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Lepus californicus.

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Lepus californicus Gray, 1837

Black-tailed Jackrabbit

Lepus californica Gray, 1837:586. Type locality "St. Antoine" ("probably on coastal slope of mts. near Mission of San Antonio, Jolon, Monterey Co.," California—Hall, 1981:326).

Lepus richardsonii Bachman, 1839:88. Type locality "California" (exact locality unknown, but probably from near Jolon, Monterey County, near type locality of *L. c. californicus*—Miller, 1912:353).

Lepus bennettii Gray, 1843:35. Type locality San Diego, San Diego Co., California.

Lepus texianus Waterhouse, 1848:136. Type locality unknown, but may be "10 mi S Alpine, Brewster County, Texas" (Hoffmeister, 1986:141).

Lepus melanotis Mearns, 1890:297. Type locality "Independence [Montgomery County—Miller, 1912:355], Kansas."

Lepus martirensis Stowell, 1895:51. Type locality "La Grulla, San Pedro Martir Mountains, Lower California [Baja California]."

Lepus merriami Mearns, 1896:444. Type locality "Fort Clark, Kinney County, Texas."

Lepus asellus Miller, 1899:380. Type locality "at the city of San Luis Potosi [State of San Luis Potosi—Miller, 1912:356], Mexico."

Lepus festinus Nelson, 1904:108. Type locality "Irolo, Hidalgo, Mexico."

Lepus tularensis Merriam, 1904:136. Type locality "Alila [= Earlimart—Hall, 1981:328] (in bottom of San Joaquin Valley), Tulare Co., California."

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Subfamily Leporinae, Genus *Lepus*, Subgenus *Macrotolagus* (Hall, 1981; Miller, 1899). There are 30 species of *Lepus* (Wilson and Reeder, 1993). Seventeen subspecies of *L. californicus* are recognized (Hall, 1981):

L. c. altamirae Nelson, 1904:109. Type locality "Alta Mira, Tamaulipas, Mexico."

L. c. asellus Miller, 1899:380, see above.

L. c. bennettii Gray, 1843:35, see above.

L. c. californicus Gray, 1837:586, see above (*vigilax* Dice is a synonym).

L. c. curti Hall, 1951*a*:42. Type locality "island, 88 miles south and 10 miles west of Matamoros, Tamaulipas, Mexico."

L. c. deserticola Mearns, 1895:564. Type locality "the western edge of the Colorado Desert, at the base of the Coast Range Mountains, in San Diego County [= Imperial Co.—Hall, 1981:326], California" (*depressus* Hall and Whitlow is a synonym).

L. c. eremicus Allen, 1894:347. Type locality "Fairbank [Cochise County—Miller, 1912:354], Arizona."

L. c. festinus Nelson, 1904:108, see above.

L. c. magdalenae Nelson, 1907:81. Type locality "Magdalena Island, Lower California [Baja California Sur], Mexico."

L. c. martirensis Stowell, 1895:51, see above.

L. c. melanotis Mearns, 1890:297, see above.

L. c. merriami Mearns, 1896:444, see above.

L. c. richardsonii Bachman, 1839:88, see above (*tularensis* Merriam is a synonym).

L. c. sheldoni Burt, 1933:37. Type locality "Carmen Island [(latitude 26° north, longitude 111°12′ west), Gulf of California], Lower California [Baja California Sur], Mexico."

L. c. texianus Waterhouse, 1848:136, see above (*griseus* Mearns and *micropus* Allen are synonyms).

L. c. wallawalla Merriam, 1904:137. Type locality "Touchet, Plains of Columbia [Walla Walla Co.—Hall, 1981:328], Washington."

L. c. xanti Thomas, 1898:45. Type locality "Santa Anita, Lower California [Baja California Sur]."

DIAGNOSIS. *Lepus californicus* (Fig. 1) possesses a black dorsal tail stripe and *L. townsendii* does not (Findley et al., 1975). A method for distinguishing skulls of *L. californicus* from those of *L. townsendii* in the Great Basin region of Nevada has not been determined. Skulls, at least of adults, of these two species in the region east of the Rocky Mountains can be distinguished by the pattern of infolding of enamel on the front of the first upper incisor teeth. *L. townsendii* has a simple groove on the anterior face of the tooth and *L. californicus*, east of the Rocky Mountains, has a bifurcation, or even trifurcation, of the infold that can be seen by examining the occlusal surface of the incisor (Hall, 1951*b*).

On the tableland of Mexico and in the southwestern United States where *L. californicus* occurs sympatrically with *L. alleni* and *L. callotis*, *L. californicus* can be distinguished by the terminal black patch on the outside of each ear and by the less extensive area of white on the flank. Eastward, in Tamaulipas, Mexico, where only *L. californicus* occurs, it too has white flanks, and some individuals lack the terminal black patch on the ear (Hall, 1981). A method for distinguishing skulls of *L. californicus* from those of all white-sided jackrabbits has not been determined (Hall, 1951*b*). However, the lower jaw of *L. alleni* is more elongate than that of *L. californicus*, especially in the diastemal region. The ramus be-

FIG. 1. *Lepus californicus melanotis* in a *Yucca-Prosopis* grassland 16 km S Tolar, Roosevelt Co., New Mexico.

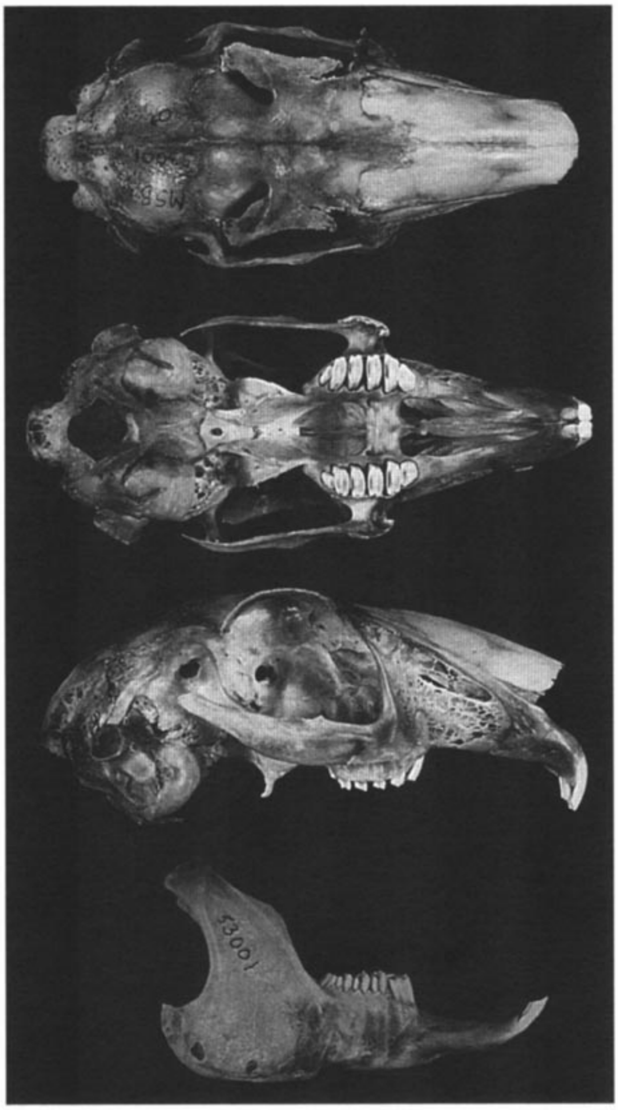

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Lepus californicus texianus* (male, University of New Mexico Museum of Southwestern Biology 53001, from Ladron Mountains, Socorro Co., New Mexico). Greatest length of cranium is 99.2 mm. Photographs by T. H. Henry.

