Cottontail Rabbits

Biology of Cottontail Rabbits (*Sylvilagus* spp.) as Prey of Golden Eagles (*Aquila chrysaetos*) in the Western United States

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U.S. Fish and Wildlife Service
Regions 1, 2, 6, and 8
Western Golden Eagle Team

Date: November 13, 2017

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Suggested Citation

Hansen, D.L., G. Bedrosian, and G. Beatty. 2017. Biology of cottontail rabbits (*Sylvilagus* spp.) as prey of golden eagles (*Aquila chrysaetos*) in the western United States. Unpublished report prepared by the Western Golden Eagle Team, U.S. Fish and Wildlife Service. Available online at: *https://ecos.fws.gov/ServCat/Reference/Profile/87137*

Acknowledgments

This report was authored by Dan L. Hansen, Geoffrey Bedrosian, and Greg Beatty. The authors are grateful to the following reviewers (in alphabetical order): Katie Powell, Charles R. Preston, and Hillary White.

Summary

Cottontail rabbits (*Sylvilagus* spp.; hereafter, cottontails) are among the most frequently identified prey in the diets of breeding golden eagles (*Aquila chrysaetos*) in the western United States (U.S.). Cottontail abundance appears to influence golden eagle breeding density, reproduction, mortality, and habitat selection. Cottontails may be key prey for golden eagles because they are optimal-sized; relatively well distributed and abundant; and occur in the kinds of open habitats favored by hunting golden eagles.

This account is limited to eastern (*S. floridanus*), desert (*S. audubonii*), and mountain (*S. nuttallii*) cottontails. Other cottontail species in western North America have more limited distributions (Chapman and Litvaitis 2003) and do not appear to be important prey for golden eagles. Jackrabbits (*Lepus* spp.) are sometimes lumped with cottontails in studies of golden eagle diets or prey relationships. Jackrabbits are important prey for golden eagles across much of the western U.S. and are discussed in a separate account (jackrabbits account).

The combined geographic ranges of the focal cottontail species in this account encompass almost the entire conterminous western U.S. Cottontails generally occur in open habitats that provide a mix of herbaceous forage and cover in the form of shrubs, small trees, rocks, or human structures, depending on the location and species. Cottontails primarily eat grasses and forbs during the growing season and woody plants during the dormant season.

Cottontail populations can exhibit substantial inter-annual fluctuations in abundance. However, there is currently insufficient information for determining whether pronounced multi-annual periodicity occurs in cottontail populations.

Cottontail populations may be influenced by a variety of environmental factors. Except for outbreaks of tularemia (*Francisella tularensis*), parasites and diseases do not appear to be a primary influence on cottontail abundance. Weather affects both survival and reproduction of cottontails. This could occur through effects on breeding condition, availability of food, thermoregulation, and ability to flee from predators. Predation may be directly responsible for most cottontail deaths. Recreational hunting is a major source of mortality for some cottontail populations but its effects on populations are unknown.

Eastern, desert, and mountain cottontails generally have low conservation rankings. However, widespread population declines may be occurring in portions of the western U.S. Habitat loss and degradation due to development, agricultural conversion, overgrazing by livestock, invasive grasses, and altered fire regimes may pose the greatest threats to cottontails.

Habitat maintenance and enhancement for cottontails could be a valuable tool for conserving golden eagles, but little is known about how cottontails respond to management activities. Much of the published information on cottontail management concerns the responses of eastern cottontails to habitat changes in human-dominated landscapes in the eastern half of the U.S. Limited bodies of information also exist for cottontails in the western U.S., particularly in regard to effects of overstory reduction in forests and woodlands and livestock grazing in grasslands and shrublands. Loss or degradation of

native shrublands and grasslands to invasive annual grasses and associated increases in wildfires could also constitute a substantial threat to cottontails across large portions of the western U.S. Cottontail management in these areas could potentially be linked to existing conservation plans for imperiled grassland and shrubland ecosystems and associated wildlife.

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Importance to Golden Eagles

Occurrence in Golden Eagle Diets

Cottontail rabbits (*Sylvilagus* spp.; hereafter, cottontails) are among the most commonly identified prey of breeding golden eagles (*Aquila chrysaetos*) in the western United States (U.S.). Bedrosian et al. (2017) synthesized data concerning the breeding season diets of golden eagles within 45 study locations in the conterminous western U.S., southern Canada, and northern Mexico. Cottontails were rarely identified to the species level in golden eagle diet studies, presumably due difficulty distinguishing among species using uneaten remains alone. Based on the percentage of identified prey individuals, cottontails were one of the top three breeding season prey taxa for golden eagles in 30 (67%) of the reviewed studies (Figure 1). Cottontails were among the top three prey in all 6 diet studies conducted in semi-arid prairie ecosystems in the western Great Plains. In intermountain basin shrub-steppe, cottontails were in the top three prey in 17 of 25 (68%) studies. They were also among the top three prey in 2 of 3 (67%) studies conducted in higher elevation areas in the Rocky Mountains and in 4 of 7 (57%) studies in Southwestern deserts, forests, and grasslands.

