

*Dipodomys ordii*. By Tom E. Garrison and Troy L. Best

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***Dipodomys ordii* Woodhouse, 1853**

Ord's Kangaroo Rat

*Dipodomys ordii* Woodhouse, 1853:235. Type locality "El Paso on the Rio Grande," El Paso Co., Texas.

**CONTEXT AND CONTENT.** Order Rodentia, Family Heteromyidae, Subfamily Dipodomysinae. The species contains 34 subspecies (Baumgardner and Schmidly, 1981; Hall, 1981):

- D. o. attenuatus* Bryant, 1939:65. Type locality "mouth of Santa Helena Canyon, 2146 feet, Big Bend of the Rio Grande River, Brewster County, Texas."
- D. o. celeripes* Durrant and Hall, 1939:10. Type locality "Trout Creek, 4,600 pieds d'altitude, Juab County, Utah."
- D. o. chapmani* Mearns, 1890:291. Type locality "Fort Verde, [Yavapai Co.] Arizona."
- D. o. cinderensis* Hardy, 1944:53. Type locality "at about 4,000 feet on sandy soil immediately north of the northern of two large cinder cones in Diamond Valley, 10 miles north of Saint George, Washington County, Utah."
- D. o. cineraceus* Goldman, 1939:352. Type locality "Dolphin Island, Great Salt Lake, Utah (altitude 4,250 feet)."
- D. o. columbianus* (Merriam, 1894:115). Type locality "Umatilla, Plains of Columbia, [Umatilla Co.] Oregon."
- D. o. cupidineus* Goldman, 1924:372. Type locality "Kanab Wash, at southern boundary of Kaibab Indian Reservation, [Mohave Co.] Arizona."
- D. o. durranti* Setzer, 1952:391. Type locality "Jaumave, Tamaulipas, Mexico" (replacement name for *D. o. fuscus* Setzer, preoccupied by *D. agilis fuscus* Boulware).
- D. o. evexus* Goldman, 1933:468. Type locality "Salida, Chaffee County, Colorado (altitude 7,000 feet)."
- D. o. extractus* Setzer, 1949:534. Type locality "1 mi. E Samalayuca, 4500 ft., Chihuahua, Mexico."
- D. o. fetusus* Durrant and Hall, 1939:14. Type locality "Deux miles au nord de Panaca, 4,800 pieds d'altitude, Lincoln County, Nevada."
- D. o. fremonti* Durrant and Setzer, 1945:21. Type locality "Torrey, 7000 ft., Wayne County, Utah."
- D. o. idoneus* Setzer, 1949:546. Type locality "San Juan, 12 mi. W Lerdo, 3,800 ft., Durango, Mexico."
- D. o. inaquosus* Hall, 1941:58. Type locality "11 mi. E. and 1 mi. N. Jungo, 4200 ft., Humboldt County, Nevada."
- D. o. longipes* (Merriam, 1890:72). Type locality "Foot of Echo Cliffs, Painted Desert, [Coconino Co.] Arizona" (*cleomophila* Goldman is a synonym).
- D. o. luteolus* (Goldman, 1917:112). Type locality "Casper, [Natrona Co.] Wyoming."
- D. o. marshalli* Goldman, 1937:223. Type locality "Bird Island, Great Salt Lake, Utah (altitude about 4,300 feet)."
- D. o. medius* Setzer, 1949:519. Type locality "Santa Rosa, Gualalupe County, New Mexico."
- D. o. monoensis* (Grinnell, 1919:46). Type locality "5600 feet altitude, Pellisier Ranch, five miles north of Benton Station, Mono County, California."
- D. o. montanus* Baird, 1855:334. Type locality "near Fort Massachusetts [Fort Garland, Costilla Co., Colorado; Hall, 1981]."
- D. o. nexilis* Goldman, 1933:470. Type locality "5 miles west of Naturita, Montrose County, Colorado."
- D. o. obscurus* (Allen, 1903:603). Type locality "Rio Sestin, northwestern Durango," Mexico.
- D. o. oklahomae* Trowbridge and Whitaker, 1940:343. Type locality "north bank of the South Canadian River, 2¼ miles south of Norman, Cleveland County, Oklahoma."
- D. o. ordii* Woodhouse, 1853:235, see above.

- D. o. pallidus* Durrant and Setzer, 1945:24. Type locality "Old Lincoln Highway, 18 mi. SW Orr's Ranch in Skull Valley, 4400 ft., Tooele County, Utah."
- D. o. palmeri* (Allen, 1891:276). Type locality "at San Luis Potosi, [San Luis Potosi], Mexico."
- D. o. panguitchensis* Hardy, 1942:90. Type locality "one mile south of Panguitch, Garfield County, Utah; altitude 6,666 feet."
- D. o. priscus* Hoffmeister, 1942:167. Type locality "Kinney Ranch, 21 miles south of Bittercreek, 7100 feet, Sweetwater County, Wyoming."
- D. o. pullus* Anderson, 1972:317. Type locality "El Rosario, Chihuahua, at 6700 ft. [Mexico]."
- D. o. richardsoni* (Allen, 1891:277). Type locality "Beaver River, Ind. Terr." Glass (1971) restricted the type locality to the confluence of Cienquilla and Currumpaw creeks, Sec. 32, T2N, R2E, Cimarron Co., Oklahoma.
- D. o. sanrafaeli* Durrant and Setzer, 1945:26. Type locality "1½ mi. N Price, 5567 ft., Carbon County, Utah."
- D. o. terrosus* Hoffmeister, 1942:165. Type locality "Yellowstone River, 5 miles west of Forsyth, 2750 feet, Rosebud County, Montana."
- D. o. uintensis* Durrant and Setzer, 1945:27. Type locality "Red Creek, 6700 ft., 2 mi. N Fruitland, Duchesne County, Utah."
- D. o. utahensis* (Merriam, 1904:143). Type locality "Ogden, [Weber Co.] Utah."