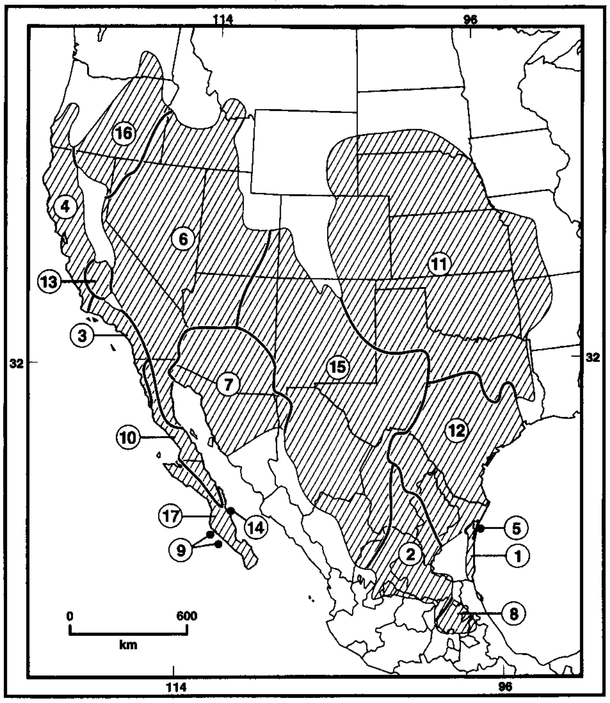

FIG. 3. Distribution of *Lepus californicus* in North America (G. G. Ceballos and C. Galindo Leal, in litt.; Hall, 1981; Hoffmeister, 1986): 1, *L. c. altamirae*; 2, *L. c. asellus*; 3, *L. c. bennettii*; 4, *L. c. californicus*; 5, *L. c. curti*; 6, *L. c. deserticola*; 7, *L. c. eremicus*; 8, *L. c. festinus*; 9, *L. c. magdalenae*; 10, *L. c. martirensis*; 11, *L. c. melanotis*; 12, *L. c. merriami*; 13, *L. c. richardsonii*; 14, *L. c. sheldoni*; 15, *L. c. texianus*; 16, *L. c. wallawalla*; 17, *L. c. xanti*.

tween the base of the incisors and the first premolar of *L. alleni* is longer, more slender, and delicate. If lower jaws of these species are lined up with symphyses, bases of incisors, and foramina parallel, the p3 of *L. alleni* is farther posterior, about opposite p4 of *L. californicus* (Dalquest et al., 1969).

GENERAL CHARACTERS. *Lepus californicus* is medium in size for the genus in all external characters (Hoffmeister, 1986). The skull (Fig. 2) is long and slender, the rostrum is long and tapering, supraorbital processes are broad (especially posterior extensions of the processes) and somewhat elevated above the frontal plane, jugals are rather narrow without a conspicuous flange projecting laterally from their dorsal margins, braincase is long and slender, anterior palatine foramina usually possesses a slight posterior constriction, palatal bridge is short and lacks a conspicuous posteromedian spine, auditory bullae vary from small to large, and molariform teeth are small (Orr, 1940).

The hind legs and ears are long, and the tail is large with a black median-dorsal stripe, and is buffy or grayish beneath (Orr, 1940). The dorsum is brownish to grizzled, sides of the body are brownish (Hoffmeister, 1986), and ventral pelage is pale with gray bases and underfur, except for the dark, dense pectoral mane; texture of the pelage is soft (Corbet, 1983). There is considerable variation in coloration among subspecies. Differences in color and other characters are indicative of corresponding changes in climatic conditions and of the ready response of *L. californicus* to such influences (Nelson, 1909). In addition to climatic conditions, substrate coloration may affect color; e.g., on the Guadiana lava field, Durango, pelage is browner than that of black-tailed jackrabbits from northern Durango, Mexico (Baker, 1960).

Ranges of average measurements (in mm) of 14 subspecies of *L. californicus* are: total length, 523–606; length of tail vertebrae, 75.0–101.0; length of hind foot, 113–135; length of dried ear from notch, 99–131; basilar length of cranium, 67.3–76.9; length of nasals, 34.9–41.8; breadth of rostrum above premolars, 21.1–26.6; depth of rostrum in front of premolars, 17.9–22.7; interorbital breadth, 24.9–28.5; parietal breadth, 29.2–32.1; diameter of bullae, 12.6–14.9 (Nelson, 1909). Body size is large on islands around Baja California (Lawlor, 1982), but *L. c. sheldoni* on Carmen Island is smaller than adjacent subspecies (Hoagland, 1992). In southern Arizona, average mass of adult males is 2,475 g (range, 1,980–3,375 g) and non-pregnant females is 2,610 g (range, 1,980–3,285 g—Vorhies and Taylor, 1933). In California, mass of males is 2,000–2,950 g and females 2,120–3,550 g. In Washington, mass of males is 1,510–1,880 g and females 1,880–2,840 g (Dice, 1926).

The pubic bone tends to be broader and shorter in females than in males (Lechleitner, 1959). In Kansas, sexual dimorphism exists in mass and length of adults; females are larger than males. As the breeding season begins, difference in mass between sexes increases until a maximum is reached in mid-summer. Toward the end of the breeding season in late summer, males begin to gain mass and females to lose mass. After the breeding season, mass is nearly the same for both sexes. Lengths of hind feet and ears of adult males and females are not different (Tiemeier, 1965).

DISTRIBUTION. The black-tailed jackrabbit ranges throughout much of western North America, from western Arkansas and Missouri westward to the Pacific Coast, and from Washington and Idaho south to Hidalgo and Querétaro, Mexico (Fig. 3; Jones et al., 1983). *L. californicus* has been introduced into Florida, New Jersey, Maryland, Massachusetts, and Virginia (Dunn et al., 1982). Its range embraces life zones from the upper border of the arid tropics through the lower and upper Sonoran, and transition zones (Vorhies and Taylor, 1933). The black-tailed jackrabbit occurs at elevations from −84 (Grinnell, 1937) to 3,750 m (Burt, 1934; Orr, 1940).

