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ECOLOGY OF THE ANTELOPE JACKRABBIT (LEPUS ALLENI)

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ABSTRACT—The antelope jackrabbit (*Lepus alleni*) is a lagomorph indicative of Neotropic savanna and thornscrub in south-central Arizona, west-central Sonora, and western Sinaloa <1,200 m elevation. We found populations in Arizona are most abundant in tropic–subtropic areas of low relief, characterized by velvet mesquite (*Prosopis velutina*) with an herbaceous understory (= Sonoran savanna grassland), and receiving a mean annual rainfall of between 200 and 450 mm, >90 mm of which falls as summer precipitation. In Mexico, this hare most commonly occurred in savanna grasslands or thornscrub interrupted by open areas receiving between 200 and 450 mm of precipitation per annum. Cacti were important habitat components for the hares and mean annual temperatures were >18°C with <60 d a year having temperatures below 0°C. Although sympatric with *Lepus californicus* over portions of its range, the two species preferred different habitats and rarely occurred together, and *L. alleni* was more prone to occur in groups than was *L. californicus*. We calculated the distributional range of *L. alleni* as ca. 102,000 km² in Arizona and Mexico.

RESUMEN—La liebre antílope (*Lepus alleni*) es un lagomorfo indicativo de la sabana del neotrópico y matorral espinoso en el centro-sur de Arizona, centro-oeste de Sonora y oeste de Sinaloa a elevaciones <1,200 m. Encontramos que las poblaciones en Arizona más abundantes estuvieron en áreas tropicales-subtropicales de bajo relieve caracterizadas por el mezquite de terciopelo (*Prosopis velutina*) con sotobosque herbáceo (= pastizal de sabana sonorense), y recibiendo un promedio de precipitación anual de entre 200 y 450 mm, de la cual >90 mm de precipitación cae en verano. En México, esta liebre ocurre más comúnmente en pastizales de sabana o matorral espinoso interrumpidos por áreas abiertas que reciben entre 200 y 450 mm de precipitación anual. Los cactus son componentes importantes del hábitat de las liebres, y las temperaturas medias anuales fueron >18°C, con <60 días al año con temperaturas debajo de 0°C. Aunque es simpátrica con *Lepus californicus* en porciones de su distribución, las dos especies prefirieron hábitats diferentes, y raras veces se presentaron juntas. *L. alleni* fue más propensa a ocurrir en grupos que *L. californicus*. Calculamos el área de distribución de *L. alleni* en aproximadamente 102,000 km² en Arizona y México.

The antelope jackrabbit (Lepus alleni) was one of the last large mammals described from North America (Mearns, 1890) and this species remains one of the least-studied hares. One of the largest members of its genus, Lepus alleni has been the subject of only one natural history study and their habitat affinities remain in need of clarification (Vorhies and Taylor, 1933). Originally described as a desert animal (Palmer, 1897), the antelope jackrabbit's long ears, legs, and lanky appearance prompted Allen (1890), Dawson and Schmidt-Nielsen (1966), and Hinds (1977) to study the animal's heat-dispersal abilities and adaptations to a hot, arid environment. Although the animal proved well adapted to arid surroundings, these authors noted that L. alleni was absent from the hottest and most-arid portions of the Sonoran Desert where the sole representative of the

genus is the black-tailed jackrabbit, *Lepus californicus*. Although Brown and Krausmann (2003) quantified the animal's use of two desert plants, velvet mesquite (*Prosopis juliflora*) and creosote (*Larrea tridentata*), as screening shade in a valley in south-central Arizona, *L. alleni* has not been documented from the Mohave or Chihuahuan deserts where these plants are common (Hall, 1981).

Descriptions of habitat affinities of the antelope jackrabbit are mostly anecdotal. Although *L. alleni* is reported to prefer the gentle terrain of valleys, plains, alluvial fans, mesas, and *bajadas* (Vorhies and Taylor, 1933; Hoffmeister, 1984; Best and Henry, 1993), there is less agreement as to the types of vegetation preferred, with some continuing to consider the species a desert animal (e.g., Best and Henry, 1993). Other investigators consider it an inhabitant of semiarid grasslands while pointing out that the hare also occurs in mesquite *bosques* and Sonoran Desert vegetation (Vorhies and Taylor, 1933; Woolsey, 1956, 1959; Hoffmeister, 1984). Nonetheless, the species is absent from most of Arizona's desert grassland, which is a semidesert grassland biotic community within a temperate climate (Brown, 1994*a*; McClaran and Van Devender, 1995).

Descriptions of habitat preferences in Mexico also have been of a general nature. Burt (1938) described the distribution of the antelope jackrabbit in Sonora only as lowlands below the oaks. Battye (*in* Allen, 1906) reported the habitat of *L. alleni* in Sinaloa to be low-elevation, open, grassy foothills with patches of low bushes, upwards to an altitude of 1,060 m. *Lepus alleni* occurs in the Sonoran Desert only in the Arizona Upland, Plains of Sonora, and Central Gulf Coast subdivisions including Tiburon Island (Hall, 1981; Turner and Brown, 1994).

The distribution and life history of *L. alleni* in Arizona was studied in the late 1920s, and it was noted that the animal occurred in several habitats but seemed to prefer grassy slopes and bajadas at moderate elevations above the giant cactus belt at elevations <1,066 m (Vorhies and Taylor, 1933). These investigators suggested that temperatures might control distribution of *L. alleni*, noting that they knew of no appreciable physical or climatic barriers other than westward, where increasing aridity might be a factor.

Studies of the behavior of antelope jackrabbits are mostly limited to the observations of Vorhies and Taylor (1933), Woolsey (1956), and the anecdotal references summarized by Best and Henry (1993) including the Master's theses of Madsen (1974) and Gray (1977). One exceptional trait of antelope jackrabbits noted is a reported tendency to occur in groups containing three or more individuals (Vorhies and Taylor, 1933; O'Connor, 1945). The objective of this study was to better understand the ecology of *L. alleni*, determine the factors limiting its distribution, and document the extent of group behavior and other differences between this species and *L. californicus*.

MATERIALS AND METHODS-We plotted representative museum records of L. alleni available on http://www.vertnet.org/ along with observations reported by Burt (1938), Armstrong and Jones (1971), and Caire (1978). Additional observations of both jackrabbit species (L. alleni and L. californicus) were geopositioned from 27 September 2009 to 15 March 2013 in areas in Arizona known to support antelope jackrabbits. Localities in Sonora were augmented by observations obtained while conducting surveys for masked bobwhite (Colinus virginianus ridgwayi) in the San Marcial, Torres, Cumpas, and Banamichi-Cananea areas and on lands belonging to the Yaqui Indians (Brown et al. 2012). Additional observations and photographs of L. alleni were provided by personnel conducting botanical, felid, and herpetological surveys in northeastern Sonora. To facilitate the preparation of distribution maps, representative localities were plotted on Google Earth where we outlined the locales and planimetered areas occupied in Maricopa, Pinal, Pima, Santa

Cruz, and Cochise counties in Arizona and the states of Sonora, Sinaloa, Chihuahua, and Nayarit in Mexico.

Habitat preferences of *L. alleni* were evaluated based on observations and frequency of pellets on the southern portion of Tiburon Island during February and March 2012. The only upland habitats occupied by *L. alleni* on Tiburon Island are areas dominated by several species of xeric microphyll shrubs (Central Gulf Coast subdivision of Sonoran Desert; Turner and Brown, 1994). Each plant was assigned a relative importance value based on relative density, relative coverage, and relative frequency values in the cover type in which *L. alleni* predominated (Aebischer et al., 1993).

Additional information included counting pellet frequencies of L. alleni and the much-less common L. californicus in Sonora along transects that sampled both bufflegrass (Pennisetum ciliare) pastures and native vegetation (Alcalá-Galván and Miranda-Zarazuá, 2012). The locations of each L. alleni and L. californicus observed were registered on a global positioning system including date, time of day, number of animals seen together, latitude and longitude, elevation, type of topography, nearest perennial plant >1 m tall, dominant vegetation, and ground cover. Also recorded was the biotic community present (Brown and Lowe, 1994), the presence and abundance of woody plant species, presence of cacti in the immediate vicinity, presence of herbaceous ground cover and, later, the approximate distance of each animal flushed when disturbed by the vehicle or person hiking. Plant nomenclature and heights followed SEINet, http://swbiodiversity.org/ and Anderson (2001). To determine the climatic parameters governing the species distribution, mean monthly precipitation and mean annual temperature data were obtained for 18 locations within or near L. alleni localities in Arizona from the U.S. Department of Commerce's (2010) NOAA summaries and for 16 locations in Mexico (Hastings and Humphrey, 1969).