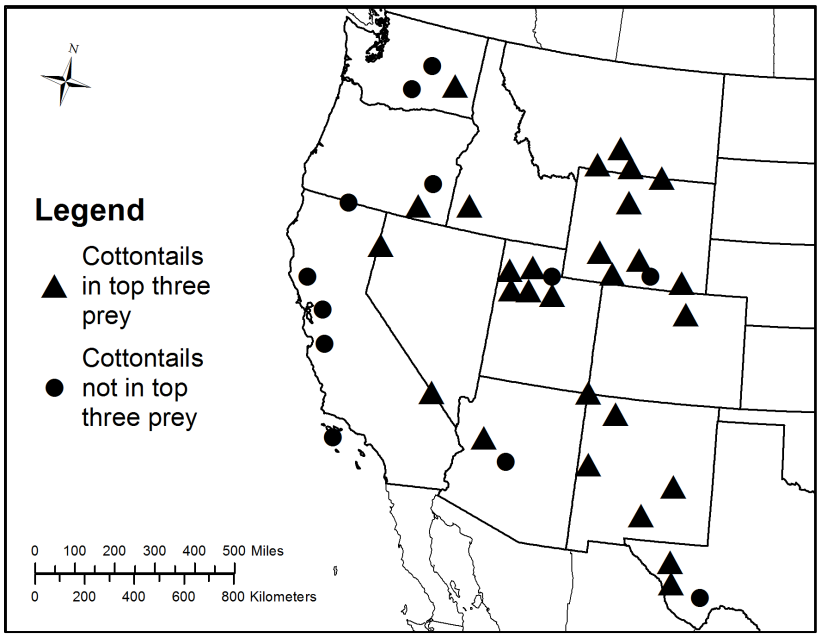

Figure 1: Locations of studies in which cottontail rabbits were in the top three breeding season prey taxa for golden eagles based on percentage of identified prey individuals (see Bedrosian et al. 2017).

Few studies have investigated the diets of golden eagles during the nonbreeding season. Leporids were found in the stomachs and crops of 38% of golden eagles collected across multiple states during September–March, but the relative importance of cottontails versus jackrabbits (*Lepus* spp.) was not determined (Arnold 1954). A study in Montana identified cottontail remains in the stomachs of just 4 of 51 (8%) golden eagles collected in March

(Woodgerd 1952). Woodgerd (1952) noted, however, that he may have misidentified some leporids when only fur was available for identification. In western Utah, Edwards (1969) found that jackrabbits were the primary prey for golden eagles during winter (occurred in ca. 98% of pellets), whereas cottontails were rarely consumed (<1% of pellets). In northeastern Wyoming, cottontails comprised only 5% of prey numbers in pellets during mid-November to mid-April, compared with 45% for jackrabbits (Hayden 1984). In contrast, an early study—primarily conducted in Kansas during the nonbreeding season—found that the stomachs of 11 of 30 (37%) golden eagles contained cottontails (Gloyd 1925). Further research is needed to determine the relative importance of cottontails to golden eagles during the nonbreeding season.

Influence on Golden Eagles

Research in portions of Montana, Wyoming, and Utah has suggested that cottontail abundance can influence golden eagle reproduction, mortality, and habitat selection (Reynolds 1969; Benson 1981; Phillips et al. 1990; Bates and Moretti 1994; Preston 2013, 2017; Crandall et al. 2015).

In southeastern Montana and northern Wyoming, Phillips et al. (1990) noted that increases in the number of breeding golden eagles occurred during years with relatively high abundances of cottontails. They also found that the number of young fledged by golden eagle pairs was significantly correlated with cottontail abundance. In one of the study years, 2 of 20 (10%) eagle nests that produced fledglings had 3 young each; an unusually high percentage of triplets, which Phillips et al. (1990) suggested was related to high cottontail numbers (also see Jenkins and Joseph 1984). In eastern Utah, Bates and Moretti (1994) similarly found that golden eagles produced more young during years with higher numbers of cottontails and jackrabbits. Reynolds (1969) reported that many golden eagles in south-central Montana failed to nest when jackrabbits and cottontails were at their lowest numbers, and that eagles nested but had low nesting success and fledged few young during years when leporid populations were recovering. Golden eagle nesting activity, success, and productivity in northwestern Wyoming was positively associated with changes in numbers of cottontails (Preston 2017). In addition, golden eagles produced triplets in only two of nine years (2015 and 2016) corresponding with highest indices of cottontail abundance (C. Preston pers. comm.)

Cottontail abundance could also influence golden eagle mortality. Benson (1981) found that the number of dead golden eagles found along power lines during the nonbreeding season in six western states was positively correlated with the number of cottontails per length of power line. The same relationship was not found for number of jackrabbits, which the author attributed to differences in how golden eagles hunt for cottontails versus jackrabbits. However, Kochert (1980) found a similar positive association between electrocution of golden eagles and densities of jackrabbits in Idaho. Benson (1981) suggested that immature eagles are at particular risk of electrocution while hunting cottontails because they are less experienced and more nomadic than adults.

Cottontails may influence habitat selection by golden eagles in some areas. In eastern Utah, golden eagles appeared to select nest locations based in part on proximity to areas with high cottontail and jackrabbit numbers (Bates and Moretti 1994). Golden eagles in

south-central Montana selected home ranges based on percent of shrub and grassland, which were included in modeling as surrogates for prey habitat, as well as terrain features that provided orographic uplift for hunting, and avoided human development, pasture, and cultivated agriculture (Crandall et al. 2015). Jackrabbits and cottontails were among the most frequently identified prey in golden eagle diet studies in that area and are both strongly associated with shrub and grassland habitats (see Habitat Associations; also see jackrabbits account). Golden eagles also appeared to select locations within their home ranges based on proximity to prey habitat, as well as terrain ruggedness, aspect, and proximity to the nest.

Prey Species Information

Physical Description

Eastern (*S. floridanus*), desert (*S. audubonii*), and mountain (*S. nuttallii*) cottontails all have gray or brown dorsal pelage and white ventral pelage, including the underside of the tail (Chapman and Litvaitis 2003). Desert cottontails have relatively long ears, while mountain cottontails have shorter, more rounded ears and large hind legs covered with dense, long fur (Orr 1940; Chapman and Litvaitis 2003). Eastern cottontails are the largest of the three species covered by this account and mountain cottontails are the smallest. Adult female eastern cottontails in the eastern U.S. weighed an average of 2.8 pounds (lbs) (1,244 grams [g]) and were an average of 17.0 inches (in) (433 millimeters [mm]) in total length, while males averaged 2.5 lbs (1,134 g) and 16.8 in (427 mm) (Chapman and Morgan 1973). In California, adult female desert cottontails weighed an average of 2.2 lbs (989 grams [g]) and males weighed an average of 1.9 lbs (841 g); both sexes were an average of 15.2 in (385 mm) in total length (Orr 1940). Female mountain cottontails in California averaged 1.8 lbs (790 g) and 14.6 in (372 mm) and males averaged 1.6 lbs (720 g) and 13.9 in (352 mm) (Orr 1940). Cottontails are considered optimal-sized prey for golden eagles (Watson 2010; Schweiger et al. 2015).