**DIAGNOSIS.** *Dipodomys ordii* is a medium-sized, relatively short-tailed, five-toed species with hind legs and feet disproportionately long as an adaptation for saltatorial locomotion (Fig. 1; Setzer, 1949). The lower incisors are awl-shaped instead of chisel-shaped as in *D. microps*. Where sympatric with *D. panamintinus*, length of hind foot of *D. ordii* is <44 mm (Hall, 1981). *D. ordii* can be distinguished from *D. compactus* by its longer, bushier, and slightly more crested tail. The ventral tail stripe of *D. ordii* is darker, less broken, and extends to the tip; its pelage is longer, silkier, and has a brownish hue, rather than the orange cast of *D. compactus* (Baumgardner and Schmidly, 1981). Length of auditory bullae and width of supraoccipital in *D. ordii* range from 14.6 to 16.7 mm and 1.0 and 2.9 mm, respectively, while in *D. compactus* they range from 12.6 to 15.7 and 2.5 to 4.2. The diploid number of chromosomes for *D. ordii* is 72 with 140 autosomal arms; in *D. compactus* the diploid number is 74 with 144 autosomal arms (Schmidly and Hendricks, 1976). There also are microhabitat differences (Baumgardner and Schmidly, 1985). All other *Dipodomys* that are sympatric with *D. ordii* have four toes on the hind feet (Hall, 1981).

**GENERAL CHARACTERS.** Color of the pelage is buffy, reddish, or blackish, depending on the subspecies, but the entire ventral surface, dorsal surfaces of the hind feet, supraorbital and



FIG. 1. *Dipodomys ordii* from near Belen, Valencia Co., New Mexico. Photograph by T. L. Best and M. R. Ruhe.



FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Dipodomys ordii oklahomae* (female, Museum of Southwestern Biology 50338, from near Norman, Cleveland Co., Oklahoma). Greatest length of cranium is 38.2 mm. Photographs by T. L. Best and J. L. Dobie.

postauricular spots, forelimbs, hip stripes, lateral stripes of the tail, and the tail at the base are pure white. The skull (Fig. 2) has a relatively short rostrum, moderate to long auditory bullae, a relatively wide interparietal, relatively wide maxillary arches, and grooved upper incisors (Setzer, 1949). The interparietal is variable in shape and number of bones (Beer, 1965). The calcaneum is long (about 7.5 mm) and narrow (about 1 mm at the narrowest width; Stains, 1959).

The subspecies show no noticeable variation in extent of the hip stripe, supraorbital and postauricular spots, basal white ring of the tail, lateral stripes of the tail, or extent of white on the venter and feet. Considerable variation exists in degree and extent of the facial markings and the dorsal and ventral stripes of the tail. Several cranial characters vary qualitatively, including the pterygoid fossae, zygomatic arches, nasal bones, braincase, and curvature of the upper incisors (Setzer, 1949). The most variable quantitative characters are greatest length of skull, bullar-premaxillary length, basal length of skull, greatest depth of skull, and length of upper diastema. In the Great Plains, where there are no other species of *Dipodomys*

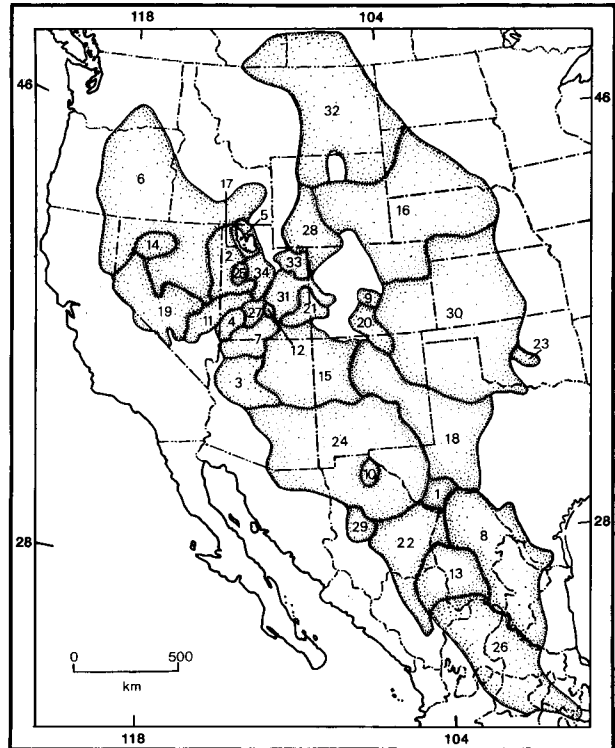


FIG. 3. Distribution of *Dipodomys ordii* (Hall, 1981): 1, *D. o. attenuatus*; 2, *D. o. celeripes*; 3, *D. o. chapmani*; 4, *D. o. cinderensis*; 5, *D. o. cineraceus*; 6, *D. o. columbianus*; 7, *D. o. cupidineus*; 8, *D. o. durranti*; 9, *D. o. evexus*; 10, *D. o. extractus*; 11, *D. o. fetusus*; 12, *D. o. fremonti*; 13, *D. o. idoneus*; 14, *D. o. inaquosus*; 15, *D. o. longipes*; 16, *D. o. luteolus*; 17, *D. o. marshalli*; 18, *D. o. medius*; 19, *D. o. monoensis*; 20, *D. o. montanus*; 21, *D. o. nexilis*; 22, *D. o. obscurus*; 23, *D. o. oklahomae*; 24, *D. o. ordii*; 25, *D. o. pallidus*; 26, *D. o. palmeri*; 27, *D. o. panguitchensis*; 28, *D. o. priscus*; 29, *D. o. pullus*; 30, *D. o. richardsoni*; 31, *D. o. sanrafaeli*; 32, *D. o. terrosus*; 33, *D. o. uintensis*; 34, *D. o. utahensis*.

(except *D. elator* in north-central Texas), *D. ordii* reaches its greatest size. To the west, *D. ordii* generally is small and is sympatric with other species of *Dipodomys* (Kennedy and Schnell, 1978). Mean measurements (in mm) of 691 adult males and 662 adult females, respectively, from throughout the range are: total length, 242.6, 241.5; length of body, 114.2, 114.0; length of tail, 128.5, 127.3; length of hind foot, 39.1, 38.6; length of ear, 12.5, 12.4; basal length of cranium, 22.1, 21.9; greatest length of cranium, 39.4, 39.1; maxillary arch spread, 21.3, 21.3; interorbital width, 13.2, 13.1; nasal length, 14.6, 14.5; intermaxillary width, 7.7, 7.7; alveolar length, 5.4, 5.5; maxillary arch width, 5.0, 5.0; basioccipital length, 5.7, 5.7; greatest depth of cranium, 13.1, 13.0; greatest width of cranium, 24.7, 24.6; zygomatic width, 18.6, 18.5 (Best, in press). Adult mass is about 52 g (Jones, 1985). At a mean body mass of 44.4 g, the total body area is 131.8 cm<sup>2</sup>, and the relative surface area is 2.97 cm<sup>2</sup>/g (Lawler and Geluso, 1986).

