WESTERN WILDLIFE

THE JOURNAL OF THE WESTERN SECTION OF THE WILDLIFE SOCIETY

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VOLUME 5 • 2018

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Coastal Vegetation Communities Affect Mesocarnivore Activity in Northern California Dune Ecosystems

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Abstract.—Dune restoration (i.e., removing invasive plant species) may influence mesocarnivore activity on the coastal dunes of Northern California. A previous study suggested mesocarnivores preferred restored areas where European Beachgrass (*Ammophila arenaria*) was removed over areas heavily vegetated with this invasive plant, but that study may have been confounded by distance to coastal forest. The aim of our study was to examine the effects of proximity to coastal forest and cover types on mesocarnivore activity in the coastal dunes. We deployed 20 motion-sensitive cameras for four weeks within the Ma-le'l Dunes Cooperative Management Area in Humboldt County, California, along transects that varied in local habitat composition and distance to nearby coastal forest. We treated photographs of the same species of mesocarnivore as separate detections if they were separated in time by at least 60 min, and we used the detection rate (total number of detections per number of viable camera checks) as an index of mesocarnivore activity. Model selection results indicate that both distance to forest and amount of Beach Pine (*Pinus contorta contorta*) habitat near a camera were important factors in mesocarnivore detection rates. We found a negative correlation between distance to forest and detection rate of mesocarnivores. Mesocarnivores may build their dens within the forest and enter the dunes to forage, thus their activity is likely highest close to the forest. Beach Pine stands may serve as cover for mesocarnivores as they forage within the dunes. By understanding these relationships, dune managers in this area can better evaluate management practices and invasive species removal.

Key Words.—*Ammophila arenaria*; camera traps; coastal dunes; European beachgrass; habitat use; Northern California; mesocarnivores

Introduction

Habitat and prey availability are factors that influence mesocarnivore habitat use (Ross et al. 2012). Invasive plants may change rodent predator avoidance behaviors and have influences up the trophic web (Johnson and De León 2015). In an experiment using artificial food trays, Johnson and De León (2015) showed that rodents may perceive less predation risk due to the cover provided by European Beachgrass (*Ammophila arenaria*, hereafter beachgrass), which can grow up to a meter in height.

Indeed, Delgado de la Flor and Johnson (2015) found that despite lower small mammal abundance in areas where invasive beachgrass had been removed, mesocarnivore activity was significantly higher in these areas, suggesting that habitat restoration could benefit the mesocarnivore community. However, the spatial extent of their study was constrained to make use of ongoing beachgrass removal, and they acknowledged that their results could have been confounded by the fact that the restored area was closer to coastal forest (Delgado de la Flor and Johnson 2015). Moreover, the dune landscape is a mosaic of several habitats, including small dense patches of Beach Pine (*Pinus contorta contorta*), dune mat (low-growing vegetation), and shrubs. Forests and densely vegetated habitats can provide important cover for mesocarnivores and could thereby affect their use of nearby open habitats, such as those in coastal dunes. Forest cover, type, and proximity are known to impact mesocarnivore habitat use in other areas (Lesmeister et al. 2015).

The term mesocarnivores refers to small to mid-sized mammalian carnivores (Roemer et al. 2009). Their diets typically include a broad variety of prey, and they far outnumber large specialist carnivores in abundance (Prugh et al. 2009; Roemer et al. 2009; Delgado de la Flor and Johnson 2015). They exhibit tremendous variation among species in terms of primary food, foraging style, and habitat associations. Within our study area in the coastal dunes of Humboldt Bay, Gray Foxes (*Urocyon cinereoargenteus*), North American Raccoons (*Procyon lotor*), and Striped Skunks (*Mephitis mephitis*) are common nocturnal mesocarnivores that prey on rodents (Delgado de la Flor and Johnson 2015). Feral Cats (*Felis catus*) are also a common introduced mesocarnivore to this area.

We examined the hypothesis that mesocarnivore activity in coastal dunes is positively influenced by forest habitats. We tested the predictions that mesocarnivore detection rates at camera traps decrease with increasing distance from coastal forest edge, and increase with increasing proportion of Beach Pine habitat within 50 m of cameras. We also sought to provide managers with an index of mesocarnivore species presence, including both native species and invasive Feral Cats. Understanding the mechanisms for apparent responses of mesocarnivores to habitat is valuable for biologists, conservationists, and managers who are concerned with habitat selection
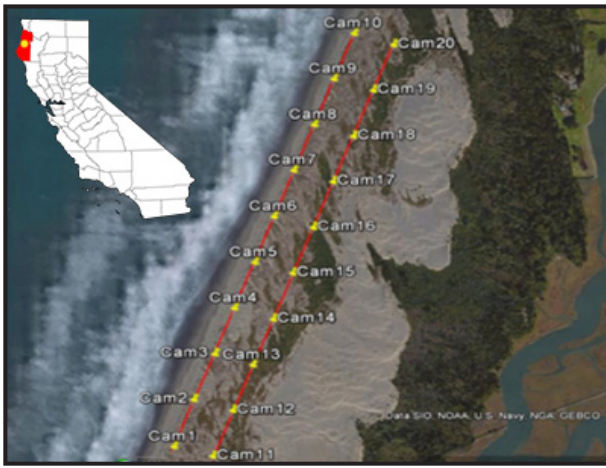
Figure 1. Camera trap site locations from 28 September to 30 October 2015 in the Ma-le'l Dunes Cooperative Management Area, Humboldt County, California, USA. The dark green band of habitat on the right side of the figure is the coastal forest. Its meandering western edge ensured a large range of distances to forest among the 20 cameras distributed among two transects (range 165–543 m). The inset map of California shows the location of Humboldt County (in red), and our study area (yellow dot).

and quality, the long-term protection of this area, and continuing efforts to remove beachgrass and conserve native wildlife.

Methods

Study site.—We studied the mesocarnivore community in the Ma-le'l Dunes Cooperative Management Area (CMA) and the Lanphere Dunes of the Humboldt Bay National Wildlife Refuge located on the North Spit of Humboldt Bay near the town of Manila in Humboldt County, California, USA (Fig. 1). This area is managed by the U.S. Bureau of Land Management (BLM) and the U.S. Fish and Wildlife Service (USFWS). The dune landscape is a mosaic composed of six habitats. For the purpose of this study, we defined these unique habitats using information from Buell et al. (1995) and Pickart and Barbour (2007). From the ocean moving inland there are: (1) beach comprising the open strip of sand immediately adjacent to the ocean; (2) native foredune grassland comprising dunes running parallel to the beach with vegetated dune ridges dominated by the native grass *Elymus mollis mollis*; (3) dune mat habitat comprising a community of over 40 low-growing herbaceous and suffrutescent native plant species (Buell et al. 1995; Pickart 1988), including Coastal Sagewort (*Artemisia pycnocephala*), Beach Bur-sage (*Ambrosia chamissonis*), Pink Sand Verbena (*Abronia umbellata brevifolia*), and Beach Pea (*Lathyrus littoralis*; Sawyer et al. 2009; NatureServe 2005); (4) herbaceous wet swales that are dominated by Dune Sedge (*Carex obnupta*) and Pacific Silverweed (*Potentilla anserina*) and woody wet swales that are dominated by Coastal Willow (*Salix*

hookeriana); (5) open dunes with little to no vegetation; and (6) dense forest stands dominated by Beach Pine, Sitka Spruce (*Picea sitchensis*), and Grand Fir (*Abies grandis*). To better understand the role of distance to forest as a confounding effect on mesocarnivore habitat use, our sampling design focused on mesocarnivore use of the dune mat habitat, which in some places is heavily invaded by beachgrass that commonly outcompete native plants. In the northern portion of the Ma-le'l Dunes CMA and Lanphere Dunes, beachgrass has been removed and the dune mat habitat restored. In this area, dune restoration has occurred and been maintained since the 1980s across more than 11.3 km of coastline in Humboldt and Del Norte counties (Pickart 2013; U.S. Fish and Wildlife Service. 2017. Dune Restoration - Humboldt Bay. Available at https://www.fws.gov/refuge/Humboldt_Bay/wildlife_and_habitat/DunesRestoration.html. [Accessed 10 July 2017]).

Sampling scheme.—We deployed 20 cameras on two transects (10 cameras per transect) within our study area. The cameras varied in brand, with each brand present on each transect: StealthCam STC-G30NGK (StealthCam, Grand Prairie, Texas, USA); Trophy Cam® (Bushnell Outdoor Products, Overland Park, Kansas, USA); and Wild Game Innovations x4x (Wild Game Innovations, Grand Prairie, Texas, USA). The model type of each camera did not influence placement and we distributed model types haphazardly at the stations such that each camera model had a wide range of distance to forest and local habitat conditions. After deployment, we confirmed there were no differences in the distribution of camera models with respect to transect number, local habitat, or distance to forest. We set cameras to take three photos in a series, on high sensitivity, and to wait 60 s before the next series of photos. Transect 1 followed the crest of the foredune grassland and transect 2 was 100 m east of, and parallel to, transect 1. We placed cameras 200 m apart along each transect. We offset northing positions of camera stations in the two transects by 100 m to alternate the camera stations and minimize attracting an animal from one camera station to the next (Fig. 1). Although the two transects were parallel to each other, the meandering edge of the forest (dark green in Fig. 1) provided variation in distance from each camera station to the nearest forest edge both within and between the transects. The meandering edge of the forest also ensured that distance to forest was not simply the inverse of distance to shoreline, which is a straight edge parallel to the two transects. We measured the distance from each camera station to the nearest forest edge using images from Google Earth (Version 7.7.8.3036) and used these data to investigate the relationship between mesocarnivore activity and proximity to forest.