FOSSIL RECORD. The genus *Lepus* had its origin in the late Pliocene or early Pleistocene in the Holarctic (Dawson, 1967). *L. californicus* is the most common fossil *Lepus* in North America, with records from early Irvingtonian or earlier (Curtis Ranch, possibly Borchers). The black-tailed jackrabbit also occurs at Slaton (late Irvingtonian) and at >35 Rancholabrean sites (Kurtén and Anderson, 1980; Lundelius et al., 1987).

FORM AND FUNCTION. Vibrissae are long and sensitive (Vorhies and Taylor, 1933). Thickness of pelage is ca. 8–9 mm (Schmidt-Nielsen et al., 1965). Banded dorsal guard hairs have a dark brown to black tip, a yellow to white band in the central shield, and a dark-brown lower shield that blends into a gray area that extends to the basal end; total length, 34–75 mm; dark tip, 3.0–6.8 mm; color band, 5–6 mm; diameter, 95–136 μm. Unbanded hair is black, 42–54 mm in length, and 75–105 μm in diameter (Moore et al., 1974).

Annual molt begins, depending on latitude, between late August and early October (Jones et al., 1983). Short summer hair is replaced by longer winter hair (Hoffmeister, 1986). The first evidence of new pelage is seen on the top and sides of the head, as a strip extending from the nose backward between the eyes to the base of the ears and as lateral bands from the sides of the nose to the cheeks. The strips of new pelage meet under the chin in the midventral line. At about the same time, new hairs appear on the back, advancing toward the nape and rump. The venter is the last region to attain new pelage, when molt lines advancing from either side meet irregularly along the midventral line (Jones et al., 1983).

The skull has pronounced supraorbital processes and fenestrate maxillary bones (Jones et al., 1983). Interparietal sutures are lost in adults (Corbet, 1983). The dental formula is i 2/1, c 0/0, p 3/2, m 3/3, total 28 (Hall, 1981).

Width of ventral parts of the anterior ribs is broad, and the transverse process of lumbar vertebrae is slender and long. There are 15 caudal vertebrae (Corbet, 1983). Masses of proximal, middle, and distal segments of the foreleg are 30.4, 12.4, and 7.0 g, respectively, and corresponding values for the hind leg are 134.0, 38.5, and 19.4 g (Hildebrand and Hurley, 1985).

The calcaneum is elongated and has three articular surfaces for the astragalus (Stains, 1959). One *L. californicus* had the posterior calcaneum enlarged and ossified, but this did not affect its ability to run (Dice, 1926).

Average length of large intestine is 164 cm (Steigers et al., 1982). In Idaho, rate of soil ingestion was 9.7 g/day (range, 9.0–10.6), with seasonal peaks in spring (March–May) and autumn (August–October—Arthur and Gates, 1988). When food is reduced by 25%, *L. californicus* had lower body mass and kidney fat indices, higher femur marrow fat, serum bilirubin, cortisol concentrations, and width of adrenal cortex, and it had depressed immune function (Henke and Demarais, 1990).

An average of 545 fecal pellets are produced each day. Sex, age, size of animals, and mass of forage consumed does not influence number of pellets voided, but size of pellets tends to increase with increase in mass of forage consumed (Arnold and Reynolds, 1943). Two kinds of feces are produced. The hard, dark feces seen in the field are the final waste product, voided during the feeding period. During the day, when *L. californicus* is resting, soft feces are formed. These pellets are taken from the anus and swallowed whole (Jones et al., 1983). Transition from hard to soft feces in the rectum may be gradual or sudden. Young animals may ingest soft feces from the mother; this could be a method of passing the flora and fauna from the intestinal tract of the mother to the offspring (Lechleitner, 1957). Moisture content of soft and hard pellets averages 80 and 74%, respectively, and protein content of soft and hard pellets averages 46 and 14%, respectively (Steigers et al., 1982). Fecal pellets are rounded, slightly flattened, and ca. 13 mm in diameter (Bailey, 1936). Time required for complete degradation of fecal pellets is ca. 4.4 years, depending upon relative humidity and precipitation (Flinders and Crawford, 1977).

Length of ear varies geographically with temperature in accordance with Allen's ecogeographic rule (Griffing, 1974). At a body mass of 2,300 g, surface area of the body is ca. 1,740 cm^2 and surface area of both ears is ca. 332 cm^2 (Schmidt-Nielsen et al., 1965). The large pinnae are potentially outstanding sites of conductive, convective, and radiative heat exchange with the environment (Hill and Veghte, 1976). As air temperature increases during the day to >40°C, circulation in the ears is reduced. Ears are held down against the back and ear vessels remain constricted. Cutaneous vasoconstriction in cold is to conserve heat, and vasodilation in a warm environment serves to dissipate heat (Schmidt-Nielsen et al., 1965). Large ears may serve as efficient radiators to the cool sky, which on clear days, may have a radiation temperature ca. 25°C below that of the animal. By seeking shade, where ground temperatures are low and solar radiation is screened out, and by sitting in a depression where radiation from the hot surface is obstructed, net radiation loss to the surroundings may be sufficient to account for necessary heat loss, without much loss of water (Schmidt-Nielsen, 1964).

In summer, *L. californicus* requires ca. 120 ml of water kg^{-1} day^{-1}, and its diet must contain at least 68% water to meet this requirement (Nagy et al., 1976). There is no evidence that *L. californicus* goes to and from water holes or other water sources, as would be necessary if free water were a requirement. Its food is succulent, with cactus increasingly consumed as drought conditions increase (Vorhies, 1945). Heat load, and therefore use of water, is reduced by seeking shade. Other factors that contribute to reducing water loss are insulation and reflectivity of pelage. Average body temperature is 39.2°C, maximum survival temperature is 43.7°C, and lethal temperature is 45.4°C. When exposed to high ambient temperature, respiratory rate may increase to 350 respirations/min. At 15–35°C, metabolic rate is 0.57 ml of oxygen g^{-1} h^{-1}. The lower critical temperature is ca. 12°C (Schmidt-Nielsen et al., 1965). *L. californicus* minimizes loss of plasma volume when exposed to dehydration (Reese and Haines, 1978).

Rectal glands, lying in both sexes on either side of the anus, secrete a substance that hardens to a yellow to orange-colored flaky material, with a strong musky odor. The characteristic odor of *L. californicus* apparently originates in these glands. Each is a simple sac ca. 12 mm deep and with a wide external opening; their function is unknown (Vorhies and Taylor, 1933). Average mass of both adrenal glands (in mg) is 388.4 for pregnant adult females, 378.8 for nonpregnant adult females, 270.0 for adult males, 243.9 for juvenile females, and 229.3 for juvenile males (Herrick, 1965). There is no difference in mass of thyroid glands between sexes. In adults, there is considerable seasonal variation in metabolism of iodine (French, 1959).