Ecological Roles

Cottontails may influence plant communities through seed dispersal (Fagerstone and Ramey 1996). Additionally, they are important prey for a wide variety of avian, mammalian, and reptilian predators (Chapman and Litvaitis 2003; see Influences on Abundance). Cottontail abundance may influence the behavior and population vital rates of golden eagles (see Importance to Golden Eagles).

Distribution

The combined geographic ranges of cottontails encompass nearly all of the golden eagle's range in the conterminous western U.S. (Figure 2). In the western U.S., eastern cottontails occur from the Dakotas south into Texas, and west into New Mexico and Arizona (Chapman et al. 1980; Figure 2). Eastern cottontails also occur in portions of Oregon and Washington, where they were introduced as game during the early 20th Century (Dalquest 1941; Graf 1955). The desert cottontail primarily inhabits lower elevation arid regions from northern

Montana south to central Mexico, and across the Southwest to the Pacific Coast (Chapman and Willner 1978; Figure 2). The mountain cottontail's range includes much of the Intermountain West, from the Rocky Mountains west to the Sierra Nevada and Cascades and from just north of the Canadian border to northern Arizona and New Mexico (Chapman 1975; Figure 2). The elevational distributions of cottontails are not well described. Desert cottontail specimens described by Orr (1940; see Physical Description) were collected from locations in California ranging from below sea level to over 5,600 ft (<0 to >1,700 m) and mountain cottontail specimens were collected between 4,500 ft (1,372 m) and 10,500 ft or higher (≥3,200 m).

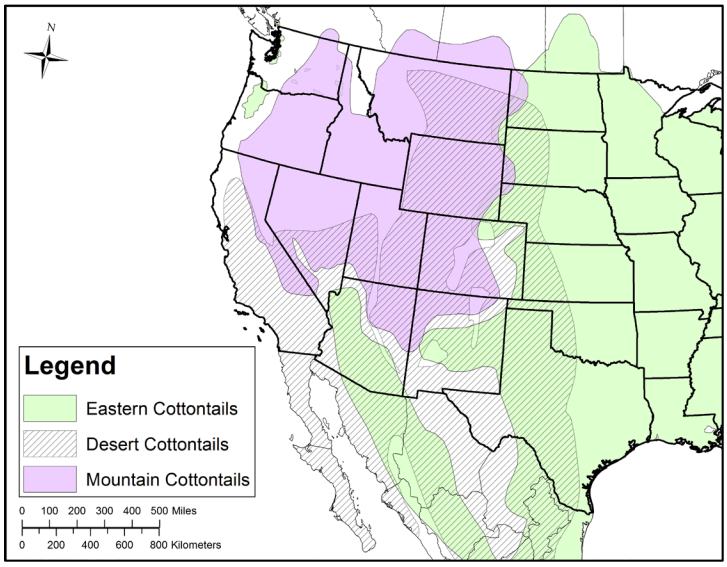

Figure 2: Approximate geographic ranges of eastern, desert, and mountain cottontails in the western U.S. (NatureServe 2015).

Habitat Associations

Research, primarily conducted in the eastern half of the U.S., has indicated that abandoned agricultural fields, shrublands, and shrub-woodlands provide good habitat for eastern cottontails (Chapman and Litvaitis 2003). Mature forests appear to provide poor habitat for eastern cottontails due to insufficient forage, while intensively cultivated lands may often lack suitable cover (Chapman and Litvaitis 2003; e.g., Mankin and Warner 1999). Eastern cottontails often use shrubs or anthropogenic habitat features, such as hedgerows, shelterbelts, and piles of brush, wood, or junk, as cover (Dalke 1942; Morgan and Gates 1983; Althoff et al. 1997). Less has been published on the eastern cottontail's habitat associations in the western U.S. In Oklahoma, eastern cottontails were studied in the cross timbers vegetation type, consisting of upland forest of oak (*Quercus* spp.) and red cedar (*Juniperus virginiana*) interspersed with tallgrass prairie consisting primarily of little bluestem (*Schizachyrium scoparius*) and Indian grass (*Sorghastrum nutans*) (Peitz et al. 1997). In Arizona, Sowls (1957) found that eastern cottontails sometimes replaced desert cottontails in higher elevation (ca. 4,000 ft [1,220 m]) oak woodlands with Mexican blue oaks (*Q. oblongifolia*), Emory oak (*Q. emoryi*), beargrass (*Nolina microcarpa*), skunk bush (*Rhus trilobata*), and manzanita (*Arctostaphylos pringlei*).

Desert cottontails occur in a variety of lower-elevation and desert habitats (Chapman and Willner 1978). They are typically found in arid and semi-arid shrublands, shrub-grasslands, and scrub and riparian habitats (Orr 1940; Davis et al. 1975). They also occur in open grasslands, provided scattered shrub cover is available (Lightfoot et al. 2010). In the Southwest, common shrubby plants in areas used by desert cottontails include mesquite (*Prosopis* spp.), creosote bush (*Larrea tridentata*), broom snakeweed (*Gutierrezia sarothrae*), yucca (*Yucca* spp.), oaks, palo verde (*Parkinsonia microphylla*), triangle-leaf bursage (*Ambrosia deltoidea*), and cacti (e.g., *Opuntia* spp., *Carnegiea gigantea*) (Sowls 1957; Davis et al. 1975; Brown and Krausman 2003; Lightfoot et al. 2010). Brown and Krausman (2003) reported that desert cottontails in Arizona were typically found in areas with bursage or other tall plants (>5 ft [>1.5 m]) that provided dense thermal cover close to the ground (i.e., lower canopy height) and were rarely in areas dominated by mesquite or creosote bush, which were generally too sparsely vegetated to provide sufficient cover. Black grama (*Bouteloua eriopoda*) is a common grass in Southwestern grasslands or shrub-grasslands used by desert cottontails (Davis et al. 1975; Lightfoot et al. 2010). In California, desert cottontails were often observed in riparian areas with oaks or willows (*Salix* spp.), on open grassy hillsides, at the edges of shrublands, along dry gullies, or in anthropogenic habitats such as under old buildings, around wood and brush piles, or in fields with tall, dense weeds (Dice 1926; Orr 1940). Orr (1940) reported that desert cottontails in Nevada were commonly associated with arrowweed (*Pluchea sericea*), screw-bean mesquite (*P. pubescens*), and catclaw (*Acacia greggii*). Desert cottontails in Montana were found in sagebrush (*Artemisia* spp.) desert and semi-desert (Hoffman et al. 1969). In Colorado, Flinders and Hansen (1973, 1975) studied desert cottontails in shortgrass prairie dominated by blue grama (*B. gracilis*), buffalo grass (*Buchloe dactyloides*), four-wing saltbush (*Atriplex canescens*), rubber rabbitbrush (*Ericameria nauseosa*), and fringed sagebrush (*A. frigida*).

