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Source: *Journal of Mammalogy*, Vol. 65, No. 2 (May, 1984), pp. 338-341
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/1381177
Accessed: 31-07-2016 15:13 UTC

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Submitted 29 June 1983. Accepted 27 September 1983.

J. Mamm., 65(2):338–341, 1984

BREEDING OF CAPTIVE KANGAROO RATS, *DIPODOMYS MERRIAMI* AND *D. MICROPS*

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The kangaroo rats (*Dipodomys*, Heteromyidae) constitute a genus of some 20 species endemic to arid and semiarid habitats of North America. Although they have been the objects of a great deal of ecological and physiological study, kangaroo rats have not become established laboratory animals, primarily because they have proven difficult to breed in captivity. According to published reports, a number of efforts to achieve laboratory breeding have produced only sporadic success (Chew, 1958; Chew and Butterworth, 1959; Butterworth, 1961; Eisenberg and Isaac, 1963); the most successful breeding program hitherto reported upon (Day et al., 1956; Egoscue et al., 1970) has produced 30 litters of *D. ordii*. In 1978, we began close monitoring of the estrous cycles of captive *D. microps* and *D. merriami*, and by the methods here described have maintained successful laboratory breeding colonies of these two species.

Maintenance.—The progenitors of the colony of *D. microps* were captured in shadscale (*Atriplex confertifolia*) scrub in the Owens Valley in the vicinity of Big Pine, Inyo Co., California. Kenagy (1973*b*) described the habitat. Progenitors of the colony of *D. merriami* were captured either in the same shadscale scrub locality (the source of 17 wild-caught breeding females and one stud male) or in creosote bush (*Larrea tridentata*) scrub near Palm Springs, Riverside Co., California (the source of 30 wild-caught breeding females and seven stud males). Parameters of reproduction in captivity did not differ between *D. merriami* from the two localities.

We maintain kangaroo rats individually in clear Plexiglas cages (33 by 17 by 28 cm) with a 0.5 l cardboard tube or can for shelter. Each cage is filled to a depth of about 3 cm with washed sand which is changed at 3-week intervals. The two species are housed in separate rooms, maintained at approximately 22°C with a 13-h day length (lights on at 22:00, off at 11:00). Mated females, presumed to be pregnant, are given short-fiber cotton for nesting material. Pups are weaned and housed individually at 25 days of age.

A diet of sunflower seeds, wheat, and rolled oats is provided ad lib., and spinach or lettuce is provided daily. Water is available ad lib., although it is little used by *D. merriami*. We supplement the diets of pregnant and lactating females of both species with ad lib. powdered skim milk. *D. merriami* is a predominantly granivorous species in nature, and is well known for its capacity to thrive without free water (Schmidt-Nielsen, 1964). However, succulent vegetation is eaten when available and may be necessary for reproduction (Reichman and Van De Graaf, 1975; Soholt, 1977); this species evidently breeds opportunistically after rainfall (Beatley, 1969; Kenagy, 1973*b*). Owens Valley *D. microps*, by contrast, are predominantly folivorous in nature and cannot survive on the same dry diets as *D. merriami* (Kenagy, 1973*a*; Csuti, 1979). Utilizing a diet of leaves of perennial shrubs, *D. microps* is a more regular annual breeder in the wild than is *D. merriami* (Kenagy, 1973*b*).

Laboratory mating procedures.—Kangaroo rats are aggressively solitary rodents and cannot be maintained in pairs. Sexual access must be confined to the female's brief estrous period, and even then must be closely monitored to avoid dangerous fights. The estrous cycle is modally 12 days in length in *D. microps*, 13 in *D. merriami*, with the potentially receptive phase of the cycle confined to a single day. This period of behavioral estrus coincides with visible changes in the female genitalia: the vulva becomes slightly swollen over the course of some two to five days, and maximal swelling is typically coincident with opening of the vaginal orifice and behavioral receptivity. Slight vaginal bleeding may precede estrus by two to three days, and a vaginal cast of pale, crusty material indicates that estrus has just passed. Characteristics of the cycle will be described in more detail in a subsequent paper.

TABLE 1.—*Frequency distribution of sizes of laboratory-born litters in* Dipodomys microps *and* D. merriami.

Species	Litter size 1	2	3	4	5	6
Dipodomys microps						
Wild-conceived		7	1	3		
Lab-conceived	5	16	15	2		
Dipodomys merriami						
Wild-conceived			5	4		1
Lab-conceived	13	59	35	11	1	

The procedures that have led to successful matings are distinct for the two species. The most successful procedure for *D. microps* has involved brief encounters in a neutral arena. Severe aggression soon ended all attempts to conduct mating trials in either animal's home cage. Forty-six matings took place in a semicircular arena of 120 cm diameter, containing a sand substrate and tin cans into which harried individuals could retreat. A female in vaginal estrus and a sexually vigorous male were simultaneously introduced into the arena and were observed for up to 60 minutes (Behrends, 1981). Female *D. microps* are highly aggressive when not receptive and even after copulation, when attacks on males may be fatal if the animals are not quickly separated.

