski and Evans, 1982). Therefore, if sociality is to evolve, special ecological conditions are required so that the benefits of associating with others will exceed the costs.

Traditionally, studies on the evolution of sociality have sought to understand the benefits of social interactions in gregarious or eusocial species (Michener, 1983, Krebs and Davies, 1984). Yet, even solitary species interact at foraging sites and territorial boundaries, and they must cooperate to produce offspring. Communication during these interactions is essential to the formation and maintenance of these social relationships. We know a great deal about social organization and communication in highly social species, such as naked mole rats and ground-

dwelling sciurids (Blumstein & Armitage, 1997, Jarvis and Bennett, 1991), but we understand little about how social interactions are shaped and regulated in more solitary species. One proposed reason for the paucity of research on solitary species is the difficulty of observation in the wild, and the difficulties involved in studies of solitary nocturnal, mammals have caused them to be specifically neglected.

It is in the areas of the evolution of sociality and communication that these less gregarious species may be of particular interest. One way to develop a more complete understanding of social evolution is to examine a continuum of behavior from the most elementary social systems seen in solitary species to those highly developed systems of eusocial species. This sequence may provide evidence of the evolutionary steps by which social behavior evolved (Brockman, 1984). Therefore, elucidating the extent of social interactions in solitary species gives us a basis of comparison.

Although solitary species such as kangaroo rats (*Dipodomys spp.*) live alone, for all species with internal fertilization, some level of cooperation is necessary to coordinate reproduction and produce the next generation. At the very least, a basic amount of social behavior and communication is essential. Because kangaroo rats are territorial and can be aggressive, communication is more likely to occur at a distance, but it may nevertheless provide the foundation for maintenance of a social structure, however rudimentary.

Despite the costs associated with sociality, there is little doubt that one of the more important benefits of social behavior is gained through the effects of reproductive competition of group members in relation to other group members (Alexander, 1974; see also Reproductive Skew Theory, Emlen 1982). Dominant individuals in a hierarchy gain because they use their superior fighting ability, speed, and strength to secure increased access to resources, such as mates. Subordinate individuals gain because they can use the interactions and cues in the hierarchy to determine if and when to display aggression. Solitary species, on the other hand, have been shown to avoid confrontation to minimize the frequency and costs of aggressive interactions (Soderquist, 1994). Bronson (1964) noted that although woodchucks are solitary, territorial, and aggressive species, they “seemed to be organized into a complex of dominance - subordination relationships which were maintained regardless of the location of interaction”. In addition, in a study of feral cats, Leyhausen (1965) argued that the cats share environmental resources such as hunting areas and sunning spots, yet are solitary. Therefore, social responses must be more complex than simple avoidance and a more evolutionary stable strategy may be to incorporate increased levels of sociality into behavioral repertoires. The thesis presented examines how a social matrix is formed between members of a solitary species and what role communication plays in that process.

The purpose of this experiment is to examine the formation of the social relationships that shape social organization in this solitary species and to assess the role of communication in that process. This knowledge can be used to build a more complete picture of the social systems and communication in the genus.

## **Methods**

**Animals and housing.** I tested 12 wild-caught adult *D. h. arenae* (6 males and 6 females) that had been in captivity for 6 weeks prior to testing and were at least 60g when trapped. I trapped the rats in Sherman live traps on 14 - 15 August 1996 at 6 separate sites on UNOCAL property near Callender, California (San Luis Obispo County), and transferred them to the captive breeding colony at the Field Station for Behavioral Research on the University of California, Berkeley campus. Because I trapped rats at different locations >300 m apart and their home ranges were no larger than 1 m, I assumed they were unfamiliar when brought into captivity.

All subjects lived in social cages at the time of testing. I used four social cages to house the 12 recently wild-caught rats in order to separate them and prevent familiarization prior to the onset of the experiment. Previously caught *D. heermanni arenae* were housed in between test animals in order to socialize them to other *D. heermanni* and to prevent the establishment of familiarity among test animals (Yoerg, 1994, 1995, 1996). Males had only female neighbors and vice versa. In other words, two of the social cages housed all six of the recently wild caught males. The females that separated them were already members of the colony. The other two social cages housed all of the recently wild caught females, separated by males that were caught and in the colony prior to the experiment. All kangaroo rats were maintained on the standard colony diet.