Mountain cottontails are often associated with sagebrush habitats, particularly in the northern part of their range (Dice 1926; Orr 1940; Powers and Verts 1971; McKay and Verts 1978b; Sullivan et al. 1989). In California, they were also observed in willow-dominated riparian areas, in cultivated fields, and in rocky ravines on the lower slopes of steep, bunchgrass-covered hills (Dice 1926). Orr (1940) suggested that mountain cottontails use rugged, rocky areas, such as hills, ridges, ravines, and canyons, in preference to plains and valleys. Rocky outcrops, which provide cover, are frequently cited as an important habitat feature for mountain cottontails (e.g., Orr 1940; Johnson and Hansen 1979; McKay and Verts 1978b; MacCracken and Hansen 1982).

Diet

Cottontails have highly variable diets that reflect the species' broad geographic ranges and diverse habitat associations (Chapman and Litvaitis 2003). The diets of cottontails also vary seasonally with changes in availability of plants. Cottontails primarily consume grasses and forbs during the growing season and the bark, buds, or branch tips of woody plants during the dormant season (Chapman and Litvaitis 2003). Cottontails may often consume cultivated crops or ornamental plants when available, though they are not generally considered to be major agricultural pests (Orr 1940; NRCS 1999; Chapman and Litvaitis 2003).

Eastern cottontails have primarily been studied in the eastern half of the U.S. (see Chapman et al. 1980 and Chapman and Litvaitis 2003). There is little information available concerning the eastern cottontail's diet in the western U.S. Eastern cottontails in Oklahoma primarily ate panic/rosette grass (*Panicum oligosanthes*), *Croton*, and composite dropseed (*Sporobolus asper*) in summer and panic/rosette grass, *Bromus* grasses, pussytoes (*Antennaria* spp.), and red cedar berries (*Juniperus virginiana*) in winter (Peitz et al. 1997).

The diets of desert cottontails have been studied in California (Orr 1940; Ingles 1941), Colorado (Hansen and Gold 1977; deCalesta 1979), Texas (Flinders and Crawford 1977; Scribner and Krysl 1982), and Arizona (Turkowski 1975). Desert cottontails in these studies consumed a wide variety of grasses (*Hesperostipa, Stipa, Festuca, Hordeum, Sporobolus, Poa, Holcus, Cynodon, Bromus, Bouteloua, Eragrostis, Dasyochloa, Agropyron*), sedges (*Cyperus* , *Carex, Eleocharis*), and rushes (*Juncus, Eleocharis*). Even broader arrays of forbs were recorded in desert cottontail diets, differing substantially among studies and regions. Woody plants and cacti found in desert cottontail diets included saltbush (*Atriplex* spp.), honey mesquite (*Prosopis glandulosa*), acacia (*Acacia* spp.), willows, and prickly pear (*Opuntia* spp.). Turkowski (1975) stated that desert cottontails are highly adaptable to drought and use cacti and succulent forbs as a source of water.

Mountain cottontails in northeastern California consumed sagebrush throughout most of the year but also ate juniper (*Juniperus* spp.) and appeared to prefer grasses when available in spring and summer (Orr 1940). In central Oregon, mountain cottontails generally ate *Bromus* grasses during spring, forbs and later-maturing grasses as *Bromus* matured and became less palatable, juniper during the peak of summer when more succulent foods were less available, and grasses (*Bromus* and *Agropyron*) when they sprouted after late summer rains (Verts et al. 1984). Mountain cottontails in that area were also observed climbing as high as 10 ft (3 m) in juniper trees in the early morning during summer to obtain moisture from wet or "waterlogged" foliage (Verts et al. 1984). The diets of mountain cottontails in Idaho consisted of grasses, including wheatgrass (*Agropyron* spp.), needle-and-thread (*Heterostipa comata*), cheatgrass (*Bromus tectorum*), bluegrasses (*Poa* spp.), and Indian ricegrass (*Stipa hymenoides*) (Johnson and Hansen 1979; MacCracken and Hansen 1984). Mountain cottontails in Idaho also consumed forbs, shrubs, and cacti, such as munro's globemallow (*Sphaeralcea munroana*), common winterfat (*Krascheninnikovia lanata*), big sagebrush (*A. tridentata*), and prickly pear.

Population Fluctuations and Densities

Cottontail densities of up to 8 per acre (ac) (20/hectare [ha]) have been reported for populations on islands or in enclosures (Chapman and Litvaitis 2003). Reported densities for free-ranging populations have ranged from 0.01 to 3.60 per ac (0.03–8.90/ha), depending on the species, season, and year (Fitch 1947; Flinders and Hansen 1973; Trent and Rongstad 1974; McKay and Verts 1978a; Chapman et al. 1982; Sullivan et al. 1989; Chapman and Litvaitis 2003).