RESULTS—We recorded antelope jackrabbit information for 412 observations and plotted these localities on a map along with the locations of 352 museum specimens (Fig. 1; Appendices 1 and 2). The total range of *L. alleni* was estimated at 102,000 km² with 12.5% (12,700 km²) of the animal's distribution being in Arizona, 76% (78,000 km²) in Sonora, 10.5% (9,500 km²) in Sinaloa, and the remaining 1% (1,800 km²) in the states of Chihuahua and Nayarit.

Lepus alleni was most often encountered in areas of low relief including level ground, gently sloping plains, alluvial fans, and *mesas*, which is consistent with previous observations (Best and Henry, 1993). Relatively few observations occurred in broken country, and steep slopes appeared to be used mainly as travel routes between mesas and *arroyo* bottoms. Elevations ranged from 440 to 1,200 m, placing the animal in mostly tropic– subtropic environments receiving mean annual rainfall amounts between 200 and 450 mm. A minimum of 90 mm falls during April through September (Hastings and Humphrey, 1969; U.S. Department Commerce, 2010). Minimum temperatures appeared to influence the distribution of *L. alleni*, as this species was documented only in areas where the mean annual temperature

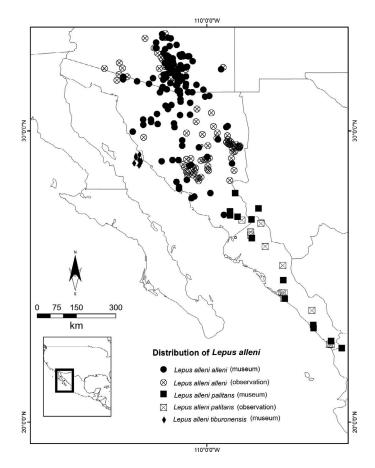


FIG. 1—Distribution of *Lepus alleni* from locations listed in Appendix 1 and 2.

exceeds 18° C and where the average number of days 0° C or colder was less than 60 (Table 1).

Most observations were in areas judged to be present or former Sonoran savanna grassland or Sonoran Savanna Grassland–Semidesert Grassland transition (67.5%; Table 2; Fig. 2A, 2B). Sixty observations occurred in vegetation characteristic of either the Arizona Upland subdivision (8%) or Lower Colorado River subdivsion (6.5%) of the Sonoran Desert (Table 2). Forty-eight (11.7%) of the 412 observations occurred in mesquite bosques or thornscrub with retired farmlands and bufflegrass pastures constituting 23 (5.6%) of the observations. Temperate oak woodlands and semidesert grasslands >1,220 m elevation accounted for <1% of the observations.

Velvet mesquites occurred at 300 (86.7%) of the observation sites and were the dominant overstory plant at 250 (76%) sites. No other plant was more-often associated with antelope jackrabbit observations than this species.

Few antelope jackrabbits were seen in or flushed from habitats having dense shrub understories. Most observations in Arizona occurred in habitats with herbaceous or bare ground understories, and the animals were infrequent in areas dominated by creosote, triangle-leaf bursage (Ambrosia deltoidea), saltbush (Atriplex polycarpa), or other shrubs (Table 2). When desert shrubs and trees did predominate, these plants were frequently accompanied by grasses or other herbaceous vegetation. Important grasses included spidergrass (Aristida ternipes), purple three-awn (Aristida purpurea), cane bluestem (Bothriochloa barbinodis), six-weeks grama (Bouteloua barbata), sideoats grama (Bouteloua curtipendula), Rothrock's grama (Bouteloua rothrockii), feather fingergrass (Chloris virgata), bush muhly (Muhlenbergia porteri), witchgrass (Panicum capillare), whiplash pappusgrass (Pappophorum vaginatum), and sand dropseed (Sporobolus cryptandrus), all of which are believed to provide both hiding cover and food. Interestingly, the height of these grasses ranges from 20 cm (8 in) to a meter or more and averages 63.7 cmapproximately the mean length of L. alleni.

A ground cover of grasses and forbs was present in 238 (58%) of the observations. Although landscapes also were dominated by bare ground during much, or even all, of the year, some seasonal grasses and forbs usually persisted, if only within the larger shrubs or mesquites. Thin-leafed grasses such as B. barbata often formed a seasonal carpet of herbaceous vegetation, and overflow areas adjacent to arroyos and other drainages contained both annual and perennial grasses from 45-90 cm tall. Dense stands of tropical grasses found along drainages and other, more-mesic areas inhabited by L. alleni included needle grama (Bouteloua aristidoides), vine mesquite (Panicum obtusum), Bermuda grass (Cynodon dactylon), tanglehead (Heteropogon contortus), sprangletop (Leptochloa species), bristlegrass (Setaria leucophila), and Arizona cottontop (Trichachne californica).

Velvet mesquite, while an important component of antelope jackrabbit habitat, often was accompanied by other leguminous trees such as ironwood (*Olneya tesota*), blue paloverde (*Parkinsonia florida*), little-leaf paloverde (*Parkinsonia microphylla*), and other trees characteristic of the Sonoran Desert or Sinaloan thornscrub. Oftentimes, large shrubs such as lotewood (*Ziziphus obtusifolia*), wolfberry (*Lycium fremontii*), or desert hackberry (*Celtis pallida*) were also present. The principal habitat requirement for *L. alleni* appears to be a potentially herbaceous understory within a velvet mesquite or other Sonoran vegetation matrix typical of a tropic–subtropic environment (Turner et al., 1995; Table 2).

Cacti often were associated with *L. alleni*, these succulents being present at 33.3% of the observation sites where this information was recorded (Table 2). Cactus species noted included saguaro (*Carnegiea gigantea*), devil cholla (*Grusonia kunzei*), the pricklypears (*Opuntia phaeacantha, Opuntia chlorotica,* and *Opuntia violacea*), chain fruit cholla (*Cylindropuntia fulgida*), cane cholla (*Cylindropuntia spinosior*), pencil cholla (*Cylindropuntia arbuscula*), staghorn cholla (*Cylindropuntia versicolor*), buckhorn cholla (*Cylindropuntia acanthocarpa*), barrelcactus (*Ferocactus wislizeni* and *Ferocactus emoryi*),