We avoided placing cameras near tall or thick vegetation to reduce false triggers. In the event that the proposed coordinates of a camera station were placed
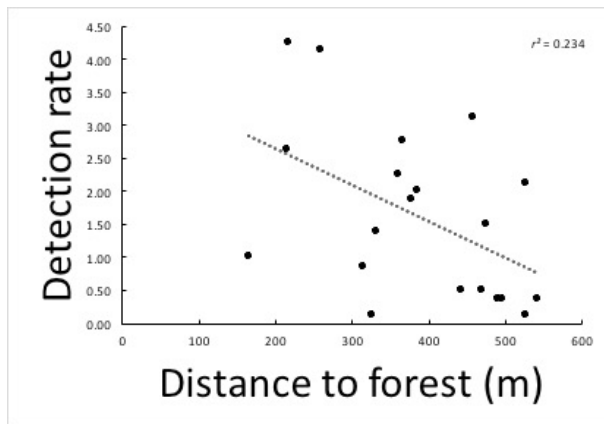
FIGURE 2. Relationship between mesocarnivore detection rate (total number of detections per number of viable camera checks) and distance to forest from 28 September to 30 October 2015 in Ma-le'l Dunes Cooperative Management Area, Humboldt County, California, USA.

in thick vegetation, we moved the camera station to the closest open area within the dune mat. We mounted each camera on a rebar pole 0.5 m above the ground, facing north, and directed the camera at bait placed 3–6 m away. We baited each camera station with a 142 g can of chicken meat. We punched three holes into each can to attract mesocarnivores and we secured each can to the ground with four stakes.

We deployed cameras 28 September 2015 and retrieved them 30 October 2015. We checked all camera stations every 4 d over a period of four weeks. We exchanged memory cards and bait cans when checking cameras. In February 2016, we revisited each camera station location to assess the vegetation cover surrounding each station. We visually estimated the percentage cover of each of the six vegetation types (to nearest 10%) in each quadrant of a 50 m circle centered upon the camera station, then averaged the quadrants to yield the percentage cover within the 50 m radius.

Analysis.—After each camera check, we sorted the photographs from each camera to determine mesocarnivore activity and distinguish false triggers from actual mesocarnivore captures. We treated photographs of the same species of mesocarnivore as separate detections if they were separated by at least 60 min, and we used the detection rate as an index of mesocarnivore activity. In a few cases (see Results), cameras malfunctioned, so we used the total number of detections per number of viable camera checks as our index of activity. We used linear regression to compare detection rates over time. We analyzed the data in Program R using detection rate as our response variable in linear correlation models to test for the effects of distance to forest and amount of local Beach Pine habitat on mesocarnivore activity (R Developmental Core Team 2008). We performed analyses on all mesocarnivore species pooled, and species-specific analyses for Feral Cat, Striped Skunk,

and Gray Fox (the three most commonly detected species). For each response variable, we created four a priori candidate models: detection rate as a function of distance to forest, percentage Beach Pine within 50 m radius, both factors, or neither (intercept only). We compared models using Akaike's Information Criterion corrected for small sample size (AICc) and selected the best model based on the lowest AICc value (Burnham and Anderson 2003).

RESULTS

There were two instances (of 160 camera checks) in which cameras failed either due to battery loss or positioning error. We excluded these sampling sessions from our analyses. Therefore, our results are based on 158 viable camera checks. There were 253 mesocarnivore detections on the cameras of which 36.4% were Feral Cat, 36.0% were Striped Skunk, 23.3% were Gray Fox, 4.0% were Virginia Opossum (*Didelphis virginiana*), and 0.4% were North American Raccoon. There were also several non-carnivore species detected, such as Black-tailed Jackrabbits (*Lepus californicus*), Common Raven (*Corvus corax*), and a number of unidentified bird and mice species. Detection rate did not significantly increase or decrease over the 28-d study period (eight checks, $F_{1,7} = 3.78$, $P = 0.100$).

The highly irregular forest edge provided a wide range of distances to forest among the 20 camera stations (165–543 m; mean ± SD = 387.6 ± 114.0 m). The percentage cover values of each of the six vegetation types ranged from 0–65% cover (16.7 ± 12.58%). There was a negative correlation between detection rate of all mesocarnivores and distance to forest ($r = -0.484$, $t = -2.344$, df = 19, $P = 0.031$), and a positive correlation with percentage of Beach Pine habitat within a 50 m radius ($r = 0.488$, $t = 2.370$, df = 19, $P = 0.029$). Analysis of these factors using the detection rate of individual species yielded correlations in the same directions, but were only significant for distance to forest and skunk detection rate ($r = -0.476$, $t = -2.294$, df = 19, $P = 0.034$) and percentage of Beach Pine and Feral Cat detection rate ($r = 0.570$, $t = 2.945$, df = 19, $P = 0.009$). The percentage of Beach Pine and distance to forest were not significantly correlated with each other ($t = -1.759$, df = 19, $P = 0.096$).

Model selection results indicate that both distance to forest and percentage of Beach Pine are important factors in mesocarnivore detection rates (Table 1). Although the single best model for total mesocarnivore detection rate included only distance to forest (Fig. 2), the models with Beach Pine were also competitive (within 2 AICc), and all fit the data more strongly than did the null model. The top model explained 34.3% of the null deviance. Distance to forest was also the single best variable for predicting the detection rate of Striped Skunks and Gray Foxes, though other models were also competitive. Percentage of Beach Pine within 50 m was the best

TABLE 1. Model selection results for generalized linear models of remote camera detection rates for all mesocarnivores and individual mesocarnivore species as predicted by distance to coastal forest and the percent of Beach Pine habitat within 50-m radius of a camera. Data were collected from 28 September to 30 October 2015 in Ma-le'l Dunes Cooperative Management Area, Humboldt County, California, USA. First entries are top models in a candidate set, though in several cases other models were also competitive (within 2 AICc).

Model	Deviance	AICc	wt	r^2
All mesocarnivores				
Distance to forest	23.764	67.706	0.146	0.241
Percent Beach Pine	23.998	67.902	0.130	0.234
Distance forest + Beach Pine	20.566	67.982	0.721	0.343
Null (intercept only)	31.309	70.427	0.003	
Striped Skunk				
Distance to forest	4.450	34.199	0.417	0.225
Distance forest + Beach Pine	4.055	35.506	0.217	0.294
Percent Beach Pine	4.711	35.342	0.235	0.180
Null (intercept only)	5.744	36.512	0.131	
Feral Cat				
Percent Beach Pine	4.352	33.754	0.706	0.327
Distance forest + Beach Pine	4.230	36.356	0.192	0.346
Null (intercept only)	6.469	38.890	0.054	
Distance to forest	5.697	39.141	0.048	0.119
Gray Fox				
Distance to forest	2.243	20.502	0.436	0.146
Null (intercept only)	2.628	20.874	0.362	
Distance forest + Beach Pine	2.243	23.668	0.089	0.146
Percent Beach Pine	2.567	23.200	0.113	0.023

predictor of Feral Cat detection rate, and this model was the most competitive among the candidate set.

DISCUSSION

We hypothesized that mesocarnivore activity in coastal dunes is affected by nearby forest habitats. Our findings support this hypothesis. There was significantly more activity of mesocarnivores closer to the forest and also in places with high percentages of Beach Pine habitat within 50 m. Results were strongest for skunks and distance to forest, and for Feral Cats and percentage of Beach Pine. However, it is important to note that our results are entirely correlative and cannot confirm or refute causation. Additional studies involving telemetry would better reveal how mesocarnivore foraging behavior varies with distance to forest and local habitat in this study system.

Mesocarnivores may be attracted to the coastal forest strip and to patches of Beach Pine habitat because they provide access to cover and potential denning sites (Pineda-Guerrora et al. 2015). These species may leave the core of their home ranges in forest and pine patches to forage for prey, such as small rodents, that are known to inhabit the dunes (Elbroch and Allen 2013; Delgado de la Flor and Johnson 2015). The open dune habitat

offers few if any denning sites, and most mesocarnivores probably rely on the forest for cover and dens. Because skunks have smaller home ranges than foxes, raccoons, and cats (Tucker 1988; Beasley et al. 2007; Horn et al. 2011; Rosatte et al. 2011), they may be less likely to travel farther from their core use areas in cover when foraging, which could explain why the effect of distance to forest was strongest for skunks in our study. Different microclimates within the habitats may also influence species habitat usage (Červinka et al. 2011).

