

*Lepus alleni*. By Troy L. Best and Travis Hill Henry

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*Lepus alleni* Mearns, 1890

Antelope Jackrabbit

*Lepus alleni* Mearns, 1890:294. Type locality "Rillito Station, on the Southern Pacific Railroad [Pima County—Miller, 1912:351], Arizona."

**CONTEXT AND CONTENT.** Order Lagomorpha, Family Leporidae, Subfamily Leporinae, Genus *Lepus*, Subgenus *Macrotolagus*. There are ca. 19 species in the genus *Lepus* (Honacki et al., 1982). Three subspecies of *L. alleni* are recognized (Hall, 1981):

*L. a. alleni* Mearns, 1890:294, see above.

*L. a. palitans* Bangs, 1900:85. Type locality "Aguacaliente (about forty miles southeast of Mazatlan), Sinaloa, Mexico."

*L. a. tiburonensis* Townsend, 1912:120. Type locality "Tiburon Island [Gulf of California, Sonora—Hall, 1981:332]."

**DIAGNOSIS.** Compared with other species of *Lepus*, *L. alleni* is large (Anderson, 1972; ca. 2.7–5.9 kg—Vorhies and Taylor, 1933)—the ears are especially large (Fig. 1; Anderson, 1972). It has long slender legs, a short tail, and a large skull (Nelson, 1909). Like *L. callotis*, but unlike *L. californicus*, which has a small white area on the venter, *L. alleni* has a wide white venter giving way to gray on the sides. This gray is sharply demarcated from the darker and buffier dorsum, especially across the hip. There is no black tip on the ears, and the distinct large throat patch is ochraceous buff (Anderson, 1972).

*Lepus alleni* can be distinguished from *L. callotis* by its larger size, long ears, and grayish sides of the body rather than whitish sides. *L. alleni* differs from *L. californicus* in having ears that are white on the outside and without black tips, sides of body that are pale grayish rather than brownish, a longer ear on average, and cranial measurements that average larger (Hoffmeister, 1986).

**GENERAL CHARACTERS.** The sexes are identical in appearance (Brown, 1987). *L. alleni* has exceptionally large, whitish ears that are nearly naked, except for long fringes of white hair on the edges and tips. The ears are sparsely covered with short, whitish or pale-fulvous down, with a few blackish hairs near the tip; bases of ears are white. The entire head has a whitish cast that is mixed with black and suffused with fulvous. The orbital ring is white, lashes are black and vibrissae are mostly black. The upperparts are yellowish brown, strongly mixed with black; this color extends from nape to rump, but does not reach the tail. The hairs of the nape are plumbeous and tipped with fulvous. The sides, including the outer side of the limbs, hips, and rump are white with fine black points on some of the hairs, giving a general pale-gray to these parts. The chin, throat, and undersurface in the median line are white, as are the inner sides of the forelegs above, inner sides of the hind limbs throughout, and upper surface of the feet. The sides of the neck are whitish above. The chest is bright fulvous; this color extends backward on the lower part of the neck and blends with the color of the back (Mearns, 1890). The tail is white (Hall, 1951) and lined above with plumbeous-black, which extends forward upon the rump. The dense coating on the underside of the feet is brown, strongly contrasting with the white upper surface of the feet (Mearns, 1890).

The skull of *L. alleni* is large (Fig. 2). The supraorbital process of the frontal bone is slightly arched, as frequently is the case in *L. californicus*. The nasal bones, premaxillaries, molars, and the entire skull have a massive appearance, contrasting in this respect with the more fragile skull of *L. californicus* (Mearns, 1890). The rostrum is long and heavy, the frontal area is broad, and the supraorbital and postorbital processes are broad and heavy. The posterior end of the postorbital process rests on small bony processes of skull and encloses the long and narrow postorbital foramen. The anterior notch

in front of the supraorbital process is small and sometimes is vestigial. The cheekteeth are heavy. The auditory bullae are small, and the basioccipital is long and not deeply constricted posteriorly. In general shape, the skull resembles that of *L. flavigularis*, but is larger (Nelson, 1909).

Average and range of measurements (in mm) of adult males and females, respectively, are: total length, 619 (553–670), 625 (597–660); length of tail, 57 (52–70), 59 (48–76—Vorhies and Taylor, 1933); length of head and body, 559 (533–584), 558 (533–584—Allen, 1906); length of ear, 163 (146–173), 161 (138–173); length of hind foot, 140 (127–150), 141 (133–150—Vorhies and Taylor, 1933); length of hind foot without claws, 128 (121–133), 127 (121–133—Allen, 1906). Average cranial measurements (in mm) of sexes combined are: basilar length, 81.5; zygomatic breadth, 46.4; postorbital constriction, 13.4; length of nasals, 45.4; width of nasals, 22.6; length of maxillary toothrow, 18.5; diameter of external auditory meatus, 6.0; breadth of braincase, 27.8; length of palatal bridge, 7.7; depth of rostrum, 22.7; parietal breadth, 27.3; length of bulla, 14.9 (Dixon et al., 1983).