| Develue of absolute, $y = 001010111$ of the solution of the solution of the solution of the subsolution of |
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| | | | | | | | | M | ean m | onthly | Mean monthly precipitation | ttion | | | | | | | | |
|--|------|-----------------|------------------|---------|-------|-------|-------|----------|-------|-----------------|----------------------------|--------|-------|--------|--------|---------------|------|-----|------|----|
| | | | Longi- | | Feb- | | | | | | | Sep- | Oc- | No- | De- | | | | | |
| Location | Α | Latitude | tude | January | ruary | March | April | May June | June | July 1 | August | tember | tober | vember | cember | \mathbf{TS} | MP | MAD | MAT | ΗT |
| Wickenburg, AZ ¹ Anache Junction | 639 | 33°58′ | 112°44′ | 33.5 | 26.2 | 19.6 | 14.5 | 4.1 | 3.8 | 36.8 | 50 | 24.4 | 17 | 17.8 | 31.5 | 279.2 | 23.3 | 65 | 18.2 | 1 |
| AZ. | 506 | 33°25′ | $111^{\circ}34'$ | 15 | 18.3 | 39.4 | 5.3 | 6.9 | 1.8 | 7.6 | 30 | 41.4 | 11.2 | 24.9 | 20.1 | 221.9 | 18.5 | 7 | 20.1 | _ |
| Maricona, AZ | 355 | 33°07′ | $112^{\circ}02'$ | 16.3 | 17.3 | 13 | 7.6 | 20 | 60 | 29.5 | 30.5 | 22.4 | 11.2 | 14.2 | 99.1 | 190.4 | 15.9 | 49 | 20.6 | 6 |
| Florence. AZ | 459 | $33^{\circ}02'$ | $111^{\circ}23'$ | 25.7 | 21.6 | 24.6 | 10.9 | 4.6 | 3.3 | 34.5 | 39.1 | 22.4 | 13.2 | 20.1 | 30 | 250 | 20.8 | 29 | 20.9 | ۱ |
| Gila Bend, AZ ¹ | 225 | 32°57′ | $112^{\circ}43'$ | 15.2 | 11.9 | 15.7 | 5.6 | 2.8 | 1.8 | 20.8 | 23.1 | 11.9 | 9.1 | 11.4 | 15 | 144.3 | 12.0 | 21 | 22.2 | - |
| Casa Grande, AZ | 428 | 32°53′ | $111^{\circ}45'$ | 19.1 | 20.6 | 17.3 | 8.1 | 2.3 | 4.3 | 31.8 | 33.5 | 19.8 | 9.7 | 19.8 | 22.1 | 208.4 | 17.4 | 42 | 21 | 1 |
| Willow Springs | | | | | | | | | | | | | | | | | | | | |
| Ranch, AZ | 1127 | $32^{\circ}43'$ | $110^{\circ}52'$ | 35.6 | 28.2 | 34.5 | 12.9 | 4.3 | 6.6 | 63 | 7.77 | 29.7 | 24.9 | 23.9 | 54.9 | 396.2 | 33.0 | 59 | 16.8 | 3 |
| San Manuel, AZ | 1085 | 32°37′ | $110^{\circ}39'$ | 24.6 | 22.9 | 21.3 | 6.6 | 5 | 7.1 | 69.3 | 64.8 | 37.1 | 20.8 | 17.8 | 36.6 | 330.9 | 27.6 | 36 | 18.3 | ы |
| Red Rock, AZ | 567 | $32^{\circ}30'$ | $111^{\circ}22'$ | 19.6 | 14.5 | 21.3 | 7.6 | 3.3 | 6.4 | 39.9 | 41.4 | 29.2 | 11.9 | 21.8 | 26.2 | 243.1 | 20.2 | 25 | 20.6 | 4 |
| Silverbell, AZ | 835 | 32°23′ | $111^{\circ}30'$ | 32.3 | 23.1 | 20.3 | 4.6 | 7.1 | 6.1 | 77 | 59.4 | 30.2 | 19.8 | 19.8 | 26.4 | 326.1 | 27.2 | 5 | 21.1 | Г |
| Ajo, AZ | 537 | 32°22′ | $112^{\circ}52'$ | 17.8 | 13.5 | 20.8 | 8.4 | 1.3 | 1.5 | 34.5 | 62.5 | 19.1 | 13 | 14 | 21.1 | 227.5 | 18.9 | x | 21.8 | Г |
| \tilde{B} owie, AZ^1 | 1145 | $32^{\circ}20'$ | $109^{\circ}29'$ | 18 | 19.3 | 15.5 | 6.1 | 4.1 | 7.9 | 52.1 | 52.1 | 22.6 | 16.8 | 14.5 | 21.1 | 250.1 | 20.8 | 68 | 16.5 | 3 |
| Tucson, AZ | | | | | | | | | | | | | | | | | | | | |
| (Rillito Creek) | 710 | $32^{\circ}17'$ | $110^{\circ}57'$ | 22.6 | 18.3 | 19.3 | 11.4 | 2.8 | 7.4 | 62.7 | 52.3 | 25.7 | 15.5 | 15.2 | 29.5 | 282.7 | 23.5 | 00 | 19.2 | 1 |
| Anvil Ranch, AZ | 838 | $31^{\circ}58'$ | $111^{\circ}23'$ | 20.3 | 17.8 | 17.8 | 7.6 | 30.5 | 7.6 | 63.5 | 60.9 | 35.6 | 20.3 | 12.7 | 22.9 | 317.5 | 26.4 | 58 | 19 | 4 |
| Santa Rita | | | | | | | | | | | | | | | | | | | | |
| Experimental | | | | | | | | | | | | | | | | | | | | |
| Range, AZ | 1311 | $31^{\circ}46'$ | $110^{\circ}51'$ | 43.2 | 39.9 | 30.1 | 15.5 | 6.9 | 16.5 | 106.4 | 107 | 48 | 18.8 | 28.4 | 35.3 | 496 | 41.3 | 27 | 17.7 | ъ |
| Tumacacori, AZ | 966 | $31^{\circ}34'$ | $111^{\circ}03'$ | 21 | 15 | 17 | 9 | 3 | 10 | 101 | 92 | 34 | 18 | 15 | 30 | 362 | 30.2 | 69 | 18.7 | ы |
| Fort Huachuca, | | | | | | | | | | | | | | | | | | | | |
| AZ | 1422 | $31^{\circ}34'$ | $110^{\circ}20'$ | 35.3 | 32.5 | 16.3 | 7.1 | 9.1 | 17.3 | 94.5 | 99.8 | 33 | 17 | 25.7 | 30.2 | 417.8 | 34.8 | 49 | 16.5 | 3 |
| 7 mi NW Sasabe, | | | | | | | | | | | | | | | | | | | | |
| AZ | 1094 | $31^{\circ}29'$ | $111^{\circ}13'$ | 31 | 25 | 18 | 7 | 3 | 9 | 98 | 94 | 50 | 14 | 25 | 58 | 429 | 35.7 | 35 | 17.5 | 9 |
| Sonoyta, SO | 393 | $31^{\circ}52'$ | $112^{\circ}51'$ | 16.9 | 9.4 | 11.8 | 4.9 | 0.9 | 0.5 | 26.7 | 48.3 | 23.3 | 17.5 | 8.8 | 26.6 | 195.6 | 16.3 | 20 | 21.1 | Г |
| Naco, SO | 1404 | $31^{\circ}19'$ | $109^{\circ}56'$ | 19 | 20.4 | 17.9 | 9.3 | 2.8 | 13.3 | 88.1 | 78.8 | 45 | 15.3 | 12.9 | 30.6 | 353.4 | 29.4 | | 17 | % |
| Cananea, SO ¹ | 1606 | $30^{\circ}59'$ | $110^{\circ}18'$ | 27.4 | 34.3 | 24.9 | 12 | 7.8 | 24.6 | 128.4 | 124 | 67 | 33 | 22.6 | 49.9 | 555.9 | 46.3 | | 15.4 | 1 |
| Altar, SO | 397 | $30^{\circ}43'$ | $111^{\circ}50'$ | 14,8 | 12.1 | 8.4 | 4 | 0.9 | 10.5 | 65.6 | 61.4 | 38,8 | 16.4 | 13.4 | 20.9 | 213.6 | 21.4 | | 22 | - |
| Santa Ana, SO | 686 | $30^{\circ}32'$ | $111^{\circ}07'$ | 14.8 | 15.5 | 11.3 | 3.7 | 2.5 | 10.8 | 73.6 | 89.3 | 40.1 | 14.4 | 14.6 | 25.2 | 315.8 | 26.3 | | 22 | - |
| Nacozari, SO | 1100 | $30^{\circ}23'$ | $109^{\circ}41'$ | 35.4 | 25.2 | 27.4 | 12.7 | 9 | 29.6 | 147.4 | 89.7 | 58.8 | 37.1 | 17.1 | 55.6 | 542 | 45.2 | | 18.9 | 5 |
| Rancho El | | | | | | | | | | | | | | | | | | | | |
| Carrizo, SO | 732 | $30^{\circ}03'$ | $115^{\circ}15'$ | 16 | 7 | œ | 5 | | | $\overline{96}$ | 121 | 43 | 14 | 8 | 21 | 343 | 31.2 | | 22.9 | × |
| Moctezuma, SO | 609 | $29^{\circ}48'$ | $109^{\circ}41'$ | 31.3 | 15.4 | 12.5 | 3.4 | 2.4 | 27.1 | 151.6 | 119 | 61.1 | 27.5 | 5.9 | 26.9 | 484.1 | 40.3 | I | 21.3 | × |
| Hermosillo, SO | 211 | $29^{\circ}04'$ | $110^{\circ}55'$ | 21.6 | 10 | 5.4 | 4.3 | | | 86.6 | 94 | 35.9 | 18.7 | 5.3 | 14.4 | 305 | 25.4 | I | 24 | - |
| | | | | | | | | | | | | | | | | | | | | |

