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History, Status, and Population Trends of Cottontail Rabbits and Jackrabbits in the Western United States

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Abstract.—**Cottontail rabbits (genus *Sylvilagus*) and jackrabbits/hares (genus *Lepus*) are keystone prey species for large avian and mammalian predators in western North America. The importance of these leporids as a prey base, and a concern that leporids may be declining, prompted this review of past population studies and evaluation of state federal-aid reports showing harvest, hunt success, and survey trends for rabbits and hares. Of the 12 states that collected data on cottontail hunt success trends, all but three reported declining trends in hunt success. Information on hunt success trends for jackrabbits was limited to California, Nebraska, Kansas, and Oklahoma; declines in jackrabbit hunt success were reported in all states except Oklahoma. Populations of Snowshoe Hares (*L. americanus*), while shown to fluctuate greatly, exhibited no evidence of long-term changes in hunt success trend in Washington, while experiencing a significant decline over time in Utah and Wyoming. No state reported data that inferred a significant increase in leporid numbers as evidenced by analyses of hunt success trends. Based on these data, both cottontail and jackrabbit numbers appear to have declined in most areas in the Western U.S. during the past 50 y with the largest decreases in California, the Great Basin, and Mid-Central Plains. We attribute the reasons for this declining trend to changes in land use and habitat quality, extended drought, and increased predation. We recommend habitat management measures to increase cottontail and jackrabbit survival rates in western states, and increased survey effort and coordination among state game and fish agencies who are primarily responsible for leporid management.**

Key Words.—Hunting pressure; leporidae; *Lepus*; population declines; population irruptions; predation; *Sylvilagus*

Introduction

The western United States has a diverse array of lagomorphs (family Leporidae) that serve as important game species for hunters, including the widespread and often plentiful cottontails (genus *Sylvilagus*) and jackrabbits (genus *Lepus*; Flinders and Chapman 2003). These species are keystone indicators for a wide range of habitats ranging from sea level to elevations > 3,650 m (Wilson and Ruff 1999). Less generally appreciated is their importance as prey for large avian and mammalian predators such as Golden Eagles (*Aquila chrysaetos*; Woodgerd 1952; Marzluff et al. 1997; Kochert et al. 1999; Stahlecker et al. 2009; McCarty et al. 2013), Ferruginous Hawks (*Buteo regalis*; Woffinden and Murphy 1977; Smith et al. 1981), Red-tailed Hawks (*B. jamaicensis*), and Great-horned Owls (*Bubo virginianus*; Smith and Murphy 1979; Steenhof and Kochert 1988; Knick 1990). Their importance in the diets of Coyotes (*Canis latrans*), Bobcats (L*ynx rufus*), and foxes (*Vulpes vulpes*, *Urocyon cinereoargentus*) is similarly well documented (Knick 1990; Wilson and Ruff 1999). Leporids can also be agricultural pests when present in large numbers (Palmer 1897; Fitcher 1953; Roundy et al. 1985; McAdoo et al. 1987, 2004).

Of the three cottontails that are most widely distributed in the western U.S., the Eastern Cottontail (*S. floridanus*), Mountain Cottontail (*S. nuttallii*), and Desert Cottontail (*S. audubonii*), the latter is the most common and most widely distributed, ranging from sea level to 1,830 m in California, most of the Southwest, much of the Great Basin, and all of the Plains states (Laundré 2018). The Eastern Cottontail is largely confined in the west to the Plains States and southwest mountain ranges (Nielson and Berkman 2018). Mountain Cottontails inhabit higher elevation areas within the Rocky Mountain and Great Basin regions up to about 3,340 m (Frey and Malaney 2006; Beever and French 2018a). The Brush Rabbit (*S. bachmani*) is confined to densely vegetated communities along the Pacific Coast (Kelly 2018) and the Pygmy Rabbit (*Brachylagus idahoensis*) to inland communities of big sagebrush (*Artemisia tridentata*; Rachlow et al. 2018). Both of these diminutive species have suffered massive alterations of their habitats with the result that some populations and/or subspecies (e.g., *S. bachmani riparius*) are considered threatened or endangered (Williams 1986).

The most widespread and abundant jackrabbit of the western U.S. is the Black-tailed Jackrabbit (*L. californicus*), which ranges northward from central Mexico to eastern Washington and eastward from coastal California to east Texas (Beever et al. 2018b). The White-tailed Jackrabbit (*L. townsendii*) is less well distributed, occurring from Canada southward to northern New Mexico and eastward from northeastern California to Iowa (Beever et al. 2018c). Locally common at higher elevations, but subject to large fluctuations in numbers, is the Snowshoe Hare (*L. americanus*; Krebs and Murray 2018). Restricted in distribution in the southwestern U.S. are the White-sided Jackrabbits (*L. callotis*) and

Figure 1. Results of a jackrabbit drive in southern Arizona in the 1940s; the animals were donated to the Salvation Army. (From Arizona Historical Society, photograph AHS # B29259; used with permission).

Antelope Jackrabbits (*L. alleni*), which are limited in the U.S. to New Mexico and Arizona, respectively (Brown et al. 2014, 2018a,b).

Leporid irruptions and rabbit drives.—Pioneer settlers of the West regarded rabbits either as a staple or an emergency food, depending on convenience and economic circumstances. Following the widespread availability of beef and the onset of commercial agriculture, rabbits were considered subsistence food for hired hands and poor immigrants (Palmer 1897). Coursing, the pursuit of jackrabbits on horseback using greyhounds, was only locally popular, and a limited sport that all but disappeared after 1900 with the advent of land fencing and settlement (Palmer 1897). As cattle ranchers and farmers settled rangelands, jackrabbit numbers increased with the animals eating irrigated crops and competing with livestock for forage (Palmer 1897; Brown 2012). By the 20th Century, leporids came to be regarded more as agricultural pests than game (Brown 2012).

Increased jackrabbit numbers resulted in an increase in complaints, prompting state and territorial legislatures to establish bounties. Beginning in 1878 in Idaho, bounty payments for rabbits spread by 1912 to Arizona, California, Nevada, Utah, Oregon, Washington, Kansas, and Texas (Palmer 1897; Brown and Carmony 2009). Depleted county treasuries and ineffectiveness in reducing jackrabbit numbers, however, resulted in bounties being discontinued after about 1915.

The impact jackrabbit and cottontail irruptions had on irrigated crops, orchards, and rangelands in the late 1800s resulted in a number of control measures being initiated including organized drives (Palmer 1897; Brown 2012). Because poisoning with strychnine and bounties proved to be ineffective, men on foot or horseback drove rabbits (primarily Black-tailed Jackrabbits, but also White-tailed Jackrabbits and cottontails) into corrals, nets, or wire mesh fences where they were shot or clubbed (Fig. 1). Irruptions and drives increased from about 1888 through the early 1900s until reaching a peak in the Great Basin and Plains states during the 1930s (Mohr and Mohr 1936; Carter 1939). The number of rabbits reported killed was not confined to farming areas. At a non-agricultural area near Canyon Diablo, east of Flagstaff, Arizona, 38,331 jackrabbits and cottontails were killed and shipped to markets in Los Angeles, California, in 1909 (Brown and Carmony 2009). In 1917, Dan Woods (unpubl. report) reported a drive in irrigated fields adjacent to desert vegetation in Casa Grande, Arizona, said to be occupied by "hundreds of thousands" of cottontails and jackrabbits.

Leporid populations, particularly jackrabbits, continued to pulse, giving rise to the belief that irruptions came in cycles (Howell 1923; Woodbury 1955; Wing 1960; Smith et al. 1981; Matchett and O'Gara 1987). Although organized drives continued into the 1950s, this method of depredation control gradually waned as had the payment of bounties. The control method favored most by the agency in charge of animal depredations after 1915, the Branch of Predatory Animal and Rodent Control (PARC) of the U.S. Biological Survey, was the use of toxicants (Foster 1932; Fitcher 1953; Brown 2012).

Having successfully lobbied for the elimination of bounties, PARC discouraged drives as only providing temporary relief and being dangerous to the participants

Figure 2. Jackrabbits (*Lepus* sp.) in a hayfield in southern Idaho during the winter of 1980–1981. (Photographed by Rich Howard).

(Evans et al. 1970). Through the 1920s and into the 1930s, PARC experimented with developing and using poison mixtures. An estimated 3,600,000 rodents and leporids were eradicated in Arizona alone in fiscal year 1929–1930, with the claim that jackrabbits had been successfully removed from 676,240 ac (Gilchrist 1930; Foster 1932). The situation was similar in other western states, including California, where Linsdale (1932) documented 285 incidences of PARC cooperators using strychnine, thallium, cyanide, and arsenic to kill prodigious numbers of Coyotes and Golden Eagles as well as ground squirrels, jackrabbits, and cottontails.

Concern over the number of animals being killed by PARC was a major reason for the first biological investigations into leporid numbers. Cooperative investigations by personnel of the U.S. Biological Survey and state universities concluded that the numbers of both Black-tailed and White-tailed Jackrabbits were excessive and in need of control (Vorhies and Taylor 1933; Donoho 1971). Other researchers, however, observed that leporids did relatively little rangeland damage except in drought years (Anderson and Shumer 1986), and that rabbits had little impact on the condition and health of browse plants (Westoby and Wagner 1973; Rice and Westoby 1978). It was now realized that many of the earlier depredation claims may have been overstated and that deer (*Odocoileus* spp.) and other wildlife species could be greater pests than rabbits and hares (Conover and Decker 1991).

The U.S. Fish and Wildlife Service (USFWS), successor to the U.S. Biological Survey, continued to discourage rabbit drives, and recommended better range management along with shooting and poisoning to prevent damage to pastures and newly planted fields (Evans et al. 1970). By the 1980s reports of irruptions had declined, depredation complaints had subsided, and the use of poisons as a control measure was on the wane (McAdoo et al. 2004). The days of prodigious rabbit numbers were drawing to a close; one of the last major irruptions documented by USFWS occurred in southern Idaho during the winter of 1981–1982 (Rich Howard, pers. comm.; Fig. 2).

Cause of irruptions.—After 125 y of depredation complaints, the questions remain: what caused these high numbers of rabbits, and why did they cease? These periodicities, once perceived as cycles (see Huey 1942), were thought to be of natural occurrence. It was believed that Black-tailed Jackrabbit and cottontail numbers systematically rose and fell on a predictable basis, not unlike Snowshoe Hare cycles (Howell 1923; Meslow and Keith 1968; Matchett and O'Gara 1987; Ganskopp et al. 1993), and, although some investigators continue to believe that cottontail and jackrabbit populations rise and fall in synchrony with weather events (Simes et al. 2015), such an explanation does not resolve why there have been no major irruptions reported for more than 30 y. Comprehensive studies by Lightfoot et al. (2010) and Hernandez et al. (2011) failed to show a cause and effect relationship between seasonal precipitation and leporid numbers, and neither drought nor other climatic phenomena have yet been shown to consistently influence jackrabbit density. Although the observed population changes are real, close examination of their timing showed that the cyclic concept provides an inadequate explanation for population changes (Wooster 1935; Bronson and Tiemeier 1958).

An explanation for rabbit irruptions, first offered by naturalist George Bird Grinnell more than 100 y ago, was that they had their basis in predator control: a cause and effect relationship denied by Animal Damage Control personnel (Evans et al. 1970). Although a study using test and control areas never demonstrated a significant relationship between predator control and irruptions, efforts to poison, bounty, trap, or otherwise reduce Coyote, Bobcat, fox, and/or Golden Eagle numbers invariably preceded major irruptions. When large-scale predator control programs were curtailed after President Richard Nixon banned the predacide Compound 1080 in 1972, reports of rabbit irruptions declined precipitously along with the need for rabbit control measures (Dave Bergman, pers. comm.).

It thus appears reasonable to assume that suppressed numbers of predators played an important role in allowing leporid numbers to increase above those found under natural conditions. Bounties, poison baits, cyanide Getters, and steel traps are now less often used to reduce predator populations than formerly, and then often only locally employed. If disease and other mortality factors can suppress a rabbit population, it is reasonable to assume that a decline in predator numbers can also increase rabbit numbers.