In Arizona, the average mass of 61 adult males was 3.69 kg (range, 2.70–4.73) and that of 55 adult females was 4.05 kg (range, 2.88–5.85). If females that were advanced in pregnancy are excluded, the average for females was 3.60 kg (range, 2.88–4.50—Vorhies and Taylor, 1933). In another sample, average mass of 46 males and females was 3.93 kg (Lipson and Krausman, 1988). In

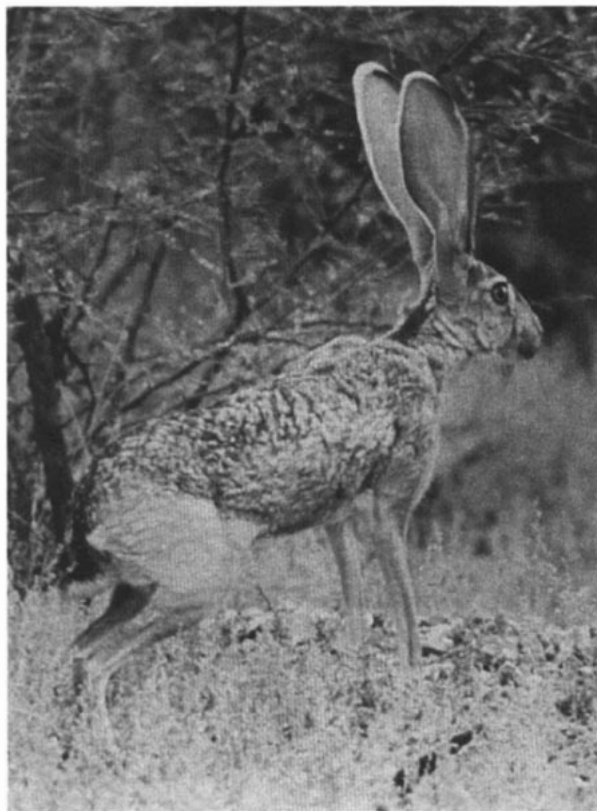


FIG. 1. *Lepus alleni* on the Buenos Aires National Refuge, Pima Co., Arizona. Photograph courtesy of R. Thompson, Arizona Department of Game and Fish.



FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Lepus alleni* from 38 miles SW Caborca on the road to Puerto Libertad, Sonora, Mexico (male, University of New Mexico Museum of Southwestern Biology 37261). Greatest length of cranium is 112.1 mm. Photographs by T. H. Henry.

Sinaloa, masses of a male and two females were 3.40, 4.30, and 2.95 kg, respectively (Armstrong and Jones, 1971).

Compared with *L. a. alleni*, *L. a. tiburonensis* is darker, is more iron-gray, and the buffiness on the back is pale and overlaid and mixed with black (Townsend, 1912). *L. a. palitans* is more brightly colored than *L. a. alleni*. The more intensely colored populations of *L. a. palitans* are in southern Sonora; these populations have a deep and vivid pinkish-buff back, heavily washed with black. The underside of the neck exhibits a richer ochraceous buff, and the sides of the body a clearer iron-gray than is found in populations in southern Sinaloa (Nelson, 1909).

**DISTRIBUTION.** *Lepus alleni* inhabits the desert plains of southern Arizona southward into northern Nayarit; an insular population is present on Tiburón Island in the Gulf of California (Fig. 3; Nelson, 1909; Townsend, 1912). The vertical range is from near sea level in Sonora (Miller, 1912) to 1,500 m in southern Arizona (Vorhies and Taylor, 1933).

**FOSSIL RECORD.** The genus *Lepus* originated in the late Pliocene or early Pleistocene in the Holarctic. The genus spread southward in the late Pleistocene and now extends (excluding introductions) into southern Africa (Dawson, 1967).

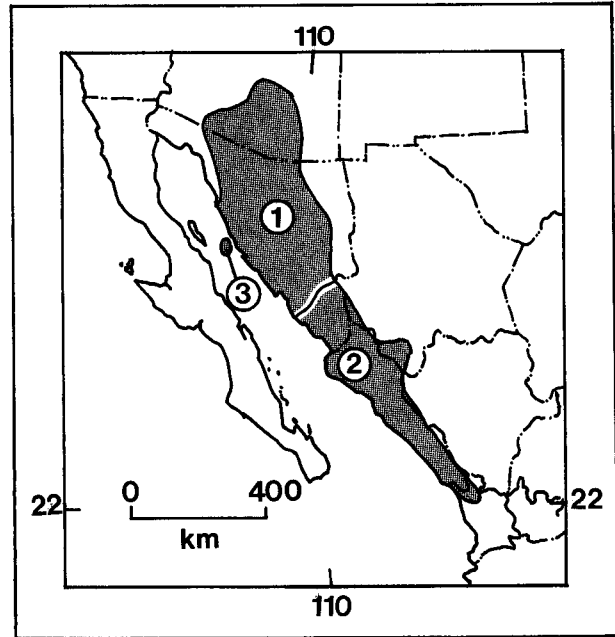


FIG. 3. Distribution of *Lepus alleni* in western North America (Hall, 1981): 1, *L. a. alleni*; 2, *L. a. palitans*; 3, *L. a. tiburonensis*.

A specimen from Burnet Cave, 1,380 m, Eddy Co., New Mexico (age,  $7,432 \pm 300$  years before present), tentatively identified as *L. alleni* (Murray, 1957; Schultz and Howard, 1935), may be *L. callotis* (Harris, 1977). Fossils closely resembling *L. alleni* are known from middle Pleistocene deposits in Sumter Co., Florida (Martin, 1974). *L. alleni* has a long history in North America, beginning in the early Irvingtonian, and may be the same species reported under the name *L. giganteus*. The Pleistocene form may have been larger than extant representatives. The sites in Florida are far from the present range. The present range appears to be much smaller than that in the Irvingtonian (Kurtén and Anderson, 1980).

A population of *L. californicus* in Mexico may have become isolated and diverged to *L. callotis*. One population of this divergent stock then became isolated on the western coastal plain where it diverged even further from the *L. californicus* stock, becoming *L. alleni*. Later, in southern Oaxaca, a second population may have been isolated from the main stock of *L. callotis* and evolved into *L. flavigularis* (Anderson and Gaunt, 1962).

**FORM AND FUNCTION.** Winter pelage is darker than summer pelage in which the black-tipped hairs have faded to brown (Burt, 1938). In Arizona on 2 April, a female was in winter pelage dorsally, which was longer and more variegated with black and fulvous than the summer coat. There were a few long hairs of the winter coat on the sides, whose broad fulvous tips indicated that the fulvous extends farther down in winter (Mearns, 1890). Average characteristics of the pelage include: reflectivity of dorsal pelage, 26%; reflectivity of ventral pelage, 42%; conductance of dorsal pelage,  $3.1 \text{ kcal/m}^2 \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}$ ; thickness of pelage, ca. 11–15 mm (Schmidt-Nielsen et al., 1965). The cuticular scales of dorsal guard hairs of *L. alleni* and *L. californicus* are identical in appearance, whether the hair samples come from museum collections, fresh specimens, or coyote feces (Short, 1978).