As a prey item for *Canis latrans*, *L. californicus* has an average gross energy of 4.8 kcal/g of dry matter, digestible energy of 3.8 kcal/g of dry matter, crude digestible protein of 64.0% of dry matter, and digestible protein of 50.6% of dry matter (MacCracken and Hansen, 1986). In a *Larrea tridentata* community in Arizona, *L. californicus* had a maintenance energy of 22,000 kcal ha^{-1} $year^{-1}$, growth energy of 1,210 kcal ha^{-1} $year^{-1}$, and energy flow of 23,210 kcal ha^{-1} $year^{-1}$. This accounted for 21.9% of energy in the community (Chew and Chew, 1970).

Lepus californicus is a biological indicator of iodine^{131} in the environment (Rickard and Price, 1984). At the National Reactor Testing Station, Idaho, strontium^{90} in bone of *L. californicus* is used as an index of environmental contamination (Fineman and Detmer, 1960). At Hanford Reservation, Washington, *L. californicus* transported radioactive materials in feces ≥1.6 km from disposal sites (O'Farrell and Gilbert, 1975). Accumulation of plutonium^{239} is greatest in bone tissue (Romney et al., 1970). Irradiated black-tailed jackrabbits had an hourly movement of 353 m compared with 294 for controls, they had a bimodal activity curve with peaks at 1700 and 0300–0500 h compared to no such pattern in controls, an average daily home range of 26.4 ha compared with 13.6 for controls, and a seasonal home range of 111.6 ha compared with 98.8 for controls (Nelson and Wagner, 1973).

No physical changes sufficiently well marked to be noticeable in the breeding period have been observed. Mammae are so flatly placed along the abdomen that they may not be obvious, even when most active. However, upon closer examination six mammae are readily found; one pair pectoral and two pair abdominal (Vorhies and Taylor, 1933). Mammae are arranged on two long mammary glands on the sides of the abdomen (Bailey, 1936).

Testes usually are in the scrotum during the breeding season. These organs are indistinguishable in *L. californicus* in the field, and only moderately conspicuous when the animal is closely examined. In midwinter, testes usually are withdrawn into the body cavity, but the inguinal canal always is open and their actual position is variable (Vorhies and Taylor, 1933). *L. californicus* does not have a baculum (Hoffmeister, 1986).

ONTOGENY AND REPRODUCTION. In California, sexually active males are present in all months (Lechleitner, 1959). In Kansas, production of spermatozoa in adults increases through December and January, but testes of adults contain spermatozoa from December until late August (Tiemeier, 1965).

There is a shorter breeding season in regions with more severe winters (French et al., 1965; Gross et al., 1974); e.g., 128 days in eastern Idaho (French et al., 1965), ca. 220 days in Kansas (Bronson and Tiemeier, 1958*a*), and >300 days in Arizona. In Arizona, November is the only month without breeding activity (Vorhies and Taylor, 1933). In Utah, percentage of pregnant females increases from January to May, then declines to July (Gross et al., 1974). In California, breeding occurs during most months (Orr, 1940), and in Kansas, the breeding season is January through August (Tiemeier, 1965).

Ovulation is induced by copulation, which occurs repeatedly after long, vigorous chases (Jones et al., 1983). Gestation period is ca. 40 days (Haskell and Reynolds, 1947). Number of young per litter (primarily based on counts of embryos) averages about two in Arizona (Vorhies and Taylor, 1933), three in Kansas (Bronson and Tiemeier, 1958*a*), three in Nevada (Hall, 1946), five in Idaho (Feldhamer, 1979), and five in California (Orr, 1940). Maximum number of young/litter is seven in California, Idaho, and Nevada (Feldhamer, 1979; Hall, 1946; Orr, 1940). However, in California average number of young per litter varies from year to year, depending upon environmental conditions (Orr, 1940); average number of embryos per female is one in January, four in April, and one in August (Lechleitner, 1959). In Arizona, size of litters vary by months, showing a correlation with precipitation (Vorhies and Taylor, 1933). In Kansas, average size of litters fluctuated by month from 1.0 in January to 4.2, usually in May, with a gradual decrease until the breeding season ended (Tiemeier, 1965). In Utah, average size of litters each month rose from one to two in January to more than six in April, and declined to three or four at the end of the season. Size of litter is positively correlated with latitude, the main difference occurring in midseason litters (Gross et al., 1974). In Idaho, no relationships were evident between litter size and age or mass of the female (Feldhamer, 1979). In Arizona, all animals, regardless of age, had a tendency to produce larger litters during the latter part of the breeding season. Age of mother has no effect on size of litters (Haskell and Reynolds, 1947).

Number of litters/female averages 3.8–4.4 in Kansas (Bronson and Tiemeier, 1958*a*; Tiemeier, 1965) and 3–6 in Arizona (Haskell and Reynolds, 1947; Vorhies and Taylor, 1933). Breeding potential is 10.2 young/year in Idaho (Feldhamer, 1979), 12.3 in Kansas (Tiemeier, 1965), and 13–14 in Arizona (Haskell and Reynolds, 1947). In California, older females maintain 100% breeding activity from January through August. There is a postpartum estrus, and pregnant females are present every month, but do not appear in large numbers until January (Lechleitner, 1959). However, consistent postpartum breeding does not occur in Kansas (Bronson and Tiemeier, 1958*a*).

Size at birth varies within a litter, but the individual in a litter of one probably is larger than any one of a litter of three or four. At 1 day old, average and range of measurements (in mm) of a litter in Arizona were: total length, 140 (140–140); length of tail vertebrae, 20 (18–20); length of hind foot, 34 (33–36); length of ear, 27 (25–30); mass, 66 g (60–71 g—Vorhies and Taylor, 1933). Compared with adults, 1-day-old young have a mass that is 3% of adult females (Goodwin and Currie, 1965).

At birth, teeth are present, eyes are open (Dickerson, 1917), and young are fully clothed with hair, including black ear tips and black tail (Haskell and Reynolds, 1947). Pelage is brown with accents of yellow and black, much richer in color than the grayish pelage of the mother (Dickerson, 1917). There is a pale-gray area that surrounds the mouth and nose (Seton, 1929). A small white patch, often present in the center of the forehead at birth, is most conspicuous when young are 2–3 weeks old. At 10 weeks, the patch begins to disappear and at 18 weeks it consists of a narrow, poorly defined line of white hairs (Goodwin and Currie, 1965). The dark, natal pelage gradually is replaced by a paler immature coat. Adult pelage becomes apparent the first winter when young are 6–9 months old (Haskell and Reynolds, 1947).