Decline of less widespread leporids.—Even though the three primary species of cottontails found in the western U.S. and Black-tailed Jackrabbits remain common animals, not all North American leporids have fared as well. Distributions of the Pygmy and Brush Rabbits, along with certain populations of the White-tailed, White-sided, and Tehuantepec (*L. flavigularis*) Jackrabbits have declined over the last 50 y, primarily due to habitat changes (Kline 1963, Traphagen 2011, Smith et al. 2018). The Pygmy Rabbit has suffered population declines due to Sagebrush (*Artemisia tridentata*) removal, and several historic populations have disappeared (Wilson and Ruff 1999). This species became extirpated and is now being re-introduced in Washington state (Becker and DeMay 2016) and is considered a Species of Special Concern in Nevada.

In California, the Riparian Brush Rabbit (*S. b. bachmani*) is listed as endangered (Williams et al. 2008), and in Mexico another subspecies, the Lower California Brush Rabbit (*S. b. exiguus*), has been recommended for threatened status and another, the Cape Santa Lucas Brush Rabbit (*S. b. peninsularis*), is thought to be extinct (Lorenzo et al. 2013). The Tehuantepec Jackrabbit is considered endangered in its limited range in Oaxaca, Mexico, due to brush encroachment and other factors (Lorenzo et al. 2008). Also, primarily in Mexico, but extending into extreme southwest New Mexico, the White-sided Jackrabbit is giving way to Black-tailed Jackrabbits due to shrub invasion of its grassland habitats (Desmond 2004; Myles Traphagen, unpubl. report 2011). Another member of the white-sided group, the Antelope Jackrabbit, while formerly feared to be in trouble due to hunting pressure (Woolsey 1956), is now relatively secure and outnumbers its black-tailed cousin where these two species are sympatric (Brown et al. 2014).

The most extensive decline that has been documented is the reduction of White-tailed Jackrabbit numbers and distribution during the last 150 y (Couch 1927; Carter 1939; Brown 1940). This cold-tolerant jackrabbit is now rare or extinct in portions of its former range in Colorado (Burnett 1926; Dalquest 1948; Donoho 1971), Kansas (Carter 1939; Brown 1940; 1947), South Dakota (Gilcrese et al. 2016), Missouri (Watkins and Nowak 1973), and Washington (Clanton and Johnson 1954; Washington Department of Fish and Wildlife 2008; Ferguson and Atamian 2012). It is a Species of Concern in California (Williams 1986) and was reported to be absent from former habitats in the Yellowstone ecosystem (Berger et al. 2005; Berger 2008), a status shown to be overly pessimistic by Gunther et al. (2009). The cause of this reduction is generally thought to center on the conversion of native prairie to shrub-steppe or agriculture and/or the arrival of expanding Black-tailed Jackrabbit populations better suited to human disturbance (Dice 1926; Brown 1940; Ferguson and Atamian 2012). Whether these declines and replacement by Black-tailed Jackrabbits were due entirely to habitat changes or reflect a continuation of climatic shifts that have occurred throughout Holocene times is difficult to state (Grayson 1977; White 1991; Schmitt et al. 2002; Fisher 2012). Because of the importance of lagomorphs as prey to large predators and to the functioning of ecosystems in the western U.S., we attempted to determine population trends and status of the more common species of *Sylvilagus* and *Lepus* west of the Missouri River. Although documenting the long-term status and population trends of these animals is difficult because no national data base exists for small mammals similar to the North American Breeding Bird Survey (Sauer and Link 2011), we used state data bases on lagomorph numbers to estimate trends in populations.

Methods

To determine population trends of these common leporids we sought out scientific literature, agency reports, and wildlife survey and hunter-based information collected by state wildlife departments. Agencies contacted included those in Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington and Wyoming. To locate peer-reviewed studies containing survey and trend information for *L. americanus*, *L. californicus*, *L. townsendii*, *S. audubonii*, *S. floridanus*, and *S. nuttallii*, we searched the data base of lagomorph literature of the International Union for Conservation of Nature (IUCN) and the species accounts in Best (1996), Best and Henry (1993a,b), Cervantes (1993), Chapman (1975), Chapman et al. (1980), Chapman and Flux (1990), Chapman and Willner (1975), Dunn et al. (1982), Flinders and Chapman (2003), Lim (1987), and Wilson and Ruff (1999). We also researched regional study summaries of mammals such as Wills and Ostler (2001), and Google Scholar and other internet search engines. Especially helpful was a compendium of articles and publications prepared by

Table 1. Survey data summaries and durations for 14 western states (excluding Oregon, New Mexico and Texas). Abbreviations are RC = roadside counts, MCR = mail carrier routes, HCS = hunter check stations, HQ = hunter questionnaires, and RTC = roadside track counts.

	Cottontails (all species)				Jackrabbits (all species)			Snowshoe Hares		All Leporids
State	RC	MCR	HCS	HQ	RC	MCR	HQ	RTC	HQ	HQ
Arizona	1966–2013		1951–2010	1961–2015						
California				1948–2014			1962–2014			
Colorado				1955–2012	1963–2013		1984–2004			1961–1967
Idaho				2008–2011					2003–2011	
Kansas				1958–2016			2006–2016			
Montana	1996–2014							1991–2012		
Nebraska		1959–2013		1960–2012		1963–2013	2002–2012			
Nevada										1960–2015
North Dakota		1999–2013		1963–2012						
Oklahoma				1986–2016			1986–2016			
South Dakota				1980–2015						
Utah	1967–2015			1967–2015					1976–2016	
Washington				1988–2016			1988–2000		1989–2016	1984–2016
Wyoming				1982–2012					1982–2012	

Simes et al. (2015) on jackrabbits in the western states and their use by Golden Eagles and other predators.

We compiled, read, and evaluated more than 225 peer-reviewed articles on leporid status, abundance, population trends, survey methodologies, and responses to environmental stimuli. We abstracted and categorized articles on both prospective and introspective studies as cottontail and jackrabbit responses to landscape alterations brought about by land use changes (e.g., grazing, fire, road construction, and woody plant encroachment), the effects of weather on recruitment and mortality, and the impacts of disease, predation, and depredation control on populations. Although only a few studies (e.g., Applegate 1997; Applegate and Williams 1998; Fedy and Doherety 2011; Fritzell 2016) were of sufficient duration over large enough areas to document population trends *per se*, these studies provided insights into developing hypotheses to explain observed population changes.

State wildlife agency surveys.—We requested each wildlife agency in western states to provide any information pertaining to *Sylvilagus* and/or *Lepus* status and/or population trends obtained through federal-aid studies, namely observation surveys, track counts, hunter harvests and hunt success. These wildlife agencies are responsible for leporid management. Our intent in assimilating these data was to compare gross trends over time within and among states to generate a broad picture of the status of leporid populations across the western U.S. All of the states responded with at least some data with the exceptions of Texas and New Mexico, where neither species of *Sylvilagus* nor *Lepus* are monitored. Twelve states provided useful cottontail and/or jackrabbit survey and/or harvest information for periods of time of 9–67 y (Table 1).

All cottontail species including brush rabbits in a state were lumped together rather than being reported separately. Survey methodologies for cottontail rabbits included spring counts of live animals recorded on roadside surveys by wildlife agency personnel in Arizona, Montana, and Utah. Rural mail carriers recorded spring or summer cottontail observations on select routes in Kansas, Nebraska, and North Dakota, where indices of wildlife observations were recorded over set numbers of days. These surveys, and similar counts of jackrabbits in Nebraska, permitted evaluations of the status and trends of both regional and statewide populations (Applegate and Williams 1998; Pitman 2013). Expressed as the number of animals seen per set number of miles, and subject to prescribed confidence intervals, these surveys are designed to provide reliable statewide indices to changes in leporid abundance.

Additional survey data included sight counts of cottontails by age class in Utah since 1967, and cottontail observations/mile (1.61 km) recorded on spring quail and dove call-count routes in Arizona since the 1960s (Smith and Gallizioli 1965; Brown et al. 1978). Spotlight surveys on select routes in six general locations were used to document cottontail population trends in Montana after 1996, and track counts were used to inventory snowshoe hares in this state since the winter of 1991–92 (Lauri Hanauska-Brown, pers. comm.). Randomized post-season mail and/or telephone hunt questionnaires have been used to index the number of cottontail hunters, cottontails harvested, and cottontail hunt success in Arizona, California, Colorado, Idaho, Kansas, Nebraska, North Dakota, Oklahoma, South Dakota, Utah, Washington, and Wyoming for periods of time ranging from nine (Idaho) to > 60 y (California). These surveys are extrapolations of a random sample of hunting license purchasers and were designed to provide statistically valid harvest and hunt success estimates (see Arizona Game and Fish Department 2014). These same questionnaires are also used to monitor jackrabbit and/or Snowshoe Hare hunters, harvests, and hunt success in California, Colorado, Idaho, Kansas, Nebraska, Nevada, Oklahoma, Utah, Washington, and Wyoming (Armstrong 1972).

Hunter check stations and/or hunter information boxes have been used to sample Desert Cottontail hunt success in Arizona since 1951 (Brown et al. 1978). More representative information from Arizona and the other states comes from post-season hunt questionnaires (Table 1). Post-hunt questionnaires were also used to index the population status of other leporids including both species of jackrabbits in Nevada. When available, we used the number of animals bagged per hunter day vs. the number/season as the more accurate indicator of population trends (Fedy and Doherety 2011).

We obtained survey and/or hunt success trend information on Snowshoe Hares from Idaho, Montana, Utah, Washington, and Wyoming. The limited survey trend information available from White-sided Jackrabbit studies in New Mexico was evaluated by Traphagan (2011). Hunter success or catch per unit effort (CUE), as measured by the number of animals taken over a set period of time, has long been used to index wildlife population trends (see Smith and Gallizioli 1965; Fritzell 2016). The numbers of animals taken or claimed per unit of hunting effort is widely accepted as a measurement of the density of an animal (Brown 1979; Fedy and Doherety 2011).

Although the Montana Fish, Wildlife and Parks Department does not collect harvest information on leporids, the agency initiated research projects in 1991 and 1996 that included cottontail spotlight surveys and Snowshoe Hare track counts. Standardized surveys of cottontails (the sum of cottontails spotted on five routes) provide an index of abundance.

Summaries of state wildlife agency hunt information.—We tabulated annual observations, harvest, and hunt success indices of each state using the number of animals seen or harvested/hunter. Because harvest levels can vary over time with the availability of other game, and hunter attitudes present unknown variables, we only used hunt success per unit effort to index possible population change. We say possible population changes because survey methodologies were not always consistent throughout the survey period and most data trends were marked by a high level of fluctuation among years in a record. Additionally, survey and hunt information, methodologies varied among states, and the duration of survey collections varied. Nonetheless, we statistically analyzed trend data of hunter success for each state. For those states providing survey and hunt success indices, we calculated Pearson's correlation coefficients ($\alpha = 0.05$) to measure the correlation of hunter success and survey results over time.

Results

Only 30 of the 225 papers reviewed compared leporid numbers over $\geq$ 20-y period of time and were useful in documenting changes in the status or distribution of a species. None of these articles, which addressed irruptions, crop depredations, the effects of weather, habitat changes, and the impact of road-kills, expressed concern over the status of any of the western cottontails or Black-tailed Jackrabbits. The only documentation of significant reductions in the status and distribution involved White-tailed Jackrabbits and Pygmy Rabbits (see Applegate et al. 2003). The contents of these articles reported that, although cottontail and jackrabbit numbers fluctuate, and the current numbers of these animals may be less than long-term means, the status of cottontails and Black-tailed Jackrabbits was believed to be secure and thus warranted an IUCN Red List conservation classification of Least Concern (LC). The only exception was in Washington state where a concern for the status of an animal has resulted in a closed season on both jackrabbit species since 2001.

By way of contrast, the White-tailed Jackrabbit is classified as Possibly Extirpated in Kansas, southern Nebraska, and Canada; Imperiled in New Mexico; Vulnerable in California; Apparently Secure in Colorado, Montana, Nebraska, Oregon, South Dakota, and Wyoming; and Secure only in Idaho and Nevada. The White-tailed Jackrabbit is a priority species in Washington where it is a Species of Greatest Conservation Need (Ferguson and Atamian 2012). There is reason to believe, however, that Black-tailed Jackrabbit and cottontail numbers after 2000 are at less than historic norms. Prior to this time densities as high as 208 Black-tailed Jackrabbits/ha were reported (Beever et al. 2018b). The last article dealing with such irruptions was published in the 1980s, and we are only aware of one publication dealing with depredations resulting from rabbit irruptions after 2000 (David Brown and Randall Babb, unpubl. report).