Males are larger than females (Best, in press; Desha, 1967; Kennedy and Schnell, 1978), and the number of sexually dimorphic characters varies geographically (Kennedy et al., 1980; Schmidly, 1971). Across the range of *D. ordii*, greatest length of skull, bullar-premaxillary length, and basal length of skull show the greatest relative differences between sexes (Kennedy and Schnell, 1978). Two of 18 nonmetric cranial traits of *D. ordii* from Oklahoma, Texas, and New Mexico differed between sexes (Hartman, 1980).

**DISTRIBUTION.** The range of *D. ordii* (Fig. 3) extends from southern Alberta and Saskatchewan to southern Hidalgo, and from central Oregon and eastern California to central Kansas and Oklahoma (Hall, 1981). Major habitats associated with its distribution are semi-arid grasslands, mixed-grasslands, scrublands (including piñon-juniper woodlands), and sandy soils (Bailey, 1931; Blair, 1943a; Hall, 1946; Hallett, 1982).

**FOSSIL RECORD.** There are two pre-Wisconsin records of *D. ordii*; one from the Slaton Quarry (late Irvingtonian) of Texas and another from the Jinglebob Local Fauna of Kansas (Sangamon; Dalquest and Carpenter, 1986). Fossils also have been recorded from: Fowlkes Cave, Culberson Co., Texas (Dalquest and Stangl, 1986); Schulze Cave, Edwards Co., Texas; Howard Ranch, Harde-man Co., Texas; Jones-Miller, Yuma Co., Colorado; Wasden, Bonneville Co., Idaho; Isleta Cave, Bernalillo Co., New Mexico; Burnet Cave, Eddy Co., New Mexico (Lundelius et al., 1983); and the west bank of the Missouri River near Pierre, South Dakota (Handley, 1953). *D. minor* or *D. gidleyi* may be the ancestor of *D. ordii* (Setzer, 1949; Wood, 1935).

**FORM AND FUNCTION.** Based upon osteology and internal anatomy, *D. ordii* is the most generalized species of the genus (Setzer, 1949). However, the anatomical structure of the brain, especially the cerebellum, indicates greater specialization of the hind limbs than in *D. merriami* or *D. spectabilis*. Little difference exists among these species in total brain volume comprising the telencephalon, diencephalon, cerebellum, and brain stem (Dressler, 1979). The hippocampal formation is about the same size as in *D. merriami*, but the anterior brain is larger. The volumes (in mm<sup>3</sup>) of the hippocampal formation and anterior brain, respectively, for three males and four females, respectively, are: 319.9 and 384.9; and 956.2 and 1,159.0 (Rylander, 1981).

Volume of the middle ear is 0.53 cm<sup>3</sup>, relative volume (middle ear volume/naso-occipital length) is 0.25, and tympanic membrane diameter is 5.30 mm. The impedance-transform ratio, representing an index to middle-ear efficiency, is 0.008. The structure of the middle ear may be an adaptation for predator avoidance (Webster and Webster, 1975).

The teeth are kleistodont (closed tooth), a type most similar to *D. deserti*, *D. nitratoides*, *D. merriami*, and *D. heermanni* (Nader, 1966). The cheekteeth are oval with P4 and M1 nearly equal in size. The enamel pattern is quickly worn away after tooth eruption (Wood, 1935). The parotid and submaxillary glands are large, which indicates the use of dry foods for nourishment. Molar glands are apparent and may be accessory parotid glands used to supply added moisture for mastication of dry foods. The harderian glands are not extensive (Midgley, 1938). The sebaceous dorsal skin gland develops from normal sebaceous glands via a proliferation of basal cells that become greatly enlarged. It differs from normal sebaceous glands in the presence of a large vesicle within each cell and in having resistant cell walls (Quay, 1954). It also differs in mean alveolar volume, is variable in size, and has two peaks in activity; one in April-May and the second in November-December. Glandular activity is similar for both sexes and shows little correlation with breeding season; however, contrary to other *Dipodomys*, glandular secretions increase during molt. The function of the gland appears to be related to scent, although maintenance of an oily secretion on the hair or skin has been proposed (Quay, 1953; Westerhaus, 1983).

The hair is non-troughed, relatively short (11.3 mm), and the widest of the genus (0.03-0.05 mm). The basal shaft and tip are straight to slightly curved, the tip tapers gradually, and the cross section is oval. Uneven rows of three to four irregularly-shaped cells constitute the medulla (Homan and Genoways, 1978). In Nevada, molt occurs from June to August (Hall, 1946).

Cheekpouch capacity as a percentage of head mass ranges from about 20% in Arizona to about 60% in California (Nikolai and Bramble, 1983). The mean volume of each cheekpouch is 0.99 cm<sup>3</sup> in Arizona (range, 0.75-1.46) and 2.48 cm<sup>3</sup> in California. Seeds of *Erodium cicutarium* and *Lesquerella gordonii* were used to determine volume. Based on daily energy expenses and the kcal/g values of the two seed types, *D. ordii* is able to satisfy its daily energy requirement with one maximum cheekpouch load of either seed species (Morton et al., 1980).

The stomach is a well-rounded, U-shaped structure, separable into distinct cardiac, fundic, and pyloric divisions. It lies in a transverse plane closely pressed against and partly covered by the left lateral lobe of the liver. This is due to the humped condition of the animal and consequent crowding of the visceral organs. The cecum is very large. The spleen is closely associated with the stomach, lying across the posterior of the fundus. A full stomach is about 17 by 14 by 7 mm (Midgley, 1938). The liver lies more dorsally and more to the right side of the body cavity than in other *Dipodomys*. The small intestine averages 237 mm in length and the large intestine is 131 mm (Setzer, 1949). Compared to other rodents, these intes-

tinal lengths are unusually short and long, respectively. Two females with hernias were in good health; the hernias apparently were caused by puncture injuries (Hubbard and Howell, 1942).

The kidney has one papilla and the medulla is divided into outer and inner zones. Relative medullary thickness (10 times the medullary thickness/cube root of the product of the length, width, and thickness of the kidney) is 8.20; ratio of inner medullary zone : cortex (thickness of inner medullary zone/cortical thickness) is 3.86; percent medullary thickness (100 times the medullary thickness/cortical + medullary thicknesses) is 83.4. Renal morphology is highly correlated with body size (Lawler and Geluso, 1986). The major urinary protein complex, thought to be produced by the liver and kidney, can be electrophoretically resolved into as many as five equidistant bands with a single band in the  $\beta$ -globulin region (Biggers et al., 1978).