Delgado de la Flor and Johnson (2015) concluded that restoring dune mat habitat by removing beachgrass likely increases mesocarnivore activity. However, our results suggest that some of their findings may be influenced by their study area, where restored dunes tended to be closer to forest habitats than unrestored and invaded habitats. Thus, we recommend future studies seek to further resolve this complexity, perhaps by using telemetry to track individual animals and determine their home range, habitat use, and visitation to cover habitats and dune mat vegetation.

Our intent was to obtain an index of activity, rather than estimate abundance or occupancy. Our camera stations were relatively close to each other (about 200 m), they were baited, and they were checked frequently (every 4 d) over a short time period (28 d). Therefore,

although our data structure is technically appropriate for an occupancy analysis, such an analysis is not informative because all stations were occupied (detected one or more mesocarnivores) and it is likely that the same individual carnivore was detected at more than one station. We could make better use of the data by analyzing variation in the number of detections, with the assumption that higher detection rates indicate greater mesocarnivore activity. With our design, it is possible that opportunistic individual animals cued into the array of baited camera stations. However, we detected no statistically significant trend in the detection rate over time.

Our results should only be interpreted within the limited spatial and temporal extent of our study. Different camera models may have introduced heterogeneity based upon different sensitivities between camera types. Our cameras were relatively close together, and in most cases, we could not identify individual animals. However, in one case we identified the same cat visiting multiple camera stations during our study. Therefore, our detection rate does not provide a measure of mesocarnivore abundance; rather, it serves as an index of mesocarnivore activity.

Mesocarnivores hold important ecological roles within plant and animal communities (Roemer et al. 2009). These species can have major influences on population sizes of birds, rodents, and other prey species, and understanding these relationships provides critical information for conservation planning (Červinka et al. 2011). Our relatively high number of Feral Cat detections (36.4% of total mesocarnivore detections; although likely only a few individuals because a single animal likely visited multiple stations in a single night) is also noteworthy and was markedly higher than the recent study (only 11% of all detections; Delgado de la Flor and Johnson 2015). Along with Striped Skunk, detections of Feral Cats were the most numerous in our study. Our camera stations were at least 2.2 km from the nearest residential area suggesting that Feral Cats may penetrate into coastal dunes, or they may live there permanently. These cats likely influence numerous prey communities, rodents and especially ground-nesting birds. Future work should be aimed at understanding effects of this introduced predator in this system.

Literature Cited

Beasley, J.C., T.L. Devault, and O.E. Rhodes, Jr. 2007. Home-range attributes of Raccoons in a fragmented agricultural region in northern Indiana. Journal of Wildlife Management 71:844–850.

Buell, A.C., A.J. Pickart, and J.D. Stuart. 1995. Introduction history and invasion patterns of *Ammophila arenaria* on the north coast of California. Conservation Biology 9:1587–1593.

Burnham, K.P., and D.R. Anderson. 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media, Berlin, Germany.

Červinka, J., M. Šálek, P. Pavluvčík, and J. Kreisinger. 2011. The fine-scale utilization of forest edges by mammalian mesopredators related to patch size and conservation issues in Central European farmland. Biodiversity and Conservation 20:3459–3475.

Delgado de la Flor, Y.A., and M.D. Johnson. 2015. Influence of invasive European Beachgrass on mesopredator activity in the coastal dunes of Northern California. Western Wildlife 2:29–34.

Elbroch, L.M., and M.L. Allen. 2013. Prey indices and behaviors at a Gray Fox den in San Mateo County, California. Western North American Naturalist 73:240–243.

Horn, J.A., N. Mateus-Pinilla, R.E. Warner, and E.J. Heske. 2011. Home range, habitat use, and activity patterns of free-roaming domestic cats. Journal of Wildlife Management 75:1177–1185.

Johnson, M.D., and Y.L. De León. 2015. Effect of an invasive plant and moonlight on rodent foraging behavior in a coastal dune ecosystem. PloS ONE, 10(2). https://doi.org/10.1371/journal.pone.0117903.

Lesmeister, D.B., C.K. Nielsen, E.M. Schauber, and E.C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. Wildlife Monographs 191:1–61.

NatureServe. 2005. NatureServe Explorer: An Online Encyclopedia of Life. Version 4.5 NatureServe, Arlington, Virginia. http://explorer.natureserve.org/.

Pickart, A.J. 1988. Dune revegetation at Buhne Point. Fremontia 16:3–5.

Pickart, A.J. 2013. Dune restoration over two decades at the Lanphere and Ma-le'l Dunes in northern California. Pp. 159–171 *in* Restoration of Coastal Dunes. Springer Series on Environmental Management. Martínez, M.L., J.B. Gallego-Fernández, and P.A. Hesp (Eds.). Springer, Berlin, Germany.

Pickart, A.J., and M.G. Barbour. 2007. Beach and dune. Pp. 155–173 *in* Terrestrial Vegetation of California. Barbour, M.G, T. Keeler-Wolf, and A.A. Schoenherr (Eds.). University of California Press, Berkeley, California.

Pineda-Guerrora, A., J.F. González-Maya, and J. Pérez-Torres. 2015. Conservation value of forest fragments

for medium-sized carnivores in a silvopastoral system in Colombia. Mammalia: International Journal of the Systematics, Biology & Ecology of Mammals 79:115–119.

Prugh, L.R., C.J. Stoner, C.W. Epps, W.T. Bean, W.J. Ripple, A.S. Laliberte, and J.S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Roemer, G., M. Gompper, and B. Van Valkenburgh. 2009. The ecological role of the mammalian mesocarnivore. BioScience 59:165–173.

Ross, S., B. Munkhstog, and S. Harris. 2012. Determinants of mesocarnivore range use: relative effects of prey and habitat properties on Pallas's Cat home-range size. Journal of Mammalogy 93:1292–1300.

Rosatte, R., P. Kelly, and M. Power. 2011. Home range, movements, and habitat utilization of Striped Skunk (*Mephitis mephitis*) in Scarborough, Ontario, Canada: disease management implications. Canadian Field-Naturalist 125:27–33.

Sawyer, J.O., T. Keeler-Wolf, and J. Evens. 2009. Manual of California Vegetation. California Native Plant Society Press, Sacramento, California.

Tucker, R. L. 1988. Home range size and habitat use of Gray Foxes on the Copiah County Wildlife Management Area in Mississippi. Dissertation Abstracts International. Section B: Physical Sciences and Engineering 49:591–591.

The members of this team included seven undergraduate students, a graduate student, and a professor from the Wildlife Department of Humboldt State University (HSU), Arcata, California. Pictured above left to right are Matthew Johnson (Professor at HSU), undergraduate students: Elizabeth Meisman, Mark Sampson, Claire Bortot, Lauren Enriquez, Sean Ihle, and Colleen Herr. This project was completed through class and group projects within two courses: Wildlife Techniques and Upland Habitat Ecology and Management. All members are passionate about conservation and interested in monitoring impacts of habitat restoration on wildlife populations. (Photographed by Matthew Delgado).

Notes

Mass Mortalities of Migratory Mule Deer (*Odocoileus hemionus*): Implications for Ecosystem Function, Conservation, or Management?

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Abstract.—Mass mortality events involving migratory Mule Deer (*Odocoileus hemionus*) in natural settings rarely have been reported. I describe two such events that occurred in the Sierra Nevada, California, during the fall migration in 2017. In both cases, large numbers of Mule Deer fell to their deaths while attempting to cross patches of ice-covered rocky terrain, a result of heavy snowfall the previous winter that persisted through summer. Heavy snowfall appears to be a precursor to mass mortality events and, if that is the case, snowpack records indicate such losses could occur more often than previously recognized. I discuss mass mortality events among Mule Deer in the context of ecosystem function and their potential relationship to life histories of two scavenging carnivores (*Gulo gulo* and *Vulpes vulpes*), and the hypothetical implications of those events for management and composition of populations of migratory Mule Deer.

Key Words.—accident; *Gulo gulo*; Red Fox; Sierra Nevada; snowpack; *Vulpes vulpes*; Wolverine

Migration is a widespread, and in some cases a threatened, phenomenon throughout the animal kingdom (Berger 2004; Wilcove 2008; Dingle 2014). In general, migratory behavior can be viewed as a basic response to adversity (Taylor and Taylor 1977), and likely evolved as an adaptation to variability in the environment (Baker 1978). Moreover, migratory behavior will be adaptive if individuals occupying specific ranges at certain times of the year achieve fitness gains greater than those incurred by resident (i.e., nonmigratory) individuals (Avgar et al. 2014).