Some authors have speculated that cottontail populations exhibit multi-annual cyclic fluctuations in abundance, similar to those reported for some hares and jackrabbits (Chapman and Litvaitis 2003). Cottontail populations indeed fluctuate among years;

however, hunter and road survey data do not indicate multi-annual periodicity in cottontail fluctuations (T. Esque et al. in prep.). A notable exception may have occurred in Wyoming, where hunter surveys indicated that population peaks have occurred every 7–10 years in recent decades (Fedy and Doherty 2011; also see Figure 3). It is possible that more noticeable periodicity in cottontail fluctuations would be evident elsewhere with longer-term data sets, at smaller spatial scales (i.e., not requiring broad geographic synchronicity among populations), and with data for individual cottontail species, rather than all cottontail species combined (i.e., not requiring synchronicity among species).

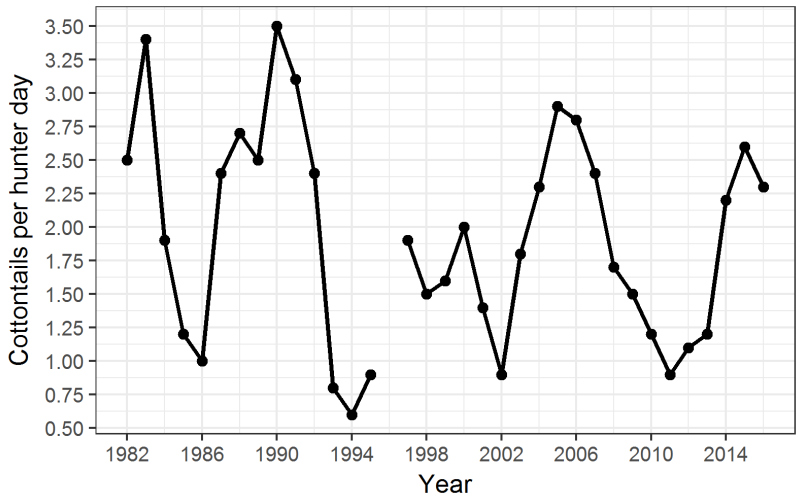

Figure 3: Cottontail rabbits (*Sylvilagus* spp.) harvest per hunter day in Wyoming from 1982–2016 (G. Frost, Wyoming Game and Fish Department, pers. comm.). Data was unavailable for the year 1996.

Influences on Abundance

Multi-annual fluctuations of cottontail populations were roughly synchronized with those of co-occurring black-tailed jackrabbits (*L. californicus*) in Idaho (Bartel et al. 2008) and greater sage-grouse (*Centrocercus urophasianus*) in Wyoming (Fedy and Doherty 2011). These findings suggest that these taxa are influenced by the same large-scale ecological phenomena, such as weather patterns or fluctuating densities of predators (Bartel et al. 2008; Fedy and Doherty 2011). Cottontail populations may also fluctuate among years in response to disease outbreaks or other factors that are more specific to leporids (Chapman and Litvaitis 2003).

Parasites and Diseases

Cottontails are hosts to a wide array of parasites and diseases (reviewed in Chapman 1974, Chapman and Willner 1978, Chapman et al. 1980, and Chapman and Litvaitis 2003). The incidence of tularemia (*Francisella tularensis*) and Rocky Mountain spotted fever (*Rickettsia rickettsi*) in cottontails and other leporids has been of particular interest to researchers, as those diseases can also infect humans (Chapman and Litvaitis 2003). Cottontails appear to rarely die from parasites or diseases, although tularemia is apparently fatal in nearly all cases (Chapman and Litvaitis 2003) and is potentially a cause

of rapid population declines (Jacobson et al. 1978). The effects of extreme cases of parasitic infection on cottontails may be similar to those for jackrabbits (e.g., Vorhies and Taylor 1933). For example, individuals are sometimes host to multiple botfly (*Cuterebra* spp.) larvae (e.g., Haugen 1942), which could be debilitating in some cases (see Vorhies and Taylor 1933 for effects on jackrabbits). Haugen (1942) reported that botfly larvae caused degeneration of the testes in two eastern cottontails. He also found that infection by a coccidian (protozoan) parasite was the cause of one captive eastern cottontail's death. Nonetheless, moderate parasite loads (defined as 5–6 individual parasites of ≥1 species) appeared to generally have little or no negative effect on rabbits in his study. Other studies, however, have suggested that endoparasites can negatively affect weight gain and reproduction by eastern cottontails (Yuill 1964; Jacobson et al. 1978).

Weather

Precipitation could influence cottontail populations through effects on both survival and reproduction. Production and survival of young mountain cottontails in Oregon appeared to be associated with amounts and timing of precipitation (McKay and Verts 1978a). In the same study area, researchers found that precipitation during pre- and post-natal development accounted for 30–64% of the variation in survival of young from the estimated mean date of birth to the end of the field season for 3 of 4 litter groups (Verts et al. 1984). If precipitation affects the production and survival of the first litter in early spring, it could subsequently influence the number of individuals in the population available to breed in the fall (Havera 1973; Applegate and Trout 1976). Drought in particular could reduce cottontail reproduction or survival by negatively impacting the availability and succulence of herbaceous foods (McKay and Verts 1978a; Verts et al. 1984; Sullivan et al. 1989). Some studies, however, have found no evidence that variation in precipitation influences abundances of cottontails (Wight 1959; Lightfoot et al. 2010).

Cold temperatures or snow accumulation could also affect cottontail populations. Severe weather may cause both mortality and delayed onset of breeding (Hamilton 1940; Wight and Conaway 1961; Conaway and Wight 1962). McKay and Verts (1978a) reported that losses of mountain cottontails in Oregon during autumn and winter of one year appeared to be associated with periods of low temperatures. Snow accumulation was associated with decreased weight of eastern cottontails in Michigan; apparently due to snow covering the rabbits' food supply (Haugen 1941). Snow cover could also make cottontails more vulnerable to predation by making them more visible or reducing their escape speed (Keith and Bloomer 1993; Brown and Litvaitis 1995).