Estrous condition was assessed every 2 days during the anestrus periods, and daily when approaching estrus. A female was considered in estrus when her vagina opening was swollen to at least a “3” and perforate. Swelling was rated on the same 5- point scale as in the field (See above and Table1). Once the female had a vaginal cast, she was considered anestrus. Weights were taken every month for both males and females.

### **Familiarization Tests**

**Experimental Design and General Procedures.** Every combination of dyads (both same and opposite sex pairs) were tested in a latin square design in pre-familiarization, familiarization and post-familiarization tests. All pre-familiarization tests were completed first and once complete, each dyad was familiarized and subsequently tested in post-familiarization tests the following night. For each rat, a one day inter-test interval was observed before it was paired with another individual. If a female came into estrus on a night in which she was to be familiarized, the familiarization was postponed until the first night the female was anestrus. If, however, the female came into estrus on the night of the Post-familiarization test (n= 7 out of 96 tests), the tests were suspended until the she was anestrus. On the first night of anestrus, the pair was re-familiarized in the familiarization room and the Post-familiarization test was run the following night. All combinations of same-sex pairs were tested followed by all combinations of mixed-sex pairs.

### **Pairings**

#### **Pre-familiarization**

I conducted pre-familiarization pairings in order to establish a baseline of rates of social and communication behaviors to be compared with the post-familiarization tests following a familiarization period. This is necessary in order to observe behavioral changes that may take place during familiarization and to determine what behavioral changes, if any, occur during the initial stages of social interactions.

**Apparatus.** I conducted paired encounters in a glass aquarium (30 x 150 x 50 cm) fitted with an acrylic lid in a 3 x 4m room with three solid walls and one wall of floor-to-ceiling wire mesh covering louvered glass. The floor of the testing arena was covered with 5 cm of sand, which was sifted and thoroughly mixed, but not changed, between tests, because sand imbued with the smell of other rats probably smells more realistic to a kangaroo rat than clean sand. A burrow consisting of a 30 cm-long section of 5-cm ABS pipe joined to a T-section was located at either end of the box. Because kangaroo rats are nocturnal, I staged all introductions at least one hour after dark under a single 100-watt red light bulb illuminated from the ceiling above the arena.

**Procedure.** I removed one kangaroo rat from its home cage and carried to the testing room in its nest jar. I then attached the jar to the far end of one of the burrows on the arena sand. I repeated this procedure with the other rat and the session began. I sat on the floor of the room 1.5 meters from the test cage. The rats habituated rapidly to my presence. Tests were 10 min, during which I recorded behaviors by continuously speaking into an audio cassette recorder (Table 2). I recorded footdrumming during pre-and post-familiarization tests as discussed below. A stopwatch was used to measure the duration of the trial. At the end of the trial, I inserted a barrier between the rats and encouraged them to return to their nest jars.

Tapes were later transcribed in real time with a stopwatch, to yield a continuous record of behaviors of both animals to the nearest s. I randomized the order of testing using a 6x6 Latin square design (Sokal, R. & Rohlf, F. 1995). Each female was paired with each female, each male was paired with each male, and each female was paired with each female to yield a total of 15 tests for the same sex pairings and 36 tests for the cross sex pairings.

### **Familiarization**

#### **Apparatus.**

Following pre-familiarization introductions, I conducted familiarizations in 3 x 4m rooms with three solid walls and one wall of floor-to-ceiling wire mesh covering louvered glass. Because kangaroo rats can be highly aggressive, the entire rooms as opposed to the glass aquarium were necessary in order to provide the rats sufficient space to interact. Objects were placed randomly throughout the room to serve as refuges in order to allow kangaroo rats the ability to hide and not interact (Figure 1). The floor was covered with 5 cm of sand, which was sifted and thoroughly mixed, but not changed, between tests. I determined the center point of the room and drew a circle (1 m in diameter) in the sand to serve as a guide for placement of the rats.

**Procedure.** I carried one rat from its home cage to the familiarization room in its nest jar and placed its home jar at a point on the edge of the circle. The procedure was then repeated with the other rat so as the rats' home jars were placed at the farthest distance apart on the circle. Once both rats were placed in the room, the session began. I recorded time of emergence and time at which each rat ventured outside the circle. Familiarization was determined to have taken place once both rats retreated into their respective burrows following interaction and remained there for greater than or equal to 30 minutes. The familiarization period lasted for 1-3 hours at which time each rat was removed from the room and returned to its home cage.