California.—Based on hunt success questionnaire data, the annual harvest of cottontails, including Brush Rabbits, has fluctuated between 300,000 and 1,200,000 animals from the late 1940s through the early 1980s, before falling to below 100,000 rabbits per annum by 1996 with a continuing decline in the 2000s (Fig. 3a). The reported number of hunters dropped from 286,488 in 1964 to just 8,361 in 2010, a 97% decline commensurate with a similar drop in the reported cottontail harvest. This reduction in harvest occurred despite a nearly 40% increase in the number of days spent hunting rabbits and parallels a significant long-term decline in cottontails claimed per hunter-day (Fig. 3b; Table 2).

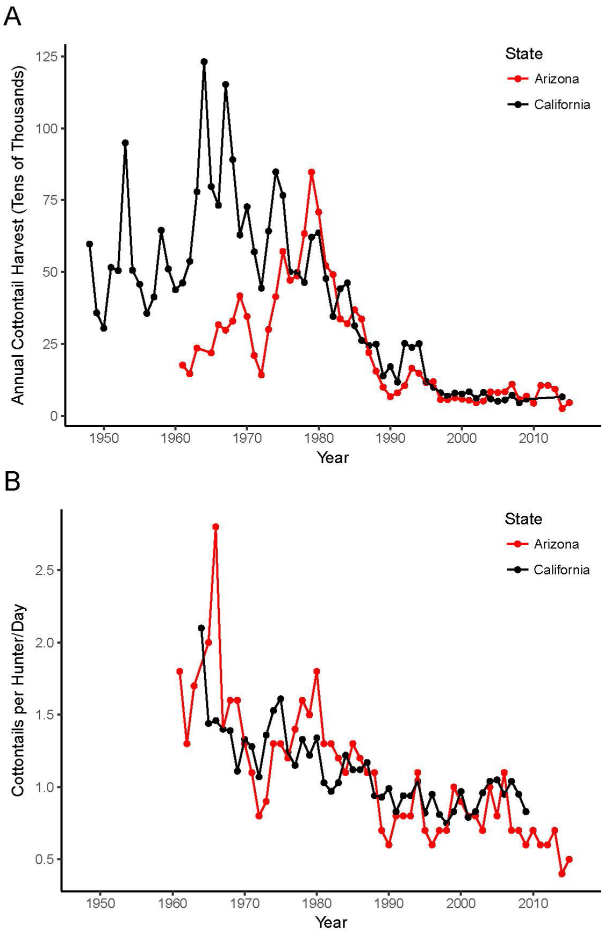

Figure 3. Annual cottontail hunt information from California and Arizona. (A) Cottontail harvest trends for California and Arizona. (B) Cottontail hunter success trends (cottontails per hunter/day) for Arizona (r = -0.78; t = 25.20, df = 52, $P < 0.001$) and California (r = -0.77; t = 21.97, df = 44, $P < 0.001$).

The reported harvest of jackrabbits in California (mostly Black-tailed Jackrabbits) shows a decline even more pronounced than with cottontails. As hunter numbers declined from 263,274 in 1964 to 87,919 in 2010 (-67%), the annual harvest of jackrabbits dropped from a high of more than 3,000,000 in 1964 to < 100,000 per year after 1997 (Fig. 4a). Similarly, the number of jackrabbits claimed per hunter-day declined significantly and relatively consistently from the 1960s to the 2000s (Fig. 4b; Table 2), although, as was the case with cottontails, hunter effort in the pursuit of jackrabbits rose during this period by nearly 40%.

Arizona.—Long-term cottontail rabbit harvest and hunter success information in Arizona show that hunter numbers dropped 58% from 28,051 in 1961 to 11,879 in 2015. Hunters harvested an increasing number of cottontails from 1961 to 1979, followed by a precipitous decline in cottontails claimed in 1990 with very low numbers of cottontails harvested from 1990 to the present (Fig. 3a). Similarly, dating back to 1961, there has been a fluctuating but significant decline in hunt success, with peaks of 2.8 cottontails/hunter day 1966, 1.8 in 1980, and 1.3 in 1985, followed by consistently lower success from 1989 to the present (Fig. 3b; Table 2).

Table 2. Summary of analyses of leporid hunt success trends and survey data for western states. Significant declines based on Pearson's Product-Moment Correlations denoted by asterisks and were $^*P < 0.050$, $^{**}P < 0.010$, and $^{***}P < 0.001$.

Species	Significant decline	No trend
Hunt Success		
Sylvilagus spp.	Arizona***	Colorado
	California***	South Dakota
	Idaho***	Washington
	Kansas***	
	Nebraska***	
	North Dakota**	
	Oklahoma***	
	Utah***	
	Wyoming*	
Lepus spp.	California***	Oklahoma
	Kansas***	
	Nebraska*	
Lepus americanus	Utah*	Washington
	Wyoming***	
Leporids	Nevada	
Survey Information		
Sylvilagus	Nebraska***	North Dakota
		Utah
Lepus	Nebraska***	

Nevada.—The annual number of hunters and harvests of all leporid species in Nevada has fluctuated greatly. Number of hunters ranged from 8,167 in 1961 to 2,230 hunters in 2005. Number of harvested cottontails ranged from 27,000–64,000 between 1961 and 1976, after which a peak of 136,500 animals were harvested in 1979, followed by a precipitous decline leading to low harvest numbers to the present (Fig. 5a). The recent peak harvest of 39,000 leporids in 2006 followed a wet winter that resulted in high hunter numbers due to increased populations of Chukar Partridges (*Alectris greca*) and other small game species (Shawn Espinoza, pers. comm.). Although the number of hunters, harvests, and days spent hunting all show a downward trajectory in Nevada, hunter success, the best measurement of leporid abundance, has shown a slight downward trend (Fig. 5b; Table 2).

Utah.—Hunt questionnaire results show a long-term downward trend in annual cottontail harvests from 1967 through 2015 (Fig. 6a). Cottontail hunter numbers similarly declined during this period from 23,249 in 1967–1968 to 12,575 in 2005–2006. More significantly, cottontails taken per hunter day show a general pattern

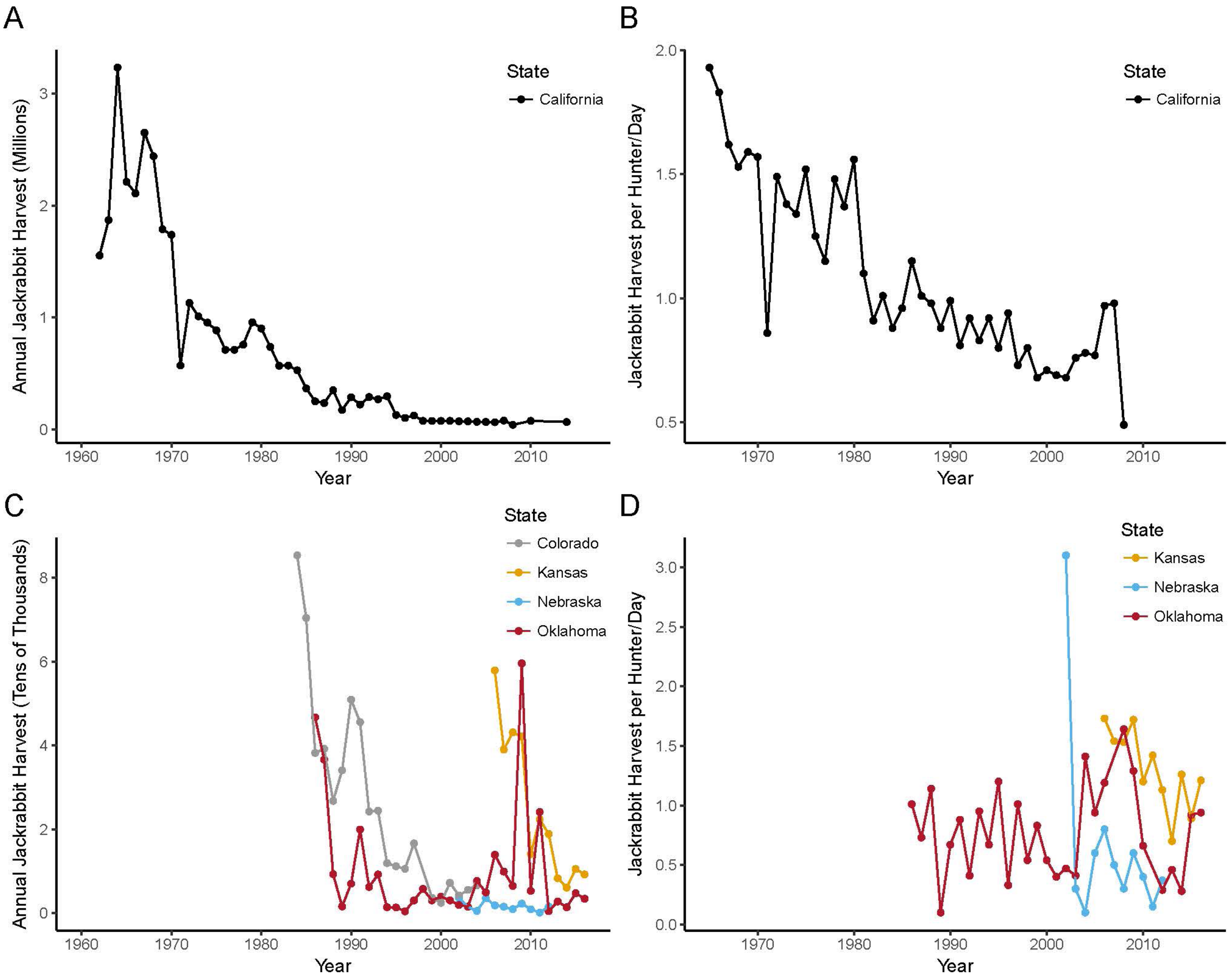

Figure 4. Annual jackrabbit hunt information from California, Colorado, Nebraska, Kansas, and Oklahoma. (A) Jackrabbit harvest trends for California; (B) Jackrabbit hunter success trends (jackrabbits per hunter/day) for California (r = -0.86; t = 38.67; df = 42; $P < 0.001$); (C) Jackrabbit harvest trends for Colorado, Nebraska, Kansas, and Oklahoma; (D) Jackrabbit hunter success trends (jackrabbits per hunter) for Nebraska (r = -0.50; t = 2.99; df = 9; P = 0.015), Kansas (r = -0.75; t = 9.05; df = 9; $P < 0.001$), and Oklahoma (r = 0.05; t = 0.25; df = 27; P = 0.808).

of decline with modest fluctuations over the same period (Fig. 6b; Table 2). Annual surveys from 1967 to 2015 of cottontails observed per mile (1.61 km) of travel also show modest fluctuations but with no overall upward or downward trend (Fig. 7; Table 2). For Snowshoe Hares, the annual harvest declined from a high of nearly 35,000 in 1979 to < 5,000 after 1997 (Fig. 8a). Even though Snowshoe Hare hunter numbers and days afield declined > 80% during this time, only a modest decline in hunter success was detected (Fig. 8b; Table 2).

Colorado.—Hunt questionnaire data collected by the Colorado Department of Parks and Wildlife are especially informative in that they include cottontail harvest information dating back to 1955 (Fig. 6c). These data show a fluctuating but steady decline in annual cottontail harvests of > 70% from 1955 to 2012. Hunter success, however, showed no obvious trend during this period (Fig. 6d; Table 2) as there was a parallel decline in the number of hunters. More impressive is the large decline in the annual jackrabbit harvest (*L. californicus*, *L. townsendii*), dropping from 11,385 hunters claiming 61,256 jackrabbits in 1976 to only 2,049 hunters claiming 6,621 jackrabbits in 2004, declines of 82% and 89%, respectively (Fig. 4c). Unlike with cottontails, jackrabbit hunter success declined considerably, ranging from a high of 7.2 jackrabbits per hunter in 1985 to fewer than four from 1999 to 2004. This trend is mirrored by the number of jackrabbits seen per survey mile (1.61 km) from 1963 to 2013, declining from a peak of 7.16 in 1968 to 0.49 in 2013.