Dipodomys merriami, by contrast, very rarely evinced sexual interest during similar encounters in a neutral arena, nor did they exhibit aggression as severe as in *D. microps*. Accordingly, a system of more prolonged mutual access was arranged. All successful matings in *D. merriami* took place in a linked cage apparatus; two adjoining clear Plexiglas cages (33 by 17 by 28 cm), occupied by the two kangaroo rats and each containing its own refuge, were connected by a 30 cm tunnel blocked by a guillotine door. When the female attained vaginal estrus, the door was lifted and the animals were given continuous access to one another. After 24 h of access, the female was examined for a copulatory plug or sign of termination of vaginal estrus; in the event of either criterion, the pairing was terminated. *D. merriami* appears to be more socially tolerant than other kangaroo rat species that we have maintained (*D. microps, D. agilis, D. deserti*). Paired animals may huddle peacefully rather than fighting. In the present procedure, fighting was rarely observed. Nevertheless, out of about 800 linked-cage pairings, we have found the male killed on four occasions, the female once, and one animal of each sex severely wounded.

Several dozen *D. merriami* males were screened for stud service, and most exhibited no sexual interest, even with females who quickly proved receptive to a reliable stud. Only ten males, eight wild-caught and two laboratory-born, have copulated in our laboratory. These successful males exhibited persistent interest in females, including even those who were not receptive. Successful and unsuccessful adult males were not reliably discriminable by degree of testicular development or other morphological characteristics.

Reproductive performance.—Between May 1978 and May 1981, 119 *D. microps* pups were born to 43 females in 49 deliveries, for a mean litter size of 2.4 (Table 1). Eleven litters were conceived in the wild and 38 in captive matings involving 10 stud males. Between April 1978 and April 1983, 322 *D. merriami* pups were born to 51 females in 129 deliveries, for a mean litter size of 2.5 (Table 1). Females of both species have six teats, but litter sizes very rarely exceeded four. Ten wild-conceived *D. merriami* litters (mean size 3.7) were significantly larger ($t_{127\ df} = 4.75$; $P < 0.001$) than 119 laboratory-conceived litters (mean size 2.4). The lower productivity of lab matings cannot be attributed to inbreeding: related animals were not mated.

Potentially pregnant females were checked for pups daily. Duration of pregnancy in *D. microps* was measured from the time of observed copulation until pups were first present; the recorded gestation period might therefore be overestimated by up to one day in the event that birth occurred shortly after the daily check. For 33 recorded gestation periods, the modal duration was 31 days (Table 2). Estimation for *D. merriami* is more problematic since most matings were not observed; estimates are from the day of mating to the day of birth and might be in error by plus or minus one day. The modal duration for 65 pregnancies in which the date of copulation was certain is 33 days (Table 2); for three pregnancies timed from observed matings, the durations were 33, 34, and 34 days. Duration of gestation in the smaller species, *D. merriami*, is significantly longer than in *D. microps* ($t_{96\ df} = 8.77$, $P < 0.001$).

Kangaroo rats do not appear to have a postpartum estrus. In our laboratory, the shortest interval between births of successfully reared pups in *D. merriami* has been 63 days; when the nursing litter is removed at 25 days of age, females may conceive again as early as four days later.

TABLE 2.—*Frequency distribution of gestation periods in* Dipodomys microps *and* D. merriami.

Species	Duration of gestation (days)					
	30	31	32	33	34	35
Dipodomys microps	1	21	9	—	2	
Dipodomys merriami			22	31	11	1

In field study of *D. merriami*, involving intensive retrapping and radio tracking of individuals, we have recorded several cases of females producing successive litters at intervals of about two months, with the minimum interval lying between 45 and 50 days. One female who lost a litter in the first week of lactation exhibited vaginal estrus between 10 and 14 days postpartum; one female who raised her litter to weaning exhibited vaginal estrus at 23 days postpartum.

It is clear that the continued presence of pups does not prevent the resumption of maternal cycling in *D. merriami*. Eighteen lactating females were examined daily from 18 days postpartum until first vaginal estrus, with pups being removed at day 25. The minimum postpartum latency to next estrus was 22 days (i.e. while pups were still present) and the median was 29 days. An additional seven females were left with their pups for 40 days, rather than the usual 25, but resumed cycling just the same; the minimum postpartum latency to next estrus was 23 days, and the median was again 29 days. Nursing behavior declines sharply at three weeks and litters left with their mothers beyond 25 days of age have not been observed to nurse at all.