*Dipodomys ordii* drinks by scooping water into the mouth with the forefeet (Allan, 1946). During 20 days, five *D. ordii* drank an average of 6.5, 11.4, 7.6, 4.3, and 7.9 cm<sup>3</sup>/day. The ratio of water intake to body mass is 0.106 cm<sup>3</sup>/g (Boice, 1972). *D. ordii* can concentrate urine to 4,290 mOsmols/l (Fairbanks et al., 1983).

In Nevada, *D. ordii* may be exposed to tritiated water in soil and plants. Lifetime chronic radiation dose is about 10 rad from internal tritium and 10 rad from radionuclides in the soil (Hatch et al., 1970). The biological half-time of tritium in body water has a 13.2-day and a 114-day component. Brain tissues show a half-time of 41 days. Visceral organ tissues of lung, heart, kidney, and liver show tritium half-times of 22 to 29 days (Martin and Koranda, 1972). In Idaho, mean dose equivalent rates are 6 mrem/day (range, 0-28; Halford and Markham, 1978).

In colder months, *D. ordii* has lower water content than in warmer months. Fat content remains nearly constant (about 2%) throughout the year and is lower than values reported for other *Dipodomys* and other small rodents. Mean annual caloric content (kcal/g body mass) is 1.390 (Schreiber and Johnson, 1975).

In self-selection feeding tests, *D. ordii* consumed the following amounts of foodstuffs (in g/100 g of body mass) during 15 days: sucrose (carbohydrate), 4.89; vitamin-free soybean casein (protein), 2.38; and cottonseed oil (fat), 0.91 (Milner and Harriman, 1972). When given a choice between pairs of sugar solutions in concentrations of 12.5, 25, and 37.5%, *D. ordii* chose the solution with the least sugar (Wagner, 1967). Given Richter-type drinking tests, *D. ordii* chose maltose and sucrose over fructose, glucose, or lactose. No preference was shown for magnesium sulfate, potassium chloride, or sodium chloride at lower concentrations; these salts, as well as hydrochloric and citric acids, were avoided at higher concentrations, suggesting taste may be a factor in food selection (Harriman and Nevitt, 1977).

Resting metabolic rate increases from June to September, decreases by January, and then remains relatively constant. Nonshivering thermogenesis increases in winter and is lowest in September. Photoperiod and cold treatment in the laboratory affect changes in resting rates of metabolism and nonshivering thermogenesis, which vary with season. Shifts in thermogenesis do not appear to result from endogenous circannual rhythms (Gettinger et al., 1986). Over a 24-h period, mean oxygen consumption ranges from 0.64 to 0.85 cc g<sup>-1</sup> h<sup>-1</sup> and is not correlated with body mass. Reflecting its nocturnal habits, mean metabolic rate during 12 h of light was 0.59 cc oxygen g<sup>-1</sup> h<sup>-1</sup> and during 12 h of dark was 0.81 cc oxygen g<sup>-1</sup> h<sup>-1</sup>; lower than for *D. merriami* and *D. panamintinus* (Kaufman et al., 1975). At running speeds <3 km/h, oxygen consumption, carbon dioxide production, and blood lactate are positively and linearly related to running velocity. At running speeds >3 km/h, oxygen consumption reaches a plateau, carbon dioxide production increases at a shallow slope, and blood lactate increases sharply (MacMillen, 1983). *D. ordii* shows a tolerance to elevated carbon dioxide concentrations without an increase in blood 2,3-diphosphoglycerate (Frederick et al., 1977). Plasma thyroxine level is 35 ng/ml (Scott et al., 1976). Mean hemoglobin concentration is 14.1 g/100 ml, mean hematocrit is 48.0%, and mean corpuscular hemoglobin concentration is 29.4% (Sealander, 1964).

During activity, *D. ordii* maintains a higher body temperature (38.9-40.0°C) than at rest (37°C), but it does not adjust body temperature to activity level or to ambient temperature. Rather, *D. ordii* simply increases body temperature 1.6 to 3°C over that at resting (Wunder, 1974). Critical thermal maximum is 45.0°C. This maximum is reached in 35 to 38 min and the rate of heating ranges from 0.20 to 0.23°C/min. Upon heat exposure, *D. ordii* becomes

inactive almost immediately, does not spread saliva or increase breathing rate appreciably, assumes a prostrate posture, and remains so until undergoing spasms. Although having a higher critical thermal maximum than other small mammals, the time to reach it is shorter (Erskine and Hutchison, 1982).

Of 124 *D. ordii* in eastern New Mexico, 65 were females, 59 were males, and 20 were male pseudohermaphrodites. These 20 individuals had functional testes and accessory male reproductive structures and rudimentary, nonfunctional female organs (Pfaffenberger et al., 1986). Mean measurements (in mm) of the length, width of the base, and height of the base of the baculum are 11.47, 1.88, and 2.14, respectively. The base of the baculum increases in size with age, while the curved distal end remains about the same size and shape (Best and Schnell, 1974). Testes of males are retracted partially into the abdominal cavity during sexual inactivity. In females, the two uterine horns join above the bladder and have a median partition for a short distance after their juncture, fusing about 0.7 mm from the vaginal orifice. The fallopian tubes appear more extensive and coiled than in other rodents (Midgley, 1938).

For *D. o. oklahomae*, size of ovaries averaged 2.1 mm over 13 months (Hoditschek and Best, 1983). The ovary is small, non-lobulate and covered by a thin germinal epithelium. Oocytes and growing follicles are in the periphery of the ovary and occur singly or in nests of two or more (Duke, 1940). Ovulation occurs when follicular diameter reaches 560 to 600  $\mu$  (Duke, 1944). The clitoris changes cyclically and is about 3 mm in length. The vulva enlarges during proestrus follicular development and may remain enlarged for long periods. Ovulation results in rapid involution of the vulva, as does cessation of ovarian activity. The epithelium of the clitorine urethra is greatly thickened during anestrus, but is thin and atrophic during periods of greatest ovarian activity. In experimental animals, ovariectomy caused involution of the vulva and thickening of the clitorine urethral epithelium. Estrogen produced swelling of the vulva and thinning of the clitorine urethral epithelium. Progesterone inhibited these actions of estrogen. Exogenous gonadotropins injected into intact females caused vulval swelling in anestrus females and rapid involution of the swollen vulva in proestrous females. Gonadotropins also produced thinning of the clitorine urethral epithelium in intact, anestrus females (Pfeiffer, 1960). Development of the distal vagina and clitorine urethra is similar to that of other *Dipodomys* (Pfeiffer, 1963).