### **Post-familiarization**

Post-familiarization tests were conducted in order to measure the change in behavior, if any, due to familiarization. If behavior changes following familiarization, it will give us an idea of the

variables involved in the formation of a social organization, i.e. if a dominance hierarchy is formed, how quickly it is formed, and how stable it may be over time. Post-familiarization Apparatus and Procedure follow the same guidelines as the Pre-Familiarization Introductions.

### Data Analysis

Based on the outcome of the dyadic encounters sociometric matrices were constructed for pre and post-familiarization tests. These matrices were reordered according to the procedure described by De Vries et al. (1993) that can be summarized as follows: 1) the dominant member of each dyad was determined on the basis of the proportion of dyadic encounters that each individual won; 2) for each dyad a score of 1 is attributed to the dominant rat and 0 to the subordinate one. In the case of a tie or when no interactions occurred for a given dyad, both members were attributed a ½ score; 3) the scores for each individual were summed and the individuals were ordered according to their scores, 4) the relative order between adjacent rats in the matrix was reversed if the dominance relationship between them contradicted the order based on their total scores.

In order to characterize the social structure formed the following variables were computed: (a) Landau's linearity index ( $h'$ ) (corrected for unknown relationships) (Landau, 1951, DeVries, 1995), (b) Kendall's coefficient of linearity ( $K'$ ), which may differ from  $h'$  when  $N$  is an even number, (c) the number of circular triads ( $d$ ) on which the statistical significance of the linearity found can be assessed from Appleby (1983); (d) the number of percent of unknown (zero or blank) relationships; (e) the number of percent of one-way relationships; (f) a chi-square goodness-of-fit test was used to test the deviation of these proportions from what could be expected if both dominant and subordinate members of a dyad had equal probabilities of initiating an agonistic interaction.

In the analysis of the social structure an individual was classified as the winner of an interaction if it initiated more fights, lunging at, approaching, or chasing its opponent. The loser of the encounter was the rat that left or fled following an approach or a chase or was supplanted without retaliation.

The effects of size and sex on the rank order of the individuals were assessed using a two-way ANOVA. The kangaroo rats were classified into two categories for sex (males vs. females) and three size categories (4 large vs. 4 medium vs. 4 small).

In order to determine changes in behavior following a familiarization period, an ANOVA using random effects individual terms was used to control for repeated testing of individuals. In addition, a non-parametric Wilcoxon tests were employed and the results compared to the random effects ANOVA.

Finally, Spearman correlations ( $Rho$ ) was used to determine how the difference in dominance rank was correlated with the difference in behavior of individuals in the post-familiarization test.

### Results

*Establishment of Dominance hierarchy.* Unfamiliar kangaroo rats established a near linear dominance hierarchy in their first interaction during the pre-familiarization tests,  $N=12$ , known dyads = 97%,  $X^2 = 66.87$ ,  $df = 20.6$ ,  $p < 0.0001$ ,  $K = 0.87$ ) thus justifying the arrangement of

dyads into a rank order dominance matrix (Figure 2). The ranking of individuals showed 3 (5%) dyadic relationships that did not fit the linear hierarchy. These occurred between individuals of similar social status (average difference of rank 2.67). The actual number of circular triads compared to the expected number were 9.25 and 55, respectively. Out of 66 relationships, two (3.03%) were unknown which indicate equal numbers of wins and losses and 96.97% were one-way relationships. Following the familiarization period, kangaroo rats establish a almost perfectly linear dominance hierarchy,  $n=12$ , known dyads = 100%,  $X^2 = 74.13$ ,  $df = 20.6$ ,  $p<0.0001$ ,  $K = 0.97$ ) with no unknown relationships (Figure 3).

There was no effect of body size or sex on dominance rank ( $F<1$ ) or sex ( $F<1$ ), both ns, and therefore neither size nor sex are a good predictor of rank order.

*Pre-familiarization vs. post-familiarization.* Figure 4 displays the substantial differences in the behavior of kangaroo rats following a familiarization period. Rats spent significantly less time fighting in the post-familiarization encounters  $F(1,5) = p<0.0001$  as compared to the pre-familiarization encounters, and significantly more time footdrumming  $F(1,5) = 5.80$ ,  $p<0.0001$ , sandbathing  $F(1,5) = 3.53$ ,  $p<0.005$ , in the burrow  $F(1,5) = 2.86$ ,  $p<0.01$ , at the burrow entrance of the other rat  $F(1,5) = 2.35$ ,  $p<0.04$  and approaching  $F(1,5) = 3.71$ ,  $p<0.003$ .