At birth, the muzzle is short and broad and the face is flat below the eyes. By 10 days old, the muzzle begins to lengthen and narrow (Dickerson, 1917). At birth, ears are <50% the length of head. By day 15, ears are as long as the head. By 28 days, ears are ca. 100 mm long, and ca. 115 mm at 35 days (Seton, 1929). The ear reaches adult size at 12–15 weeks (Tiemeier, 1965). Except for ear measurements, there is no obvious difference between sexes (Haskell and Reynolds, 1947).

Average lengths of ear, hind foot, and body of newborns are 22, 17, and 29%, respectively, of comparable measurements of adults. One month after birth, length of body has completed 50% of its growth, but mass is only 13% of adult mass. Apparently, most energy used by young is devoted to development of the body frame. Ears and hind feet develop quickly. By 2.5 months, average lengths of ear, hind foot, and body surpass 90% of adult measurements, but mass is only 65% of adult mass (Goodwin and Currie, 1965). Mass reaches that of adults at 32 weeks, and total length at 28 weeks (Haskell and Reynolds, 1947).

After parturition, mothers remove all afterbirth from young. Mothers continue to lick sexual organs and navels of young throughout the nursing period (Haskell and Reynolds, 1947). For the 1st 10 days after birth, young are nursed exclusively, followed with solid food to supplement nursing. They may continue to suckle until 12–13 weeks old (Hoffmeister, 1986), but may only be suckled 17–20 days (Tiemeier, 1965). Until ca. 1 week old, they suckle by lying on their backs with their hind feet around the neck of the mother. Thereafter, they change their nursing posture to an upright position, or occasionally reverting to prostrate feeding. At ca. 10 days old, young supplement their milk diet with solid food, and at an age of ca. 3 weeks, they will eat a dry ration of rolled barley and alfalfa (Haskell and Reynolds, 1947).

Young do not exhibit well-coordinated hopping until 2–3 days old (Haskell and Reynolds, 1947). During the 1st few days, young have a generalized sense of fear, squatting with lowered ears at any sound or movement; they can turn and jump while emitting a low-pitched sound. For 1–2 days they keep close to the nest, and they have some difficulty with orientation and balance. By 3 days, they have considerable coordination. On day 4, they begin digging, and until ca. 5 weeks old they spend much time digging (Dickerson, 1917).

In California, mortality seems to be equally divided between sexes (Lechleitner, 1959). In Idaho, mortality during the 1st year of life was ca. 91% and ca. 98% by 3 years (Feldhamer, 1979). In Kansas, populations contained 71–82% young-of-the-year in autumn (Bronson and Tiemeier, 1958*a*). In Utah, populations were comprised of 72–93% young-of-the-year in September and October (Gross et al., 1974). Under natural conditions, black-tailed jackrabbits probably do not live >7 years (Haskell and Reynolds, 1947).

ECOLOGY. *Lepus californicus* seems to favor places where grazing has been severe or where grasses are not abundant and cacti and low shrubs are scattered (Baker, 1956); it does not readily move into areas of tall grass or forest where visibility is obscured (Jones et al., 1983). In Arizona, the black-tailed jackrabbit is an animal of open country; it is found in habitats with *Prosopis*, *Artemisia*, desertscrub, and *Pinus-Juniperus* (Hoffmeister, 1986). In Colorado, the black-tailed jackrabbit was most abundant on pastures with light and moderate grazing (Flinders and Hansen, 1975). In Mexico, *L. californicus* is almost entirely a desert dweller; it often is common on desolate stretches of cactus desert or on adjoining *Prosopis*-grasslands that have been so overgrazed that the ground is almost bare (Leopold, 1959).

A sitting black-tailed jackrabbit taking advantage of the sparse shade of a clump of *Prosopis* or other plant is a characteristic sight in the Chihuahuan Desert (Anderson, 1972). *L. californicus* often builds shelter forms to protect itself from heat by making horizontal excavations in sand beneath vegetation (Burt, 1934). Shelter forms often are 10–20 cm wide and 30–45 cm long. Some are slight depressions in the surface and others are excavated to depths of 3–11 cm. Usually, the depression fits the haunches of the reposing animal, being deepest at the rear and sloping out to ground level at the front. Frequently, forms are in clumps of grass or other vegetation (Vorhies and Taylor, 1933). In Utah, average traits of shelter forms were: temperature inside form, 8°C; temperature outside form, 9°C; light inside form, 1,369 footcandles; light outside form, 2,990 footcandles; wind inside form, 0 km/h; wind outside form, 2.5 km/h; volume of form, 118.5 cm^3; length of form, 30 cm; width of form, 15 cm; depth of form, 2.5 cm; height of shrub with shelter form, 93 cm; and distance to nearest cover, 175 cm (Flinders and Elliott, 1979).

Throughout much of its range, adult black-tailed jackrabbits rarely take shelter in holes or burrows, but some may enter holes dug by *Cynomys* or *Taxidea taxus* (Cahalane, 1939; Long, 1940; Vorhies and Taylor, 1933). In the Mojave Desert, *L. californicus* may retreat to burrows during hot days in summer (air temperature >42°C), but for only 3–5 h in the afternoon. Self-constructed burrows begin as shelter forms and gradually are deepened by digging during hot afternoons. After several days, burrows are deep enough to enclose the entire animal. Burrows are not used during high winds or in cold winter months, although they are available (Costa et al., 1976).

The black-tailed jackrabbit also makes conspicuous trails and runways through brush, weeds, meadows, fields, and over the dusty or sandy surface of desert valleys (Bailey, 1936). It seems to prefer the easiest route for travel. Thus, when vegetation is broken down by former movements, it continues to use these routes and soon definite trails develop (Lechleitner, 1958*a*).

Components of diet are variable among locations and seasons (Dunn et al., 1982). In Utah, e.g., *L. californicus* ate nearly all species of plants including *Artemisia tridentata, Atriplex confertifolia, Atriplex nuttallii, Eurotia lanata,* and *Halogeton glomeratus* (Currie and Goodwin, 1966; Westoby, 1980). Black-tailed jackrabbits also may consume fungi (Maser et al., 1988), gravel, or sand (Vorhies and Taylor, 1933), but they reportedly will not eat fish, flesh, fowl, reptiles, and insects (Seton, 1929). However, in Tamaulipas and Texas, *L. californicus* has been reported to feed on carcasses of horses (Vorhies and Taylor, 1933).

A mature black-tailed jackrabbit may consume ca. 390 g of forage/day, of which ca. 45% is assimilated. Succulent forages are better assimilated than dry, woody foods used during winter months (Johnson and Peek, 1984). Average amount of green alfalfa and grama grass (*Bouteloua*) consumed in feeding trials was 307.4 g/day (range, 146.5–631.2 g—Vorhies and Taylor, 1933). In New Mexico, average mass of stomach contents was 67 g; lactating females had heavier stomach contents than nonlactating animals (Griffing and Davis, 1976).