Oregon.—The only survey and hunt information collected by the Oregon Department of Fish and Wildlife are harvest data collected on an introduced population of Eastern Cottontails on the E. E. Wilson Wildlife Area in the northwestern portion of the state. Thirty years of harvest and hunt success trends indicate a robust cottontail population in this area with no discernable trends up or down.

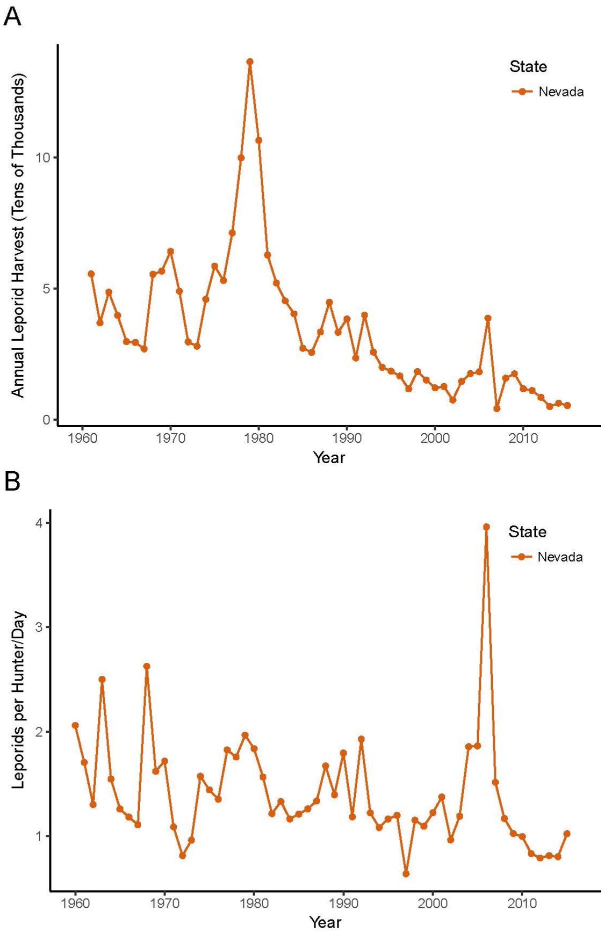

Figure 5. Annual leporid hunt information from Nevada. (A) Leporid harvest trend; (B) Leporid hunter success trend (leporids per hunter/day) (r = -0.26; t = 2.57; df = 54; P < 0.050).

Washington.—The number of cottontail hunters in 1988 was 18,966 vs 2,489 in 2012, and the number of cottontails claimed in 1988 (5,803 animals) versus 2012 (only 950) reflect declines of 68% and 84%, respectfully. A high of 31,335 cottontails were harvested in 1989, with the lowest total of animals harvested (4,296) occurring in 2016 (Fig. 6a). Hunter success remained relatively constant over this period (Fig. 6b; Table 2).

The total number of jackrabbits harvested declined substantially between the 1988 and 2000 (peaking at 6,680 in 1992 and falling to 383 in 1999) that the jackrabbit hunting season was closed in 2000, presumably to protect a declining population of White-tailed Jackrabbits. The number of Snowshoe Hare hunters dropped from 1,959 in 1988 to 622 in 2012, a 68% decline. Snowshoe Hare harvests dropped even more, from 5,803 in 1988 to 950 in 2012 (down 84%; Fig. 8a). As was the case with cottontails, however, hunter success remained relatively constant (Fig. 8b; Table 2).

Idaho.—During the nine recent years from 2003 to 2011, cottontail hunters declined 48% from 4,013 to 2,100, while the reported harvest went from 26,157 to 5,500, a reduction of 79%. With only these years of data, hunt questionnaire data indicated a significant decline in hunt success (Fig. 6d; Table 2). Harvests peaked at 27,500 cottontails in 2004 and fell to 5,500 by 2011 (Fig. 6c). Correspondingly, the number of cottontails taken per hunter fell from 6.47 in 2001 to 2.62 in 2009 (Fig. 6d; see also Knetter 2014).

Snowshoe Hare harvests fluctuated wildly, and no trend was detected during this period (Fig. 8a; see also Knetter 2014). From 2003 to 2011 the number of hunters hunting Snowshoe Hares rose from 619 to 700, while harvests increased from 1,488 to 2,300. The number of Snowshoe Hares taken by hunters varied widely among years (0.7–4.3 hares/hunter) with no apparent pattern.

Montana.—The index of abundance of cottontails varied widely among years, ranging from 215.7 in 2008 to 14 in 2010. The index was nearly equivalent in the first year of the surveys (28.5 in 1996) to the last year (27.8 in 2014). Snowshoe Hare abundance as indicated by an index of track counts was also subject to considerable variation. Highs > 8,000 were recorded in 1998 and 1999, while a low abundance of 478 was recorded in 1992. The index of abundance was nearly equivalent in the first year of the surveys (1,119.6 in 1991) as the last survey reported (1,154.5 in 2011).

Wyoming.—The statewide data indicate an 84% decline in the number of cottontail rabbit hunters from 21,755 in 1982 to 3,561 in 2012; the number of rabbits harvested during this period declined 96%, from 307,173 to 13,025. Harvests peaked at 462,837 in 1983 and fell to a low of 11,802 by 2011 (Fig. 6a). Coupled with a decline in hunter numbers, cottontail hunt success fluctuated annually with descending peaks occurring in 1983, 1991, and 2006 (Fig. 6b; Table 2). Statewide hunt information on Snowshoe Hares in Wyoming also shows a general decline in number of annual hunters from of 1,031 in 1982 to 314 in 2012 (down 70%), while harvests dropped from 3,267 to 193 over the same period (down 96%, Fig. 8a). Hunt success also showed a significant decline marked by wide fluctuations (Fig. 8b; Table 2).

North Dakota.—Cottontail observations by rural mail carriers show a gradual decline in the number of cottontails seen/100 miles (160.9 km) of survey from 1999 through 2011 prior to an irruption in 2012 after which observations receded to a near all-time low in 2013 (Fig. 7). Statewide cottontail hunter estimates fluctuated from 16,323 in 1963 to 3,388 in 2012, with a major decline in harvests taking place in the late 1970s and early 1980s followed by a general downward trend thereafter (Fig. 9a). A general but significant decline in seasonal hunt success after the mid-1960s was followed by a slight rise in the mid-1970s and a lower range of annual fluctuations (Fig. 9b; Table 2).

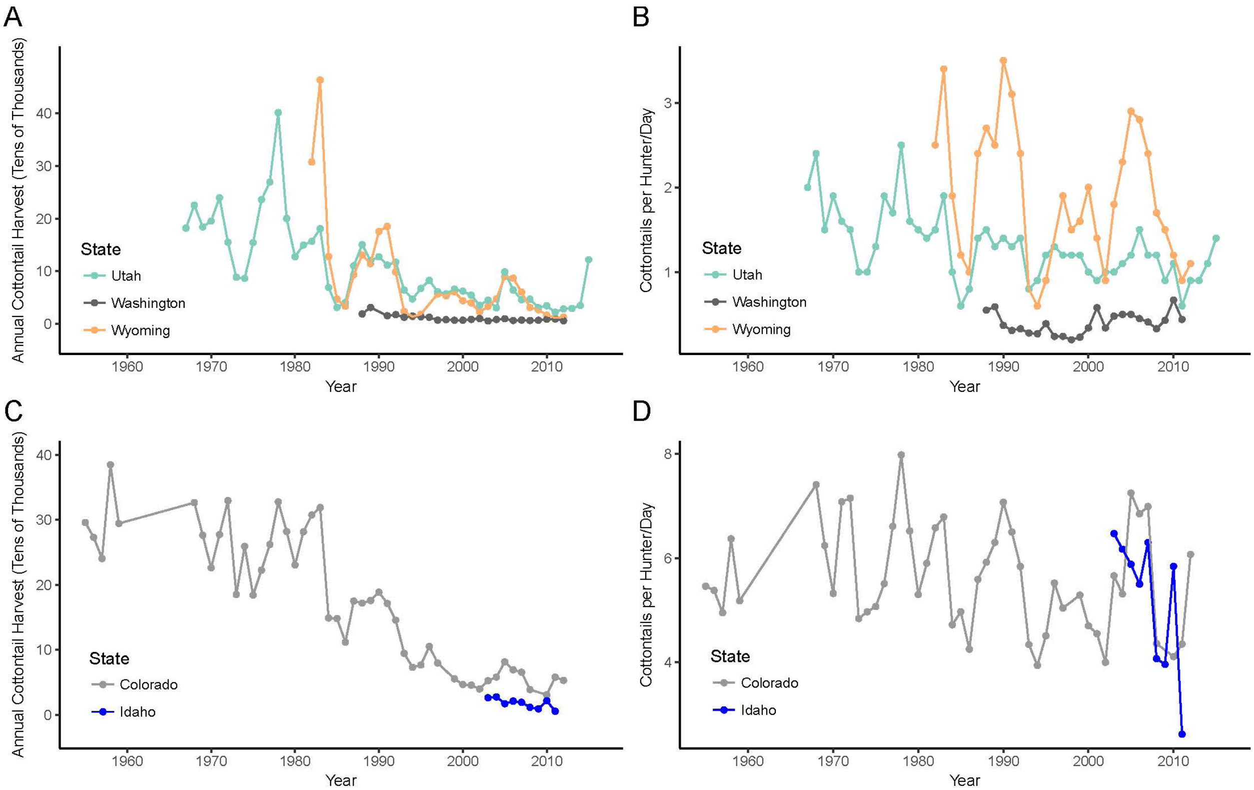

Figure 6. Annual cottontail hunt information from participating Utah, Washington, Wyoming, Colorado, and Utah. (A) Cottontail harvest trends for Wyoming, Washington, and Utah; (B) Cottontail hunter success trends (cottontails per hunter/day) for Wyoming (r = -0.30; t = 2.27; df = 28; P < 0.050), Washington (r = 0.27; t = 1.70; df = 22; P = 0.104), and Utah (r = -0.58; t = 9.50; df = 47; P < 0.001); (C) Cottontail harvest trends for Colorado and Idaho; (D) Cottontail hunter success trends (cottontails per hunter) for Colorado (r = -0.21; t = 1.81; df = 46; P = 0.077), and Idaho (r = -0.74; t = 7.61; df = 7; P < 0.001).

South Dakota.—Hunt questionnaire data show a history of fluctuating annual cottontail hunters and harvests before descending to low levels in 2011-2014 (Fig. 9a). There was no significant long-term decline in the seasonal bag/hunter; however, these data exhibit extreme fluctuations (Fig. 9b; Table 2).

Nebraska.—Mail carrier surveys show long-term declines for cottontail rabbits, with the highest numbers and greatest fluctuations reported prior to 1980 (Fig. 7). Cottontail hunter numbers declined from 46,600 in 1960 to just 7,867 in 2007, a decline of 83%. Annual reported harvests fell from 366,400 to 50,496 during the same period (-86%; Fig. 9c). There was also a significant, albeit fluctuating, downward trend in hunter success, with data from 2010 to 2012 being roughly half that of data from the 1960s (Fig. 9d; Table 2).

Hunt information for jackrabbits was only collected 2002–2012. Over 3,500 jackrabbits were harvested in 2002 by 571 hunters, with a low of 102 animals harvested in 2011 (Fig. 4c). There is no overall trend in the small sample of highly fluctuating data on hunter success for jackrabbits in Nebraska (Fig. 4d). A more robust data set includes the number of jackrabbits observed per mile (1.6 km) from 1963–2013. This census trend indicates a consistent and significant decline in jackrabbits over this period (Fig. 7; Table 2).

Kansas.—Nearly 60 y of hunt questionnaire data indicate long-term declines in cottontail hunters (down 83%), days spent hunting, and cottontails harvested (down 95%). A high of over two million cottontails were harvested in 1958, the first year of the survey, whereas the lowest number of cottontails was harvested in 2016, the last year of available data (Fig. 9c). Hunt success indices, which while fluctuating over time, have trended significantly downward from peaks in the late 1950s, mid-1960s, and early 1980s (Table 2). Seasonal bags have remained at fewer than eight rabbits per hunter/season since the 1980s, and hunters reported near all-time lows in cottontail hunt success in the years between 2010 and 2012 (Fig. 9d). Jackrabbit harvest data have only been collected in Kansas since 2006, but there has been a precipitous decline from that time to the present (Fig. 4c). There has been a more modest, but significant decline in jackrabbit hunter success during this same period (Fig. 4d; Table 2).