The dental formula of *L. alleni* is  $i \ 2/1, \ c \ 0/0, \ p \ 3/2, \ m \ 3/3$ , total 28, as in all *Lepus* (Nowak and Paradiso, 1983). This large species has a relatively small p3 (Kurtén and Anderson, 1980). Cheekteeth of *L. alleni*, *L. californicus*, and *L. townsendi* are similar, but the lower jaw of *L. alleni* is more elongate than that of the other two species, especially in the diastemal region, which is longer, more slender, and delicate. If lower jaws of the three species are lined up with symphyses, bases of incisors, and foramina parallel, the p3 of *L. alleni* is farther posterior than in the other species, approximately opposite p4 of *L. californicus* (Dalquest et al., 1969).

There is no evidence that *L. alleni* requires free water. Its food, mainly mesquite (*Prosopis*) and cactus, is highly succulent, with cactus increasingly consumed as drought conditions become

more severe (Vorhies, 1945). Digestive powers are rapid and efficient. Apparently, food traverses the alimentary tract in ca. 12 h (Vorhies and Taylor, 1933).

An average of 175.5 g of forage is consumed each day in the laboratory, and an average of 522 fecal pellets is produced. Sex, age, size of animals, and mass of forage consumed do not influence the number of pellets voided, but the size of individual pellets increases as mass of forage consumed increases. There is no difference between *L. alleni* and *L. californicus* in the number of pellets produced, but those of *L. alleni* are larger (Arnold and Reynolds, 1943). Fecal pellets produced by *L. alleni*, while subsisting on dried *Bouteloua aristidoides*, were 7–9 mm in diameter, whereas a diet of green alfalfa produced feces 6–7 mm in diameter and almost black (Vorhies and Taylor, 1933).

The ears may be >21 cm long (Vorhies and Taylor, 1933) and >10 cm wide (Brown, 1987), adding ca. 25% to the total surface area of the body. The ears potentially are significant sites of conductive, convective, and radiative heat exchange with the environment. Changes in blood flow in the pinnae may play a major role in modulating conductance of heat (Hill and Veghte, 1976).

Heat load and use of water are reduced when *L. alleni* seeks shade. Insulation and reflectivity of the pelage also reduce water loss. Using the clear sky as a radiation heat sink is not possible during the hottest part of the day, but becomes possible in the mid-afternoon when solar and reflected radiation is lower, even when air temperature is high. Blood flow in the ears increases when conditions permit heat loss, but there is immediate vasoconstriction when net heat flux is unfavorable, thereby minimizing heat gain. A relatively high lethal temperature possibly provides a safety factor in marginal situations (Schmidt-Nielsen et al., 1965).

At high ambient temperature, *L. alleni* primarily depends on evaporation for dissipating heat. The use of water is less than predicted if only body size is considered. When ambient temperature is below body temperature, conductance increases by 2–3 fold as ambient approaches body temperature. This facilitates dry heat loss and contributes to water economy. At ambient temperatures above body temperature, heat flows from the environment to the body. In this situation, heat flow into the body is impeded by a decrease in conductance to minimal values, thus achieving a considerable reduction in the use of water for evaporation (Dawson and Schmidt-Nielsen, 1966).

At ambient temperatures <25°C, rate of water loss is 0.06% of body mass/h (Dawson and Schmidt-Nielsen, 1966). Evaporative water loss begins to increase at ambient temperatures >30°C and increases with increasing heat load (Schmidt-Nielsen et al., 1965). There is a gradual increase in evaporation at >25°C, reaching 0.9% of body mass/h at 45°C (Dawson and Schmidt-Nielsen, 1966). At a temperature of 51°C, evaporation is ca. 1.3% of body mass/h (Schmidt-Nielsen et al., 1965).

Evaporation accounts for 8–10% of heat loss from the animal until the difference between body and ambient temperature is ca. 18°C, i.e., ambient temperature is ca. 20°C. When the difference between body and ambient temperatures is <15°C, evaporation becomes increasingly important in dissipating the metabolic heat load, accounting for ca. 50% when the difference between body and ambient temperatures is 5°C and 100% when there is no difference. A further increase in evaporation occurs when ambient temperature exceeds body temperature; the excess in evaporation >100% serves to eliminate heat that now flows into the animal from the hotter environment (Dawson and Schmidt-Nielsen, 1966).

In summer, water loss averages 0.09% of body mass/h and shows no correlation with ambient temperature of 5–20°C. A 3,300-g antelope jackrabbit would thus lose 2.97 g/h. Conversely, evaporative water loss increases exponentially at 3–25°C in winter. At 10°C, water loss during winter is ca. 50% that in summer. At an ambient temperature of 23°C, active evaporative cooling begins. At 25–45°C, there is no significant seasonal difference in evaporative cooling (Hinds, 1977).

Average and range of temperatures (°C) are: rectal temperature, 39.2 (37.6–39.9); maximum survivable temperature, 43.7 (43.0–44.1); lethal temperature, 45.4 (44.9–45.9). When exposed to 51°C for up to 4 h, *L. alleni* is able to maintain a stable body temperature for several hours. When exposed to lethal temperatures, antelope jackrabbits struggle, lose coordination, and have jerky movements; then they experience a rapid decline in respiration rate, followed by a slow, irregular, and gasping respiration, and die at a body temperature of 45.4°C. *L. alleni* can recover from a rectal

temperature of 44°C after exposure to 51°C ambient temperature in the laboratory (Schmidt-Nielsen et al., 1965). The lower critical temperature is ca. 20°C (Dawson and Schmidt-Nielsen, 1966).