Explanations for prehistoric mass mortality events have been varied and diverse (Keim 1969; Guthrie 1990), but often are attributed to natural deaths in a rigorous environment (Pewe 1975). Descriptions of contemporary mass mortality events are encountered infrequently (Berger 1983), but recently have been reported for several migratory artiodactyls, among which are Saiga Antelope (*Saiga tatarica*; Kock et al. 2018), Wildebeest (*Connochaetes taurinus*; Subalusky et al. 2017), Reindeer (*Rangifer tarandus*; Henrik Libell, unpubl. report), and Mule Deer (*Odocoileus hemionus*; Jones 1954; Bleich and Pierce 2001). As a result, the potential role of mass mortality events in ecosystem function is receiving increased attention (Pennisi 2017). In this note, I add to the literature on mass mortality events, and consider their potential role in ecosystem function and in the conservation and management of migratory Mule Deer in the Sierra Nevada of California.

The importance of unimpaired migration to Mule Deer occupying the Sierra Nevada is well established (Longhurst et al. 1952; Kucera and McCarthy 1988; Loft and Bleich 2014). Migration typically occurs along traditional routes (Sawyer et al. 2009), and Mule Deer inhabiting those mountains move to and from seasonal ranges each year (Longhurst et al. 1952). During spring, they travel through high-elevation passes to summer ranges west of the Sierra crest and return eastward through those passes to winter ranges during autumn (Kucera 1992; Bleich et al. 2006; Monteith et al. 2011, 2014). Although migration is a widespread phenomenon, there are benefits and tradeoffs associated with that behavior (Nicholson et al. 1997). For example, Mule Deer remaining longer on summer ranges incurred significant nutritional advantages, but likely faced greater threats to survival than did those that migrated earlier (Monteith et al. 2011).

Accidental deaths of individual Mule Deer are not uncommon (Heffelfinger 2006), but at least two mass mortality events previously have occurred in the Sierra Nevada at Bishop Pass (3,680 m; 37°06'54"N, 118°32'41"W) when dozens of deer slipped and fell while traversing steep, ice-covered slopes during autumn migrations in 1952 and 1995 (Jones 1954; Bleich and Pierce 2001). In late October and early November 2017, at least 76 additional Mule Deer fell to their deaths near Bishop Pass, and at least 44 others died in a separate event near Shepherd Pass (3,672 m; 36°40'21"N, 118°20'44"W) about 50 km SSE of Bishop Pass (Paula Brown-Williams, unpubl. report). In both of those cases, deer slipped on ice that had persisted through summer and, unable to regain their footing, plunged to their deaths as described previously (Jones 1954; Bleich and Pierce 2001). Among the dead at both locations were adult males and females, as well as young-of-the-year (Fig. 1). Blood trails likely associated with crippled deer

FIGURE 1. At least 76 Mule Deer (*Odocoileus hemionus*) representing all age classes and both sexes were killed in a mass mortality event in the Sierra Nevada near Bishop Pass, which separates Inyo and Fresno counties, California, in Fall 2017. (Photograph courtesy of California Department of Fish and Wildlife).

indicated others were injured at each location, but their fate is unknown. The 2017 incident at Bishop Pass was the third such loss documented there, and the event at Shepherd Pass is the fourth such incident in the Sierra Nevada of which I am aware. Those four events all followed winters of exceptionally high snowfall that resulted in ice-covered terrain persisting near those passes. Based on preliminary information, Bleich and Pierce (2001) hypothesized that mass mortality events have occurred at Bishop Pass more frequently than previously reported.

The Sierra Nevada is a massive mountain range, reaching elevations > 4,400 m above sea level (ASL) and extending 640 km in a north-south direction while separating the Great Basin from the San Joaquin and Sacramento valleys (Storer and Usinger 1968). Vegetation on winter ranges ($\bar{x} \approx 1,600$ m ASL) east of the Sierra crest is representative of the Great Basin and conforms to the Sagebrush (*Artemisia* sp.) belt of Storer

and Usinger (1968). Summer ranges west of the crest range in elevation from 2,200 to 3,600 m ASL (Kucera 1988). Vegetation zones on summer ranges include the Lodgepole Pine-Red Fir, Subalpine, and Alpine belts (Storer and Usinger 1968; Kucera 1992). High-elevation passes used during migration are in the Alpine belt, which is characterized by vast, rocky areas that are nearly devoid of vegetation (Wehausen 1980).

Summer ranges are more mesic than winter ranges, and average annual rainfall is substantially less on the east side of the mountains because of the rain shadow cast by the Sierra Nevada (Mulch et al. 2008). On typical summer range near Huntington Lake, Fresno County (2,260 m ASL; 37°22'N, 119°13'W), mean annual precipitation is 101 cm, whereas mean annual precipitation is 13 cm at Bishop, Inyo County (1,260 m ASL; 37°22'N, 118°24'W), and is representative of winter ranges east of the Sierra crest (Bleich and Taylor 1998).
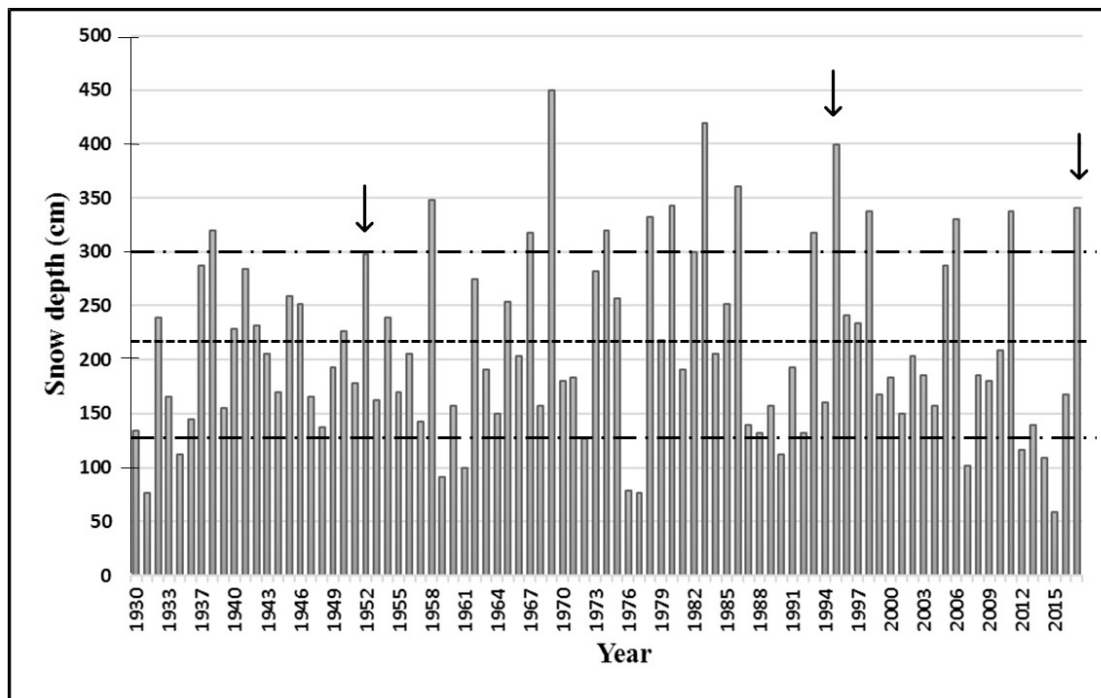
Figure 2. Depth of April snowpack at the Bishop Pass Snow Survey Station (BSH), Fresno County, California, 1930–2017. For reference the long-term mean (-----) and ± 1 standard deviation (– • – • –) are shown. Snowpack during April was ≥ 297 cm, the minimum known to have been followed by a mass mortality event at Bishop Pass in 17 y from 1930 to 2017; no information was available for 1936. Years in which mass mortality events were documented are indicated by downward arrows.

Mean annual snowfall is 465 cm and 15 cm at Huntington Lake and Bishop, respectively. Mean annual temperature at Huntington Lake (7.1° C) is substantially less than at Bishop (13.3° C). Weather conditions at high elevations are quite variable and can be extreme during winter. Years of heavy snowfall result in icy conditions on bare talus slopes near some of those passes, and ice persisting on steep hillsides through summer presents a danger to migrating deer (Jones 1954; Bleich and Pierce 2001).

Among carnivores capable of preying on Mule Deer, Grizzly Bear (*Ursus arctos*) and Wolverine (*Gulo gulo*) have been extirpated from the Sierra Nevada (Storer and Tevis 1955; Aubrey et al. 2007; Schwartz et al. 2007); historical presence of Gray Wolf (*Canis lupus*) remains uncertain (Schmidt 1991; Shelton and Weckerly 2007). Mountain Lion (*Puma concolor*) and Coyote (*Canis latrans*), however, are important predators of Mule Deer (Pierce et al. 2000) and occur throughout the range (Storer and Usinger 1968). Black Bears (*Ursus americanus*) prey extensively on neonatal Mule Deer on summer range, but prey on fawns infrequently east of the Sierra crest (Monteith et al. 2014). Sierra Nevada Red Fox (*Vulpes vulpes necator*) remain extant but are a threatened taxon (Barrett and Golightly 1994), and feed on Mule Deer as carrion when it is available (Perrine 2005). The deer population occupying the Round Valley winter range (37°25'N, 118°36'W), 33 km north of Bishop Pass, declined rapidly from ≥ 6,000 in 1985 to about 1,000 in 1991, where it remained until 1992 when it began to increase slowly (Pierce et al. 2012).