In *D. microps*, changes in the appearance of the external genitalia were monitored in 13 mothers, beginning at 25 days postpartum, when pups were weaned. The first vaginal estrus occurred at 34.2 ± 2.9 days postpartum (range 29 to 39). Four of these females were paired with a testosterone-treated castrate at this first postpartum estrus, and one copulated.

The maximal litter production by a single female *D. merriami* in our laboratory has been eight litters, each consisting of two pups, over a 23-month period; maximal offspring production has been 25 pups in seven litters in 22 months. Potential productivity is certainly higher, since we have made no effort to breed individuals at consistently minimal intervals and since the female reproductive lifespan extends from about two months of age into at least the fifth year.

Reproductive maturity.—Laboratory-born female *D. merriami*, when weaned and separated at 25 days of age, typically exhibit a prolonged period (about 4 to 30 days) of vulvar swelling, often accompanied by discharges that are not characteristic of the swollen phase of mature estrous cycles. This early swelling is not associated with the opening of the vaginal orifice that accompanies the brief swelling of mature cycling estrus. Young females in this state are evidently not sexually receptive, but fertile mating can occur at the first cycling estrus. The youngest mother in our laboratory conceived at 64 days of age and gave birth at 97 days.

Our field records suggest somewhat earlier sexual maturity. One young female, who was first marked as a juvenile when accompanying her mother in early departures from the natal burrow, produced a first litter which must have been conceived when she was between 40 and 50 days old. A second female exhibited not only vulvar swelling but a copulatory plug at approximately 25 days of age, although no litter was produced.

This research has been supported by National Research Council of Canada Grant A7026 to M. Daly. Laboratory assistance was provided by D. Eggers, M. Kasprowicz, T. Mark and J. Yanch. Thanks are extended also to W. Mayhew, A. Muth, and V. Muth for permitting and facilitating field work at the University of California Boyd Deep Canyon Desert Research Center.

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Submitted 15 June 1983. Accepted 23 November 1983.

J. Mamm., 65(2):341–342, 1984

COMMENTS ON REPRODUCTIVE SENESCENCE AMONG FEMALE JAPANESE MACAQUES

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Wolfe and Noyes (1981) reported on the relationship between age and fertility among female Japanese monkeys (*Macaca fuscata*) of the Arashiyama West troop. One analysis they performed revealed that old females (18 years and older) of the troop during 1976–1979 had a significantly lower reproductive rate than did the young females (defined as 6 to 17 years of age) of 1979. A computational error in that analysis should be brought to attention: Wolfe and Noyes failed to subtract births to 5-year-old females from the total births to young females (as they had done in all similar analyses). This error has a bearing on the conclusions drawn by Wolfe and Noyes. Young females during 1979 produced 37 (not 42) infants, and the number of females of this age class was 59 (not 58). These corrected figures yield a birth rate that is not significantly different from that of Arashiyama West old females during the period (1976–1979) considered by Wolfe and Noyes (1981) ($G = 0.72$, $P > 0.30$, d.f. = 1). As a result, none of the comparisons between Arashiyama West old and young females during periods discussed by Wolfe and Noyes (1981) yielded significantly different birth rates.

A further point should be clarified to avoid conflicting published statements on the Arashiyama troop. Wolfe and Noyes (1981) stated that between arrival in Texas (in February 1972) and December 1973, the Arashiyama troop experienced a 29% decrease in size, "from 184 members including those born during the 1972 birth season to 129 members just before the 1973 (sic) birth season," (p. 700). Wolfe and Noyes (1981) clearly meant to refer to the 1974 birth season here because December 1973, the point in time they were considering, came after the 1973 birth season. It is not clear to us how Wolfe and Noyes arrived at their figure of 184 monkeys. The troop produced 27 infants in 1972, and 150 monkeys were transported to Texas originally. At no time during the stated period did the troop actually number 184 individuals: in the first six months in Texas the troop decreased from 150 to 146 monkeys, through a loss of 31 individuals and recruitment through births of 27 infants in the 1972 birth season (Clark and Mano, 1975). Between transplantation in February 1972 and February 1974, just prior to the 1974 birth season, the troop actually experienced a decline of only 12%, from 150 members to 132 members.

The possibility of reproductive senescence among aged female Japanese monkeys, as well as females of other species of nonhuman primates, is a question deserving continued attention. However, the present evidence from the Arashiyama West population of *M. fuscata* does not indicate such a decline in fertility occurred.