Predators

Cottontails are prey for a variety of avian predators, including golden eagles, hawks (*Buteo* spp.), accipiters (*Accipiter* spp.), and great horned owls (*Bubo virginianus*); mammalian predators, such as coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), American badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and weasels (*Mustela* spp.); and both rattlesnakes (*Crotalus* spp.) and gopher snakes (*Pituophis catenifer*) (reviewed in Chapman 1974, Chapman and Willner 1978, and Chapman et al. 1980). Chapman and Litvaitis (2003:118) stated that "predation

is probably the major factor in the death of most cottontails, and is the primary direct cause of cottontail population regulation." Predators were responsible for 24 of 27 (85%) deaths of radio-tagged eastern cottontails in Wisconsin; the remainder were due to unknown causes (Trent and Rongstad 1974). Most (74%) of the mortalities in that study occurred during fall and winter and were apparently due to increased exposure to predators when shrubs lost their leaves and no longer provided concealment.

Recreational Hunting

Cottontails are important game animals in the U.S. (Chapman and Litvaitis 2003). In California, Arizona, and Colorado, tens of thousands—sometimes hundreds of thousands—of cottontails have been harvested each year in each state (D. Brown et al. in prep.). Less than ten thousand per year per state may be harvested in most other Western states (D. Brown et al. in prep.). We were unable to find information concerning effects of recreational hunting on cottontail populations.

Population Status

Eastern, desert, and mountain cottontails are all globally ranked as species of "least concern" by the International Union for Conservation of Nature (IUCN 2016); and globally and nationally "secure" by NatureServe (2015). NatureServe (2015) ranks the three species as secure or "apparently secure" in most western states (Appendix 1). However, eastern cottontails are ranked as "vulnerable" in New Mexico and Wyoming; desert cottontails are ranked as vulnerable in Oklahoma; and mountain cottontails are ranked as vulnerable in Arizona and "presumed extinct" in North Dakota (NatureServe 2015). These cottontail species are either not mentioned or are not recognized as being in need of conservation measures in most western states' Wildlife Action Plans or Conservation Strategies (Appendix 1). The exception is in Arizona, where two subspecies of mountain cottontail (*S. n. grangeri* and *S. n. pinetis*) are listed as "Tier 1B" (vulnerable) (AGFD 2012).

Despite their generally low conservation rankings, widespread declines in cottontail populations may be occurring (Chapman and Litvaitis 2003). Hunter success surveys in 5 of 15 western states (AZ, CA, KS, NE, and UT) showed significant downward trends through time, as did road surveys in three states (AZ, NE, and NM) (T. Esque et al. in prep.). No significant upward trends were apparent in long-term monitoring surveys for cottontails in the West. Some states may lack sufficiently long-term monitoring data for detection of statistically significant trends. For example, though a statistically significant trend was not evident (T. Esque et al. in prep.), hunter success data suggest a long-term downward trend in cottontail populations in Wyoming (Figure 3).

Habitat loss or degradation may constitute the greatest threat to cottontails in the western U.S. (Chapman and Litvaitis 2003). Homogenization of landscapes due to intensive agriculture or overgrazing by livestock may have caused declines of eastern cottontails in some portions of their range (Allen 1984; Chapman and Litvaitis 2003). Urban and agricultural development appear to threaten mountain cottontails in British Columbia, Canada (COSEWIC 2006). Widespread habitat loss could negatively affect mountain cottontails and other leporids associated with sagebrush, which is being converted to exotic

annual grassland in large portions of the western U.S. (see Management Considerations). Climate change is projected to cause substantial changes in the range, composition, and ecological functioning of native shrub and grass habitats in arid and semi-arid regions of the West and could therefore affect both leporids and golden eagles (Brown et al. 1997; Wagner 1999; Neilson et al. 2005; Weiss and Overpeck 2005).

Management Considerations

Cottontails are among the golden eagle's most important prey (see Importance to Golden Eagles). Management activities that increase cottontail populations could therefore indirectly benefit golden eagles. Cottontails are often managed to increase local populations for recreational hunters (Chapman and Litvaitis 2003). Broader conservation efforts may also be needed, however, as cottontails may be experiencing widespread declines (Chapman and Litvaitis 2003; see Population Status). Based both on management studies and the species' natural histories, cottontails likely generally benefit from management activities that maintain or enhance a mix of dense, low cover and openings with grasses and forbs (Chapman and Litvaitis 2003). In imperiled ecosystems, such as sagebrush steppe, management for abundant cottontail populations could potentially be incorporated into conservation strategies for multiple wildlife species, such as greater sage-grouse and jackrabbits.

Creating Cover in Exurban and Agricultural Areas

Intensive agriculture and urban development may have contributed to declines of some cottontail populations, particularly in the eastern and Midwestern U.S. (Chapman and Litvaitis 2003). In contrast, low-density human development could benefit cottontails in some areas. For example, in southwestern Arizona, Bock et al. (2006) found that desert and eastern cottontails were more abundant in low-density exurban neighborhoods than in rangelands with bunchgrasses, scattered shrubs, and forbs. The authors stated that this was likely due to increased cover provided by human structures and landscaping; especially in more open grasslands.

Creating brushpiles to provide cover has long been a primary management approach for eastern cottontails in exurban and agricultural areas (reviewed in Allen 1984 and Chapman and Litvaitis 2003). Brushpiles created for cottontails should be located near the edges of vegetation types that provide food but limited cover, such as fields or pastures; be at least 13–20 ft (4–6 m) in diameter and 3–7 ft (1–2 m) in height; be distributed 55–110 yards (50–100 m) from each other; and be replenished or replaced every few years, as they often lose their effectiveness as cover within 3–5 years (Chapman et al. 1982; Allen 1984).

Planting hedgerows has been another commonly used form of habitat improvement for eastern cottontails (reviewed in Allen 1984 and Chapman and Litvaitis 2003). Hedgerows can provide a valuable source of cover in otherwise open landscapes (Chapman and Litvaitis 2003). Thorny shrub species with low, dense canopies may be optimal for hedgerows intended to provide cover for cottontails (Chapman et al. 1982).