*Rank difference correlations.* Rank difference between individuals was positively correlated with the difference in both footdrumming ( $R_s = 0.630$ ,  $p<0.0001$ ) and in burrow ( $R_s = 0.712$ ,  $p<0.0001$ ). Rank difference was negatively correlated with sandbathing ( $R_s = -0.659$ ,  $p<0.0001$ ), at burrow ( $R_s = -0.699$ ,  $p<0.0001$ ), digging ( $R_s = -0.631$ ,  $p<0.0001$ ), and approach ( $R_s = -0.598$ ,  $p<0.0001$ ).

**Table 1**

Scoring system for estrous condition (after Villablanca, unpublished)

Swelling of Genitals	Discharge
1 = Clitoris large, vulva not swollen	1 = none
2 = vulva slightly risen, diameter greater than clitoris	2 = dry white crust
3 = Vulva noticeably risen, longer than wide	3 = striated cast
4 = Vulva large, top flat, edges round	4 = plug (mucous, black, post-copulatory noted)
5 = Vulva taut, top flat, edges straight	5 = fresh or dried blood

\*As a female goes into estrus, the opening of her vulva is assessed. There are three categories: NP - Not Perforate, AP - Almost Perforate and P - Perforate. Behavioral estrus is correlated with a perforate condition. However, because estrous periods during each cycle can range from a few hours to a few days, females were considered in estrus when the swelling was at least a '3' and her vulva opening was almost perforate to perforate.

**Table 2**

Behavior	Description
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Approaches/Leaves	animal moving toward/away from the other animal
Chase/Flee	rapid movement toward/away from the other animal
In burrow	entire body within one of the burrows
At burrow	head oriented toward burrow opening while burrow occupied
Fight	sparring, biting, or locked attack
Jump/Avoid	animal jumps upwards and back while facing the other
Sandbathing	rubbing side, or ventrum against the sand
Digging	movement of sand with either forefeet and/or hindfeet
Footdrumming	alternate striking of hindfeet on the ground