TABLE 1—Continued

| | | | | | | | | Z | 1ean m | Mean monthly precip | precipit | ation | | | | | | | | |
|----------------------|------|---|------------------|---------|------|----------------------|--------|-------|--------|----------------------------|----------|------------------|-------------|-----------------|---------------|---------------|------|-----|---------|-----|
| Location | A | Longi- Feb- A Latitude tude January ruary | Longi- tude | January | | March April May June | April | May . | June | July | August | Sep- tember t | Oc- ober | No- vember o | De- cember | \mathbf{TS} | MP | MAD | MAT 1 | HT |
| Punta de Agua, SO | 066 | 98°95/ | 100°95′ | | 04 | ъ | и х | _ | 107 % | 193.6 | | 43.4 | г | 90.6 | 40.9 | 465 S | | | 7 66 | x |
| vmas, SO | 0 00 | 27°56' | $110^{\circ}53'$ | 12.1 | 5.8 | 3.5 3.5 | 1.6 | 0.0 | 6 | 45.5 | 66.7 | 50.2 | 18.6 | 7.8 | 20.5 | 235.2 | 19.6 | | 25 1 | - 1 |
| Ciudad Obregon, | | | | | | | | | | | | | | | | | | | | |
| SO | 51 | 27°29′ | $109^{\circ}56'$ | 14.1 | 4 | 3.5 | 1.1 | 0.2 | 6.8 | 79.2 | 84.9 | 58.9 | 21.9 | 5.6 | 20.8 | 301 | | | 25.6 | 6 |
| nos, SO | 389 | $27^{\circ}01'$ | $108^{\circ}57'$ | 39.3 | 16.7 | 7.7 | 1.7 | 0.8 | 34.7 | 172.7 | 173 | 92.5 | 47.7 | 10.2 | 41.9 | 638.9 | | l | 23.5 | 10 |
| Choix, SI | 310 | $26^{\circ}43'$ | $108^{\circ}16'$ | 43.9 | 14.4 | 8.4 | 3.6 | 2.3 | 58.3 | 215.8 | 207 | 115 | 48.7 | 16.7 | 47.9 | 782 | 65.2 | l | 24.9 | 10 |
| ll Fuerte, SI | 100 | $26^{\circ}26'$ | $108^{\circ}38'$ | 25.8 | 11 | 4.6 | 5 | 1.4 | 32.4 | 167.1 | 167 | 102 | 41.3 | 11.2 | 34.1 | 599.9 | | I | 25.2 | 6 |
| Guasave, SI | 20 | $25^{\circ}34'$ | $108^{\circ}28'$ | 12.2 | 5.6 | 4.8 | 0 | 1.3 | 14.9 | 123.8 | 125 | 83.3 | 60.2 | 19.4 | 7.4 | 457.9 | | I | 26 | 6 |

pincushions (*Mammillaria* species), night-blooming cereus (*Cereus greggii*), hedgehog cactus species (*Echinocereus engelmannii*, and *Echinocereus fasciculatus*), and the "endangered" Pima pineapple cactus (*Coryphantha scheeri* var. *robustispina*). Based on the evidence of tracks, fecal pellets, and teeth marks at the base of the cacti, we believe that the consumption of cacti pulp and fruits allows the hare to survive without free water, as was also reported by Vorhies and Taylor (1933).

Although nearly one third of *L. alleni* observations were in locations having significant areas of bare ground, herbaceous grasses and forbs (or both) were present in 68% and 39% of the locations, respectively. Important species in the more-arid areas included winter annuals such as globe mallows (*Sphaeralcea*), native and nonnative mustard species (*Brassica, Sisymbrium, Lesquerella, Descurainia*), nievitas (*Coryphantha*), plantains (*Plantago*), filaree (*Erodium cicutarium*), California poppy (*Eschscholzia mexicana*), broadleaf combseed (*Pectocarya platycarpa*), and red-maids (*Calandrinia ciliata*). Summer rains resulted in significant areas occupied by plants such as Mexican poppy (*Kallstroemia grandiflora*), amaranth species (*Amaranthus*), and purselane species (*Portulaca*).

We observed <10 antelope jackrabbits in dense grass or in semidesert grasslands above 1,220 m elevation and populated by such temperate bunchgrasses as curly mesquite grass (Hilaria belangeri), tobosagrass (Hilaria mutica), black grama (Bouteloua eriopoda), and sideoats grama (B. curtipendula; Brown, 1994a). Lepus alleni was rarely encountered in thick, matted stands of Johnsongrass (Sorghum halepense) or tangled thickets of mesquites and other thorny plants such as lotewood and pricklypear. Although this hare may forage in areas opened up for agriculture or bufflegrass pasture, large irrigated fields were avoided, especially those subject to "clean farming" practices. Antelope jackrabbits appeared more reluctant than were L. californicus to reoccupy abandoned farmlands, this species being more-often seen in native vegetation between retired fields (Table 2).

We recorded 69 observations of *L. alleni* in Sonora, not including 16 photo locations examined from camera sets. Elevations ranged from 185 to 1,175 m and included areas mapped as Sonoran Desertscrub (12%), through Sonoran Savanna Grassland (16%) to Sinaloan Thornscrub (55%), with the remainder in Sinaloan Tropical Deciduous Forest and Madrean Evergreen Woodland (Brown and Lowe, 1994). Hares using thornscrub, deciduous forest, and riparian areas were usually seen or photographed in clearings or along roadsides. Although some habitats used by *L. alleni* in Sonora were savannas similar to those used in Arizona, others possessed a more-closed aspect similar to that in mesquite bosques.

No grassland or savanna vegetation occurs on Tiburon Island, where *L. californicus* is lacking. Relative importance values of plants associated with antelope jackrabbit

| | | | 1 | alent wo cies pres | , | | | Unde | rstory no | oted |
|--|-----------|------|------|-----------------------|-------|-------|-------|---------|-----------|------|
| Habitat type | No. hares | Prju | Olet | Ladi | Atspp | Other | Cacti | Grasses | Forbs | Bare |
| Sonoran Desertscrub | | | | | | | | | | |
| Arizona Upland Subdivision | 33 | 28 | 29 | 14 | 0 | 16 | 30 | 20 | 18 | 8 |
| Lower Colorado River Subdivision | 27 | 24 | 15 | 25 | 3 | 8 | 17 | 13 | 17 | 13 |
| Sonoran Savanna Grassland | 129 | 123 | 61 | 79 | 14 | 57 | 63 | 97 | 66 | 50 |
| Sonoran Savanna–Semidesert Grassland | 149 | 139 | 8 | 0 | 0 | 7 | 17 | 121 | 52 | 42 |
| Mesquite bosque and Sinaloan Thornscrub | 48 | 23 | 30 | 5 | 2 | 14 | 8 | 18 | 4 | 6 |
| Retired farmland and bufflegrass pasture | 23 | 5 | 1 | 3 | 2 | 3 | 2 | 18 | 4 | 1 |
| Sinaloan Tropical Deciduous Forest | 1 | _ | _ | 0 | 0 | 1 | | | _ | _ |
| Madrean Evergreen Woodland Savanna | 2 | _ | _ | 0 | 0 | 2 | _ | | _ | _ |
| Total | 412 | 342 | 144 | 126 | 21 | 108 | 13 | 287 | 16 | 12 |

sign and observations in the Central Gulf Coast subdivision of Sonoran Desertscrub (xeric microphyll shrub) were: brittlebush Encelia farinosa (55.3%), creosote L. tridentata (38.2%), the saltbush Atriplex barclayana (32.9%), and elephant tree Bursera microphylla (31.0%) with lesser frequencies for physicnut Jatropha cuneata (22.7%) and ironwood O. tesota (18.5%). Mangroves and other halophytic vegetation were avoided. To calculate a population density of jackrabbits on Tiburon Island, we conducted day and night observations along line transects that considered the perpendicular distance from the observer to the transect to obtain a density function (f(0))(Buckland et al. 1993). A total of 76 adult jackrabbits were observed on three transects traveled 30 times for a total of 92.6 km. The estimated density averaged 3.56 rabbits/ km². Given an area of 1,208 km² of potential habitat, we estimated a population of 4,300 L. alleni on Tiburon Island.