Oklahoma.—Hunt statistics from 1986 to 2016 show that the numbers of cottontail hunters and cottontails harvested in that state have been in decline since the mid-1980s (down 77% and 85%, respectfully), reaching a low in 2015 (Fig. 9c). During that same time the number of cottontails harvested per hunter day fluctuated widely while showing a slight but significant decline (Fig. 9d;

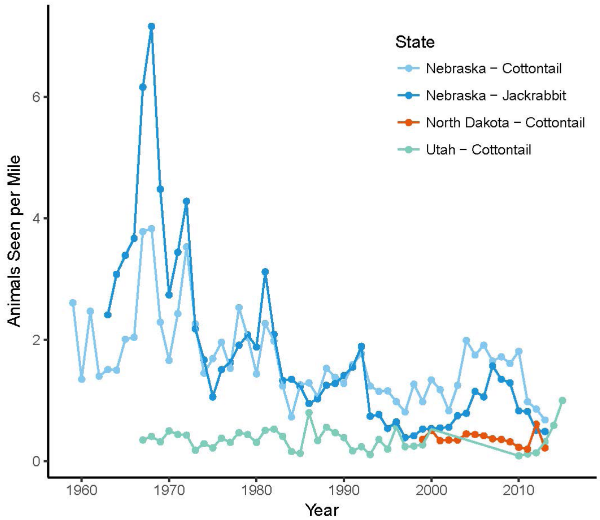

Figure 7. Annual leporid survey information (animals seen per mile); cottontails from Utah (r = 0.01; t = 0.03; df = 38; P = 0.976), Nebraska (r = -0.52; t = 7.81; df = 53; P < 0.001), and North Dakota (r = -0.28; t = 1.39; df = 13; P = 0.188), and jackrabbits from Nebraska (r = -0.72; t = 17.69; df = 49; P < 0.001).

Table 2). Jackrabbit hunters, harvests, and hunter success in Oklahoma have been highly variable over time and show no clear overall trends due to the small sample size of hunters in some years (Fig. 4c,d; Table 2).

Discussion

There have been significant declines in cottontail hunt success in nine of the 12 states; there were no significant trends in hunt success in Colorado, Washington, and South Dakota. Hunt success on jackrabbits has significantly declined in three of the four states collecting this information, with no significant change in Oklahoma. Survey data show a significant decline for cottontails and jackrabbits in Nebraska, but not for cottontails in Utah or North Dakota. No state reported a statistically valid increase over time in either leporid survey or hunt success data. Other survey results show similar trends.

New Mexico.—Research studies in extreme southwestern New Mexico (Hidalgo County) provide local population trends for White-sided Jackrabbits, Black-tailed Jackrabbits, and cottontail rabbits. Traphagen (unpubl. report) compared recent survey data for these species (1997–2010) with similar animal/mile information collected in 1976 and 1981 (Bednarz and Cook 1984). These data showed a declining population trend for both jackrabbits and cottontails after 1998 despite a rise in Black-tailed Jackrabbit and cottontail observations from 1976 to 1998. Traphagen (unpubl. report) attributed this overall decline in rabbit numbers primarily to an increase in mesquite density and drought but considered other issues such as changes in fire management, increased road kills, and an increase in cattle grazing and exotic grasses as possible contributing factors.

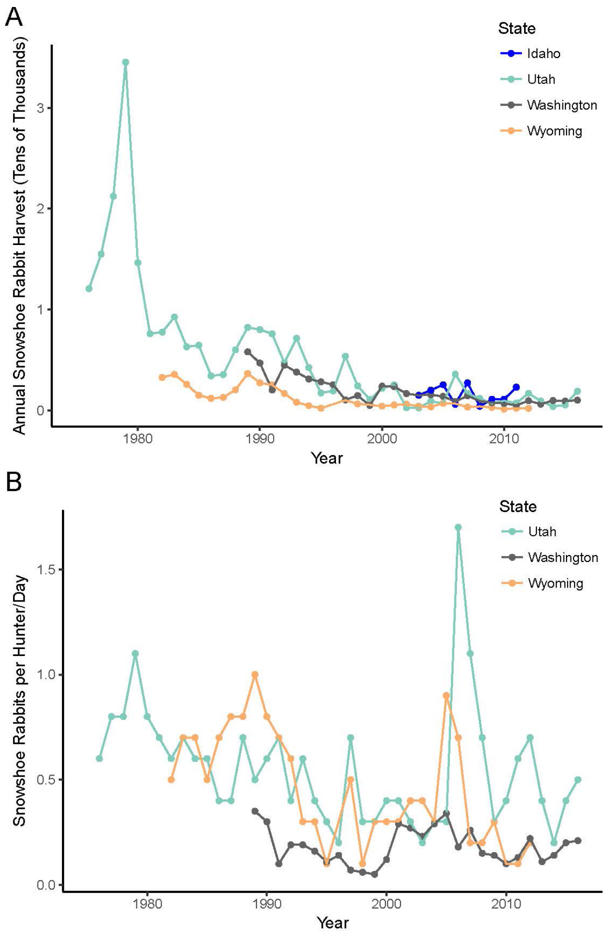

Figure 8. Annual Snowshoe Hare hunt information from Utah, Idaho, Wyoming, and Washington. (A) Snowshoe Hare harvest trends for Utah, Idaho, Wyoming, and Washington; (B) Snowshoe Hare hunter success trends (snowshoe hares per hunter/day) for Utah (r = -0.25; t = 2.04; df = 39; P < 0.050), Wyoming (r = -0.60; t = 7.83; df = 28; P < 0.001), and Washington (r = -0.07; t = 0.36; df = 26; P = 0.720).

Nevada.—Specific investigations into leporid trends in Nevada are limited to six years of surveys on the Yucca Mountain test site between 1990 and 1995 (TRW Environmental Safety Systems, Inc., unpubl. report). Night time spotlight surveys showed an abundance of both cottontails and Black-tailed Jackrabbits in 1992, 1993, and 1994, with low numbers in 1990, 1991 and 1995. Jackrabbit observations ranged from a low of 0.01 animals/km in 1991 to 1.5 animals/km in 1994, with no apparent trend, with the number of jackrabbits seen per km dropping to 0.4 animals/km in 1995. Although of short duration, the study concluded that both cottontail and jackrabbit abundance appeared to correlate with the amount of winter precipitation (TRW Environmental Safety Systems, Inc., unpubl. report).

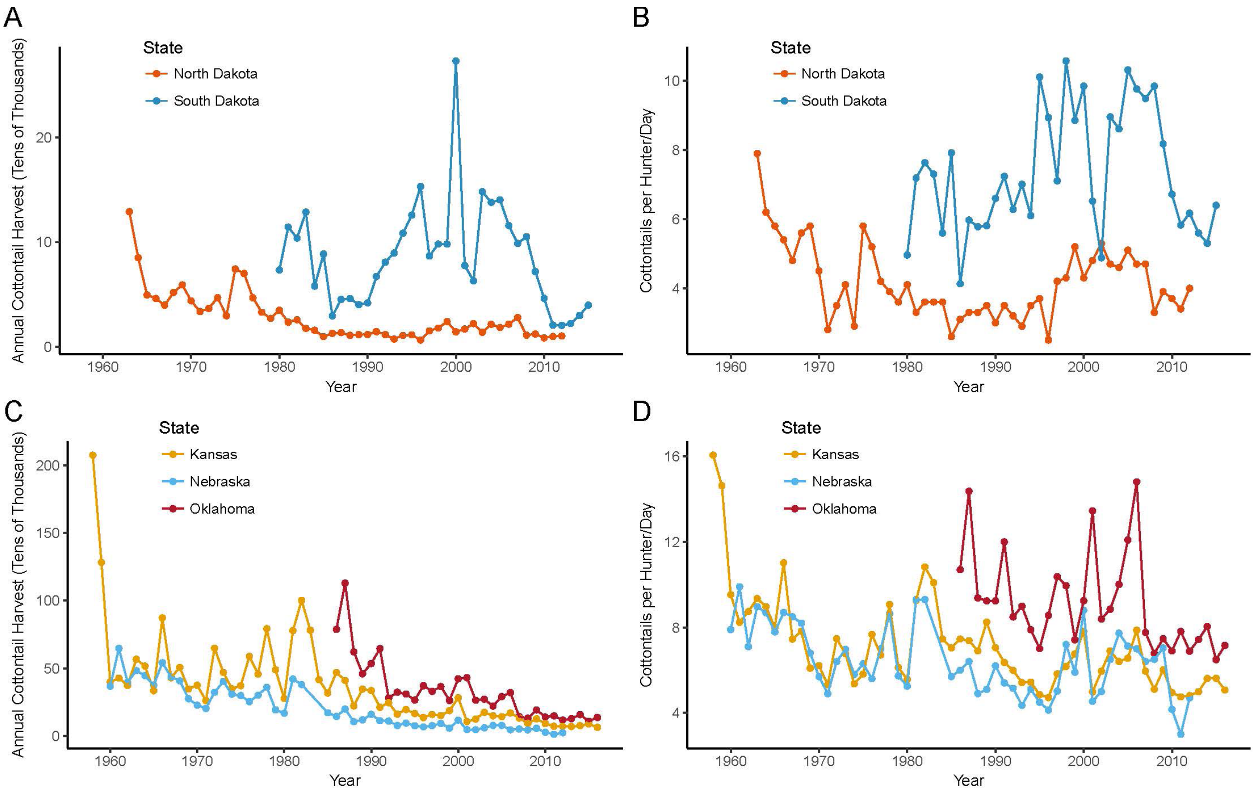

Figure 9. Annual cottontail hunt information from North Dakota, South Dakota, Nebraska, Kansas and Oklahoma. (A) Cottontail harvest trends for North Dakota and South Dakota; (B) Cottontail hunter success trends (cottontails per hunter) for North Dakota (r = -0.31; t = 3.10; df = 48; P < 0.010), and South Dakota(r = 0.21; t = 1.53; df = 34; P = 0.135); (C) Cottontail harvest trends for Nebraska, Kansas, and Oklahoma; (D) Cottontail hunter success trends (cottontails per hunter/day) for Nebraska (r = -0.50; t = 7.00; df = 49; P < 0.001), Kansas (r = -0.62; t = 12.35; df = 57; P < 0.001), and Oklahoma (r = -0.43; t = 4.04; df = 29; P < 0.001).

Utah and southern Idaho.—These states are unique among the western states in that these states hosted several studies that attempted to determine the causes and impacts of large numbers of leporids from the 1950s through the mid-1980s. A discussion of situations leading up to a series of erratic population increases in jackrabbit numbers in the Rush and Tooele valleys of Utah was provided by Christensen and Hutchnson (1965), who concluded that jackrabbit numbers, while fluctuating wildly after settlement and the introduction of livestock, had declined by the time of their study. An abundance of Black-tailed Jackrabbits was also reported to occur in 1958 in the Curlew Valley of north-central Utah prior to a decline in 1959–1960, which lasted to 1968 (Gross et al. 1974). The jackrabbit population then again rose rapidly to peak in 1970, density estimates ranging from 11.7–102 jackrabbits/km² (Gross et al. 1974). Variations in local jackrabbit population numbers led Gross et al. (1974) to question the then prevailing concept that these changes were the result of natural cycles or regional weather patterns. Nor did these authors find that jackrabbit population increases were due to increased natality as they observed no increase in breeding season length, ova produced, or litter size in years of good reproduction versus bad years (Gross et al. 1974). These researchers also concluded that variations in the presence of green feed was not a factor in that reproductive success was relatively constant and breeding season length varied mostly with latitude (Gross et al. 1974). Instead, Gross et al. (1974) attributed 85% of the changes in jackrabbit population size to variations in mortality, with Coyotes being the primary predator.

To determine the causes of population changes along the Utah-Idaho border, Clark (1972) noted that a drop in Black-tailed Jackrabbit numbers preceded a decline in Coyote numbers from 1963 to 1968. When jackrabbit numbers rose in 1969 and 1970, so did those of Coyotes (Clark 1972). Although Clark (1972) found Coyote density to correlate with jackrabbit density the previous year, he attributed most Coyote mortality and population decreases to be the result of predator control, a relationship not unlike the case with San Joaquin Kit Foxes (*Vulpes macrotis mutica*) in the southern San Joaquin Valley (Cypher et al. 1994, 2000).