The barrier separating the fetal and maternal blood streams in the labyrinth of the chorioallantoic placenta consists of the fetal endothelium and its associated basal lamina (basement membrane), one layer of trophoblast that is cellular rather than syncytial, and the maternal endothelium and its associated basal lamina. The chorioallantoic placenta is of the endotheliochorial type (King and Tibbitts, 1969). The trophospongia layer of the near-term placenta is divisible into two cellular zones, an inner zone adjacent to the labyrinth and a basal zone located mesometrial to the inner zone. Maternal blood draining from the trophospongia layer always is contained in channels lined by a layer of squamous cells that is separated from the trophospongia cells by a basal lamina (Tibbitts and King, 1975).

**ONTOGENY AND REPRODUCTION.** Timing of reproduction varies from one or two breeding seasons (Flake, 1974; Hall, 1946; Johnston, 1956) to some reproductive activity in all months (Hoditschek and Best, 1983). Overall, the length of the breeding season is about 6.8 months of the year (Conley et al., 1977). In Texas, males are capable of reproduction every month. Breeding and parturition occur from August through May. Young born in the early part of the reproductive season may bear young during the following winter and spring (Garner, 1974). In Texas and Oklahoma, *D. o. richardsoni* usually begins breeding in August or September, ends in March, and seldom breeds from April to July. Rate of reproduction is associated with precipitation, food supply, and population densities (McCulloch and Inglis, 1961).

The onset of reproductive activity is correlated with rainfall and appearance of green vegetation and may be related to energetic costs of gestation and care of offspring. In New Mexico, number of embryos is significantly correlated with rainfall in the previous month; size of ovaries is significantly correlated with temperature (Best and Hoditschek, 1986). In Oklahoma, there is a significant correlation between the number of corpora lutea and the greatest daily precipitation during the month. The reproductive cycle, timing, and length

of the breeding season are regulated by the female's cycle, which is strongly affected by the environment (Hoditschek and Best, 1983). Age at sexual maturity is about 83 days (Jones, 1985).

Most males are capable of reproduction all year, even though length and mass of testes and sperm counts fluctuate. For *D. o. oklahomae*, mean testis length is 9.7 mm, mean testis width is 5.9 mm, and mean testis mass is 0.20 g. Testes  $\geq 6.8$  mm with a mass  $\geq 0.07$  g usually contain mature spermatozoa. Testicular measurements are significantly different among age groups, and except for testicular width, significantly different among months (Hoditschek and Best, 1983). Using *D. ordii* from Washington, an equation for estimating mass of testis =  $1.015 (\text{length} \times \text{width}^2) + 15.833$  (Kenagy, 1979).

Gestation is from 28 to 32 days (Day et al., 1956; Duke, 1944). Embryos of *D. o. columbianus* from Utah are considered near term at 22 mm in length (Duke, 1944). Number of embryos ranges from 1 to 6 with a mean of 3.5 (Hall, 1946). There may be two litters each year (Alcorn, 1941). In captivity, the maximum litter size was 6, maximum number of litters/year was 5, maximum number of young/year was 20, maximum number of litters/lifetime was 9, and the maximum number of young/lifetime was 38. The lifespan in captivity may reach 7 years 5 months (Egoscue et al., 1970).

Growth rate is correlated with age from birth to 70 days. Measurements (in mm) for four age classes (1-3, 4-15, 16-29, and 30-70 days, respectively) are: total length, 74.4, 149.9, 210.6, 237.5; length of tail, 23.3, 75.2, 117.9, 133.0; length of ear, 2.7, 9.0, 13.2, 13.7; length of hind foot, 16.6, 36.2, 38.9, 39.2; body mass (in g), 7.0, 18.7, 34.1, 55.2. However, none of these is reliable in predicting age (Smith et al., 1978).

Juvenile, subadult, and adult age classes may be determined by completeness of dentition, tooth wear, translucence of auditory bullae, and convexity of cranium. In juveniles, the auditory bullae are opaque and rough in texture, permanent dentition usually is absent, incomplete, or with no wear, and the lateral view of the skull is markedly convex on the dorsal surface. In subadults, the auditory bullae are less opaque, permanent dentition has little wear, and convexity of the skull is intermediate. In adults, the bullae are translucent and smooth, the molars and premolars show wear, and convexity of the upper surface of the skull is barely evident (Best and Schnell, 1974).

**ECOLOGY.** *Dipodomys ordii* lives in a diversity of habitats. In Idaho, it is found in several vegetative communities (Groves and Keller, 1983), but is most abundant in the *Juniperus* community with *Chrysothamnus* and *Eurotia* as the understory (Allred, 1973). In Oregon, it is found in *Artemisia tridentata*, *Juniperus occidentalis* (Rogers and Hedlund, 1980), and *Sarcobatus vermiculatus* associations (Feldhamer, 1979). In Utah, it has a strong affinity for open shrublands and grasslands on sandy soils (Armstrong, 1979) and for *Artemisia*, *Pinus-Juniperus*, and *Atriplex* communities above 1,350 m (Honeycutt et al., 1981). In Wyoming, it is an abundant resident of sand dune communities where mean height of vegetation is  $>25$  cm and bare soil is  $>40\%$ . It also occurs in the *Yucca* and *Artemisia* grassland communities, though in smaller numbers. The essential feature of the habitat in which *D. ordii* is associated is sandy, fine-textured soils (Maxwell and Brown, 1968). In New Mexico, *D. ordii* is found in *Yucca*, *Quercus*, *Prosopis*, and *Atriplex* communities (Best and Hoditschek, 1986; Dice, 1930). In Texas, it occurs where the predominant vegetation is *Prosopis glandulosa*, *Artemisia filifolia*, *Yucca*, *Quercus havardi*, and *Gutierrezia sarothrae* (Garner, 1974).