Lepus alleni is sympatric with L. californicus in Arizona and much of northern Sonora. Although the latter was thought to be present in lower than historic numbers during our surveys, we observed mixed groups of the two species only thrice. Partly for this reason, but also because of our intent to describe the habitat affinities of L. alleni, our observations of antelope jackrabbits outnumbered those of black-tailed jackrabbits by nearly 4:1 (421 vs. 106). Lepus californicus ranged both lower (390 vs. 440 m) and higher (to 2,133 m) in elevation than antelope jackrabbits, which rarely occurred >1,200 m. Vorhies and Taylor (1933) and O'Connor (1945) reported seeing groups of up to 35 L. alleni individuals but the most animals we observed together was eight. Nonetheless, the group variance incidence of 1.32 L. alleni vs. 1.18 L. californicus only approached statistical significance, indicating that more L. alleni were seen per sighting than L. californicus (t-ratio = 2.39, df = 223, P = 0.18; Table 3).



FIG. 2—A) Habitat of *Lepus alleni* in Arizona. Note the herbaceous understory and savanna-like aspect in the vicinity of Sopori Wash west of Amado in Pima County, Arizona. The trees are mostly *Prosopis juliflora*. Summer aspect. B) Habitat of *L. alleni* near Pueblo Viejo, Sonora. Spring aspect. Photo by Anibella Carlón Flores.

Lepus californicus also was less-often associated with mesquites than were L. alleni (47% of the observations vs. 83%). Sixty-three (57.3%) of the L. californicus observations were in Sonoran Desert vegetation with the number of observations associated with bare ground (36) being greater than with either grasses (17) or forbs (32). Lepus californicus was more prone to use agricultural areas and seral stages of abandoned farm fields than were L. alleni, with 15% of the observations of the former vs. 5.6% of the latter being in retired farm fields or pastures (Table 4). One result of the antelope jackrabbit being absent or poorly represented on lands devoted to irrigated agriculture is that this species now has a more-disjunct distribution than does L. californicus and is absent over much of its former range.

Only three live jackrabbits less than half grown were observed during this study. A *L. californicus* was seen motionless in its form on 16 June 2012 within dense brush under a fruiting saguaro. Two young *L. alleni* were found dead on 25 July 2013 and 20 September 2013. The former, an obvious neonate, had its skull bitten into and ears chewed away and appeared to have been killed by a round-tailed ground squirrel (*Xerospermophilus tereticaudus*). The second animal was about half grown but still displayed a white-marked forehead and appeared to have been dropped by a great horned owl (*Bubo virginianus*). Both of the young antelope jackrabbits would have been born after the onset of summer rains.

Like other hares, this species is adapted to open country and, based on our observations, generally avoids rough topography and steep terrain. Employing both "see and flee" and "skulking-down" escape strategies, adult antelope jackrabbits are most-often encountered on level valley floors, gentle slopes, and alluvial fans <1,070 m elevation.

There was only a minor difference in the flushing distances recorded between the two hares (*t*-stat = -0.336, df = 126, P = 0.37), with both height and amount of cover appearing to be more of a factor than the species involved. The mean flushing distance for *L. alleni* was 65.4 m (n = 90) and was 61.1 m for *L. californicus* (n = 38).

No *L. alleni* were observed in areas of <400 ha of suitable-appearing habitat that were isolated by freeways or by irrigated fields devoted to agriculture (or both), indicating that this species might require a substantial-sized home range.

DISCUSSION—Our observations, coupled with fossil, paleontological, archeological, and historic evidence, suggest that antelope jackrabbits evolved in subtropical grasslands, landscapes that presently exist in Arizona and Sonora in a much-altered state (Kürten and Anderson, 1980; Szuter, 1991; Brown, 1994*b*; Rea, 1998). Even now, however, some tropical grasses persist, with habitats supporting the most *L. alleni* having an herbaceous

ground cover of ephemeral forbs and grasses beneath a velvet mesquite overstory. Today this species is an endemic relic restricted to low-elevation plains, valleys, and foothills within the Sonoran and Sinaloan biotic provinces of Arizona and northwest Mexico (Swarth, 1929; Dice, 1939, Brown et al., 2012).

Centered in west-central Sonora, the species distribution extends northward through subtropic south-central Arizona to approximately latitude 33°23'N southeast of Apache Junction and southward to the Sinaloa-Nayarit border at ca. 21°54'N. Its eastern limits are the steep slopes of Arizona's sky-islands and Mexico's Sierra Madre Occidental, where populations extend upward in the interior valleys of central Sonora, western Chihuahua, and Sinaloa to ca. 1,066 m. Western limits approximate a 100-mm summer rainfall isoline from Florence, Arizona, southwest to the Sonora coast in the vicinity of Libertad, and then southward along the coast (including Tiburon Island) to the Marismas Nacionales in extreme southern Sinaloa. Of the seven hares native to North America, L. *alleni* has the most-restricted range ($<100,000 \text{ km}^2$) other than the tropical and similar Tehuantepec jackrabbit (Lepus flavigularis; Lorenzo et al., 2006).

The western distribution of *L. alleni* appears controlled by aridity. Precipitation amounts within the range of the hare increase from a low of ca. 200 mm on the mist-prone seacoasts of Tiburon Island and southwestern Sonora to a high of ca. 460 mm in interior valleys and foothills. A more-important limiting factor appears to be the amount of summer (June-September) moisture, this precipitation amount ranging from a minimum of 90 mm in areas subject to coastal fog to 360 mm or more in south-central Sonora. A greater tolerance for low humidity is thought to explain why L. californicus ranges farther west into the "Gran Desierto" region of Sonora and California's Imperial Valley. Conversely, the relatively higher humidity of the Central Gulf Coast and Tiburon Island may explain the persistence of L. alleni in these areas as well as in southern Sonora and Sinaloa, both of which lack populations of L. californicus.

The antelope jackrabbit reaches its greatest abundance in what are, or were, tropic–subtropic grasslands within and adjacent to Sonoran Desertscrub and Sinaloan Thornscrub (Brown, 1994*b*, 1994*c*; Brown and Lowe, 1994). Within Sonoran Desertscrub the animal is mostly restricted to the more-mesic Arizona Upland, Plains of Sonora, and Central Gulf Coast subdivisions, being absent from most of the desert's Lower Colorado River subdivision (Turner and Brown, 1994). *Lepus alleni* is poorly represented in areas dominated by creosote, saltbush, and other low-growing shrubs (<2 m) including triangleleaf bursage. Nonetheless, this species is able to persist in degraded savannas dominated by velvet mesquite and nearly devoid of herbaceous cover.

Although antelope jackrabbits extend upward into semidesert or desert grassland communities in south-

| Month | No. of singles | No. of pairs | No. of triples | No. of fours | No. of fives | No. of sixes | No. of sevens | No. of eights | Total observations | % Singles | % Pairs | $\frac{\%}{3+}$ |
|------------|----------------|-----------------|-------------------|-----------------|-----------------|-----------------|---------------|------------------|-----------------------|--------------|------------|-----------------|
| WOITIN | singles | pairs | uipies | louis | lives | 51205 | sevens | eignis | observations | Singles | 1 4115 | 5 + |
| Antelope | e jackrabbi | t | | | | | | | | | | |
| Jan | 13 | 6 | 1 | 0 | 0 | 0 | 0 | 1 | 21 | 61.9 | 28.6 | 9.5 |
| Feb | 22 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 25 | 88 | 8 | 4.5 |
| Mar | 12 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 17 | 70.6 | 17.6 | 11.8 |
| Apr | 35 | 8 | 3 | 0 | 1 | 0 | 0 | 0 | 47 | 74.5 | 17 | 8.5 |
| May | 47 | 8 | 4 | 1 | 1 | 0 | 0 | 0 | 61 | 77 | 13.1 | 9.8 |
| June | 74 | 19 | 3 | 1 | 3 | 0 | 0 | 0 | 100 | 74 | 19 | 7 |
| Jul | 81 | 13 | 1 | 0 | 1 | 0 | 0 | 0 | 96 | 84.3 | 13.5 | 2.2 |
| Aug | 60 | 8 | 3 | 1 | 1 | 1 | 0 | 0 | 74 | 81.1 | 10.8 | 8.1 |
| Sept | 49 | 7 | 2 | 0 | 1 | 0 | 0 | 0 | 59 | 83.1 | 11.9 | 5.1 |
| Oct | 10 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 83.3 | 16.7 | 0 |
| Nov | 32 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 39 | 82.1 | 12.8 | 5.1 |
| Dec | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 90 | 10 | 0 |
| Total | 444 | 82 | 22 | 3 | 8 | 1 | 0 | 1 | 561 | 79.1 | 14.6 | 6.3 |
| Black-tail | led jackrab | bit | | | | | | | | | | |
| Jan | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 100 | 0 | 0 |
| Feb | 12 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 13 | 92.3 | 0 | 7.7 |
| Mar | 10 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 83.3 | 16.7 | 0 |
| Apr | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 9 | 66.7 | 22.2 | 11.1 |
| May | 16 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | 84.2 | 15 | 0 |
| Jun | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 66.7 | 22.2 | 0 |
| Jul | 22 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 88 | 12 | 0 |
| Aug | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 100 | 0 | 0 |
| Sep | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 100 | 0 | 0 |
| Oct | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 100 | 0 | 0 |
| Nov | 8 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 10 | 80 | 10 | 10 |
| Dec | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 99 | 12 | 2 | 0 | 1 | 0 | 0 | 0 | 114 | 86.8 | 10.5 | 1.8 |