Lepus californicus prunes *Gutierrezia sarothrae* during November to March. Presumably, it consumes only new growth stems of this species. It also prunes stems from *Larrea tridentata* during dry winter months at an average height of 44 cm above ground, yielding a severed stem 30–70 cm in length and 11–50 g in mass. *L. californicus* eats new woody stems from the previous season allowing leaves and old wood to fall to the ground. It preferentially prunes stems of shrubs with higher moisture content in tissues, and it also prunes stems from the same shrubs in successive years (Steinberger and Whitford, 1983).

The black-tailed jackrabbit is an important disperser of seeds. In Kansas, ca. 15 kg of seed of *Sporobolus cryptandrus* was deposited in fecal pellets on 1 ha (Brown, 1947). It also is important in disseminating seed of *Opuntia,* and may be responsible for much of the rapid spread of this plant (Timmons, 1942). *L. californicus* will eat *Opuntia* during autumn and winter; seeds consumed are defecated and randomly scattered while it feeds. Pellets containing cactus seeds were most numerous in overgrazed shortgrass areas (Riegel, 1941).

Size of home range may be 20–140 ha (Harestad and Bunnell, 1979; Lechleitner, 1958*b*). In Kansas, movement range of juveniles was 4–28 ha with a mean of 14, while that of adults was 5–78 ha with a mean of 17 (Tiemeier, 1965). In Idaho, *L. californicus* seldom moved >0.4 km, indicating a home range of <16 ha. Dispersal movements of greater distances occurred in ca. 18% of the population; greatest distance moved was 45 km in a 17-week period. Seasonal moments involve short distances, but may result in dense local concentrations (French et al., 1965).

Techniques used to determine density include road counts, drive counts, and a variety of transects (Smith and Nydegger, 1985). The black-tailed jackrabbit exhibits a 10-year cycle in population density (Anderson and Shumar, 1986), but it may increase in numbers when an extensive control program of predators, such as *C. latrans,* has been carried out (Hoffmeister, 1986). In Idaho, densities ranged from 0.1 to 1.5/ha during a 4-year study (Smith and Nydegger, 1985). In Utah, populations fluctuated by nine fold (Gross et al., 1974). In Kansas, densities varied from 0.2–0.3/ha in pastureland to 5.6/ha on a wheat field; average density was 0.8–1.3/ha (Tiemeier, 1965). Near Bakersfield, California, densities have reached 208/ha (Seton, 1929).

Lepus californicus may cause damage to agricultural crops, including lawn and pasture grasses, ornamental shrubs, orchards, grape vines, alfalfa, seeding grain crops, and potato plants (Burt, 1934; Johnson and Peek, 1984; Tiemeier, 1965; Westoby and Wagner, 1973). In Kansas, most crop damage was restricted to fields near daytime resting areas, and buffer fields restricted the amount of damage (Bronson and Tiemeier, 1958*b*).

The black-tailed jackrabbit has been kept from causing damage to crops by fencing, rabbit drives, organized hunts, shooting, trapping, snaring, poisoning (Bailey, 1936), and bounties. One rabbit drive involved ca. 6,000 persons and resulted in destruction of ca. 20,000 black-tailed jackrabbits near Fresno, California. In 207 drives, 494,634 were killed (Palmer, 1897). During a typical drive, a pen with woven-wire sides was built. From a narrow opening on one side, two wings of wire fence were set up in the shape of a "V." A line of persons converged on the wide end of the V driving the jackrabbits into the pen; there the animals were killed (Hall, 1955). Black-tailed jackrabbits killed in massive drives were processed and shipped to market, scalped for collection of bounty, used as food for humans, fed to swine, used for fertilizer, or discarded (Palmer, 1897).

Poisons that have been used to control populations include sodium fluoroacetare (compound 1080—Johnson and Peek, 1984), strychnine (Seton, 1929), zinc phosphide (Hood, 1972), and the anticoagulant diphacinone (Johnston, 1978). Unfortunately, many of these chemicals also harm non-target species (Johnson and Peek, 1984). In Idaho, in an area of 8,502 km^2, 168,166 black-tailed jackrabbits were killed with 24 kg of strychnine applied to bait (Seton, 1929). Use of chemosterilants to inhibit reproduction is impractical because black-tailed jackrabbits are widely distributed during the breeding season, reproduction of non-target species can be affected, and recurrence of estrus after induced litter loss requires multiple treatments (Johnson and Peek, 1984).

In southern Arizona, *L. alleni* and *L. californicus* occur in equal numbers. These species often are seen together, sometimes sitting under the same bush or running away side by side (Swarth, 1929). However, their different gaits, when running, distinguishes them (Mearns, 1890). On grassy bahadas at elevations of ca. 1,050 m, *L. alleni* usually is several times as numerous as *L. californicus.* However, in *Prosopis* along valley bottoms and on barren *Larrea* desert, *L. californicus* usually is more numerous (Vorhies and Taylor, 1933). In New Mexico, a decline in density of *L. callotis* was accompanied by an increase in relative numbers of *L. californicus* and *Sylvilagus audubonii.* It appears that the numbers of *L. callotis* may have decreased as density and vigor of grass plants declined, while populations of *L. californicus* and *S. audubonii* increased in response to a concurrent increase in cover of forbs and shrubs (Bednarz and Cook, 1984).

Lepus californicus may be infected with, e.g., *Borrelia burgdorferi* (Lane and Burgdorfer, 1988), *Toxoplasma gondii* (Franti et al., 1975), *Coxiella burnetti, Pasteurella tularensis* (Vest et al., 1965), *Pasteurella pestis* (Kartman, 1960), *Yersinia pseudotuberculosis* (Hubbert, 1972). Endoparasites include protozoans (e.g., *Eimeria*—Dunn et al., 1982; *Trypanosoma*—Ward, 1934), cestodes (e.g., *Taenia*—Dunn et al., 1982; *Cysticercus*—Ward, 1934), nematodes (e.g., *Dirofilaria*—Dunn et al., 1982; *Obeliscoides*—Ward, 1934). Ectoparasites include a variety of ticks (e.g., *Dermacentor, Haemaphysalis*—Dunn et al., 1982), mites (e.g., *Androlaelaps*—Whitaker and Wilson, 1974; *Euschoengastia*—Wrenn and Loomis, 1974), fleas (e.g., *Hoplopsyllus*—Dunn et al., 1982; *Monopsyllus*—Stark, 1958), lice (e.g., *Haemodipsus*), and dipterans (e.g., *Cuterebra*—Vorhies and Taylor, 1933).