*Dipodomys ordii* primarily is a granivore. Throughout its range a wide variety of food is consumed; the most common are seeds of grasses and forbs, followed by green vegetation, other vegetative material, and rarely animal material. In Oklahoma, *D. o. oklahomae* had *Cycloloma atriplicifolium*, *Strophostyles helvola*, *Cassia fasciculata*, *Corispermum hyssopifolium*, *Helianthus*, *Aristida*, *Populus deltoides*, and green vegetation (mostly *Trifolium* and unidentified leaves) in its cheekpouches. Cheekpouches never contained animal material; the only non-plant material was sand (Best and Hoditschek, 1982). In Texas, foods included dry stems, *Paspalum stramineum*, *Prosopis juliflora*, *Andropogon halli*, *Ambrosia artemisiifolia*, *Gaillardia puchella*, *Croton glandulosus*, *Sorghum halapense*, *Helianthus annuus*, the fungus *Endogone*, and insects and other arthropods made up 18% of the diet. There was no

significant variation among seasons. Foods were eaten in proportion to their abundance, except *Solanum eleagnifolium*, *P. juliflora*, and *G. puchella* (Alcoze and Zimmerman, 1973). In Colorado, the diet primarily consisted of seeds (74%), forbs (13%; including *Kochia scoparia*), grasses and sedges (5%; the most common being *Bouteloua gracilis*), arthropods (4%), fungi and mosses (2%), and shrubs (1%; Flake, 1973). In Idaho, seeds and leaves of *Halogeton glomeratus* were the most frequent food items found in stomachs. Also present were arthropods, *Lepidium perfoliatum*, *Descurainia pinnata*, *Atriplex confertifolia*, *Salsola kali*, *Opuntia*, *Artemisia tridentata*, and grasses (Johnson, 1961).

The mean mass of seeds in 35 cheekpouches was 1.25 mg. No pattern of seed-size selection exists among *D. ordii*, *D. merriami*, and *Perognathus flavus*, though there was a marked seed-species selection. Of the seeds taken by *D. ordii*, 68% were of two species of *Euphorbia* (Lemen, 1978). When seeds are placed on the surface, *D. ordii* will recover 100% of them; when buried at a depth of 0.6 or 1.3 cm, only 5% are recovered (Johnson and Jorgensen, 1981). *D. ordii* readily colonized a seed-supplemented plot of shortgrass prairie in Colorado where it previously had been absent (Abramsky, 1978).

In Nevada, *D. ordii* shows a tendency to increase size of home range in spring and again in late autumn and early winter. There is no difference between mean home range sizes of males and females for the year. Annual composite home ranges, using the circular and principal component methods, respectively, are: 0.62 and 0.43 ha (O'Farrell, 1978). Population size on 2.7 ha ranged from one to five (O'Farrell, 1980). In Texas, density over a 2-year period was 15.6/ha (range, 9.9–26.9/ha). Movements of adult males were within about 0.20 ha 95% of the time; female movements were within about 0.22 ha (Garner, 1974). In New Mexico, home ranges of males in a *Prosopis* association showed little variation over time and averaged 1.36 ha. Home ranges of females varied from a mean of 0.44 in March to 1.32 ha in April and May (Blair, 1943b). Density is correlated with rainfall and primary productivity. During seasons with favorable conditions, *D. ordii* acts as an immigrant species moving into communities dominated by *Larrea* (Whitford, 1976). Density may reach 53/ha (Conley et al., 1977). Density in campgrounds is not different from that outside of campgrounds (Clevenger and Workman, 1977).

In Oregon, *D. ordii* is associated with *Perognathus parvus*, *Peromyscus maniculatus*, *Onychomys leucogaster* (Rogers and Hedlund, 1980), *Eutamias minimus*, *D. microps*, *Microdipodops megacephalus*, *Spermophilus townsendii*, *Neotoma lepida*, *Microtus montanus*, and *Reithrodontomys megalotis* (Feldhamer, 1979); in Nevada with *Perognathus longimembris*, *P. formosus*, *Microdipodops megacephalus*, *D. merriami*, *D. panamintinus*, *D. microps*, *P. maniculatus*, *R. megalotis*, *O. leucogaster*, *O. torridus*, and *N. lepida* (O'Farrell, 1974); in Utah with *Eutamias dorsalis*, *Ammospermophilus leucurus*, *Peromyscus crinitus*, *P. maniculatus*, *P. truei*, *O. leucogaster*, and *N. lepida* (Honeycutt et al., 1981); in Wyoming with *Spermophilus pilosoma*, *S. tridecemlineatus*, *Perognathus fasciatus*, *P. flavescens*, *P. flavus*, *Chaetodipus hispidus*, *R. megalotis*, *R. montanus*, *P. maniculatus*, *O. leucogaster*, and *Microtus ochrogaster*; in New Mexico with *P. flavescens*, *Chaetodipus intermedium*, *D. merriami*, *Neotoma albigula*, *Peromyscus eremicus* (Lemen and Rosenzweig, 1978), *D. spectabilis*, *S. pilosoma*, *Geomys bursarius*, *C. hispidus*, *P. flavus*, *Reithrodontomys*, *Peromyscus leucopus*, *Sigmodon hispidus*, *Neotoma micropus*, *Mus musculus*, *Lepus californicus*, *Sylvilagus audubonii*, *O. leucogaster*, *Canis latrans*, *Vulpes*, *Taxidea taxus*, *Mustela frenata*, and *Antilocapra americana* (Best, 1972); and in Chihuahua with *Thomomys umbrinus*, *P. flavus*, *Reithrodontomys fulvescens*, *R. megalotis*, *P. boylii*, *P. maniculatus*, *P. truei*, *Baiomys taylori*, *Sigmodon minimus* (= *fulviventris*), *S. ochrogaster*, *Neotoma mexicana*, *Rattus rattus*, *M. musculus*, *L. californicus*, *L. gaillardi*, *S. audubonii*, and *S. floridanus* (Anderson and Long, 1961). When *D. ordii*, *D. spectabilis*, and *D. merriami* are removed from experimental enclosures, the abundance of smaller (7–39 g) granivorous rodents increases, while populations of small omnivores remain stable (Munger and Brown, 1981). In enclosures devoid of other rodents, *D. ordii* is displaced by *O. leucogaster* into open microhabitats with short vegetation (Rebar and Conley, 1983).

In laboratory feeding experiments between *D. ordii* and *P. flavus*, differences in size of seeds selected are apparent, but proportion of seed-types selected is not. When placed together, both species store fewer seeds. *D. ordii* selects a greater proportion of

intermediate-sized seeds and a lesser proportion of small-sized seeds, is more consistent in amounts of seeds stored, is more efficient at gathering clumped seeds, and is less affected by the presence of another species than is *P. flavus* (Hutto, 1978); this and microhabitat differences allow them to coexist (Lemen and Rosenzweig, 1978).

Among eight commercial seeds, *D. ordii* selected greater numbers of smaller thistle and millet seeds than larger seeds (Mares and Williams, 1977). In sand dune habitats, seed-size selection and microhabitat use appear responsible for coexistence between *D. ordii* and other species. The sizes (in mm) of seeds selected most often by *D. ordii*, *D. merriami*, and *D. deserti* are: 3.33–3.96, 1.40–1.65, and >4.70, respectively (Brown and Lieberman, 1973).