TABLE 3—Group observations of the antelope jackrabbit, *Lepus alleni*, and the black-tailed jackrabbit, *Lepus californicus*, from 2009–2014.

central Arizona and north-central Sonora, this species appears to avoid temperate grasslands with mean annual temperatures less than 18°C (Table 1). The antelope jackrabbit is lacking from southeastern Arizona, southern New Mexico, and most of the Mexican highlands, where it is replaced by either *L. californicus* or white-sided jackrabbit (*Lepus callotis*).

The function of group behavior in *L. alleni* is not known but may be related to mating and involve either multiple males or multiple females (Angerbojorn and

TABLE 4—*Lepus californicus* observations by habitat-type and associated plant species. Areas visited included, but were not limited to, Altar Valley, Avra Valley, McLellan Valley, Marana Air Park, Santa Cruz Flats, Vekol Valley, Stanfield-Maricopa area, Coolidge Air Park, Oracle Junction, upper Santa Cruz Valley, Sopori Valley, and the Santa Rita Experimental Range. Additional observations were recorded in these same areas by cooperators familiar with *L. alleni*. Prju = *Prosopis juliflora*; Olte = *Olnea testota*; Ladi = *Larrea tridentata*; Atspp. = *Atriplex* species; Other = other leguminous tree.

| | | Most pre | valent wood | y plant spec | ies present | | Unde | erstory n | oted | |
|----------------------------------|----------|----------|-------------|--------------|-------------|-------|-------|-----------|-------|------|
| Habitat type | No. Seen | Prju | Olte | Ladi | Atspp | Other | Cacti | Grasses | Forbs | Bare |
| Sonoran Desertscrub | | | | | | | | | | |
| Arizona Upland Subdivision | 22 | 2 | 8 | 8 | 0 | 9 | 13 | 1 | 0 | 0 |
| Lower Colorado River Subdivision | 41 | 11 | 1 | 22 | 11 | 2 | 20 | 4 | 14 | 19 |
| Sonoran Savanna Grassland | 15 | 13 | 0 | 2 | 0 | 0 | 2 | 2 | 4 | 8 |
| Sonoran Savanna–Semidesert | | | | | | | | | | |
| Grassland ecotone | 11 | 11 | 2 | 0 | 0 | 2 | 4 | 9 | 4 | 3 |
| Mesquite bosque and thornscrub | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Retired farmland and pasture | 17 | 15 | 0 | 1 | 0 | 0 | 0 | 1 | 10 | 6 |
| Total | 106 | 52 | 11 | 33 | 11 | 13 | 39 | 17 | 32 | 36 |

Flux, 1995; Nowak, 1999; Rioja et al., 2008). Evidence questioning such an assumption is that group behavior occurred throughout the year with a log-linear regression model showing no significant difference between months ($\chi^2 = 5.855$, df = 11, = P < 0.088) including the jackrabbit's reproductive season from February through September (Vorhies and Taylor, 1933; Table 3). Only three observations were made of groups containing both jackrabbit species.

Antelope jackrabbits in southern Arizona range westward from the San Pedro River to just beyond Organ Pipe Cactus National Monument. *Lepus alleni* in Arizona is found north of the Gila River only in the vicinities of Apache and Florence junctions. Southward the animal ranges at elevations from as low as 260 m on the Cabeza Prieta National Wildlife Refuge (Simmons, 1966) to nearly 1,520 m in an area on Fort Huachuca in western Cochise County (Hoffmeister, 1984).

Most sightings in Arizona occurred in valleys and on alluvial fans drained by the Santa Cruz River and its tributaries-Rillito Creek, Cañada del Oro, Brawley Wash, Robles Wash, Quijotoa Wash, Santa Rosa Wash, and Vekol Wash-areas also occupied by L. californicus. Other Arizona locations occupied both by L. alleni and L. californicus included areas drained by McClellan Wash and Queen Creek. Important areas included Altar and Avra valleys, Santa Cruz Flats, McClellan Valley, the Santa Rita Experiment Range, the Papago Indian Reservation, and the Oracle Junction area. Drainages in Arizona that have a more-sporadic or lower density of L. alleni include the watersheds of the Sonoyta and San Pedro rivers such as Babocomari Creek. Antelope jackrabbits in Arizona are therefore limited to select habitats within Santa Cruz, Pima, Pinal, southern Maricopa, and extreme western Cochise counties; the species is absent from the extensive semidesert grassland areas found in Greenlee, Graham, and most of Cochise county.

We believe that both winter and summer season annual plants, together with mesquite stems and the new growth on perennial grasses, materially contribute to the animal's diet during the warmer months (Vorhies and Taylor, 1933; Arnold, 1942). We know of no *L. alleni* observations from areas having less than 100–200 mm of summer precipitation, and we believe the need for green forage may prevent the antelope jackrabbit from occurring in habitats subject to extended drought and areas with little or no summer flooding or otherwise lacking herbaceous vegetation. Although reported to not drink water, antelope jackrabbits were repeatedly photographed by Pima County Parks and Recreation personnel drinking at wildlife catchments in the Sopori Wash area west of Green Valley Arizona (K. Baldwin, pers. comm.).

Areas of special interest near the northern terminus of the range of *L. alleni* are the Santa Cruz Flats and adjacent drainages bordering the Santa Cruz River and Santa Rosa Wash in Pinal County. Here, the species is confined to level plains of alluvial fill, overflow areas, and stabilized dunes that are more mesic than the adjacent desert scrub. One of the most-striking features of these flood-prone habitats is the numerous small bolsones or playacitas outside the river channels. These ephemeral wetlands, which include a few vernal pools and which may be a hectare or more in size, experience standing water for days or even weeks after heavy rains and run-off. Other areas, at least formerly, were subject to periodic overflows of the Santa Cruz River, Vekol Wash, or other drainages. Excess surface water deposited on these fine soils permits the establishment of mesquite savannas of C. virgata and other grass species, which are more mesic than the adjacent desert scrub. As in thornscrub regions in Sonora, Mexico, L. alleni persists in woodlands (bosques) when open adjacent areas are present.

A specimen in the University of Arizona collection from near Fort Bowie is of particular interest (Roth and Cockrum, 1976; Hoffmeister, 1984). This location is some 80 km east of any known population and is from outside the temperature parameters of the locations of any other specimen. We have examined the specimen collected by Roth on 23 September 1976 and it is indeed *L. alleni*. The habitat of this individual, and another reportedly seen by Roth nearby, is atypical of the species, however, and we regard it as an anomaly. Fort Bowie National Historic Site Naturalist Larry Ludwig (pers. comm., 2011) has no record of anyone seeing one of these hares in the Fort Bowie–Apache Pass vicinity since his arrival in 1972.