At ambient temperatures of 3–25°C, body temperature remains at an average of 37.9°C. Above an ambient temperature of 25°C, body temperature increases as ambient temperature increases, reaching ca. 40.3°C at an ambient temperature of 39°C (Dawson and Schmidt-Nielsen, 1966). At ambient temperatures of 15–35°C, the metabolic rate averages 0.57 ml of oxygen g<sup>-1</sup> h<sup>-1</sup>. This is similar to the rate of other animals of similar size (Schmidt-Nielsen et al., 1965).

When exposed to high ambient temperatures in the laboratory, respiratory rate increases to >350 respirations/min. Breathing takes place through the nose, even at the highest rates. Only in terminal stages after respiration rates have decreased is there some open-mouth breathing and gasping (Schmidt-Nielsen et al., 1965). At low ambient temperature the respiration rate is ca. 40 cycles/min, increasing to >700/min at high ambient temperatures. A marked increase in respiration does not occur until ambient temperature is within 4°C of body temperature. At high ambient temperatures is not markedly elevated. At low ambient temperatures, heart rate increases by ca. 50% relative to that occurring in the thermoneutral range, as does respiration rate (from ca. 36 to 50 cycles/min—Dawson and Schmidt-Nielsen, 1966).

Acclimatization to winter conditions primarily is metabolic. Reduction of evaporative heat losses at low ambient temperatures is important. Acclimatization to summer conditions occurs through decreasing heat production and increasing dry heat losses when body temperature slightly exceeds ambient temperatures. *L. alleni* is physiologically able to survive the full impact of desert conditions if avoidance is not possible (Hinds, 1977).

The rectal glands, lying in both sexes on either side of the anus, secrete a substance that hardens to a nearly dry yellow to orange-colored flaky material, with a strong musky odor. The substance producing this characteristic odor of the animal apparently originates in these glands. Each gland is a sac ca. 12 mm deep and has a wide external opening. The glands do not appear to be more active in the breeding season. Their function is unknown. Possibly by means of these glands, the individual leaves a record in the shelter form or wherever it pauses to sit (Vorhies and Taylor, 1933).

There are six mammae; one pair is pectoral and two pair are abdominal. They are so flatly placed along the abdomen that they are not noticeable even when most active. However, they easily are found in lactating females (Vorhies and Taylor, 1933).

**ONTOGENY AND REPRODUCTION.** The breeding season is from late December through September (Vorhies and Taylor, 1933), with pronounced peaks in spring and mid-summer (Brown, 1987). No physical changes are noticeable in the breeding period, but testes of males usually are in the scrotum at this time. These organs are not visible in the living animal in the field. In mid-winter, testes usually are within the body cavity, but their position is variable (Vorhies and Taylor, 1933).

Two copulations have been observed in the field, one at 1125 h on a dark misty day, the other just before sundown. The manner of copulation was almost identical to that of the domestic rabbit (*Oryctolagus cuniculus*). In one instance, immediately after copulation the female chased the male a few meters, uttering a peculiar growl or grunt. In the other instance, coition was preceded by a chase and vigorous combat accompanied by continuous growling (Vorhies and Taylor, 1933).

The gestation period is ca. 6 weeks in length. In Arizona, the number of young per litter averaged 1.93 (range, 1–5). A female may have three or four litters per year (Vorhies and Taylor, 1933). In Mexico, young usually appear in June (Allen, 1906). In Sinaloa, a female had six embryos with a crown-rump length of 52 mm on 16 November (Armstrong and Jones, 1971). In Chihuahua, a lactating female was observed on 7 December (Burt and Hooper, 1941). In Arizona, a female had two embryos that were 85 mm in length on 1 April (Dice and Blossom, 1937). On 23 April, a female was suckling young, and young 30–50% grown also were present (Burt, 1933). On 14 May, a half-grown female was observed (Swarth, 1929). Females suckling young also occur in October (Vorhies and Taylor, 1933).

The young are precocial, as are all hares (Brown, 1987); i.e., at birth the young are fully clothed with hair, eyes are open, and they can hop. Neonates do not show the characteristic white rump,



FIG. 4. Habitat occupied by *Lepus alleni* 15 km E Durango, Durango, Mexico (above) and at the Santa Rita Experimental Range, Pima Co., Arizona (below). Photographs by T. L. Best.

but one young ca. 19 days old showed the rump flash for the first time when alarmed and running (Vorhies and Taylor, 1933).

Caesarian operation has been used as a technique to obtain animals for research (Arnold, 1942). In Arizona, three young were removed from a female by caesarian operation on 13 March. Upon removal from the uterus, breathing began as in a normal birth, the eyes were open, and they immediately made attempts to suckle. Their masses were 108.0, 103.5, and 90.0 g. No bleeding occurred when the umbilical cords were cut. They were successfully fed warm, diluted milk with a pipette. Attempts to get them to suckle a mother house cat were successful, but all died by 18 March. Measurements (in mm) of two that survived to 18 March were: total length, 150, 150; length of tail, 8.0, 8.5; length of hind foot, 40, 45; length of ear, 37, 40 (Vorhies, 1921).

One neonate weighed 184 g. Two others that were 1–2 days old measured (in mm): total length, 155 and 158; length of tail, 25 and 22; length of hind foot, 39 and 43; mass, 133 and 183 g (Vorhies and Taylor, 1933). By 5 days of age the incisors are well developed as is the pelage. The young are fully clothed in short fur. In coloration, young have white posterior edges of the ears and are slightly darker in body color than adults. They possess a small and distinct white spot in the center of the forehead, which is not present in the adult. The white of the side and belly does not extend upward to the back and side during the first few days after birth (Vorhies, 1921). Until nearly grown they are more wary than adults, more nocturnal, and less prone to leave their shelter forms (Vorhies and Taylor, 1933).