Eberhardt and Van Voris (1986) evaluated two high and three low jackrabbit populations during a 21-y period (1965-1985) on the Dugway Proving Grounds in northwestern Utah. These authors found jackrabbit population increases to last from 5–10 y, while abrupt declines occurred over two years with reductions of 90%. Although increases in 1969 and 1977 coincided with longer breeding seasons, these investigators concluded that juvenile mortality rates were the principal factor determining jackrabbit population size (Eberhardt and

Van Voris 1986). These researchers also noted that jackrabbit population highs were considerably lower on their study area than on off-site ranches, suggesting that Coyote control might be involved. Nonetheless, they attributed fluctuations in jackrabbit populations to an unknown factor and survey irregularities.

Bartel et al. (2008) counted leporids in the Curlew Valley for 30 y and on the Idaho National Laboratory in central Idaho for 11 y. These researchers disagreed with the findings of Clark (1972) relating Coyote numbers to lagomorph numbers, describing the relationship between Coyotes and jackrabbits as complicated. Instead, these authors detected 10–11-y cycles in Black-tailed Jackrabbit numbers with peak populations in 1971, 1981, and 1991–1993. No overall trend was noted, however, nor were any changes in Pygmy Rabbit or cottontail numbers reported (Bartel et al. 2008).

Information concerning trends in rabbit populations in southern Idaho can also be inferred from raptor population and dietary studies conducted in this part of the Great Basin (Smith and Murphy 1979; Woffinden and Murphy 1989; Grant et al. 1991; Hoffman and Smith 2003). Most of these studies indicate fluctuating but declining jackrabbit numbers. Steenhof et al. (1997) reported Black-tailed Jackrabbit population highs in 1971, 1979, and 1992, but noted that each peak was less than the one before. More recently, Julie Heath and Michael Kochert (unpubl. report) found that Golden Eagle numbers in the Snake River Birds of Prey Area in Idaho declined from 1980 to 2011 attendant with extensive fires, habitat changes, and lower numbers of leporids.

Colorado.—Craig McLaughlin of the Colorado Department of Parks and Wildlife (pers. comm.) does not believe that harvest figures or hunt success for Colorado accurately reflect population trends. Survey effort and protocols have varied over the 50+ y interval, and the switch from mail hunt questionnaires to telephone interviews is thought to have corrected a bias that favored sampling the more successful hunters before 1998. Other variables are involved, and the department is of the opinion that these data are reliable and that any trends should be regarded as suggestive of a need for further investigation rather than to represent actual population trends.

Oregon.—The only concern expressed for leporids in Oregon that we are aware of is a possible reduction in the number of Black-tailed Jackrabbits in marginal range west of the Cascade Range. This concern is based on 20 y of fewer animals seen on road counts in the Willamette Valley by Verts and Carraway (1998).

Washington.—Wide fluctuations in leporid numbers do not appear to occur on the 1,400 km² Hanford Site in Washington where there is no farming, livestock grazing, or predator control (Rickard and Poole 1989). After a 45-y study of the wildlife in the area, Rickard and Poole (1989) described Black-tailed Jackrabbits as abundant with no major fluctuation or evidence of jackrabbit cycles. In 1990, Fitzner and Gray (1991) considered Black-tailed Jackrabbits at Hanford as abundant, Pygmy Rabbits as extirpated, Mountain Cottontails as common, and White-tailed Jackrabbits as uncommon and confined to the highest elevations.

Wyoming.—Fedy and Doherty (2011) reported finding a high correlation (r = 0.77) between Greater Sage-grouse (*Centrocercus urophasianus*) seen on lek counts in Wyoming and cottontail hunt success between 1982 and 2007. No explanation for the similarities in population variation was offered, but the trends for both species were downward, with the peak in cottontail hunt success in 2006 being lower than the one in 1980 (Fedy and Doherty 2011).

Kansas.—An analysis of more than 40 y of small mammal surveys conducted by rural mail carriers for the Kansas Department of Wildlife, Parks and Tourism showed a decline in both cottontail rabbit and Black-tailed Jackrabbit observations since the 1970s (Applegate 1997; Applegate and Williams 1998). Black-tailed Jackrabbits were no longer observed in 24 counties where they were formerly present, and White-tailed Jackrabbit distributions had been so reduced that this species is now regarded as extirpated from the state (Applegate 1997; Applegate and Williams 1998). While noting that the mail carrier survey technique has inherent biases, Applegate et al. (2003) considered the declines in leporids to be real and the result of cleaner farming practices, an increase in the application of herbicides, urbanization, and a greater acreage of forested land.

Mail carrier generated survey indices for Eastern Cottontails and Black-tailed Jackrabbits during the recent 10-y (2003–2013) period have indicated relatively stable or slightly declining numbers (Pitman 2013). A decline in cottontail observations in western Kansas has been attributed to severe drought, while only one Kansas region reported a decline in Black-tailed Jackrabbit observations (Pitman 2013).

It thus appears that hunt success questionnaires and survey indices suggest that populations of cottontails and jackrabbits in most western states have experienced long-term declines, and that leporid numbers in many areas are at or near historic lows. Observation indices for cottontails and jackrabbits in those states that survey these animals (Kansas, Nebraska, Utah, Montana, and North Dakota) are lower or at the same levels as in previous years, hunt information from most western states shows a general decline in the popularity of rabbits as game animals. Of particular interest is that hunt questionnaire indices indicate a declining trend in cottontails and jackrabbit populations in most of the states sampled. Significant declines in cottontail hunt success were reported in California, Arizona, Utah, Idaho, Wyoming, North Dakota, Nebraska, Kansas, and Oklahoma. Current jackrabbit numbers appear to be at historic lows in California, Colorado, Washington, Nebraska, Kansas, and possibly elsewhere. Snowshoe Hare indices, while subject to great fluctuations, show no appreciable trends in Idaho, Montana and Washington, while showing declines in Utah and Wyoming. Several studies support the above indices in assuming a long-term decline in cottontail and jackrabbit numbers in the Great Basin and central Great Plains (e.g., Steenhof et al. 1997; Applegate and Williams 1998). None of the reports we examined suggest an increase in leporid population trends in any of the western states after 1990.

Although both state federal-aid surveys and the literature review suggest some populations of cottontails and Black-tailed Jackrabbits are below historic levels, there is no reason for concern when it comes to the status of these species. With local exceptions, the three species of widely distributed cottontails and the Black-tailed Jackrabbit remain common game animals and retain maximum historic distributions. The habitat restrictions affecting Pygmy Rabbits, White-sided Jackrabbits, and some Brush Rabbit subspecies are well recognized, and Snowshoe Hare populations continue to fluctuate with no universal trend in status. As such, no species appears in need of increased legal protection at this time. Nor is there any evidence that sport hunting is involved in the observed declines. Indeed, with the exceptions of California and possibly Oklahoma, state surveys show declines in hunting pressure: markedly so in most states. This decline in interest, while possibly influenced by lower rabbit and hare populations, can also be attributed to improved economic conditions, an increased availability of more attractive game species, changing demographics, and an aging hunter population.

Determination of the reasons for long-term changes in leporid populations is difficult due to natural population fluctuations caused by such environmental variables as weather, livestock grazing intensity, and predator control programs. Recognized and unrecognized biases in survey sampling frames undoubtedly also lead to changes in reporting rates. As a result, the logical, and most often given explanation for any perceived declines has been attributed to changes in habitat quality (Applegate et al. 2003).

Land use and habitat change as causes for leporid declines.—Exurbanization, highway construction, agricultural expansion and changes in farming practices have reduced the amount of available habitat for western state cottontails and jackrabbits. More subtle are the changes in habitat quality due to changes in grazing intensity, vegetation composition, and fire occurrence. Such changes have likely resulted in both short term and long-term changes in leporid abundance. Several informative studies using repeat photography and the testimony of early settlers have documented western-wide landscape changes from early in the 20th Century through to the present (Phillips 1963; Christensen and Hutchinson 1965; Bahre and Shelton 1993; Gruel 1996; Van Auken 2000; Turner et al. 2003). These studies generally agree that western landscapes now have less grass, more trees and shrubs, more annuals, and more irrigated farmland than were present formerly. It has also been demonstrated that Black-tailed Jackrabbits, and to a lesser extent, cottontails, have benefitted from some of these changes while White-tailed Jackrabbits have suffered (Dalquest 1948; Ferguson and Atamian 2012).

Several studies (Vorhies and Taylor 1933; Taylor et al. 1935) have suggested that the thinning of grasses and their replacement by shrubs increased Black-tailed Jackrabbit numbers. Unfortunately, determining actual leporid population trends in the face of vegetation change has been little studied, particularly before 1950 when the most pronounced landscapes changes were taking place. The effect of vegetation changes on leporid numbers may be species specific and not always the same from place to place. Although it is generally assumed that Black-tailed Jackrabbits and cottontails benefit from an increase in shrubs and woody plants, White-tailed Jackrabbit numbers have been shown to suffer from the removal of native grasses and cereal crops. Nor are the results of habitat changes always as expected. Clearing portions of a dense cover of Velvet Mesquite (*Prosopis velutina*) in Arizona resulted in no change in Black-tail Jackrabbit observations despite an increase in Antelope Jackrabbit sightings (Germano et al. 1983).

Livestock grazing and water developments.—That western landscapes have changed due to the impacts of water developments, livestock grazing, and fire suppression is well accepted (Humphrey 1957; Bahre and Shelton 1993; Van Auken 2000; Turner et al. 2003; Brown and Makings 2014). Prolonged grazing by sheep and cattle has been shown to reduce the presence of perennial grasses and increase the density of junipers (*Juniperus* spp.), mesquites (*Prosopis* spp.), and such woody shrubs as sages (*Artemisia* spp.), Snakeweed (*Gutierreizia sarothrae*), Burroweed (*Isocoma tenuisecta*), and rabbit brush (*Ericameria* spp.; Van Auken 2000; Brown and Makings 2014). Complicating the issue, however, is the likelihood that climate change and a reduction in numbers of days of freezing temperatures may also be involved in the replacement of grasses by woody plants (Van Auken 2000; Turner et al. 2003).

Decreases in the density of bunchgrasses due to livestock grazing have been identified as contributing to both a reduction in overall wildlife abundance and diversity (Germano et al. 1983; Gruell 1996; Miller et al. 2011; Brown and Makings 2014). Although White-tailed Jackrabbits have been reported to decline with the reduction of grasses (Dalquest 1948; Ferguson and

Atamian 2012), Black-tailed Jackrabbits are said to generally increase (Vorhies and Taylor 1933; Taylor et al. 1935; Daniel et al. 1993; Brooks 1999). The reason why grazing results in an increase in Black-tailed Jackrabbit numbers is complex. Although once thought to be primarily due to the increased presence of annuals on grazed ranges (Vorhies and Taylor 1933), another factor may be that more shrubby rangelands favor Black-tailed Jackrabbits because they provide better escape cover for this species (Desmond 2004). A more relevant question given the findings presented here may be whether the cessation or reduction of livestock grazing results in fewer Black-tailed Jackrabbits.

Black-tailed Jackrabbit habitat selection has been shown to be based on both habitat quality and predation avoidance, and moderately grazed ranges with a high incidence of grasses and forbs have been shown to be favored over heavily grazed habitats (Flinders and Hansen 1975; Nelson et al. 1997; Marín et al. 2003). Similarly, Boch et al. (2006) found that cottontails were more abundant in rural neighborhoods that were ungrazed rather than grazed sites due to the better cover provided. Further, jackrabbits are not significant contributors to overgrazing as was once thought (Rice and Westoby 1978). Shrub communities protected against jackrabbits possessed little or no differences in general plant condition and health than the communities available to large numbers of jackrabbits (Rice and Westoby 1978). Clark and Wagner (1984) suggested that a decline in historic populations of Black-tailed Jackrabbits in northern Utah was due to overuse of the forage plant Greenmolly (*Neokochia americana*) by sheep and not jackrabbits. Although livestock grazing may have initially generated better habitat for Black-tailed Jackrabbits by opening up dense grasslands and increasing the number of shrubs, continued grazing has not improved habitats for jackrabbits, cottontails, or Pygmy Rabbits. Although grazing may initially have facilitated an increase in Black-tailed Jackrabbit distribution and abundance, neither continued grazing, better range management, nor the cessation of grazing explains the recent decline in Black-tailed Jackrabbit numbers.