In New Mexico, *D. ordii* is sympatric with *D. merriami* and *P. flavus*. *D. ordii* selects the grass habitat, *D. merriami* occupies stands of *Larrea tridentata*, and *P. flavus* is found in both habitats (Lemen, 1978). In Nevada, spatial overlap between *D. ordii* and *D. microps* occurs only in summer, between *D. ordii* and *D. panamintinus* in winter, spring and summer, and between *D. ordii* and *D. merriami* in all seasons. *D. ordii* is more restricted to sandy soils than *D. merriami*, which ranges through *Artemisia* habitat, including the habitats of *D. ordii*, *D. panamintinus*, and *D. microps*. Microhabitat choice and specialization, as well as social factors such as the dominance hierarchy structures, appear responsible for the coexistence of these species (O'Farrell, 1980). In the laboratory, *D. ordii* is dominant to *D. merriami* and subordinate to *D. panamintinus*; body size may be responsible for this hierarchy (Blaustein and Risser, 1976).

*Dipodomys ordii* and *D. merriami* are ecologically separated on the basis of microhabitat specialization (Hallett, 1982; Schroder and Rosenzweig, 1975). *D. merriami* is found on harder soil (Benson, 1933), while *D. ordii* is found in more sandy soils. The diets of the two also are different. For example, in Guadalupe Mountains National Park, Texas, the main food items taken by *D. ordii* are *Bouteloua* (18%), *Sporobolus* (17%), *Nerisyrenia* (9%), and *Atriplex* (6%). These foods represent <6% of the diet of *D. merriami*, suggesting these species coexist on the basis of difference in diet (O'Connell, 1979). Herbicide treatment of a desert shrub community resulted in the reduction of *L. tridentata* and an increase in *Muhlenbergia porteri*; subsequently, *D. merriami* was replaced by *D. ordii* as the dominant species (Whitford et al., 1978). Neither *D. ordii* nor *D. merriami* uses habitats in the available proportions; both stop more frequently at burrow locations beneath *Larrea*, the dominant shrub, and also use sand dunes more than expected. Habitat selection facilitates coexistence between these species (Schroder, 1987).

Predators include *Vulpes macrotis* (Egoscue, 1956), *Canis latrans* (Johnson and Hansen, 1979a, 1979b), *Tyto alba* (Anderson and Long, 1961; Rickart, 1972), *Bubo virginianus*, *Asio otus* (Marti, 1969; Maser et al., 1980; Stickle and Stickle, 1948), and *Speotyto cunicularia* (Smith and Murphy, 1973). In Nevada, *D. ordii* is under-represented in the diet of *A. otus* in proportion to the population size. Here the morphologic adaptations of a bipedal gait and enlarged auditory bullae are correlated with decreased predation (Kotler, 1985). In Nebraska, *B. virginianus* takes more than twice as many *D. ordii* as *T. alba* (7 and 3%, respectively; Rickart, 1972).

Bacteria that infect *D. ordii* include *Coxiella burnetii*, *Rickettsia rickettsii*, *Francisella tularensis*, and *Yersinia pestis* (Whitaker, in press). These are pathogenic in man, resulting in Q fever, Rocky Mountain spotted fever, tularemia, and plague, respectively. *D. ordii* is resistant to inoculations of > 1,000,000 plague organisms (Marchette et al., 1962). Protozoans include *Eimeria balphae*, *E. chobotari*, *E. dipodomys*, *E. scholtzsecki*, *E. utahensis*, and *Besnoitia jellisoni*. Cestodes include *Raillietina retractilis* and nematodes include *Capillaria americana*, *Heligmosomum*, *Heteromoxys deserti*, *Protospirura muris*, *P. numidica*, *Trichuris dipodomis*, and *T. minuta* (Whitaker, in press). In Texas, the yearly infection rates for *Raillietina*, *P. muris*, and *H. deserti* are 5, 3, and 8%, respectively. The peak occurrence of *P. muris* and *H. deserti* in January and June is correlated with reproductive behavior of female *D. ordii*. Parasitism occurs throughout the year, with the greatest intensity in the warmer months. *Raillietina* increase in late spring, remain relatively high throughout the summer, and rapidly decline in August (Garner et al., 1976).

Mites of nine families occur on *D. ordii*, including *Cheyletus linsdalei*, *Androlaelaps fahrenheitii*, *Brevisterna mortani*, *Echinonyssus hilli*, *E. incomptis*, *E. longichelae*, *E. neotomae*, *E. triacanthus*, *E. utahensis*, *Eubrachylaelaps crowei*, *E. debilis*, *Haemogamasus ambulans*, *H. reidi*, *H. onychomydis*, *Hypoaspis*

*leviculus*, *Ischyropoda armatus*, *I. furmani*, *Laelaps kochi*, *Geomylichus dipodomys*, *G. texanus*, *Macrocheles*, *Ornithonyssus bacoti*, *Radfordia bachai*, *Uropoda*, *Proctolaelaps*, *Sertitypanum contiguum*, *S. exarमतum*, and *Euryparasitus*. Chiggers include *Comatacarus americanus*, *Euschoengastia cordiremus*, *E. criceticola*, *E. decipiens*, *Euschoengastoides arizonae*, *E. loomisi*, *E. tumidus*, *Eutrombicula alfreddugesi*, *E. batatus*, *E. belkini*, *Hexidionis allredi*, *H. breviseta*, *H. doremi*, *H. harveyi*, *Hyponeocula arenicola*, *H. fovea*, *H. montanensis*, *Odontacarus linsdalei*, *O. micheneri*, *Otorhinophila baccusi*, *O. parvisola*, *Parasacia gurneyi*, *Pseudoschoengastia farneri*, *P. hungerfordi*, *Trombicula bakeri*, and *Xenodontacarus plumosus*. Ticks include *Dermacentor andersoni*, *D. parumapertus*, *Haemaphysalis leporispalustris*, and *Ixodes kingi*. Sucking lice include *Fahrenholzia pinnata*, *Hoplopleura arboricola*, *H. hesperomydis*, *Neohaematompinus neotomae*, and *Polyplax auricularis*. Fleas include *Aetheca wagneri*, *Anomiopsyllus amphibolus*, *A. novomexicanensis*, *A. nudatus*, *Callistopsyllus terinus*, *Catallagia decipiens*, *Echinopaga gallinacea*, *Epitedia stanfordi*, *E. wenmanni*, *Eumolpianus eumolpi*, *Foxella ignota*, *Malaraeus telchinus*, *Megabothris quirini*, *Megarhthroglossus divisus*, *Meringis altipectin*, *M. bilsingi*, *M. dipodomys*, *M. disparalis*, *M. facilis*, *M. hubbardi*, *M. nidi*, *M. parkeri*, *M. rectus*, *Orchopeas leucopus*, *O. sexdentatus*, *Oropsylla aridis*, *O. bacchi*, *O. fota*, *O. francisi*, *O. hirsutus*, *O. labis*, *O. montana*, *O. tuberculata*, *Pleochaetis exilis*, and *Rhadinopsylla sectilis* (Whitaker, in press).