Predation by *C. latrans* may affect abundance of black-tailed jackrabbits (Wagner and Stoddart, 1972). Conversely, density, demography, movement, and reproductive success of many predators are related to abundance of *L. californicus* (e.g., *Buteo regalis, Aquila chrysaetos, Bubo virginianus*—Smith and Murphy, 1979; *C. latrans*—Clark, 1972; *Lynx rufus*—Knick and Bailey, 1986; *Vulpes macrotis*—Egoscue, 1975). Hunter-killed black-tailed jackrabbits may serve as a source of exposure of lead to *A. chrysaetos* and *Haliaeetus leucocephalus* (Craig et al., 1990).

Humans, with motorized vehicles, spotlights, and guns, probably cause the greatest mortality (Tiemeier, 1965). In addition to predation and shooting by humans, automobiles, forest fires, drought, hail, and extremely cold weather can cause death of black-tailed jackrabbits (Vorhies and Taylor, 1933). In California, automobiles and fires kill considerable numbers. Predators, except dogs, appeared to have little influence on the adult population. Greatest loss occurred in winter. About 20% of deaths may have been due to intestinal coccidiosis, but the remainder may have died of a condition resembling shock disease (Lechleitner, 1958*b*). The number of carcasses on highways have ranged from <1/km in uncultivated areas of Kansas (Sprague, 1939) to ca. 130/km in Idaho (Williams and Nelson, 1939).

A long-range pulsing transmitter equipped with a thermistor has been used to detect rate, time, and cause of mortality. Of 25 test animals, 64% were killed by coyotes, 12% died of unknown factors, 20% were partially eaten by birds, and one was shot by a hunter 10 km from the study area (Stoddart, 1970). Radiotelemetry collars cause increased grooming, but mobility is not hindered. Vulnerability to avian predators is greater for collared animals, but deaths due to *C. latrans* are not different from control animals (Wywialowski and Knowlton, 1983).

Skins of *L. californicus* have been used for hats (Kellogg, 1937). The black-tailed jackrabbit has been used to train racing dogs (Jackson, 1962), has been exhibited in zoos (Dolan and Moran, 1969), and has served as food for man. Domestic chickens will eat flesh of black-tailed jackrabbits, and the result is production of eggs at an accelerated rate (Vorhies and Taylor, 1933).

BEHAVIOR. *Lepus californicus* primarily is nocturnal (Vorhies, 1945). Evening feeding periods seem to vary greatly with weather, season, and phase of the moon. Calm and dry evenings appear to be more favorable for longer feeding periods than windy and wet evenings (Lechleitner, 1958*a*). On cloudy days, rarely otherwise, it may feed during midday (Vorhies and Taylor, 1933). Wind is the most important weather factor limiting activity. Falling snow and fog limits nocturnal activity, while rain and temperature seem to have little effect on movement (Tiemeier, 1965). Following cold nights, these jackrabbits may lie on their sides in morning sunshine, apparently basking. On hot summer days, this species usually begins panting (through the nose only) in early afternoon, and becomes restless (Costa et al., 1976).

When foraging, the body is hunched up. Gradually it is stretched out as the animal attempts to reach farther away. Ultimately, the hind legs are again brought up beneath the body with a hop and the original position is assumed. Consequently, while feeding it moves slowly. It is constantly alert for signs of danger and frequently shifts its large, erect ears around in an attempt to detect unusual sounds. The head is raised every 20–30 s to inspect the surroundings. During this pause, chewing continues. The tail is almost always elevated so that it is pressed back against the rump (Orr, 1940). In browsing *Prosopis, L. californicus* rears up on its hind feet, its forefeet hanging limp, its ears flopping freely, or wishing to reach higher, stands on its toes, places its forepaws on a branch, and proceeds to crop off leaves, bark, or buds. It is especially fond of tufts of green leaves that appear in axils of *Prosopis* spines. Bark may be striped for a distance of ca. 60 cm above ground (Vorhies and Taylor, 1933).

No regularly recurrent seasonal migration occurs. However, there are noticeable changes in numbers of black-tailed jackrabbits through the year; perhaps, there is some movement to areas with more food or more favorable temperatures. Amount of daily movement varies with distance between shelter and foraging areas. It may only travel from brushy washes to nearby grassy mesas, but it also may move up to 16 km round trip from desert to alfalfa fields. Black-tailed jackrabbits may invade outskirts of desert cities, moving onto green lawns in late afternoon (Vorhies and Taylor, 1933).

Lepus californicus cleans itself by licking the body and also by licking the paws and rubbing them over parts not accessible to its tongue, such as the top of the head and ears (Orr, 1940). It dusts itself by rolling in shallow depressions it has dug in loose sand. When the dusting process is finished, it will sit on its hind legs, lick its forepaws, and brush the sides of its head (Tiemeier, 1965). Black-tailed jackrabbits may shake their heads vigorously from side to side to dislodge mosquitoes from the long ears. Sometimes the hind feet are used to scratch the ears (Orr, 1940).

When *L. californicus* is in a shelter form in the middle of the day, it may remain motionless to avoid detection. When undisturbed and moving about slowly, the tail usually is elevated over the back; ears frequently are partly lowered (Orr, 1940). *L. californicus* appears to rely on hearing more than any other sense to detect danger. Sense of smell seems to be used for identification of foods and to detect conspecifics. It is able to see movements, but apparently cannot distinguish still objects at any distance. When danger threatens, the first sign of alertness is raising of the ears in an attentive attitude. If danger seems remote, it often stands on the hind feet with front feet held limply in front, ears erect, and nose vigorously twitching. If an individual becomes alerted, alarm somehow is spread quickly to others in the vicinity. When danger is imminent, *L. californicus* reacts by either fleeing or remaining motionless. In dense vegetation, it often reacts to a distant stimulus by sneaking away or by running with the body close to the ground and ears held low (Lechleitner, 1958*a*). Generally, after running directly away from the source of disturbance, the jackrabbit veers off its course so that when it stops it is faced at a right angle to, rather than directly away from, the point of danger (Orr, 1940).

The black-tailed jackrabbit is a good runner and leaper, prime assets in avoiding *C. latrans*, its principal predator (Hoffmeister, 1986). It can run up to 64 km/h (Garland, 1983), and may leap over small bushes or similar obstacles, but it is more prone to sneak away without making itself conspicuous by long leaps, and even when frightened pursues a flatter course, not bounding high from the ground in its observation leaps (Vorhies and Taylor, 1933). Often it runs into obstacles; fences apparently go unnoticed and it often runs directly into them (Lechleitner, 1958*a*). One loping along made 20 hops in 5.5 s; i.e., at a rate of 218 hops/min, and at ca. 3 m/hop it can travel >650 m/min. Observation hops are high, ca. 1.1 m, and take 3× as much time as low bounds (Seton, 1929).

Lepus californicus usually avoids entering water (Hawbecker, 1942), but it will cross rivers at ice jams (Couch, 1928) and is known to forage on vegetation in ca. 5 cm of water (Lechleitner, 1958*a*); one was found on a pelagic raft of giant kelp (*Macrocystis pyrifera*) 24 km off the coast of California (Prescott, 1959). The black-tailed jackrabbit swims with all but the head and ears submerged; ears are lowered over the back (Orr, 1940). It swims rapidly and well, and when emerging from water, it will shake the water off (Lechleitner, 1958*a*).