Fire.—The role of fire on leporid abundance is also complex, and fires have been documented as being beneficial to both cottontails and jackrabbits. Both rabbits and hares are fire-adapted to some degree, and Keane et al. (2008) demonstrated that large fires are an historic norm in western forests, Pinyon-Juniper Woodlands, and Chaparral. Fires were thought to be more prevalent in plains and semi-desert grasslands where jackrabbits evolved before the introduction of livestock (Brown and Makings 2014). Lochmiller et al. (1995) reported that herbicides and prescribed fires increased cottontail abundance on his study areas in the Cross Timbers and Sacramento Valley of California, and Amacher et al. (2011) found that Black-tailed Jackrabbit observations increased dramatically within one year of a burn in a mixed conifer forest. Although an increase in precipitation and reduced predation could not be ruled out as the cause of the increases, these authors attributed larger jackrabbit numbers to a flush of herbaceous vegetation resulting from fire and the more open aspect of the forest.

An important exception to rabbits increasing after fire is in the Great Basin where intermountain grasslands now burn more often due to the presence of the invasive Cheatgrass (*Bromus tectorum*; Weddell 2001; Link et al. 2006; Keane et al. 2008). Here, the native bunchgrasses are damaged by fire and the resulting Cheatgrass-dominated landscape becomes increasingly prone to catastrophic burns. Both rabbits and hares avoid Cheatgrass communities and their numbers are generally fewer where this plant predominates (Woffinden and Murphy 1989). As a result, large areas of Cheatgrass now have lower jackrabbit and cottontail numbers than adjacent sagebrush communities, at least temporarily (Julie Heath and Michael Kochert, unpubl. report).

Knick and Dyer (1997) concluded that wildfires in Sagebrush from 1980 to 1992 within the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho reduced the amount of Black-tailed Jackrabbit habitat. In 1985 fires burned 50% of the NCA reducing small mammal populations for at least a year. Miller et al. (2011) calculated that about 57% of the existing Sagebrush cover type in the Great Basin of southeast Oregon, southern Idaho, and portions of northeast California, Nevada, and western Utah were at moderate or high risk of elimination over the next 30 y due to Cheatgrass expansion. It has been estimated that there is a 100% chance of fire when the land cover is > 45% Cheatgrass (Link et al. 2006). It thus appears that both fires and fire suppression can result in a decrease in leporid numbers depending on the plant communities involved.

Changes in agriculture practices.—Although the planting of domestic grasses and food plants may have initially benefited cottontails and jackrabbits, causing numerous depredation complaints, large concentrations of rabbits in agricultural fields are largely a past phenomenon. Instead, clean farming, the conversion of adjacent rangelands to farmlands, and the application of pesticides and herbicides have now reduced the quality of leporid habitat over large areas. Mankin and Warner (1999) found that cottontail hunter success in Illinois declined from 70-90% as a result of land use changes, particularly in regard to agriculture. Tiemeier (1965) and others have reported that Black-tailed Jackrabbits did not do well in agricultural areas compared to natural vegetation, and that the elimination of natural cover adjacent to farmland resulted in some areas having fewer rabbits than formerly. Leporid populations, previously assisted by agriculture, now appear reduced when compared to former numbers. The effects of recent applications of weed killers and other newly-developed chemicals remain unknown. Although changes in agricultural practices cannot explain jackrabbit declines in rangelands, a systematic collection and analysis of rabbits in areas subject to such treatments is much needed.

Increase in road-kills.—Another cause of increased leporid mortality is the increase in graded roads, paved highways, and freeways since 1950. Road kills now account for an estimated one million or more animals killed per day in the U.S. (Road Ecology Center (REC). 2011. Annual report: wildlifecrossing.net/California. California Roadkill Observation System. Available from http://www.wildlifecrossing.net/california/ [Accessed 11 September 2017]). Even prior to World War II, the toll on rabbits and hares by vehicles was impressive. Williams and Nelson (1939) counted 1,209 rabbit carcasses on a trip over a 586 km stretch of highway between Nyss, Oregon, and Twin Falls, Idaho, an average of 2.1 rabbit carcasses/km in a landscape that was then 60% Sagebrush. After the war, an even more impressive rate of 16 leporid carcasses per km was recorded by Adams and Adams (1959) while traveling from California to Nevada. Lechleitner (1958) reported more than 100 road kills on his Gray Lodge study area in the Sacramento Valley of California, noting this to be the major cause of mortality for this population.

A random evaluation by Caro et al. (2000) showed that jackrabbits were the most common road killed animal in the Central Valley of California between 1997 and 1999 with 1.2 carcasses/100 km. Roads through prime wildlife habitat take a larger toll. Gerow et al. (2010) reported an average of 29,377 vertebrates killed per 1.1 km a day in Saguaro National Park in Arizona between 1994 and 1999. Many of these animals were cottontails and jackrabbits. During a period when jackrabbit densities ranged from 2.2–45.0/km², Ferguson and Atamian (2014) found about 130 road killed jackrabbits/km in their Idaho study area.

As high as some of these road kill estimates are, the actual number of leporids removed is thought to be greater than reported for a variety of reasons. Some road kills remain undetected, and scavenging predators often remove carcasses before they can be tallied. Regardless of the numbers of animals killed, the proliferation of well-traveled roads since 1950 may have reduced not only the density of leporids in adjacent areas, but also may have influenced their distribution. An additional cause of mortality in such situations may be that road-killed carcasses provide a hyper-food source for increased numbers of scavenging predators such as Coyotes and Golden Eagles, which then prey on living leporids (Teixeira et al. 2013).

Weather and climate change.—Rabbit populations fluctuate both seasonally and annually, but the factors that cause rabbit numbers to increase are complex and imperfectly understood. Although linear correlations between precipitation amounts and lagomorph recruitment rates have not been convincingly demonstrated, there is some evidence of a cause and effect relationship between precipitation, green food biomass, and leporid abundance (Sowls 1957; Hungerford et al. 1974; Gray 1977; and Nelson et al. 1997). In a three-year investigation of declining leporid populations in the Mojave Desert, Sosa Burgos (1991) found an apparent relationship between precipitation and Desert Cottontail abundance, but not Black-tailed Jackrabbit numbers. Although she found a similarity in cottontail and jackrabbit population trends, changes in jackrabbit numbers depended on precipitation, food availability, and Coyote abundance. Coyote numbers, in turn, determined cottontail abundance (Sosa Burgos 1991). Hernandez et al. (2011) found only a weak relationship between Black-tailed Jackrabbit abundance and precipitation/grass production in their 10-y study within the Chihuahuan Desert ($r^2 = 0.34$; $P = 0.28$). In another 10-y study in semi-desert grassland, jackrabbit numbers were determined more by variation in predation than by variation in weather-related recruitment (Lightfoot et al. 2010). Portales-Betancourt et al. (2012), working within the Chihuahuan Desert region, found that cottontail ovary weights correlated with photoperiod, temperature, and precipitation. It thus appears that, while cottontail and jackrabbit numbers may be influenced by rainfall and recruitment, much of the variation is due to mortality caused by predation or disease. Although rainfall determines the plant production needed for recruitment, leporid population levels may actually be determined by the predators that influence the mortality rate.

Interactions between precipitation, natality, and mortality may be particularly complex in northern populations where rainfall fluctuation is less pronounced. Although Hayden (1966a) attributed a drop in jackrabbit natality in the Great Basin to low precipitation and a lack of green vegetation, Gross et al. (1974) concluded that jackrabbit population increases in that area were not due to an increase in green feed, as there was no increase the number of ova produced by female jackrabbits during years when green feed was present. Nor did these investigators find an increase in breeding season length and litter size in wet years versus poor years. Age ratios did not significantly differ between years, and 85% of the variation in population size was attributed to variations in mortality (Gross et al. 1974).

French et al. (1965) attributed a jackrabbit population increase in southern Idaho between 1955 and 1960 to mild years allowing for longer breeding seasons and resulting in females having more embryos. Litter size and frequency of pregnancy was nonetheless independent

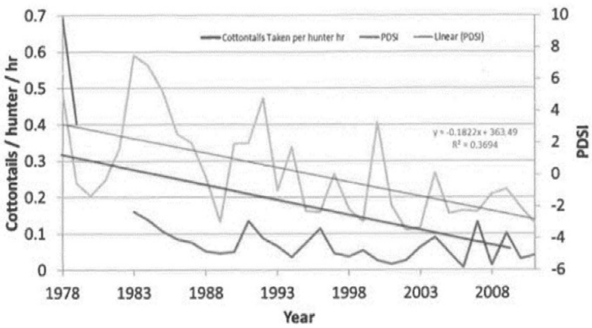

Figure 10. Cottontail hunt success at Oracle Junction, Arizona, compared with the Palmer Drought Severity Index for Southeast Arizona, 1979–2012 (from Levi Heffelfinger et al., unpubl. data).

of weather, and the authors concluded that reproductive success was density dependent with mortality more important than recruitment in determining jackrabbit population size. Although Eberhardt and Van Voris (1986) attributed Black-tailed Jackrabbit population peaks in northern Utah to juvenile recruitment rates > 50%, they reported no increase in precipitation or grass biomass prior to the years of increasing populations. Nor, as did Gross et al. (1974), did they find a relationship between fluctuating age ratios and population indices. Nonetheless, the availability of herbaceous vegetation has to be important as the spring and early summer diets of jackrabbits and cottontails consists mostly of green grasses and forbs (Hayden 1966b). MacCracken and Hansen (1962) noted that both cottontails and jackrabbits were most abundant on the Idaho National Engineering Laboratory where the herbaceous biomass was the greatest: Black-tailed Jackrabbits being most numerous where grasses proliferated, cottontails preferring forb-rich sites.

Extreme weather can also cause rabbit numbers to fluctuate. Stoddart (1985) reported that 34% of the jackrabbits in Curlew Valley, Utah, died during a 68-h period in February, 1962, due to a severe freeze and snow event. He attributed this high mortality to increased predation due to the rabbits being immobilized by chilling winds. As in most unusual events, however, the population quickly recovered to resume an irregular pattern of population fluctuations.

Increased incidence of drought.—The response of leporids to drought is an aspect of changing weather that needs more evaluation. Wooster (1935), Bronson and Tiemeier (1958), and Tiemeir (1965) attributed Black-tailed Jackrabbit population increases in Kansas to lower juvenile mortality during times of drought. On the contrary, drought was stated as an explanation for a 10-y downward trend in cottontail populations in eastern counties of that state (Pittman 2013). This latter explanation is supported by Fitch (1947), who reported that cottontails in the Sacramento Valley of California failed to reproduce during the summer dry season. Moreover, Lightfoot et al. (2010), Hernandez et al. (2011), and Portales-Betancourt (2012) found that Black-tailed Jackrabbits had higher reproductive success and population levels following periods of high precipitation and forage production than during times of drought.

Using survey and hunt data from Oracle Junction and two other areas in southeastern Arizona, Levi Heffelfinger et al. (unpubl. data) compared the mean number of cottontails observed on 20-mi quail call-count survey routes each year with regional precipitation amounts and the Palmer Drought Severity Index (PSDI). Although their comparisons did not show a significant annual correlation coefficient between survey numbers with either winter precipitation or seasonal PDSIs, there was a parallel decline in the number of cottontails observed in spring and the preceding October-March precipitation. A similar parallel relationship was also shown between the number of cottontails taken per hunter trip and the October-March PDSI (Fig. 10).

Given that much of California and the west are experiencing a long-term drought, it appears likely that prolonged aridity could account for a decline in cottontail and jackrabbit numbers. U.S. Drought Monitor maps prepared by the National Oceanic and Atmospheric Administration and its cooperators in March 2015 show Exceptional long-term drought in California and western Nevada, with severe to moderate long-term droughts impacting Arizona, southern Colorado, extreme southwest Idaho, western Kansas, western Oklahoma, Utah, and eastern Washington (http://droughtmonitor.unl.edu/Home.aspx) with some of these states also experiencing significant declines in leporid survey indices.