April snowpack is a reliable measure of maximum winter snow depth (Mote et al. 2005) and, apart from 1936, has been recorded annually at the Bishop Pass Snow Survey Station, Fresno County (3,414 m; 37°06'00"N, 118°33'25"W) since 1930 (California Department of Water Resources. 2017. Bishop Pass [BSH]. Available from http://cdec.water.ca.gov [Accessed 26 November 2017]). I reviewed those records and explored snowpack conditions over the previous 87 y. April snowpack ($\bar{x}$ = 211 ± 84.7 [SD] cm) ranged from a low of 58 cm in 2015 to a high of 419 cm in 1969 (Fig. 2). In 1952, when ice persisted at Bishop Pass and a mass mortality event occurred there during fall migration (Jones 1954), April snowpack was 297 cm. Additional mass mortality events are known to have occurred during Fall of 1995 and 2017, when April snowpack was 399 cm and 340 cm, respectively (Bleich and Pierce 2001; this paper). Thus, I considered any year with April snowpack ≥ 297 cm to be a precursor for a mass mortality event at this location during the subsequent fall migration, but interannual variation in local conditions affects persistence of snowpack (Mote et al. 2005), and the threshold for such could be less. During 17 of the 86 y (20%) for which data are available, April snowpack was ≥ 297 cm. On average, April snowpack ≥ 297 cm has occurred about once every 5 y (Fig. 2).

Historical distributions of Sierra Nevada Red Fox and now extirpated Wolverine coincided closely with that of Mule Deer in the Sierra Nevada, and both occurred at high elevations (Schempf and White 1977; Barrett and Golightly 1994; Statham et al. 2012) used by Mule Deer during migration. Red Fox and Wolverine are opportunistic feeders and large mammals in their respective diets likely originate as carrion (Wilson 1982; Pasitschniak-Arts and Lariviere 1995; Copeland and Whitman 2003; Cypher 2003; Perrine 2005). Thus, carrion resulting from mass mortality events might have been an important food source for Wolverine prior to extirpation and may yet play a role in the foraging ecology of Red Fox on a seasonal, even if irregular, basis. To the best of my knowledge, this note is the first to posit a potential role of mass mortality events in the ecology of those secretive carnivores.

Density independent events occur unpredictably and complicate management in highly variable ecosystems (Mackie et al. 1990; Bleich and Taylor 1998). Hypothetically, April snowpack of a depth adequate to persist into the period of fall migration could play a role in the demographics of some migratory deer populations following winters of heavy snowfall. For example, deep April snowpack (as precursors to potential mass mortality events) occurred in 1985 and 1986 (Fig. 2) during the precipitous crash of deer occupying the Round Valley winter range, a decline attributed largely to drought (Pierce et al. 2012). Thus, the rate of decline may have been exacerbated by undocumented mass mortality events during autumn migrations in 1985 and 1986, when April snowpack was 250 cm and 360 cm, respectively. Rate of recovery of that population might also have been slowed by similar events. Since 1992, when the population began to recover, April snowpack > 297 cm has been recorded six times, and was 287 cm in a seventh year. Neither of these possibilities had been considered previously (Kucera 1988; Pierce et al. 2012). Clearly, better understanding of the relationship between annual snowfall and mass mortality events, as well as quantification of the population-level impacts of such events, is necessary to interpret their demographic consequences.

Heavy snowfall during winters of 1968–1969, 1982–1983, 1984–1985, and 1985–1986 (Fig. 2) promulgated regulatory changes to reduce harvest of deer throughout the eastern Sierra Nevada. Those changes were based on the deaths of several hundred deer during the winter of 1968–1969, and early fall storms in 1983, 1985, and 1986 that resulted in extremely high harvests (Blankinship 1987). That accidental deaths of the type described here played a role in the dynamics of some migratory populations in the Sierra Nevada remains hypothetical but, given the relative probability (20% in any given year) of April snowpack ≥ 297 cm as a precursor to such a mass mortality event, I suggest that metric be a consideration when formulating harvest regulations during population

declines of the magnitude described previously (Kucera 1988; Pierce et al. 2012).

The composition of deer populations exhibiting partial migration (Chapman et al. 2011) may also be affected by mass mortality events, a factor not considered by previous investigators (Kucera 1992; Monteith et al. 2011). In the Sierra Nevada, timing of deer migration from summer to winter ranges is mediated by phenological changes in forage and by body condition of migrants (Monteith et al. 2011). At the onset of migration, however, deer cannot be aware of risks associated with ice conditions at isolated high-elevation locations on steep, north-facing slopes described herein. The proportion of Mule Deer occupying the Round Valley winter range but that migrates across the Sierra crest each year declined from 87% in 1987 to 58% in 1998 and was ≤ 50% in 2009 (Kucera 1988; Monteith et al. 2014). Much of that change has been a demographic consequence of predation on neonatal deer by Black Bears west of the Sierra crest and the near absence of bear predation on offspring of deer that do not cross the range (Monteith et al. 2014). Mass mortality events would exacerbate selection against the migratory component of a deer population (i.e., migration thus becomes maladaptive; Avgar et al. 2014) and, thereby, contribute to an increase in the relative abundance of deer that remain east of the Sierra Crest during winter but co-occur with migrants on winter range. Such mortality would be additive (Bowyer et al. 2014) to that attributed to predation and compound the already severe shift in population structure described by Monteith et al. (2014).

It is often through observations of unanticipated or unusual events that questions arise and our understanding of nature ultimately is enhanced (Estes 2016). Mass mortality events involving Mule Deer in the Sierra Nevada have been reported only infrequently and observations of those events may have been serendipitous. The rarity of such reports, however, begs questions about whether mass mortality events truly are rare, or have simply gone undetected or not been reported when they do occur, and where in the Sierra Nevada they might occur. That those events take place at high elevations in remote, rugged, and isolated terrain immediately prior to winter is consistent with the notion that they may well go unnoticed. Historical snowpack records indicate that climatic conditions as possible precursors to such losses occur at Bishop Pass, on average, about every 5 y; hence, mass mortality events may be more frequent than recognized. If so, those accidental deaths have greater implications, both for ecosystem function and for management of migratory Mule Deer than considered previously and warrant further investigation.

1969 and its impacts to Mule Deer. Pep Partridge and, the late, Earl Brown and Dick Noles provided many hours of animated conversation regarding the management of Mule Deer and never hesitated to share advice; I learned a great deal from them. I thank Kevin Monteith and Jim Heffelfinger for many helpful suggestions that improved the manuscript. This is Professional Paper 124 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

Aubrey, K.B., K.S. McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the Wolverine in the contiguous United States. Journal of Wildlife Management 71:2147–2158.

Avgar, T., G. Street, and J.M. Fryxell. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology 92:481–490.

Baker, R.R. 1978. The evolutionary ecology of animal migration. Homes and Meier Publishers, New York, New York.

Barrett, R., and R. Golightly. 1994. Sierra Nevada Red Fox. Pp. 84–85 in Life on the Edge: A Guide to California's Endangered Natural Resources. Thelander, C. (Ed.). BioSystems Books, Santa Cruz, California.

Berger, J. 1983. Ecology and catastrophic mortality in wild horses: implications for sociality in fossil assemblages. Science 220:1403–1404.

Berger, J. 2004. The last mile: how to sustain long distance migration in mammals. Conservation Biology 18:320–331.

Blankinship, T.E. 1987. Buttermilk Deer Herd Management Plan. California Department of Fish and Game, Bishop, California.

Bleich, V.C., and B.M. Pierce. 2001. Accidental mass mortality of migrating Mule Deer. Western North American Naturalist 61:124–125.

Bleich, V.C., and T.J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of Mule Deer. Great Basin Naturalist 58:265–272.

Bleich, V.C., B.M. Pierce, J. Jones, and R.T. Bowyer. 2006. Variance in survival rates among young Mule Deer in the Sierra Nevada, California. California Fish and Game 92:24–38.

Bowyer, R.T., V.C. Bleich, K.M. Stewart, J.T. Whiting, and K.L. Monteith. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. California Fish and Game 100:550–572.

Chapman, B.B., C. Bronmark, J.A. Nilsson, and L.A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

Copeland, J.P., and J.S. Whitman. 2003. Wolverine (Gulo gulo). Pp. 672–682 in Wild Mammals of North America: Biology, Management, and Conservation. 2nd Edition. Feldhamer, G.A., B.C. Thompson, and

J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.

Cypher, B.L. 2003. Foxes (Vulpes species, Urocyon species, and Alopex lagopus). Pp. 511–546 in Wild Mammals of North America: Biology, Management, and Conservation. 2nd Edition. Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.

Dingle, H. 2014. Migration: The Biology of Life on the Move. 2nd Edition. Oxford University Press, Oxford, UK.

Estes, J.A. 2016. Serendipity: An Ecologist's Quest to Understand Nature. University of California Press, Oakland, California.