Young removed by caesarian operation were reared in an incubator at 22–35°C and were fed a diet composed of dry milk and barley water administered every 4 h by means of an eye dropper over a period of 2–3 weeks. Subsequently, they were transferred to an indoor hutch where they were fed milk in larger quantities at longer intervals. When 6–8 weeks old, they were released into outdoor pens and the diet changed to hay and grain (Arnold, 1942).

Under favorable conditions, breeding age is attained during the 2nd year (Brown, 1987; Vorhies and Taylor, 1933). The sex ratio

of adults in southern Arizona was 47.5% males : 52.5% females. Longevity is not known (Vorhies and Taylor, 1933).

**ECOLOGY.** *Lepus alleni* occurs in a variety of habitats in Arizona, usually on grassy slopes at moderate elevations (Fig. 4). It appears to favor the bajadas or mesas above the saguaro cactus (*Carnegiea gigantea*) belt, where grasses, mesquites, and catclaws (*Acacia*) abound (Vorhies and Taylor, 1933). It seemingly is most common in areas with a good growth of grass under moderately high and open, desert shrubs, but it also occurs in desert habitats having little grass (Dice and Blossom, 1937). It occurs less commonly in creosotebush (*Larrea*) desert and in the dense growth of mesquite along valley bottoms (Vorhies and Taylor, 1933). In Reddington Pass, Arizona, *L. alleni* occurs in hilly country among scattered oaks (*Quercus*) and junipers (*Juniperus*), a few mesquites, clumps of manzanita (*Arctostaphylos*), and beargrass (*Nolina*), small cacti, and sparse grass (Lange, 1960). At the limit of its range in Yuma Co., Arizona, it occurs in stabilized sand dunes where the dominant vegetation is *Hilaria rigida*, *Opuntia stanleyi*, and some *Larrea tridentata*, but this is not typical habitat for this species (Simmons, 1966).

In Mexico (Fig. 4), *L. alleni* is found singly and in pairs in the low and open grasslands and in the open grassy foothills with patches of low bushes. It is most numerous in the foothills near the coast (Allen, 1906). In southern Sonora, Sinaloa, and northern Nayarit, it occupies the arid upper-tropical subzone. In Sonora, it occupies the lower Sonoran life zone, characterized by the low and arid plains west of the mountains between the Arizona border and southern Sonora. *L. alleni* also occupies the Sonora biotic province; the desert-plains region extending from southwestern Arizona to western Sonora (Goldman, 1951). On the road between Nogales and Guaymas, Sonora, the antelope jackrabbit was common from Cibuta south to Guaymas, but none was seen in the oak-covered hills between Cibuta and Nogales. It was common in the lowlands between Guiracoba and the Río Yaqui. On Tiburón Island, it is fairly numerous and rather wild compared to mainland populations (Burt, 1938).

In southern Arizona, *L. alleni* lives in dry valley slopes distant from water sources. However, if water is available, it does not drink. The diet primarily consists of green grass, other green vegetation, and many species of cactus. It feeds on pulps and pods of *Opuntia engelmannii* more than on any other species of cactus. Dissected stomachs contained considerable amounts of the moist mucilaginous pulps of cactus pads; these pads have a moisture content of 78%. It also feeds on the common visnaga cactus (*Echinocactus wislizeni*; 94% water) and on the underground tubers of *Talinum angustissimum* (70% water—Ghobrial and Nour, 1975).

In the laboratory, average daily food consumption by *L. alleni* was 126 g of alfalfa hay (leaves) and rolled barley, 167 g of air-dry native forage, and 171 g of air-dry green forage. Forage consumption as a percentage of live weight of *L. alleni* for these three forage classes are 5.8, 6.1, and 6.5%, respectively. *L. alleni* usually selects weeds, followed by grasses and browse. Weeds and grasses are about equal parts of the diet suggesting why this species may contribute to overgrazing. If antelope jackrabbits and range cows eat the same foods, then 48 antelope jackrabbits consume the same amount of food as a 450-kg range cow. If the two species compete only for perennial grasses, then 164 antelope jackrabbits consume as much as one range cow (Arnold, 1942). Another estimate is that eight antelope jackrabbits consume the same quantity of forage as one sheep, and 41 consume the same as one range cow. When these estimates are adjusted to reflect actual overlap in diet of these species, 15 antelope jackrabbits consume as much as one sheep, and 74 consume as much as one domestic cow (Vorhies and Taylor, 1933).

When range is moderately deteriorated, antelope jackrabbits force succession toward the climax stage, whereas on range that has deteriorated to the point of having more weeds than grasses, the effect is toward further deterioration (Bond, 1945). They select grazed areas more often than areas under total protection or areas that are lightly grazed (Taylor et al., 1935).

Based upon analysis of the contents of 179 stomachs, 36% of the diet was mesquite (*Prosopis juliflora*), 45% grass (e.g., *Aristida*, *Bouteloua*, *Eragrostis*, *Trichloris mendocina*, *Valota saccharata*, *Panicum*, *Cenchrus*, *Sporobolus*, *Eriochloa acuminata*, *Agrostis*), 7.8% cactus (e.g., *Opuntia engelmannii*, *O. phaeoacantha*, *O. fulgida*, *O. spinosior*, *Echinocactus wislizeni*, *E. fendleri*, *Mammillaria*, and *Carnegiea gigantea*—Vorhies and Taylor, 1933), and small amounts of other foods (e.g., *Celtis pallida*—Van Dersal,

1938; *Amorpha*, *Portulaca*, Boraginaceae, *Boerhaavia*, *Eriogonum*, *Karwinskia*, Scrophulariaceae, *Ambrosia*, Compositae—Vorhies and Taylor, 1933). Arthropods were found in 20 of the 179 stomachs, but appeared accidental in the diet. Diet is closely related to the alternating dry and rainy seasons. Following winter rains, when a number of perennial grasses put forth leaves, the percentage of grass in the diet markedly rises, whereas the amounts of mesquite and cactus consumed decrease almost to complete absence. During May and June, the most arid period of the year, the grass dries, and less is eaten, whereas mesquite remains a high percentage of the diet and cactus increases. In July and August, following the summer rains, grass becomes the most important item in the diet, forming 80% of food eaten in July and 84% in August. Mesquite falls to its lowest point for the year at this period of maximum grass development, and cactus also decreases. Through the autumn months the proportion of grass in the diet declines somewhat, whereas that of mesquite increases proportionately. Although deciduous, mesquite does not shed its leaves in early autumn; some leaves remain on individual trees all winter, and therefore are available for consumption (Vorhies and Taylor, 1933).