Increasing understory density in shelterbelts might also improve availability of cover for cottontails in agricultural landscapes (Swihart 1981; Chapman and Litvaitis 2003). In contrast with conifers, palatable shrubs planted in shelterbelts may also provide a source of food during winter (Swihart and Yahner 1983). Mowing between shelterbelt rows may be helpful if grass is dense and lacks spaces for cottontails to move through (Morgan and Gates 1983), whereas not mowing may allow establishment of preferred winter forage (e.g., *Ribes* spp. or *Rubus* spp.) (Swihart and Yahner 1982–83).

Setting Back Succession in Forests and Woodlands

Reducing tree canopy cover to facilitate growth of shrubs, grasses, or forbs is the primary management approach used to increase local populations of cottontails in the eastern U.S. (Chapman and Litvaitis 2003). The limited available information suggests that setting back succession in forests and woodlands is also beneficial to cottontails in the West.

In clearcut pine forest in eastern Texas, eastern cottontails were found in "all the stages of early second growth" but were most abundant 5–12 years after harvesting (Taylor and Lay 1944). Herbaceous vegetation was most diverse and abundant during this period. Subsequently, sapling pines and brushy hardwoods dominated the area and cottontails were replaced by other species.

In the oak-dominated cross timbers vegetation type in Oklahoma, eastern cottontails were in better physiological condition following both overstory removal with herbicides and subsequent prescribed burning (Lochmiller et al. 1995). The benefits of both types of disturbance appeared to be due to increased production and nutritional quality (e.g., protein content) of herbaceous foods, particularly forbs.

In pinyon-juniper woodlands in New Mexico, shrubs provided the primary cover for desert cottontails (Kundaeli and Reynolds 1972). The highest cottontail pellet numbers occurred in plots with a shrub density of approximately 85 per acre (210/ha). At high densities (>160/ac [395/ha]), live trees appeared to negatively influence habitat conditions for cottontails by suppressing shrubs. However, uprooting, piling, and burning of all trees in treated areas lowered use by cottontails. Down trees appeared to provide important sources of cover in areas with limited shrub cover. *Add mention of prevalence of P-J removal?*

In Southwest ponderosa pine (*Pinus ponderosa*) forests, cottontails may prefer small openings with abundant logging residue (Ffolliott 1990). Slash piles and dense shrub cover may improve habitat conditions for cottontails in managed ponderosa pine forests by increasing cover (Costa et al. 1976).

Livestock Grazing

It is unclear if reports of effects of livestock grazing on cottontails are contradictory or indicate that grazing has different effects, depending on the ecological setting, type of livestock, season or intensity of grazing, or other factors.

Multiple researchers have reported that cottontails were absent or occurred at relatively low densities in areas grazed by livestock. Crouch (1982) reported that (*species*) cottontails

were relatively abundant on ungrazed bottomlands along a river in northeastern Colorado but were "almost nonexistent" in grazed areas (*type of livestock*). In southern Arizona, densities of cottontails (species not reported) appeared to be consistently higher in ungrazed plots than in plots grazed by cattle (Taylor et al. 1935). In southeastern Arizona, Bock et al. (2006) found that desert and eastern cottontails were more abundant on ungrazed than grazed lands (cattle, cattle and horses, or sheep). Ungrazed areas had taller ground cover than grazed areas. In southeastern Idaho, mountain cottontails were less abundant in areas grazed by sheep and cattle than in areas closed to grazing for at least 25 years (MacCracken and Hansen 1982). MacCracken and Hansen (1984) speculated that heavy grazing by livestock reduced the availability of forage for cottontails in the study area. In eastern Texas, Taylor and Lay (1944) found that eastern cottontails were more numerous in areas where livestock grazing was light or absent (type of livestock not reported). The next highest abundance was in an area that was moderately grazed (not described).

Sightings of desert cottontails in the Chihuahuan Desert in New Mexico did not significantly differ between conservatively versus more heavily grazed rangelands (30–35% vs. 40–45% use of key forage species by cattle) (Nelson et al. 1997). Shrub and grass cover were similar on the two types of rangeland. In shortgrass prairie in Colorado, desert cottontails were more abundant in moderately grazed pastures (27–30 yearling heifers/320 ac pasture) than in lightly (20/pasture) or heavily (45/pasture) grazed pastures (Flinders and Hansen 1975). Flinders and Hansen (1975) noted that, in the moderately grazed pastures, cattle tended to lightly or moderately browse four-wing saltbush, causing the foliage to grow more densely and provide better cover for cottontails. Together, these two studies suggest that effects of livestock grazing on cottontails could vary depending on whether and how grazing influences plants used for food and cover.

Fire and Invasive Grasses

Millions of acres of shrublands and grasslands across the West have been invaded by cheatgrass, red brome (*B. madritensis, B. rubens*), and other exotic annual grasses (Pellant and Hall 1994; Salo 2004). In western shrublands and grasslands, continuous fuel provided by annual grasses has fostered the spread of fires far larger than those that occur in areas dominated by native vegetation or that typified the pre-settlement period (Brooks and Pyke 2001; Keane et al. 2008; Balch et al. 2013; Brooks et al. 2016). Many areas of the West are now locked in a grass/fire cycle, wherein fire-adapted annual grasses facilitate fires, which kill sagebrush and other fire-intolerant native competitors, and thereby promote even greater spread of annual grasses (D'Antonio and Vitousek 1992; Brooks et al. 2004; Balch et al. 2013).