Guthrie, R.D. 1990. Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. University of Chicago Press, Chicago, Illinois.

Heffelfinger, J.R. 2006. Deer of the Southwest. Texas A&M University Press, College Station, Texas.

Jones, F.L. 1954. An unusual cause of deer mortality. Journal of Wildlife Management 18:142.

Keim, C.J. 1969. Aghvook, White Eskimo: Otto Geist and Alaskan Archaeology. University of Alaska Press, Fairbanks, Alaska.

Kock, R.A., M. Orynbayev, S. Robinson, S. Zuther, N.J. Singh, W. Beauvais, E.R. Morgan, A. Kerimbayev, S. Khomenko, H.M. Martineau, et al. 2018. Saigas on the brink: multidisciplinary analysis of the factors influencing mass mortality events. Science Advances 4(1):eaao2314. doi:10.1126/sciadv.aao2314.

Kucera, T.E. 1988. Ecology and Population Dynamics of Mule Deer in the Eastern Sierra Nevada, California. Ph.D. Dissertation, University of California, Berkeley, California. 207 p.

Kucera, T.E. 1992. Influences of sex and weather on migration of Mule Deer in California. Great Basin Naturalist 52:122–130.

Kucera, T.E., and C.W. McCarthy. 1988. Habitat fragmentation and Mule Deer migration corridors: a need for evaluation. Transactions of the Western Section of The Wildlife Society 24:61–67.

Loft, E.R., and V.C. Bleich. 2014. An historical perspective on deer ranges in California: terminology and its relevance to wildlife conservation. California Fish and Game 100:451–472.

Longhurst, W.M., A.S. Leopold, and R.F. Dasmann. 1952. A survey of California deer herds: their ranges and management problems. Game Bulletin 6:1–136.

Mackie, R.J., K.L. Hamlin, D.F. Pac, G.L. Dusek, and A.K. Wood. 1990. Compensation in free-ranging deer populations. Transactions of the North American Wildlife and Natural Resources Conference 55:518–526.

Monteith, K.M., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in Mule Deer: effects of climate, plant phenology, and life-history

characteristics. Ecosphere 2(4):art47. doi:10.1890/es10-00096.1.

Monteith, K.M., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, J.G. Kie, and R.T. Bowyer. 2014. Life history characteristics of Mule Deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–63.

Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Mulch, A., A.M. Sarna-Wojcicki, M.E. Perkins, and C.P. Chamberlin. 2008. A Miocene to Pleistocene climate and elevation record of the Sierra Nevada (California). Proceedings of the National Academy of Sciences 105:6819–6824.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of Mule Deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Pasitschniak-Arts, M., and S. Lariviere. 1995. *Gulo gulo*. Mammalian Species 499:1-10.

Pennisi, E. 2017. Drowned Wildebeest provide ecological feast. Science 356:1217–1218.

Perrine, J.D. 2005. Ecology of Red Fox (*Vulpes vulpes*) in the Lassen Park Region of California, USA. Ph.D. Dissertation, University of California, Berkeley, California. 236 p.

Pewe, T.L. 1975. Quaternary geology of Alaska. U.S. Geological Survey Professional Paper 835:1–145.

Pierce, B.M., V.C. Bleich, and R.T. Bowyer. 2000. Prey selection by Mountain Lions and Coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462–472.

Pierce, B.M., V.C. Bleich, K.L. Monteith, and R.T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from Mountain Lions and Mule Deer. Journal of Mammalogy 93:977–988.

Sawyer, H., M.J. Kauffman, R.M. Nielson, and J.S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Schempf, P.M., and M. White. 1977. Status of six furbearer populations in the mountains of northern California. U.S. Department of Agriculture, Forest Service, Region 5. San Francisco, California.

Schmidt, R.H. 1991. Gray wolves in California: their presence and absence. California Fish and Game 77:79–85.

Schwartz, M.K., K.B. Aubrey, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation of Wolverines in California using historical DNA. Journal of Wildlife Management 71:2170–2179.

Shelton, S.L., and F.W. Weckerly. 2007. Inconsistencies in historical geographic range maps: the Gray Wolf as an example. California Fish and Game 93:224-227.

Statham, M.J., A.C. Rich, S.K. Lisius, and B.N. Sacks. 2012. Discovery of a remnant population of Sierra Nevada Red Fox (*Vulpes vulpes necator*). Northwest Science 86:122–132.

Storer, T.I., and L.P. Tevis, Jr. 1955. The California Grizzly. University of California Press, Berkeley, California.

Storer, T.I., and R.L. Usinger. 1968. Sierra Nevada Natural History. University of California Press, Berkeley, California.

Subalusky, A.L., C.L. Dutton, E.J. Rosi, and D.M. Post. 2017. Annual mass drownings of the Serengeti Wildebeest migration influence nutrient cycling and storage in the Mara River. Proceedings of the National Academy of Sciences 114:7647–7652.

Taylor, L.R., and R.A.J. Taylor. 1977. Aggregation, migration, and population mechanics. Nature 265:415–421.

Wehausen, J.D. 1980. Sierra Nevada Bighorn Sheep: History and Population Ecology. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan. 240 p.

Wilcove, D.S. 2008. No Way Home: The Decline of the World's Great Animal Migrations. Island Press, Washington, D.C.

Wilson, D.E. 1982. Wolverine. Pp. 644–652 *in* Wild Mammals of North America: Biology, Management, and Conservation. 2nd Edition. Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (Ed.). Johns Hopkins University Press, Baltimore, Maryland.

Vern Bleich was a Wildlife Biologist with the California Department of Fish and Game for 34 y, where his responsibilities centered largely on the conservation and management of large mammals occupying the eastern Sierra Nevada and the Great Basin, Mojave, and Sonoran deserts. Currently, he is Research Professor in the Department of Natural Resources and Environmental Science at the University of Nevada Reno. Although he has emigrated from California to North Dakota, he continues to contribute to the conservation and management of large mammals inhabiting arid landscapes throughout the western United States. He serves as an advisor to the Society for the Conservation of Bighorn Sheep, the Texas Bighorn Society, the Wild Sheep Foundation, and the California Chapter of the Wildlife Sheep Foundation, and is midway through his second term on the Montana-Dakotas Resource Advisory Council of the Bureau of Land Management. (Photographed by Riley Heater).

PEER EDITED

NOTES

PREDATION OF A WESTERN POND TURTLE (*ACTINEMYS MARMORATA*) BY A GREAT EGRET (*ARDEA ALBA*)

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Abstract.—The Western Pond Turtle (*Actinemys marmorata*) is an endemic turtle of the Pacific coast of North America and understanding which species are predators can be useful to the conservation of the species. We photographed a Great Egret (*Ardea alba*) catching and consuming a small Western Pond Turtle at a pond near Gorman, California. We estimated that the turtle was about 30 mm carapace length, the size of a hatchling turtle.

Key Words.—California; turtles; predators; birds

Western Pond Turtles (*Actinemys marmorata*) are eaten by a variety of predators including carnivorous mammals, such as the Northern River Otter (*Lontra canadensis*), American Mink (*Mustela vison*), Northern Raccoon (*Procyon lotor*), Gray Fox (*Urocyon cineroargenteus*), Coyote (*Canis latrans*), and Black Bear (*Ursus americanus*; Bury 1972; Manning 1990; Bury and Germano 2008). Several bird species, including the Bald Eagle (*Haliaeetus leucocephalus*), Osprey (*Pandion haliaetus*), Great Blue Heron (*Ardea herodias*), and gulls (*Larus* sp.), are also suspected of eating Western Pond Turtles (Bury and Germano 2008). Like other turtle species, Western Pond Turtles are most vulnerable as eggs and small turtles because of the greater number of predators that can eat turtles when they are small. Both introduced America Bullfrogs (*Rana catesbeiana*) and fishes such as Largemouth Bass (*Micropterus salmoides*) are known to eat young Western Pond Turtles (Moyle, 1973; Nussbaum et al., 1983) but the effect of these predators on turtle populations is unknown (Germano and Riedel 2015).

On 23 May 2018, the junior author photographed a small Western Pond Turtle being eaten by a Great Egret (*Ardea alba*) at a pond near Gorman, California (Fig. 1). To estimate the size of the turtle eaten, we determined the mean length of the bill of Great Egrets from two specimens in the collection of the Department of Biology at California State University, Bakersfield (CSUB). The bill length from its tip to the anterior of the eye was 120 mm in CSUB #A-47 and 130 mm in CSUB #A200. Based on the mean length of the bill from these two egret specimens (125.0 mm), the turtle appeared to be a hatchling about 30 mm carapace length (Fig. 2).

The senior author has studied turtles at this site since 2007, and when the pond is full, the turtle population is robust (Germano and Riedel 2015). The pond has not filled since 2011, has had limited water only in the late winter/early spring, and has dried completely by summer (David Germano, pers. obs.). The senior author trapped turtles in spring 2017 and caught 36 individuals when the pond was only about 20% full and drying of the pond meant trapping could no longer occur by the beginning of June (unpubl. data). It is not known how predation affects populations of Western Pond Turtles. The pond does not fill in all years and the periodicity of filling may influence the persistence of the population more than predation events, like the one documented. If and when the pond fills again will likely determine the outcome of this once thriving population of Western Pond Turtles.