Although much of the area within the antelope jackrabbit's former range no longer contains suitable habitat, recent observations show little change in the limits of distribution. An exception may be in the northwest along the lower Santa Cruz, Vekol, Greene, and Santa Rosa drainages (Arnold, 1942). Here, below an elevation of 400 m in Komatke Thicket and other portions of the Gila River Indian Reservation, the species may no longer be present due to agricultural developments, an expanded network of concrete canals, and the loss of native grasses and forbs (Rea, 1998).

Major habitat losses have occurred in Arizona within the range of *L. alleni* due to the conversion of its habitat to irrigated farmlands and urbanization. These losses have been particularly acute in southern Maricopa, Pinal, and Pima counties, where 58,131 ha or an estimated 20% of the animal's historic range is no longer occupied. Farmlands in Arizona removing the most habitats are located along the Santa Cruz River including the Santa Cruz Flats, Santa Rosa Wash, and in the Casa Grande, Coolidge, Marana, and Queen Creek irrigation districts. Urban losses have been the most severe in the vicinities of the towns of Apache Junction, Maricopa, Casa Grande, Arizona City, Chandler, Oracle Junction, and north, east, and south of Tucson.

In Sonora and Sinaloa, antelope jackrabbits occur on level to rolling terrain between sea level and the oak belt at from 945–1,070 m elevation, with most observations below 460 m (Allen, 1906; Burt, 1938; Armstrong and Jones, 1971; Caire, 1978). Armstrong and Jones (1971) reported that *Lepus alleni palitans* occurs at low to moderate elevations throughout Sinaloa but is most abundant in the north where it merges with *Lepus alleni alleni* in the vicinity of Alamos, Sonora. The southernmost record is from the vicinity of Acaponeta, Nayarit, just south of the Sinaloa border (Hall, 1981).

Desert habitats included Arizona Upland, Plains of Sonora, and the Central Gulf Coast subdivisions of the Sonoran Desert (Turner and Brown, 1994). Only one animal was seen in the Lower Colorado River Valley subdivision of the Sonoran Desert. As in Arizona, minimum summer rainfall or the presence of maritime dew (or both) appeared to be a factor limiting the distribution of L. alleni in Sonora. Also, as in Arizona, tropical grasses such as B. barbata and herbaceous vegetation accompanied most observations. The overstory situation in Sonora and Sinaloa is more diverse, however, with several species of columnar cacti such as organ pipe cactus (Stenocereus thurberi), Indian comb (Pachycereus pecten-arboriginum), and senita cactus (Pachycereus schottii) often present. In addition, as in Arizona, mesquite bosques or other leguminous thickets of thornscrub were often nearby, such habitats providing thermal and screening cover for resting animals.

In central Sonora, Alcalá-Galván and Miranda-Zarazuá (2012) found that *L. alleni* pellets in buffelgrass pastures were more likely to be observed along the edges near natural habitats than in the fields. They reported greater densities of *L. alleni* in native vegetation, with pellet densities decreasing as the center of buffelgrass fields was approached, despite the use of this grass as a food item during the late winter and early spring when native grasses were less available (Alcalá-Galván and Miranda-Zarazuá, 2012).

Massive losses of L. alleni habitat comprising some 1,560,000 ha of irrigated farmland have occurred in Sonora and Sinaloa. Livestock have reduced the herbaceous vegetation throughout the animal's range, including within the Tohono O'Odham nation (Brown and Carmony, 2012). Although we often observed L. alleni near stock tanks, we suspect that this was due to these features being fringed with mesquites, as stock tanks are generally detrimental to the hare in that they concentrate cattle overuse, interrupt moisture flow, reduce water distribution, contribute to soil erosion, and result in reduced grass cover (McAuliffe, 1998; Brown and Carmony, 2012). Another potential threat brought on by grazing or fire suppression (or both) is a reduction in habitat quality due to an increase in woody vegetation (Turner et al., 2003). By way of contrast, retired farmlands in Avra Valley managed by Pima County and the City of Tucson as "open space" appear to have improved as L.

alleni habitat due to reversion to a more-natural state and an increase in herbaceous cover.

Antelope jackrabbit densities and abundance appear to vary over time with variations in weather, habitat quality, livestock grazing intensity, predator control, and probably other activities (Vorhies and Taylor, 1933). Quantifying population changes was outside the scope of this study but our observations, coupled with harvest information, indicate that L. alleni is not being replaced by L. californicus as is the case with the closely related L. callotis (Desmond, 2004; Burhans and Heffelfinger, 2010 in litt.; Traphagan, 2011 in litt., Desmond, 2004). Indeed, 5 y of check station information show robust populations of L. alleni despite a decline in numbers of L. californicus. No instances of hybridization between L. alleni and L. californicus were noted either in the field or at a hunter check station where \sim 300 hares were examined (Burhan and Heffelfinger, 2010 in litt.)

Based on specimen records, available climate data, and the archeological record, we have concluded that *L. alleni* is a grassland relict that occurs in tropic–subtropic savannas within and adjacent to Sonoran Desertscrub and Sinaloan Thornscrub. Antelope jackrabbits persist only within Sonoran Desertscrub habitats having sufficient summer precipitation and humidity or where the more arid-adapted *L. californicus* is lacking or poorly represented. An essentially savanna species, *L. alleni* has adapted to living in mesquite bosques and other thornscrub-like vegetation, provided open landscapes occur nearby.

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APPENDIX 1—Gazetteer of select *Lepus alleni* (antelope jackrabbit) museum specimen locations plotted on Google Earth and used in Figure 1. Localities are ordered by subspecies, state, institution, and catalog number or source, with decimal latitude and longitude coordinates in brackets. ? indicates specimen number unknown.

Lepus alleni alleni-ARIZONA: American Museum Natural History (AMNH)-MS2413 [32.7174, -111.4975], MS2412 [32.4257, -111.1568], MD 7876 [32.26738, -110.8816], M-137011 [32.2537, -110.6975]; Arizona State University (ASU)-2013 [33.77126, -111.552407], 2814 [33.3707, -111.5507], 589 [33.2213, -111.2531], 2041 [33.061899, -111.76172];California Academy Science (CAS)-17464 [32.267531, -110.882702], 5906 [31.774531, -110.867864], 5908 [31.74994, -110.92074], 6887 [31.673873,-111.260969], 5902 [31.58431, -110.739098]; Charles R. Conner Museum (CRCM)-68-12 [31.851495, -110.873639], 57-63 [31.631507, -110.346823]; Field Museum Natural History (FMNH)-15040 [32,580948, -111.321349], 910 [32.269743, -110.884051], 54315 [31.613532, -111.031632]; Humboldt State University (HSU)-1032 [32.863321, -111.454611]; University Kansas Natural History Museum (KU)-79083 [33.006118, -111.055898], 8228 [31.787295,-110.994528]; University of New Mexico Museum of Southwestern Biology, Albuquerque (MSB)-162731 [31.6417731, -110.357073]; Museum Vertebrate Zoology University of California, Berkeley (MVZ)-? [31.83701, -110.953102], 19129 [31.791927,-110.942849], 27849 [32.316895, -111.128888]; San Diego Museum Natural History-24047 [33.210409, -112.15097], 212 [32.286677, -110.903411], 211 [32.184537, -110.974495], 213 [32.011003,-110.989765], 24776 [32.012807, -111.349517], 24636 [31.972728, -111.38628], 931 [31.937593, -110.979848],23484 [31.852701, -111.852653]; University of Arizona (UA)—15323 [33.243101, -111.343561], 15327 [32.978023, -111.282323], 12758 [32.665968],-887088], 12757 [32.61355, -110.641658], 3057 [32.610188, -110.884012], 775 [32.589855,-111.395413], 17898 [32.544076, -111.165938], 1650 [32.4378, -110.49756], 22857 [32.376976, -111.436764],21284 [32.303884, -110.905512], 22853 [32.28706,