The reason that leporid populations do not always respond positively to years of moderate to high precipitation amounts remains unknown. Especially intriguing is the lack of recovery experienced by Southwest rabbit populations after the wet years in the late 1980s. This lack of response, and the failure of populations to always decline in dry years, suggests that drought may be synergistic with some other factor or factors in maintaining populations of rabbits at low levels.

Disease.—Diseases and parasites have long been suspected as agents capable of reducing leporid numbers. Rabbit fever, or Tularemia (*Francisella tularensis*), and other fatal bacterial pathogens have been found in a number of western state rabbit populations (Bacon and Drake 1958; Bowen et al. 1960; Eberhardt and Van Voris 1986). Rabbits are also prone to harbor the tick *Dermacenter parumapertus* and other vectors for Tularemia such as Q-fever (*Coxieila burneti*) and Rocky Mountain Spotted Fever (*Rickettsia rickettsia*), which have been reported as occurring in western state leporids (Rosasco 1957; Bacon and Drake 1958). Tiemeier (1965) thought that disease could reduce jackrabbit populations to a few individuals within a month or two, and Woolf et al. (1993) presented evidence that Tularemia might be regulating some semi-isolated populations of Eastern Cottontails. Actual investigations, however, have yet to document disease as a regulating factor in populations of western leporids. An investigation of a high-density population of Black-tailed Jackrabbits near Battle Mountain, Nevada, in 1951 failed to implicate either Tularemia or Plague (*Yersinia pestis*) as the cause of a die-off despite the report of dead rabbits being present (Phillip et al. 1955). The only pathogens noted were antibodies for Colorado tick fever and western equine encephalomyelitis, neither of which could be implicated as a serious cause of mortality.

In an intensive study involving 558 rabbits of four species collected in eastern and central Washington during a time of high rabbit populations from July 1953 to June 1956, Bacon and Drake (1958) found only three animals with high titers for Plague, five positive reactions to Tularemia, and five staphylococcus infections. Even though the number of potential vectors was high, they concluded that there was no correlation between bacterial infections and leporid density. Lechleitner (1958) found little mortality attributable to Tularemia or other diseases in a high density jackrabbit population in Sacramento Valley, California. He did note non-lethal incidences of intestinal coccidiosis, but not enough to impact population levels. Eberhardt and Van Voris (1986) attributed declines in jackrabbit numbers to an unknown factor and to survey irregularities after their long-term study (1954–1985) of this animal on the Dugway Proving Grounds in Utah. Having failed to show other than a low but increasing incidence of Tularemia and Q-fever, they found that the only high incidence of disease involved Rocky Mountain Spotted Fever, which was independent of jackrabbit population density. Nor has radioactivity and nuclear contamination been shown to decrease leporid numbers (Turner et al. 1966).

No cases of jackrabbits having Plague or Lyme disease have been reported (Henke and Bryant 1999), and disease has yet to be implicated in any large-scale lagomorph decline in the western U.S. Diseases rarely reduce population levels over a large area, even in relatively dense populations (Bowen et al. 1960). Most epidemics are more or less regional, and not believed to impact wide areas, much less entire states (Schaible et al. 2011). Moreover, the likelihood of pathogens being so persistent so as to extract a continued reoccurring toll on leporids for periods of 30 y or more is reason to doubt disease as a cause of the present decline.

Disease, however, does pose a possibility for causing future declines, as the introduction of *myxomatosis* in the 1950s, and Rabbit Hemorrhagic Disease Virus (RHDV) in the 1990s had devastating impacts on introduced populations of European Rabbits (*Oryctolagus cuniculus*) in Australia and elsewhere (Jaksic and Yanez 1983; Saunders et al. 2010; Lavazza and Cooke 2018). Although highly successful at reducing rabbit numbers in Australia, these introduced viruses are now a problem for native leporids in portions of Europe (Mutze et al. 2010; Lavazza and Cooke 2018). The monitoring of diseases is therefore worthy of consideration even if endemic pathogens have not been shown to cause major declines in rabbit numbers in western North America.

Parasites.—Parasite infestations have also been suggested as contributing to reduced rabbit numbers, especially after a population experiences a rapid decline. But even though high nematode infestations and the presence of bot-flies (*Culebra* spp.), ticks, and lice often accompany high rabbit densities, most parasite infestations wax and then wane with the cessation of warm weather (Vorhies and Taylor 1933; Rosasco 1957). Clemons et al. (2000) found a high incidence of ecotoparisites, roundworms (78%), and bot fly larvae in 54 jackrabbits in a northern California jackrabbit population but noted no stressed animals. An investigation into a declining White-tailed Jackrabbit population in South Dakota found no evidence of bacterial infections in 314 animals and only four livers infected with the nematode parasite, *Calodium hepaticum* (Schaible et al. 2011), leading to the conclusion that neither disease nor parasites were responsible for the decline. It thus appears that landscape change, drought, and other phenomena are more often the cause of reductions in leporid numbers than disease or parasites (Wooster 1935; Lechleitner 1958; Stoddart 1985; Smith 1990).

Changes in predation rates.—Jackrabbits, and to some extent cottontails, are not unlike Mule Deer (*Odocoileus hemionus*) and other herbivores in that their population levels are not always controlled by reduced food plant availability (Longland 1991). Rather than their numbers being reduced by starvation, leporid populations are more often controlled either by reduced recruitment rates or increased predation rates that lower population numbers to carrying capacity or below (Anderson and Shumar 1986; Meslow and Keith 1968). Hence, the population dynamics of cottontails and jackrabbits is such that numbers can be maintained below carrying capacity if high numbers of predators are able to persist during times of low population levels due to the presence of alternate prey species (Boutin and Cluff 1989; Gibson 2006). Put another way, a multitude of predatory species, if present in sufficient numbers, can result in leporids persisting at below optimum numbers (Jerome Letty et al., unpubl. data).

Several researchers have concluded that jackrabbit numbers, and to a lesser extent cottontail numbers, depend on predator numbers (Eberhardt and Van Voris 1996; Steenhof et al. 1997). Bartel et al. (2008) considered numbers of Black-tailed Jackrabbits in northern Utah to be controlled by periodicities in predator numbers that occurred at 10–11-y intervals. In actuality, most predator populations are thought to be controlled by the abundance of their principal prey species, and researchers have reported jackrabbit numbers to influence Bobcat (Knick 1990), Coyote (Cypher et al. 1994), and Golden Eagle (Steenhof et al. 1997) population sizes. It therefore stands to reason that changes in predator populations can impact leporid numbers over the same time period.

That rabbit population changes can be attributed to mortality resulting from increased predation rates is well documented. Lord (1961) reported finding a high turnover of cottontails in all monthly age-classes, and Stoddart (1970), while noting low mortality rates for adult jackrabbits, found that more than two-thirds of a semi-annual mortality rate of 41% was due to Coyote predation with another 20% attributable to raptors and scavengers. Wagner and Stoddart (1972) determined that an increasing population of Coyotes was the major source of increased jackrabbit mortality from 1962 to 1970 in Curlew Valley, Utah, hastening if not causing a 1963–1967 jackrabbit population decline.

By way of contrast, an increase in jackrabbit numbers in Curlew Valley, Utah, from 1968 to 1970 was thought to be due to increased Coyote mortality resulting from predator control (Wagner and Stoddart 1972). An example in reverse was presented by Knick (1990), who attributed a 90% decrease in Bobcat distribution, density, and survival in southeastern Idaho in 1981 to a major decline in cottontail and jackrabbit numbers. Further evidence that at least some leporid populations are influenced by changes in predator numbers is provided by Henke and Bryant (1999), who found that jackrabbit numbers in west Texas increased with Coyote removal as did medium-sized predators such as the Striped Skunk (*Mephitis mephitis*), while cottontail and raptor numbers remained unaffected.

Predator/prey relationships may not be the same in one region of the country as another. For example, a predator/prey relationship between leporids and Coyotes may be less obvious where predator/prey diversity is high. Coyotes are optimal foragers, and a study in a Chihuahuan Desert region of Mexico having high prey variability found no functional relationship between Black-tailed Jackrabbit abundance and Coyote numbers (Hernandez et al. 2002, 2011).

Although predator numbers may control leporid numbers, rabbit numbers do not always determine predator abundance. Despite a decline in both cottontail and jackrabbit numbers in southeastern Idaho in 1981, Stoddard et al. (2001) found that the number of Coyotes continued to rise until peaking in 1984. Also, Coyote numbers in Curlew Valley, Utah, did not correlate with a decline in jackrabbit numbers, the number of Coyotes remaining high due to alternate prey availability (Bartel et al. 2008).

A more complex example was found in the Mojave Desert where Sosa Berger (1991) determined that cottontail and jackrabbit numbers determined Coyote population size, but Coyote numbers controlled only jackrabbit population numbers and not cottontails. Cottontail numbers were influenced by precipitation amounts and forage production. Jackrabbit numbers, while affected by Coyote numbers, were also influenced by precipitation. Given the synergistic relationship between leporids and their predators, it appears reasonable to assume that a long-term increase in predator numbers and/or the variety of predators can result in lower populations of rabbits. Just as jackrabbit irruptions can be facilitated by predator control, it stands to reason that increased predation levels, particularly during times of drought, can not only keep rabbit populations in check, but result in declining population levels (Jerome Letty et al., unpubl. data).

Despite the last 30 y being a time of drought in much of the western U.S., most western states report increased predator populations. This trend is evidenced by increasing harvests of Coyotes, foxes, Bobcats, and other mammalian furbearers by varmint hunters and sportsmen in states such as Arizona (ADGF 2014). This phenomenon is attributed, at least in part, to a decrease in predator control and fur trapping activity since the 1980s (Roberts and Crimmins 2010). The reasons for an increase in predators may actually be more diverse; in addition to less trapping and predator control, the proliferation of wildlife waters, an increase in roadside carrion, and adaptations to living with humans have contributed to a better environment for several species of predators including Coyotes (McClure et al. 1996; Lombardi et al. 2017).

Avian predators also appear to have increased in number as a result of habitat enhancements both intentional and otherwise. In addition to the provision of artificial roosts and nesting platforms, thousands of kilometers of power line poles now provide hunting perches and other raptor amenities not historically present. The killing of raptors by rural people and predator control agents greatly declined after 1960 to be replaced by projects designed to increase raptor nesting success and reduce raptor mortality (David Brown, pers. obs.). The retirement of DDT and its derivatives has resulted in an improvement in the recruitment of most raptor species, and the North American Breeding Bird Index (BBI) shows a steadily increasing trend for Red-tailed Hawk observations in every western state and bioregion since 1966 (e.g., Bierregaard et al. 2014, Sauer et al. 2003). During this time the Ferruginous Hawk BBI increased in six of the seven bio-provinces in which this species occurs (Sauer et al. 2003, Sauer and Link 2011). Golden Eagle numbers appear to have declined only in areas preceded by declines in leporid numbers (Greg Beatty, pers. obs.). The most dramatic decline in lagomorph hunt success indices occurred before 1982 and may have been due to the reduction of abnormally high leporid populations brought on by widespread predator control. Should lagomorph populations continue to decline, and alternate prey is scarce, Golden Eagle and other avian predator populations, will likely suffer.

Recommendations

Although little can be done to combat the effects of drought, and detrimental land use changes will continue to degrade habitats, leporid populations, and the predators who rely on them, could benefit from an improved status and recognition by the states that have management authority over these species. Declining hunter numbers and harvests should concern wildlife management agencies seeking to increase hunter recruitment as lagomorphs are traditional entry level game animals. It would therefore be advantageous from a management perspective if state federal-aid coordinators developed standardized data collection techniques through the aegis of the Association of Eleven Western State Game and Fish Commissioners.

Research is also needed to determine if, and how much, populations of resident lagomorphs can be increased through better land management practices. The provision of more shrub cover should benefit cottontail rabbits (Lochmiller et al. 1995), and jackrabbits benefit from open landscapes of native vegetation. Additional investigations into the population dynamics of leporids are much needed, and future studies should formulate habitat improvement measures that might improve juvenile survival rates. Investigations into the possible detrimental impacts of agricultural chemicals and changes in crop production are also needed. Improvements in leporid management practices can provide a win-win situation for both hunters and predators, while improving ecosystem dynamics throughout the western U.S.

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