LITERATURE CITED

Bury, R.B. 1972. Habits and home range of the Pacific Pond Turtle, *Clemmys marmorata*, in a stream community. Ph.D. Dissertation, University of California, Berkeley, California. 205 p.

Bury, R.B., and D.J. Germano. 2008. *Actinemys marmorata* (Baird and Girard, 1852) – Western Pond Turtle, Pacific Pond Turtle. *In* A.G.J. Rhodin, P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, and J.B. Iverson, Eds. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5, pp 001.1-001.9, doi:10.3854/crm.5.001.marmorata.v1.2008.

Germano, D.J., and J.D. Riedle. 2015. Population structure, growth, survivorship, and reproduction of *Actinemys marmorata* from a high elevation site in the Tehachapi Mountains of Southern California. Herpetologica 71:102–109.

Manning, T. 1990. Summer feeding habits of River Otter (*Lutra canadensis*) on the Mendocino National Forest, California. Northwestern Naturalist 71:38–42.

Moyle, P.B. 1973. Effect of introduced Bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18–22.

Nussbaum, R.A., E.D. Brodie, Jr. and R.C. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University Press of Idaho, Moscow, Idaho.

Figure 1. Great Egret (*Ardea alba*) eating a small Western Pond Turtle (*Actinemys marmorata*) at a pond near Gorman, Los Angeles County, California. (Photographed by Bill Buchroeder).

Figure 2. Great Egret (*Ardea alba*) with a small Western Pond Turtle (*Actinemys marmorata*) in its bill at a pond near Gorman, Los Angeles County, California. (Photographed by Bill Buchroeder).

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 (*Lynx 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.

| State | Cottontails (all species) | | | | Jackrabbits (all species) | | | Snowshoe Hares | | All Leporids |
	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).

A

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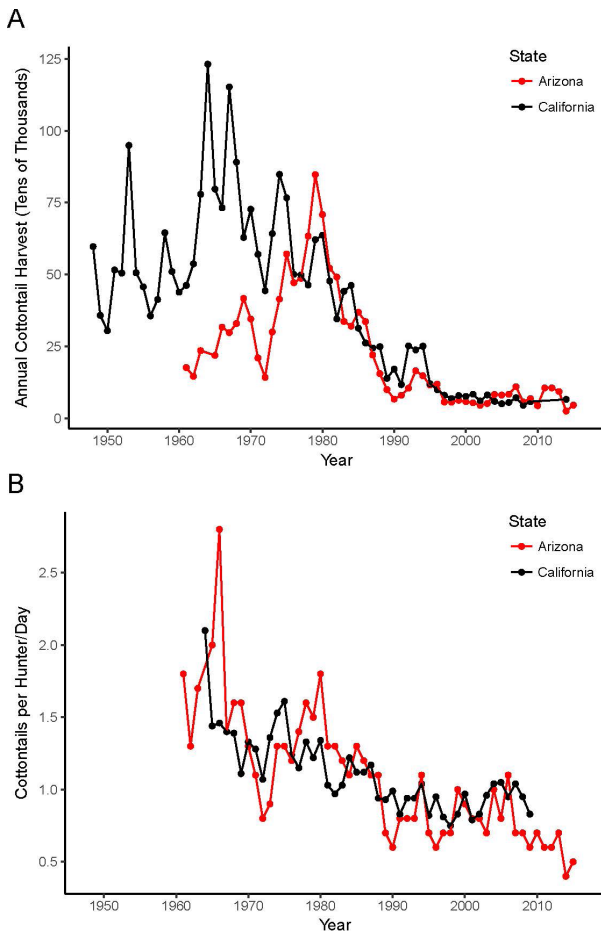
FIGURE 3. Annual cottontail hunt information from California and Arizona. (A) Cottontail harvest trends for California and Arizona. (B) Cottontail hunter success trends (cottontails per hunter/day) for Arizona ($r = -0.78$; $t = 25.20$, df = 52, $P < 0.001$) and California ($r = -0.77$; $t = 21.97$,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

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***	

1.3 in 1985, followed by consistently lower success from 1989 to the present (Fig. 3b; Table 2).

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
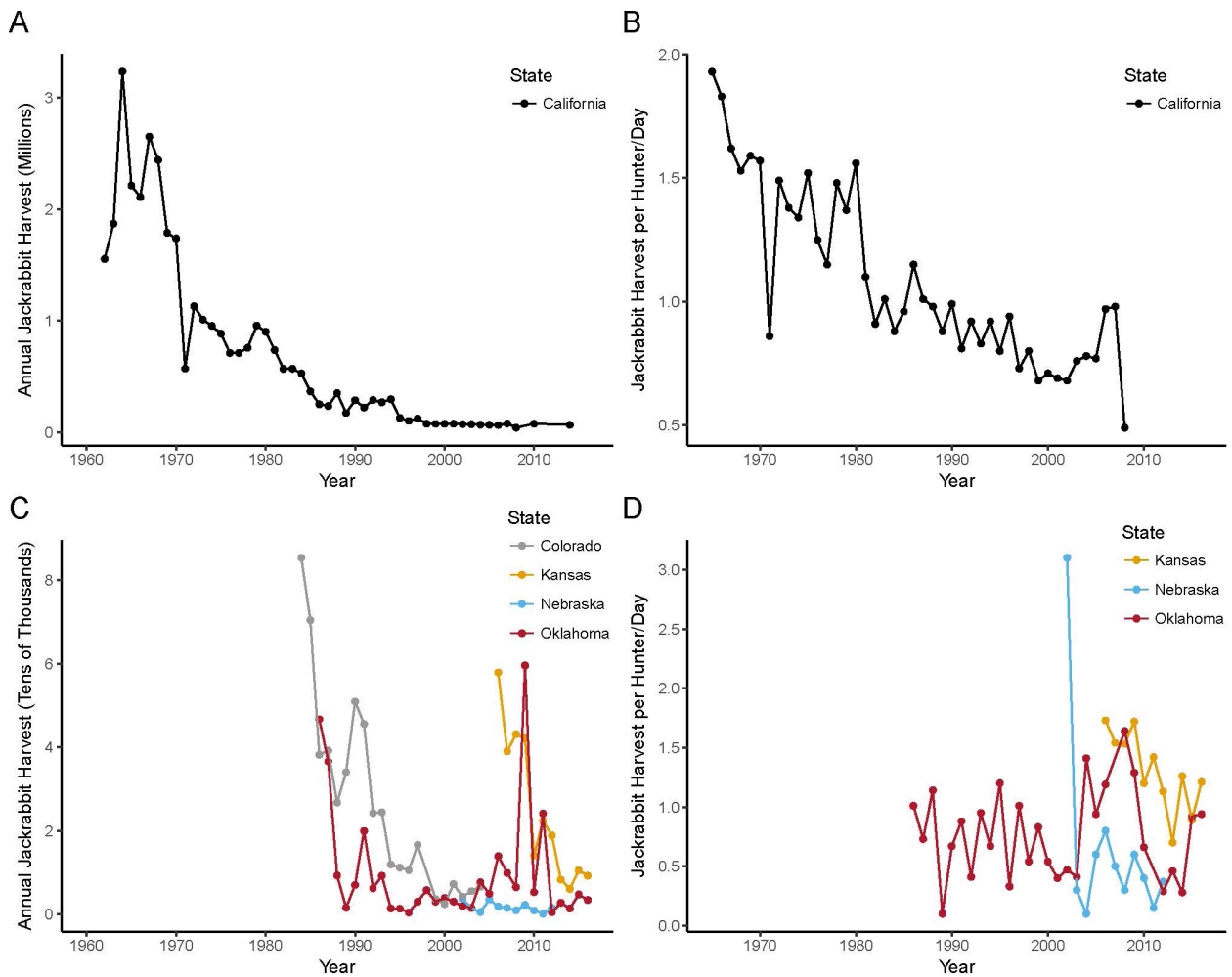
FIGURE 4. Annual jackrabbit hunt information from California, Colorado, Nebraska, Kansas, and Oklahoma. (A) Jackrabbit harvest trends for California; (B) Jackrabbit hunter success trends (jackrabbits per hunter/day) for California ($r = -0.86$; $t = 38.67$; df = 42; $P < 0.001$); (C) Jackrabbit harvest 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. 6; 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.