*Lepus alleni* seeks minerals by digging and biting the soil. Analysis of the soil did not show salt or saline constituents. Fecal pellets may become covered with soil upon defecation; 97 of 179 stomachs contained gravel or sand (Vorhies and Taylor, 1933).

Average size of home range is 642.8 ha and population density is 0.3/ha (Swihart, 1986). On the Santa Rita Experimental Range, Pima Co., Arizona, populations reach ca. 1 antelope jackrabbit/2 ha (Reynolds, 1958). More were seen in undisturbed mesquite, and in mesquite with clearings, than in mesquite-free range (Germano et al., 1983). In this region, *L. alleni* apparently is least abundant in the semidesert vegetation type (0.025/ha), only slightly more abundant in the foothill vegetation type (0.030/ha), and most abundant in the mesa vegetation type (0.086/ha—Vorhies and Taylor, 1933). It was reported as abundant in the vicinity of Tucson, especially about one-third of the distance from Florence to Tucson. On the Santa Rita Experimental Range, it was so numerous that it was common in the early morning to see 12–15 at once (Swarth, 1929). In recent years, the number of *L. alleni* has decreased significantly in areas of southern Arizona where the introduced Lehmann lovegrass (*Eragrostis lehmanniana*) has been established (R. Thompson, in litt.).

In much of southern Arizona, *L. alleni* and *L. californicus* occur in equal numbers (Doutt, 1934; Swarth, 1929). 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, allow easy identification (Mearns, 1890). On the grassy bajadas at altitudes of ca. 1,050 m, *L. alleni* usually is several times as numerous as *L. californicus*, but in the mesquites along the valley bottoms and on the barren creosotebush desert, *L. californicus* usually is more numerous (Vorhies and Taylor, 1933).

There is a notable difference in the distribution of *L. alleni* and *L. californicus* by vegetation types on the Santa Rita Experimental Range. There appear to be 2.85 *L. alleni* to each *L. californicus* in the semidesert type, 5.00 *L. alleni* to each *L. californicus* in the foothill type, and 11.35 *L. alleni* to each *L. californicus* in the mesa type (Vorhies and Taylor, 1933).

In southern Arizona, *L. alleni* occupies the same habitat as *Spermophilus tereticaudus*, *Ammospermophilus harrisi*, *Neotoma albigula*, *Chaetodipus penicillatus*, *C. baileyi*, *Perognathus amplus*, *P. flavus*, *Dipodomys merriami*, *D. spectabilis*, *Onychomys leucogaster*, *Mus musculus*, *Lepus californicus*, *Sylvilagus audubonii*, *Spilogale gracilis*, *Mephitis mephitis*, *M. macroura*, *Vulpes macrotis*, *Taxidea taxus*, *Canis latrans* (Spencer, 1941) *Dipodomys ordii*, *Peromyscus eremicus*, *P. maniculatus* (Reynolds, 1958), *Tayassu tajacu*, *Odocoileus hemionus* (Germano et al., 1983), *Thomomys bottae*, *T. umbrinus*, *Urocyon cinereoargenteus*, *Lynx rufus*, *Spermophilus spilosoma*, *Sigmodon hispidus*, *Chaetodipus hispidus*, *C. intermedius*, *C. goldmani*, *Reithrodontomys megalotis*, *R. flavescens*, *Onychomys torridus*, *Notiosorex crawfordi*, *Dipodomys deserti*, *Peromyscus crinitus*, and *Neotoma lepida* (Best et al., 1990). Remains of other species associated with *L. alleni* (one of the most abundant species) in cave deposits in southern Arizona were many of the previously listed mammals and *Antilocapra americana*, *Spermophilus variegatus*, *Erethizon dorsatum*, *Odocoileus virginianus*, *Felis concolor*, *Canis lupus*, *Ursus americanus*, and *Bassariscus astutus* (Colbert, 1950).

Though once rather common near Organ Pipe Cactus National

Monument, Arizona, antelope jackrabbits have almost disappeared due to rabbit plague (Huey, 1942). These jackrabbits also may have a severe skin disease similar to mange (Lipson and Krausman, 1988). One had a large spherical tumor 2.5 cm in diameter in the spleen. A number of cases of infections or ulcer-like sores were noted on the genital organs of both sexes (Vorhies and Taylor, 1933).

Parasites include: the cestodes *Cittotaenia*, *Taenia multiceps* (Lipson and Krausman, 1988), *Multiceps*, and *Raillientina*; the nematodes *Dermatoxys veligera* (Vorhies and Taylor, 1933; Wetzel, 1932), *Wellcomeia longejector* (Hannum, 1943), *Nematodirus arizonensis* (Dikmans, 1937), and *Passalurus ambiguus* (Lipson and Krausman, 1988); the chigger *Hexidionis allredi* (Lucas and Loomis, 1968); the ticks *Haemaphysalis leporispalustris*, *Dermacentor albipictus* (Lipson and Krausman, 1988), and *D. parumapertus* (Vorhies and Taylor, 1933); the fleas *Hoplopyllus affinis* (Lipson and Krausman, 1988; Vorhies and Taylor, 1933), and *Cediopsylla* (Lipson and Krausman, 1988). In Sonora, an adult male had three large botfly larvae (*Cuterebra*) in the skin of the throat (Dice and Blossom, 1937). The larvae of *Cuterebra princeps* and *C. americana* were present in 31% of antelope jackrabbits; 60% in the throat and 40% in the rump. One *L. alleni* contained 16 larvae (Vorhies and Taylor, 1933).