This hare usually is silent, but when cornered, injured, or handled, it may emit a piercing cry. Some handled animals respond by emitting a guttural growl or grunt. This low growl or grunt sometimes is heard from females reacting aggressively toward approaching males (Lechleitner, 1958*a*).

Except during the breeding season, *L. californicus* is not gregarious, but groups sometimes as large as 200–250 are seen in winter months. These are concentrations of feeding animals on winter wheat or grain sorghum. Smaller groups of two to five occur during the breeding season (Tiemeier, 1965). There is no social organization among animals in the same field. The only semblance of family structure exists between young and mother; these interactions cease by the time young are weaned (Lechleitner, 1958*a*).

Aggressiveness is uncommon in natural situations. Typically two animals close together will ignore each other, but they may butt, bite, jump 30–60 cm into the air, run in circles at high speed around another animal, or simply avoid the other animal. Often, two black-tailed jackrabbits will cease usual activities and turn to face each other, one will either attempt to butt heads or run a tight circle around the other, the second will then chase the first for a short distance, often attempting to bite the pursued on the flanks, and as if by mutual consent, such action shortly ceases and both animals will resume their original activities (Tiemeier, 1965). Perhaps this is fighting or a playful contest (Orr, 1940). Females often charge other black-tailed jackrabbits that approach within 5–10 m of their position. This antagonism seems to lead to a spacing and may be a type of territorial behavior (Lechleitner, 1958*a*).

Males frequently fight by rearing up on their hind legs and striking at each other with their forefeet, usually causing fur to fly. Biting each other, especially on the ears, also occurs (Hoffmeister, 1986); ears may be torn and seriously injured (Vorhies and Taylor, 1933). A sexually active male, with nose close to the ground, seeks a female. If a male is encountered, a fight or a chase may ensue (Hoffmeister, 1986).

Sexual activities can be classified as hunt, approach, chase, boxing match, and copulation. Any of these activities can end quickly and be replaced by some other behavior (Lechleitner, 1958*a*). Some females accept males on the day of parturition. In

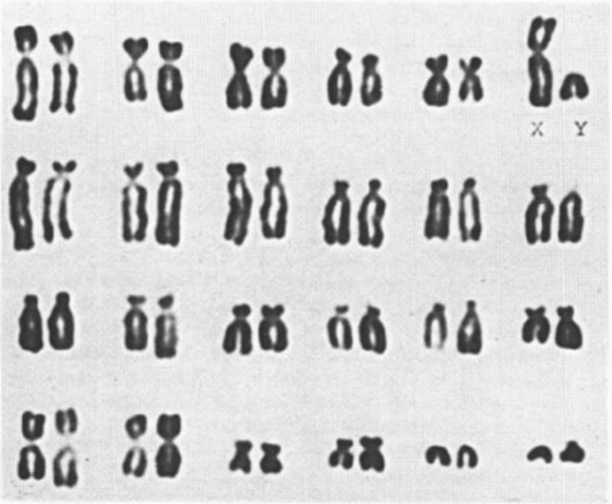

FIG. 4. Karyotype of *Lepus californicus eremicus* from near Tucson, Pima Co., Arizona (Hsu and Benirschke, 1967).

such instances, males sometimes assist females in disposing of afterbirth. Breeding is promiscuous; females accept the first interested male (Haskell and Reynolds, 1947). Courtship behavior is intense and involves circling, male and female approaches, long chases, and urine emission during jumping and chasing activity. Complex behavior involving combinations of all of these components may last 5–20 min. Copulation usually follows. After copulation, the male may jump backward, fall to the ground, emit a hissing squeal, and leap up again renewing the chase with up to four more copulations. The black-tailed jackrabbit may exhibit displacement behavior when excited during escape or reproductive behavior (Blackburn, 1973).

Lepus californicus may place its young in a prepared nest, with some hair as a lining. Along ridges in an alfalfa field, nests were sunk into the ground, level with the surrounding surface. Each was thickly lined with fur and only a small opening was left at the top. Nests were invisible except when plowed up. In areas with adequate aboveground cover and hard soil, the nest was hardly more than an enlarged shelter form beneath heavy grass clumps or brush (Vorhies and Taylor, 1933). In California, one nest consisted of an unlined shallow depression in the ground and resembled shelter forms used by adults (Lechleitner, 1958*a*).

For at least the 1st week postpartum, a litter generally is grouped during day and night and has a strong fidelity for a particular resting site. In situations of potential danger, young remain motionless. If harm becomes imminent, litter mates move away from the threat independently. The mother plays an active role in retrieving and regrouping a litter if it is disturbed. Except during periods of nursing, the female stays some distance from the litter and does not act to distract predators or watch over young (Stoddart, 1984). Nursing females move to their litters at night, and away from them in daytime (Vorhies and Taylor, 1933). In California, several young were found in dense grasses and weeds. They remained motionless until closely approached; then they crept a short distance away and crouched again. Young were active at night and remained almost motionless during day. This pattern of behavior persisted until they were ca. 2 months old. At this time, a gradual change to more diurnal habits occurred (Lechleitner, 1958*a*).

Lepus californicus is difficult to capture and keep in captivity. If a wild animal is placed into a cage, it incessantly throws itself against the screen until it kills itself (Schmidt-Nielsen, 1964). In addition, some die, presumably of shock, upon being handled for the first time (French, 1959).

GENETICS. The diploid number of chromosomes is 48; there are 42 metacentrics, submetacentrics, or subtelocentrics, 4 acrocentrics, the Y chromosome is a small acrocentric, and the X chromosome is a large submetacentric (Fig. 4; Hsu and Benirschke, 1967). The fundamental number of chromosomal arms is 88 (Uribe-Alcocer et al., 1989). An albino *L. californicus* occurred in New Mexico (Kennedy, 1949).

REMARKS. A morphometric analysis of 16 subspecies of *L. californicus* produced two groups that were separated geographically by a line running from the Colorado Rockies to the Gulf of California. There also was a definite separation of *L. insularis* from *L. californicus* in Baja California (Dixon et al., 1983). Shamel (1942) regarded the eastern subspecies of *L. californicus* as more closely related to *L. callotis*, but Hall (1951*a*) considered them to be subspecies of *L. californicus*.

The Latin word *Lepus* means hare (Jaeger, 1955). The specific epithet *californicus* refers to California. Additional common names are Californian jackrabbit, gray-sided jackrabbit, narrow-gauge mule, jackass-hare, Texas jack, Texan hare (Seton, 1929), liebre, liebre de cola negra (Leopold, 1959), and Great Plains jackrabbit (Jones et al., 1983).

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