Figure 1

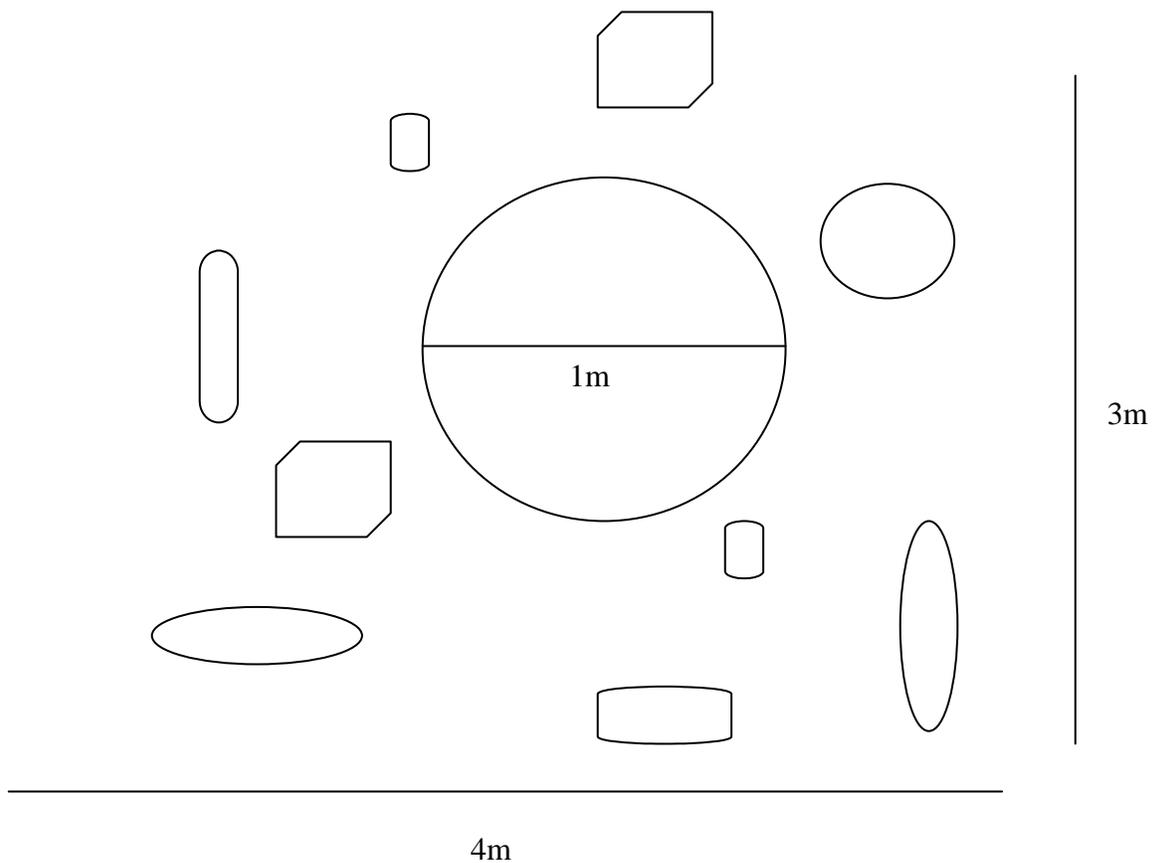


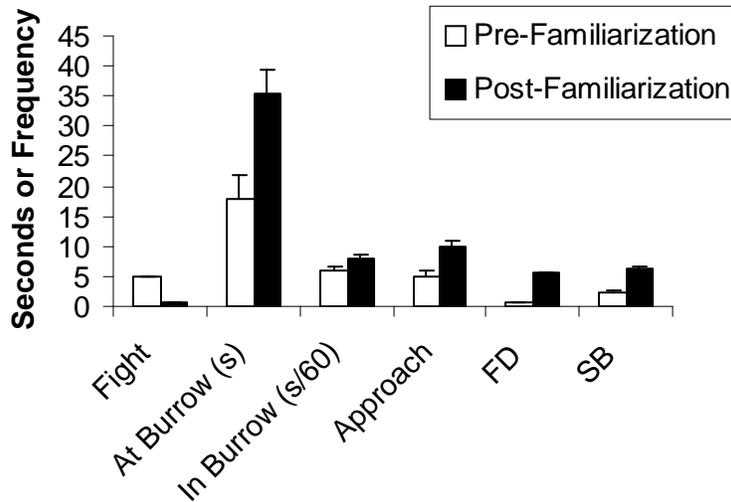
Figure 2

	ME	FB	MD	FE	FD	MB	FC	FF	MA	MC	FA	MF	Total
<b>ME</b>	*	1	1	1	1	1	1	1	1	1	1	1	11
<b>FB</b>	0	*	1	1	1	1	1	1	1	1	1	1	10
<b>MD</b>	0	0	*	1	1	1	<u>0</u>	1	1	1	1	1	8
<b>FE</b>	0	0	0	*	1	<u>0</u>	1	1	1	1	0	1	6
<b>FD</b>	0	0	0	0	*	1	1	1	1	1	1	1	7
<b>MB</b>	0	0	0	<u>1</u>	0	*	1	1	1	1	1	1	7
<b>FC</b>	0	0	<u>1</u>	0	0	0	*	1	<u>0</u>	1	1	1	5
<b>FF</b>	0	0	0	0	0	0	0	*	1	1	1	1	4
<b>MA</b>	0	0	0	0	0	0	<u>1</u>	0	*	1	1	1	4
<b>MC</b>	0	0	0	0	0	0	0	0	0	*	1	1	2
<b>FA</b>	0	0	0	0	0	0	0	0	0	0	*	0	0
<b>MF</b>	0	0	0	0	0	0	0	0	0	0	0	*	0
<b>Total</b>	0	1	3	4	4	4	6	7	7	9	9	10	64