Predators include the bobcat *Lynx rufus* (Vorhies and Taylor, 1933; Young, 1958), the coyote *Canis latrans* (Short, 1979; Vorhies and Taylor, 1933), and the golden eagle *Aquila chrysaetos*. Automobiles and irresponsible shooters also kill antelope jackrabbits (Vorhies and Taylor, 1933).

In Arizona, antelope jackrabbits are valuable for their skin, as human food, as food for furbearers, and as a safety factor for game and domestic livestock by attracting the attention of coyotes and other carnivores (Vorhies and Taylor, 1933). They are hunted as nongame mammals with no closed season or bag limit (Dunn et al., 1982). On the Papago Indian Reservation, Arizona, they are used as food (Brown, 1987), and remains of food animals from an Indian village site in southern Arizona indicated that *L. californicus* was more common in the area than *L. alleni* (Burt, 1961).

*Lepus alleni* is not rare (Dunn et al., 1982), but expanding agriculture encouraged by impoundments of rivers flowing from the Sierra Madre Occidental to the coasts of Jalisco, Nayarit, Sinaloa, and Sonora is causing massive habitat alteration. Thus far, the impact on populations of *L. alleni* has been slight, but as the trend continues population declines are expected (Chapman et al., 1983).

**BEHAVIOR.** *Lepus alleni* is nocturnal and crepuscular (Vorhies, 1945). In Sonora, groups of four to six were seen feeding at dusk, usually in pairs (Caire, 1978). In Arizona, it feeds at night, before and after sunrise, and for several hours in the morning (up to 0800–1000 h). Toward evening it begins to feed at 1600–1800 h, depending on the time of year. On cloudy days, rarely otherwise, it feeds during midday hours. All of 179 stomachs contained food, no matter what time the animals were taken. The ratio of the weight of stomach contents to weight of the animal is low, ranging from 0.7 to 3.5% and averaging 1.7% (Vorhies and Taylor, 1933).

When browsing on mesquite (*Prosopis*), *L. alleni* rears up on its hind feet, its forefeet hanging limp, its ears flopping freely; or, attempting to reach higher, stands on its toes, places its forepaws on a branch partly for support and partly to hold down the branch, and crops off leaves, bark, or buds. It favors the tufts of green leaves that grow in the axils of mesquite spines (Vorhies and Taylor, 1933).

*Lepus alleni* rarely utters sounds. When caught or wounded it cries loudly and often continuously until released. Rarely, it makes a peculiar growling or grunting vocal sound, or a rapidly uttered chuck, chuck, chuck (Vorhies and Taylor, 1933).

The antelope jackrabbit rests by day in sitting places known as shelter forms. These shelter forms may be made by backing up under clumps of grass, weeds, or brush, but often are merely a sitting place beside a cactus or mesquite trunk on top of the ground where no digging or scratching effort has been done, and without the protection of vegetation. Sitting in such a shelter form the occupant is in full view from at least three sides, but is protected from the sight of aerial predators and sheltered from the midday sun. Sometimes the shelter form is dug out so as to be a slight depression or a somewhat deeper excavation. The resulting depression usually fits the haunches of the reposing animal, being deepest at the rear end and sloping upward to ground level at the front. Most shelter forms are under mesquite, cactus, catclaw, or hackberry (*Celtis pallida*), although any plant of sufficient size to afford some

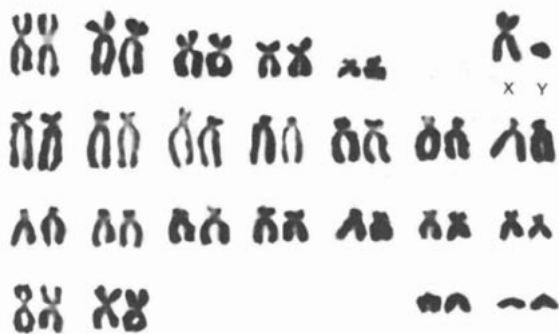


FIG. 5. Karyotype of a male *Lepus a. alleni* from near Tucson, Pima Co., Arizona (Hsu and Benirschke, 1967).

overhead cover may be used. Shelter forms average 8–15 cm wide and 28–46 cm long. These shelter forms are used for only a short time (perhaps a few days), before the animal moves to another (Vorhies and Taylor, 1933).

The antelope jackrabbit always seeks shade in shelter forms during hot seasons. Frequently, its shelter form under these conditions is in the shade of large and densely foliated shrubs, such as the desert hackberry, or the trunk of a large mesquite. When prevented for 0.5 h by gentle harassment from obtaining protection from the bright sunshine of May or June, it evidently becomes uncomfortable and continually seeks shade. If harassment continues, it becomes more persistent in clinging to some shady spot. The location of the shelter form in which it sits during the day is variable in its relation to the amount of shade (Vorhies, 1945).

The antelope jackrabbit may sit on its haunches in the shelter form, with forefeet on the ground, and extended to the front. This position allows a sudden leap and a quick escape. When more relaxed, it crouches low in its shelter form, folding its forelegs back underneath the front part of the body, with the backs of the forefeet facing downward, the palms up. In this position, the animal must rise to the palms-down position before starting off; a slight alarm brings this response (Vorhies and Taylor, 1933).