**BEHAVIOR.** *Dipodomys ordii* is nocturnal and active all year (Jorgensen and Hayward, 1965; Kenagy, 1976). Males generally are more abundant and active than females. Activity increases under cloudcover, particularly in winter. It decreases during inclement weather, clear nights, under moonlight, and ceases when temperatures are below  $-11^{\circ}\text{C}$  or when snow cover is  $>40\%$  (O'Farrell, 1974). In moonlight, there is a shift in use of microhabitat from more open areas to areas with greater cover (Kaufman and Kaufman, 1982). Daytime activity has been observed (Moore, 1929). In Kansas, almost no activity occurs during the first hour following sunset or the hour of sunrise; activity is variable from nights with moonlight and no cloudcover (4.3 animals/h), to moonlight with cloudcover (18.4/h), to starlight, but no moonlight (33.2/h; Kaufman and Kaufman, 1982). In Nevada, activity occurred only after midnight in winter; trimodal activity was prevalent in spring, and there was a bimodal pattern with the preponderance of activity occurring after midnight in summer (O'Farrell, 1974). When dominant adults are removed, activity patterns develop a peak just after sunset and decline thereafter (Jorgensen et al., 1980).

Intraspecific aggression is rarely observed in nature. In captivity fighting occurs, but usually is not serious. During confrontations, a tooth chattering sound occurs; the loser retreats making faint chuckling noises and squeaky snorts (Allan, 1946).

Mating behavior of a captive pair of *D. o. richardsoni* was initiated by the female chasing the male for 15 min, followed by the male chasing the female for about 20 min, with both nosing the other's genitalia. Following this, copulation occurred 13 times in the next 20 min. A 5-min period of inactivity was followed by another bout of pursuit and coition (Allan, 1944).

In Kansas, *D. ordii* was observed to mate in nature. The first attempted copulation occurred at 2115 h and lasted about 8 s, apparently without intromission. Two more unsuccessful attempts occurred at 2120 h (5 s) and 2122 h (15–20 s). Modified sand-bathing, sparring with the forelegs, and one chasing the other occurred between attempts. At 2129 h, a 30-s copulation took place with apparent intromission. The female was in a trench of her own making, the male approached from the side and quickly moved to the rear and mounted, grasping her inguinally with his forelegs, his chin appressed to her neck. She responded by assuming the lordosis position with her chin on the ground and back arched. After 20 s the female moved about while the male retained his grip (riding) and thrustured continuously. After separation, both sat a little apart, the male grooming his genital region (Engstrom and Dowler, 1981).

*Dipodomys ordii* has parental response to neonate vocalizations in the frequency range corresponding to that used in predator detection and avoidance. Neonate vocalizations become variable and infrequent at 14 days of age, which coincides with a marked increase in physical activity, thermoregulatory ability, and solid food intake. When young are born either prematurely or ill, they cannot vocalize and are ignored or eaten by the mother (LeVick, 1982).

Grooming occurs by sliding and rolling in sand and dust. The underparts and sides are dusted by sliding over the sand propelled by strong thrusts of the hind legs. The feet and tail receive careful grooming (Allan, 1946). *D. ordii* can swim (Stock, 1972). Mean response time to electric shock is 12.2 s, compared to 4.8 s for *Mus musculus* (Boice et al., 1968).

**GENETICS.** *Dipodomys ordii* has a diploid number of 72 chromosomes with all autosomes biarmed. There are 140 autosomal arms, of which 4 pairs are metacentric, 26 pairs are submetacentric, and 5 pairs are subtelocentric. The X chromosome is submetacentric and the Y chromosome is acrocentric to subtelocentric (Stock, 1974).

Mean number of alleles/locus/population is 1.03, mean proportion of polymorphic loci/population is 0.030–0.207, and mean genic heterozygosity is 0.008–0.024. The degree of genetic variability is relatively uniform regionally, with the overall average heterozygosity varying from 0.006 to 0.017; there are no recognizable geographic patterns. The range of coefficients of genetic similarity is from 0.93 to 1.00 (Beck et al., 1981; Johnson and Selander, 1971).

Over 50% of the nuclear DNA is composed of families of highly repetitive nucleotide sequences that appear as density satellites in a cesium chloride gradient (Prescott et al., 1973). Alkaline cesium chloride strand densities (g/ml) of satellite DNA are 1.709, 1.796 for HS- $\alpha$  satellite; 1.762, 1.771 for HS- $\beta$  satellite; and 1.737, 1.759 for MS satellite DNA (Mazrimas and Hatch, 1977). The most commonly repeated nucleotide sequence of the highly repetitive satellite HS- $\alpha$  fraction is six nucleotides long and represents about 25% of the total HS- $\alpha$  satellite DNA, while the remaining DNA is composed of sequence variants related to the most common sequence (Fry and Salser, 1977). Binding of anti-nucleoside antibodies reveals different classes of DNA in the chromosomes of *D. ordii* (Schreck et al., 1977); the HS- $\alpha$  satellite from *D. ordii* resembles the alpha satellite of the guinea pig (Salser et al., 1976).

**REMARKS.** Usually, *D. ordii* is placed in a group of its own (Grinnell, 1922; Johnson and Selander, 1971; Lidicker, 1960; Stock, 1974; Wood, 1935). However, *D. ordii* is considered most similar to *D. compactus* (Schnell et al., 1978; Setzer, 1949; Stock, 1974). *D. ordii* does not synthesize the  $\beta$  subunit of lactate dehydrogenase, suggesting that the Heteromyidae and Geomyidae might be better placed in the Suborder Myomorpha than in Sciuromorpha (Baur and Pattie, 1968).

*Dipodomys* is from the Greek, *di* (two), *podos* (foot), and *mys* (mouse; Jaeger, 1955), and refers to the bipedal mode of locomotion. The specific epithet *ordii* is in honor of George Ord, President of the Academy of Natural Sciences of Philadelphia when the species was described in 1853.

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