In shrub-steppe ecosystems, leporids are typically among the golden eagle's primary prey (reviewed in Bedrosian et al. 2017). Research in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho indicated that the grass/fire cycle has caused large-scale habitat loss for leporids and thereby negatively affected golden eagles (Kochert and Pellant 1996; USDI 1996). Golden eagle reproduction in the NCA was initially negatively impacted by declines in leporids following major wildfires and loss of shrub cover in the 1980s and 1990s but then rebounded after a few years; apparently due to eagles switching to alternate foraging habitats and prey (Marzluff et al. 1997; Kochert et al. 1999; Heath and Kochert 2016). However, the number of golden eagle territories in the

NCA has substantially declined since the mid-1970s, possibly due primarily to declining jackrabbit populations (USDI 1996; Kochert and Steenhof 2013). Remaining golden eagles in the NCA may be at greater risk of mortality than prior to fires. Heath and Kochert (2016) found that, after major fires, eagles in the NCA switched from jackrabbits and mountain cottontails to a variety of other prey, including rock pigeons, which are carriers of trichomaniasis, an often fatal disease. Forty-one percent of golden eagle nestlings in the NCA and surrounding area recently tested positive for the protozoan that causes trichomaniasis (Dudek and Heath 2015).

Preventing or interrupting loss of leporid habitat to the grass/fire cycle could be crucial to the conservation of golden eagles in the western U.S. (USFWS 2016). Conservation of leporids and other prey is largely concordant with existing strategies for preserving or restoring habitat for protected wildlife species, such as greater sage-grouse and Brewer's sparrows (*Spizella breweri*) (e.g., GBBO 2010; RISCT 2012; BLM 2015). However, it is possible that, at finer scales, management prescriptions to benefit these species differ from those that are optimal for cottontails and other golden eagle prey.

Information Gaps

- Additional studies are needed to determine how cottontails influence golden eagles. Distinguishing between cottontails and jackrabbits in golden eagle diets, rather than lumping them as leporids, could help better elucidate the relative influence of cottontails on golden eagles. Little is known about golden eagle diets during the nonbreeding season, including the potential importance of cottontails versus other prey.

- Most of what is known about eastern cottontails is limited to the eastern half of the U.S. Additional research of eastern cottontail diets, habitat associations, and responses to management activities is needed in the western U.S.

- The status of cottontail populations in the western U.S. is poorly known. Cottontails are generally ranked as being of low conservation priority. However, experts on cottontails have suggested that widespread population declines are occurring in North America. This suggestion is supported by hunter success and road survey data from multiple western states.

- In the last several decades, recreational hunters in western states have harvested anywhere from thousands to more than a million cottontails (e.g., California in the 1960s) per state per year. The effects of large-scale harvesting on cottontail populations is unclear.

- Some researchers have suggested that cottontails exhibit cyclic multi-annual population fluctuations but there is little evidence supporting this and true cycles may be limited to specific geographic populations. Studies limited to individual species and populations may be needed to determine whether pronounced periodicity occurs in cottontail populations.

- Weather appears to influence cottontail behavior and demography in a variety of ways. The potential impacts of climate change on cottontails therefore merits further study.

- In contrast with some other mitigation measures, such as retrofitting power poles, there are currently no quantitative standards for using prey enhancement to mitigate take of golden eagles. A before-after-control-impact (BACI) study design could be used to assess the effects of habitat enhancement protocols for cottontails and other prey. BACI studies should take into account potential periodicity in cottontail populations and related fluctuations in golden eagle reproduction.

- Cottontails have traditionally been managed as game for recreational hunters. However, their importance to golden eagles, other predators, and ecosystem functions, as well as evidence of declining populations and habitats, indicate that they merit additional research and inclusion in conservation planning. Furthermore, the threats facing cottontails in many shrubland and grassland ecosystems also impact other wildlife species of conservation concern (e.g. greater sage-grouse), suggesting that cottontail management can be linked to existing conservation plans for imperiled landscapes and protected wildlife species.

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Appendix 1: Conservation Status of Cottontails in the Western United States.

Location	NatureServe Status	State Wildlife Action Plan/ Conservation Strategy	State Hunting (season; limit)
Global	Secure	N/A	N/A
United States	Secure	N/A	N/A
Arizona	Secure (*S. audubonii, S. floridanus*); Vulnerable (*S. nuttallii*)	Tier 1B—vulnerable (*S. nuttallii*)	Open all year; 10/day
California	Unranked	No mention	Jul 1–end of Jan; 5/day
Colorado	Secure (*S. nuttallii, S. floridanus*); Apparently secure (*S. audubonii*)	No mention	Oct 1–end of Feb; 10/day
Idaho	Secure	No mention	Aug 30–end of Feb; 8/day
Kansas	Secure (*S. floridanus*); Apparently secure (*S. audubonii*)	No mention	Open all year; 10/day
Montana	Apparently secure	No mention	Open all year; no limit
Nebraska	Secure (*S. floridanus*); Apparently secure (*S. audubonii*)	Non-tier (not at risk)	Sep 1–end of Feb; 7/day
Nevada	Secure	Not a species of conservation priority	2nd Sat in Oct–end of Feb; 10/day
New Mexico	Secure (*S. audubonii*); Apparently secure (*S. nuttallii*); Vulnerable (*S. floridanus*)	No mention	Open all year; no limit
North Dakota	Unranked (*S. audubonii, S. floridanus*); Presumed extinct (*S. nuttallii*)	No mention	Open all year; no limit
Oklahoma	Secure (*S. floridanus*); Vulnerable (*S. audubonii*);	Not a species of greatest conservation need	Oct 1–Mar 15; 10/day
Oregon	Apparently secure (*S. nuttallii*); Not applicable (*S. floridanus*)	No mention	Open all year; no limit
South Dakota	Secure (*S. audubonii, S. floridanus*); Apparently secure (*S. nuttallii*)	Not a species of greatest conservation need	Sep 1–end of Feb; 10/day
Texas	Secure	No mention	Open all year; no limit
Utah	Secure	No mention	Sep 1–end of Feb; 10/day
Washington	Secure (*S. nuttallii*); Not applicable (*S. floridanus*)	No mention	Sep 1–Mar 15; 5/day
Wyoming	Secure (*S. audubonii, S. nuttallii*); Vulnerable (*S. floridanus*)	Not a species of greatest conservation need	Sep 1–Mar 1; 10/day