Figure 3

	ME	FB	MD	FD	MB	FE	FC	FF	MC	MA	FA	MF	Total
<b>ME</b>	*	1	1	1	1	1	1	1	1	1	1	1	11
<b>FB</b>	0	*	1	1	1	1	1	1	1	1	1	1	10
<b>MD</b>	0	0	*	1	1	1	1	1	1	1	1	1	9
<b>FD</b>	0	0	0	*	1	1	1	1	1	1	1	1	8
<b>MB</b>	0	0	0	0	*	1	1	1	1	1	1	1	7
<b>FE</b>	0	0	0	0	0	*	1	1	1	1	1	1	6
<b>FC</b>	0	0	0	0	0	0	*	1	1	<u>0</u>	1	1	4
<b>FF</b>	0	0	0	0	0	0	0	*	1	1	1	1	4
<b>MC</b>	0	0	0	0	0	0	0	0	*	1	1	1	3
<b>MA</b>	0	0	0	0	0	0	<u>1</u>	0	0	*	1	1	3
<b>FA</b>	0	0	0	0	0	0	0	0	0	0	*	1	1
<b>MF</b>	0	0	0	0	0	0	0	0	0	0	0	*	0
<b>Total</b>	0	1	2	3	4	5	7	7	8	8	10	11	66

Figure 4



## Discussion

Unfamiliar kangaroo rats established a near linear dominance hierarchy almost immediately upon introduction. Following familiarization the dominance hierarchy becomes linear with only one relationship out of place. Though the current mechanism for the establishment of the hierarchy is not known, it is clear that body size and sex are not important factors. Current understanding of social behavior suggests that only social species establish stable dominance hierarchies. However, it is clear that solitary kangaroo rats are able to establish a stable linear dominance hierarchy and suggests that solitary species may be preadapted for sociality and therefore have the potential to be behaviorally flexible in response to environmental variability. Though kangaroo rats live alone and their burrows are diffusely spaced, in years where population densities are extremely high, solitary kangaroo rats have been observed to live close together (i.e. multiple males in a precinct Randall, 1997).

Following familiarization, several behaviors changed. Kangaroo rats were much less likely to engage in fights, but were more likely to communicate through sandbathing and footdrumming. They were also more likely to approach, dig, spend time at the burrow entrance of the other rat and were less likely to interact as evidenced by the time spent in the burrow. This suggests that initial assessment happens very rapidly and is a good indicator of the strategy the rat will eventually use when interacting with a particular conspecific.

Difference in rank was highly positively correlated with the difference in footdrumming and in burrow. This indicates that low ranking rats, footdrummed and spent significantly more time in burrow than other rats. Shier and Yoerg, 1999 have shown that footdrumming in this species is a communicative signal that means approximately "Get away from my home". Therefore, an effective strategy for subordinate rats may be to stay in their burrow and footdrum, thus decreasing the likelihood of costly fights. In addition, difference in rank was highly negatively

correlated with the difference in sandbathing, time spent at the burrow entrance of the other rat, digging and approaching. This indicates that rats that were higher ranking spent more time sandbathing, at the burrow entrance of the other rat, digging and approaching which can be interpreted as more interactive. There seemed to be three strategies. The more dominant individuals emerged from their burrows quickly and began to approach, dig, etc. The rats in the middle of the hierarchy switched their strategy dependent on their partner. The subordinate rats almost always stayed in their burrows and footdrummed.

## **General Discussion**

Over the final two years of the project, we were able to deepen our understanding of pair compatibility through detailed analysis of copulatory, communication, and social behavior. Copulatory behavior in Heermann's kangaroo rat appears more complex than previously thought. Kangaroo rats of this species engage in multiple mounts (~191 s), extensive mate guarding and communicative displays of footdrumming following copulation.

Studies of communication in this species elucidated interspecific differences in the genus. Female Heermann's kangaroo rats in estrus preferred to spend more time and sandbathe in male scented sand to clean sand or sand imbued with their own scent. These results suggest that females may be communicating estrous condition to males through sandbathing.

Footdrumming in this species is also different than documented accounts of footdrumming in other *Dipodomys spp.*. Heermann's kangaroo rats footdrum primarily within their burrow and the signal appears to mean "Get away from my home". This suggests that subordinate rats that are reluctant to interact are doing the majority of footdrumming in this species.

Finally our results suggest that solitary kangaroo rats are more social than previously thought. They are able to establish stable linear dominance hierarchies almost immediately upon introduction to an unfamiliar rat. It is possible that with respect to social behavior, solitary kangaroo rats may be preadapted for sociality and therefore have the potential to be behaviorally flexible in response to environmental variability. This information may be particularly important for housing protocols and mating strategies and may become imperative in the coming years as kangaroo rat natural habitat continues to be fragmented and degraded.

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