The ears are laid along the back in a relaxed position as the antelope jackrabbit rests or dozes. At slight alarm, the animal rises to a leaping posture and brings the ears upward to a position of attention. If it chooses to trust to concealment rather than flight, it hunches down lower than ever in the shelter form, pressing the ears tightly against the back. When observed from a distance, the ears may be erect, but when approached, the ears are slowly lowered to become inconspicuous. Frequently, it rests flat in its shelter form with forelegs extended and sometimes in the open it stretches out flat on one side to bask in the sun like a house cat. Other behaviors include taking a long, lazy stretch when made to leave its shelter form unwillingly, feeding, washing its face, extracting thorns from front or hind feet, rolling in dust or sand, and many stages of flashing the white rump (Vorhies and Taylor, 1933).

*Lepus alleni* has no burrows (Schmidt-Nielsen, 1964), but it may have nests beneath the ground level with some hair as lining. One nest located under a bunch of beargrass was round and covered with bits of beargrass, providing excellent concealment. The nest was lined with fur from the mother, and contained two young. Another nest was located under a mesquite in the edge of a clump of sacaton grass. It was in a depression ca. 20 cm below ground level, lined with fur, and contained one young. A third nest was within the hollowed-out shell of a barrel cactus (*Echinocactus*) 40.6 cm in diameter, which had been excavated to a depth of ca. 35.6 cm. Two young large enough to hop around were in the nest, and were well covered with fur from the mother (Vorhies and Taylor, 1933).

It has been postulated that *L. alleni* scatters its young at or soon after birth (Vorhies and Taylor, 1933). The mother returns at night to suckle them. The duration of parental bonds and care is short and the young hares become independent in a matter of days (Brown, 1987).

Young removed from the uterus by caesarian operation immediately attempted to suckle. A marked tendency to nocturnal habits was noted on the 2nd day after birth, and this became more marked in succeeding days. None would accept milk in midday, but

milk was accepted in the morning, late afternoon, and night. Alertness and activity were more marked at night than in daylight hours (Vorhies, 1921).

*Lepus alleni* may be the fastest member of the genus (Allen, 1906) with running speeds up to 72 km/h (Garland, 1983). It can easily clear bushes >1 m in height (Allen, 1906) and can clear fences >1.5 m high with little change in stride (Brown, 1987; Vorhies and Taylor, 1933). One leap of 7 m was recorded (Howell, 1944). Ordinarily, netting 0.75 m high suffices to exclude other jackrabbits (Vorhies and Taylor, 1933).

The antelope jackrabbit runs in a nearly horizontal plane for several strides then may make a stride higher than the others. Although not common, this behavior usually takes place in tall grass or when brush obstructs its sight of possible danger (Howell, 1944). As it starts to run, it makes four or five long hops on the hind legs alone, kangaroo fashion, then reverts to the usual mode of locomotion. Occasionally, with ears erect, the kangaroo hops are again displayed, apparently to see or hear possible pursuers (Swarth, 1929).

*Lepus alleni* can be approached more closely when there is vegetation between it and the observer, as opposed to a direct approach without vegetation. The leisurely moving, unfrightened individual that is not flashing its white sides does not make observation leaps. When the antelope jackrabbit runs away from an observer, a conspicuous white area is displayed on the rump. This area appears to shift each time the animal turns, the white being kept toward the observer, partly by the manner of holding the skin and partly by the zigzag course taken by the running animal. The white is flashed by a set of skin muscles that pulls the skin of the hind quarters over the back and up one side and at the same time everting the hairs, thereby exposing a surprisingly large white area on the left or right rear. Individuals hopping about to feed, or running but not alarmed, as in play or chasing each other, do not show this white (Vorhies and Taylor, 1933).

Males may fight by rearing up on hind feet and hitting each other vigorously and with great rapidity for several seconds. These contests usually are fought in silence. The fight usually ends with the victor pursuing the vanquished. Rarely does the combat end in a draw. Antelope jackrabbits may have scars from wounds, and ears frequently are torn. One had lost a part of its scalp, one had lost skin from its side, and another had a compound fracture of the lower foreleg; the stub was dried but still in use, the foot dangling from it (Vorhies and Taylor, 1933).

*Lepus alleni* is difficult to capture and maintain in captivity. A wild animal placed in a cage throws itself against the screen incessantly until it kills itself (Schmidt-Nielsen, 1964).

**GENETICS.** *Lepus alleni* has a diploid number of 48 chromosomes (Fig. 5). There are 42 metacentrics, submetacentrics, or subtelocentrics, and 4 acrocentrics or telocentrics. The X chromosome is submetacentric and the Y is acrocentric (Hsu and Binirschke, 1967). *L. alleni*, *L. flavigularis*, and *L. californicus* share the same diploid number ( $2n = 48$ ) and the same number of banded chromosomes ( $FN = 88$ ); sizes of the chromosomes are similar (Uribe-Alcocer et al., 1989).

**REMARKS.** There is no evidence of intergradation between *L. callotis* and *L. alleni*. *L. flavigularis* and *L. callotis* are more alike than either is to *L. alleni*. *L. flavigularis* is geographically and morphologically distinct from *L. callotis* (Anderson and Gaunt, 1962).

A numerical taxonomic analysis of 12 cranial characters of the three subspecies of *L. alleni* did not produce clusters, either of the insular subspecies, *L. a. tiburonensis*, or of the other two subspecies, *L. a. alleni* and *L. a. palitans*. This indicates the insular subspecies may not be distinct from the subspecies on the adjacent mainland of Mexico (Dixon et al., 1983).

The Latin word *Lepus* means hare (Jaeger, 1955). The name *alleni* honors Joel Asaph Allen, Curator of the Department of Mammals and Birds, American Museum of Natural History (Mearns, 1890). The common names of Allen's hare (Mearns, 1890), Allen's jack rabbit, wandering jack rabbit (Elliot, 1905), blanket jack, saddle jack, Mexican jackrabbit, burro jack, and jackass rabbit (Seton, 1929) have been applied to this species. The conspicuous flash of white while running resembles that of the pronghorn (*Antilocapra americana*), thus the name antelope jackrabbit (Vorhies and Taylor, 1933).

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