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-111.296799], 18410 [32.24988, -111.2206538], 21244 [32.245602, -111.344402], 21242 [32.162037,-111.25071], 23465 [32.15166, -109.532535], 4473 [32.096686, -111.057422], 8193 [31.927753,-110.718311], 1964 [31.85943, -111.394638], 19400 [31.848531, -110.955955], 76 [31.835358]-110.870014], 5289 [31.551821, -111.526756], 13346 [31.506048, -111.557258], 17137 [31.439884]-110.113552], 14146 [31.429729, -110.931679]. University Colorado Museum Natural History (UCM)-3197 [31.824157, -110.888414]; University Illinois in Hoffmeister 1984-[33.252616, -111.518346, 32.207704, -110.72803, 31.635152, -110.358904, 31.632836,-110.717477, 31.489734, -111.377806, 31.36725,-110.649697, 31.361579, -110.519716]; U.S. National Museum = Smithsonian (USNM)-149701 [32.873262, -111.760872], 16848 [32.621129, -110.787626], 223552 [32.273002, -110.892771], 19517 [32.231624, -110]689463], 19516 [32.1806, -110.889168], 19520 [32.164386, -110.858237], 209848 [31.966942,-111.475695], 307400 [31.90796, -110.973266], 564045 [31.891532, -110.868386], 250055 [31.809857]-110.856908; 235482 [31.805982, -110.887462]; 36500 [31.805027, -110.965055], 203028 [31.79109,-110908456], 209237 [31.784796, -111.493126], 59001 [31.497529, -111.557113], 18220 31.42995,-110.986594], University Texas at El Paso (UTEP)-3362 [32.083645, -111.226466], 3581 [32.041293, -111.232015]; Western New Mexico University-5474 [32.684410, -110.845231], 5786 [32.509872],-111.290062], 6196 [32.220297, -110.766026], 6808[32.16316, -111.245279].

SONORA: AMNH—MS5372 [30.165, -109.3249]; ASU-588 [30.35099, -111.9851]; Centro de Investigaciones Biológicas del Noroeste (CIB)—14506 [29.021541, -110.98.477]; FMNH—1167 [30.874261, -111.031632]; KU—100414 [29.118863, -110.012426], 67553 [28.013361, -110.969731]; Los Angeles County Museum (LACM)—4915 [27.862142, -109.92021]; Louisiana State University (LSU)—31.481206, -111.54498]; MSB—36154 [31,263629, -109.922463], 37261 [30.384348, -112.255549], 83774 [39.060492, -112.29593]; MVZ—76205 [31.801402, -112.87407], 106139 [27.743863, -110.523473], New Mexico Museum Natural History (NMMNH)—4812 [29.715017, -109.64016]; SDMNH-7062 [31.36629, -111.607645]; Texas Technical University (TTU) in Caire 1978-[31.224611, -110.026633, 29.688081, -110.854541,28.809488, -110562136, 28.808697, -110.615429, 28.808409, -110.592374, 28.07266, -110.957526]; UA-1246 [29.953791, -112.624944]; Universidad Nacional Autónoma de México (UNAM)-1B3268 [31.104881, -110.917384], 1B12150 [30.569744, -111.80488], 1B25747 [29.502687, -110.851009]; USNM-59292 [31.864463, -112.875215], 59228 [31.753032],-112.417551], 17812 [30.630485, -110.947363], 97448 [30.58778, -110.579264], 51228 [31.632476,-112.014246], 17812 [30.630485, -110.947363], 97448 [30.587781, -110.579264], 250849 [30.208206],-111.111224], 250851 [30.152856, -109.330113], 509004 [28.874124, -109.172635], A46057 [28.309828, -110.689587]; University Washington Burke Museum (UWBM)—? [30.068408, -111.092879, 28.2532, -111.028287]; UTEP-1595 [30.994232, -110.566546], 4616 [29.456007, -110.273376];

Lepus alleni palitans—SONORA: USNM—96478 [27.029687, -108.967002].

SINALOA: AMNH—M23957 [26.9411, -108.468; M-23944, 22.833, -105.7695]; M24699, 23.3813, -106.3941]; CIB—14507H [27.238, -109.307, 18869M [27.085101, -109.324]; KU—79458 [27.294301, -108.240411], LACM—70176 [23.3, -106.41]; UNAM—1132574 [24.217919, -107.368103]; USNM—97447 [24.78776, -107.411163]; UWBM—81684 [26.2675, -108.58855];

NAYARIT: USNM—509004 [22.480419, -105.372956]. Lepus alleni tiburonensis—SONORA: AMNH—M31991 [28.9305, -112.2495], CIB—15563ND [29.133219, -112.404247], KU—95250 [28.999072, -112.222237], MSB—42639 [28.999626, -112.29593], 83774 [29.060492, -112.29593]; MVZ—76202 [28.962104, -112.22556], SDMNH—19866[28.87215, -112.532356]; UNAM—1B24360 [29.2453, -112.265], 1B28528 [28.9955, -112.358], 1B24361 [28.7585, -112.358]; USNM—198403 [29.046437, -112.252559].

APPENDIX 2—Gazetteer of global positioning system localities in Figure 1 where *Lepus alleni* (antelope jackrabbits) were observed, photographed, or referenced in peer-reviewed publications. Localities are ordered by subspecies and state with latitude and longitude coordinates in brackets.

Lepus alleni alleni—ARIZONA: Huey 1942 [31.941483, -113.017082, 31.871882, -112,753379]; JC [31.906862, -111.538369, 31.82005, -111.233]; Simmons 1966 [32.186016, -112.918951, 32.156255, -113.539832, 31.94703, -113.539832]; This Study (TS)—[33.389991, -111.450985, 33.2768, -111.44175, 32.895906, -111.85217, 32.716, -111.708, 32.7068, -111.708, 32.613415, -110.881966, 32.56988, -111.58558, SONORA: Burt 1938—[31.060098, -110.903375, 30.8635, -110.220806, 30.782364, -111.3382, 30.309947, -111,979854, 30.242601, -111.715712,30.21634, -112.272507, 28.965958, -111.53845,27.114063, -109.433662]; J. Childs (JC)-[29.611982, -109.238039, 29.59542, -109.267, 29.58428, -109.272,29.563171, -109.230497, 29.55978, -109.263, 29.552213,-109.246638, 29.5427, -109.23, 29.509734, -109.123502,29.45982, -108.902, 29.45288, -108.958, 29.449704,-108.923875, 29.43482, -109.036, 29.43473, -108.939,29.42902, -108.920]; R. Thompson (RT)-[29.624957, -109.312104, 29.620419, -109.335106, 29.582385,-109.241723, 29.567181, -109.239022, 29.525035,-109.027585, 29.483726, -109.972158, 28.301849,-109.277925]; T. Van Devender (TR)-[30.63722, -109.84028, 30.352127, -110.373043, 29.950254,-109.647101, 29.93000, -110.70694, 29.907646,-110.15698, 29.857104, -109.3167, 29.782633,-109.666226, 29.701431, -109.288729, 29.40487,-109.16151, 29.291543, -109.083796, 29.272785,-109.132031, 29.098003, -109.98436, 29.062264,-109.19305, 29.056772, -110.553365, 29.04028,-110.70139, 29.03292, -110.049223, 29.031466,-109.994644, 28.9963, -110.12389, 28.9825,-11021387, 28.92944, -110.19222, 28.77167,-109.99111, 28.72972, -110.4225, 28.67917, -109.9955,28.658522, -109.974582, 28.635879, -109.12584,28.3969, -110.24139, 28.3875, -110.2897, 28.38600, -10.35472, 28.296205, -110.299349]; TS-[31.757508, -113.100943, 30.770127, -110.332879, 30.183415,-109.776096, 29.794611, -112.149638, 29.783538,-109.6834, 28.852467, -110815327, 28.794662,-110.523835, 28.760945, -110.764747, 28.722913,-110.438312, 28.72000, -110.44000, 28.71832,-110.467, 28.6169, -110.4168, 28.600877, -110698206,28.5646, -110.6852, 28.560026, -110.460795, 28.529866, -110.684524, 28.50467, -110.50018, 28.5003, -110.6718,28.49295, -110.649], DB-[31.40028, -112.94897, 31.43048, -112.92476, 31.42027, -112.92491].

Lepus alleni palitans—SONORA: TR—[26.857186, -108.840361].

SINALOA: Armstrong and Jones 1971—[26.771074, -108.228724, 26.492113, -108.628388, 26.37365, -109.062112, 26.361069, -108.643067, 26.008307, -107.987462, 25.321209, -107.421659, 24.390907, -107.421659, 24.390907, -107.373001, 24.237639, -107.395224, 23.039507, -106.437252, 22.665519, -105.832445, 22.634368, -105.832445]; B. Gibbons (BG)—[26.41, -108.62].