A

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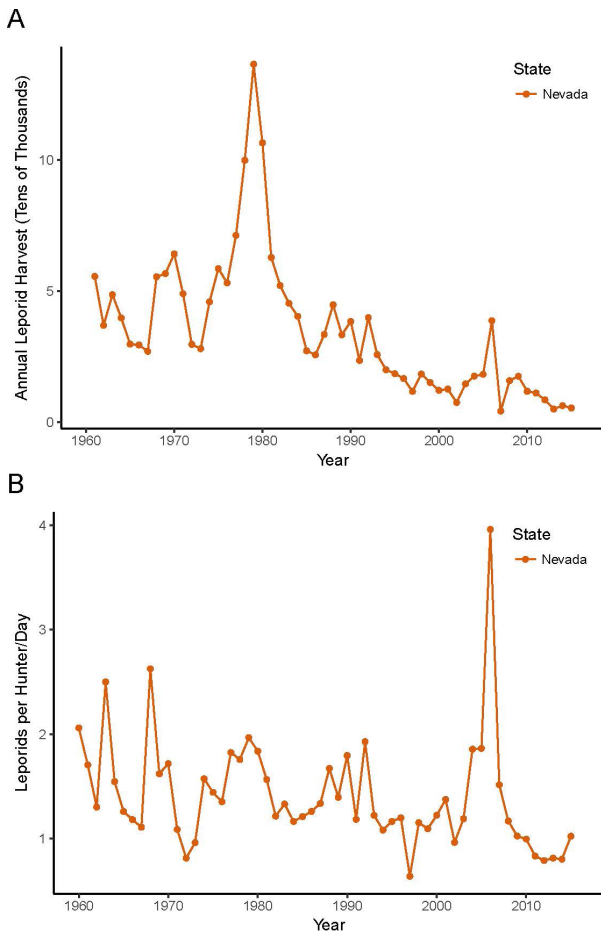
Figure 5. Annual leporid hunt information from Nevada. (A) Leporid harvest trend; (B) Leporid hunter success trend (leporids per hunter/day) (r = -0.26; t = 2.57; df = 54; P < 0.050).

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).
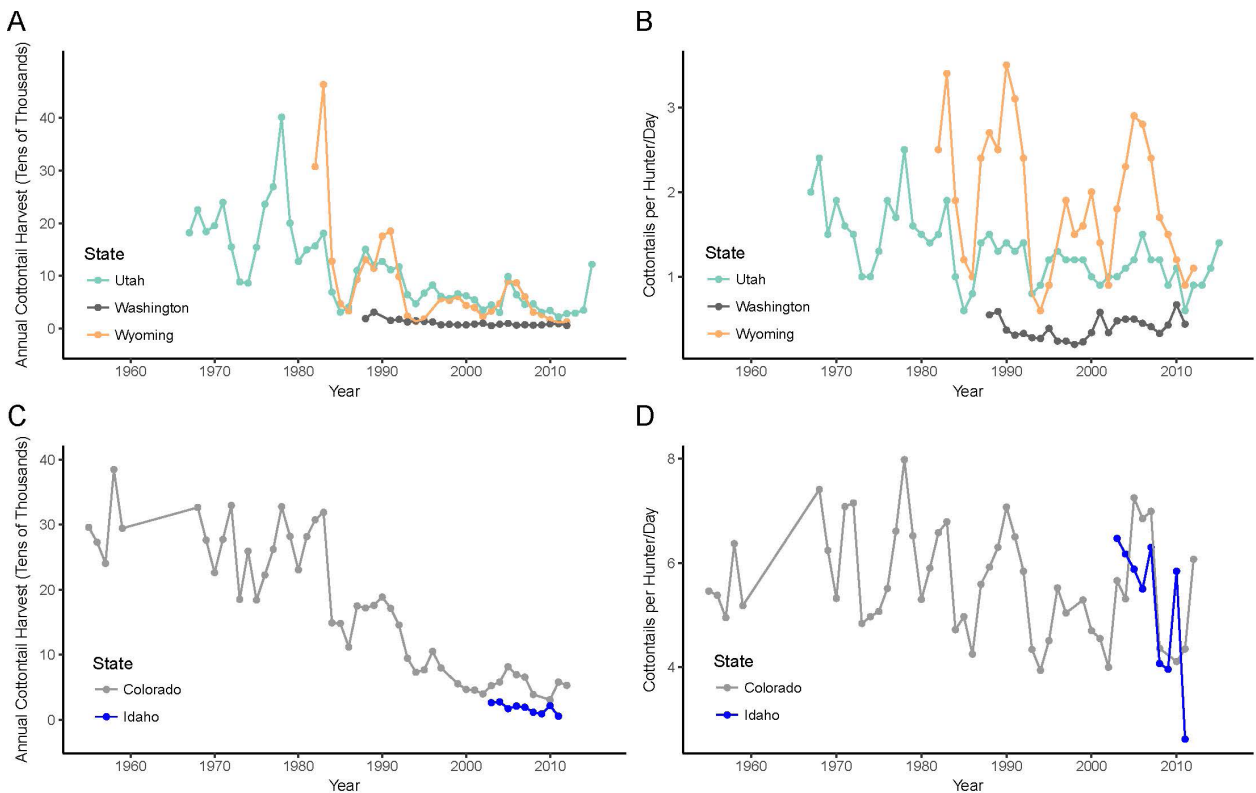
FIGURE 6. Annual cottontail hunt information from participating Utah, Washington, Wyoming, Colorado, and Utah. (A) Cottontail harvest trends for Wyoming, Washington, and Utah; (B) Cottontail hunter success trends (cottontails per hunter/day) for Wyoming ($r = -0.30$; $t = 2.27$; df = 28; $P < 0.050$), 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;
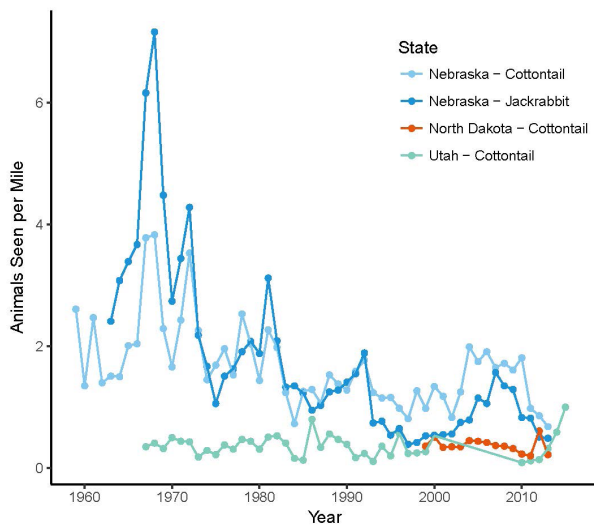
Figure 7. Annual leporid survey information (animals seen per mile); cottontails from Utah ($r = 0.01$; $t = 0.03$; df = 38; $P = 0.976$), Nebraska ($r = -0.52$; $t = 7.81$; df = 53; $P < 0.001$), and North Dakota ($r = -0.28$; $t = 1.39$; df = 13; $P = 0.188$), and jackrabbits from Nebraska ($r = -0.72$; $t = 17.69$; 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
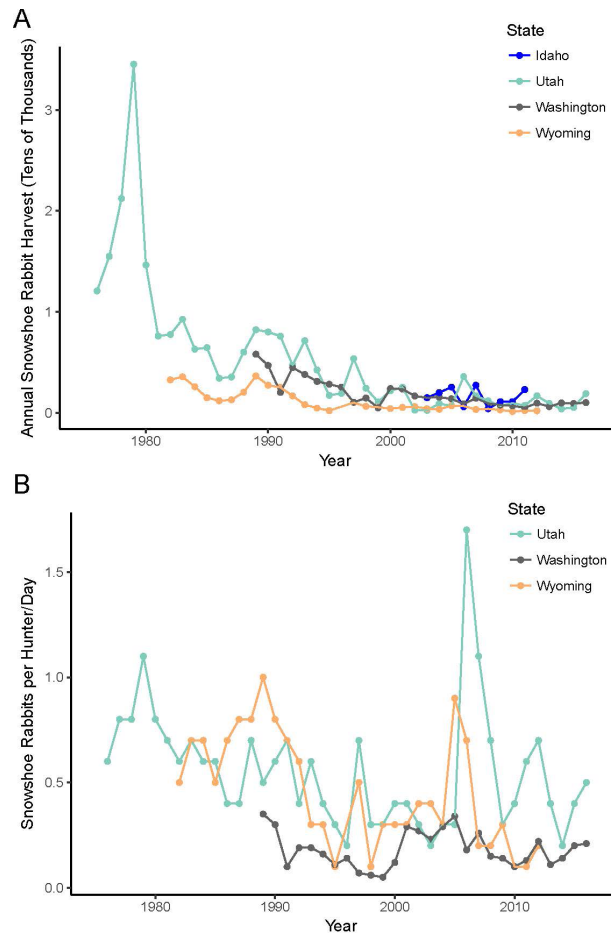

Figure 8. Annual Snowshoe Hare hunt information from Utah, Idaho, Wyoming, and Washington. (A) Snowshoe Hare harvest trends for Utah, Idaho, Wyoming, and Washington; (B) Snowshoe Hare hunter success trends (snowshoe hares per hunter/day) for Utah ($r = -0.25$; $t = 2.04$; df = 39; $P < 0.050$), Wyoming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

cattle grazing and exotic grasses as possible contributing factors.

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).
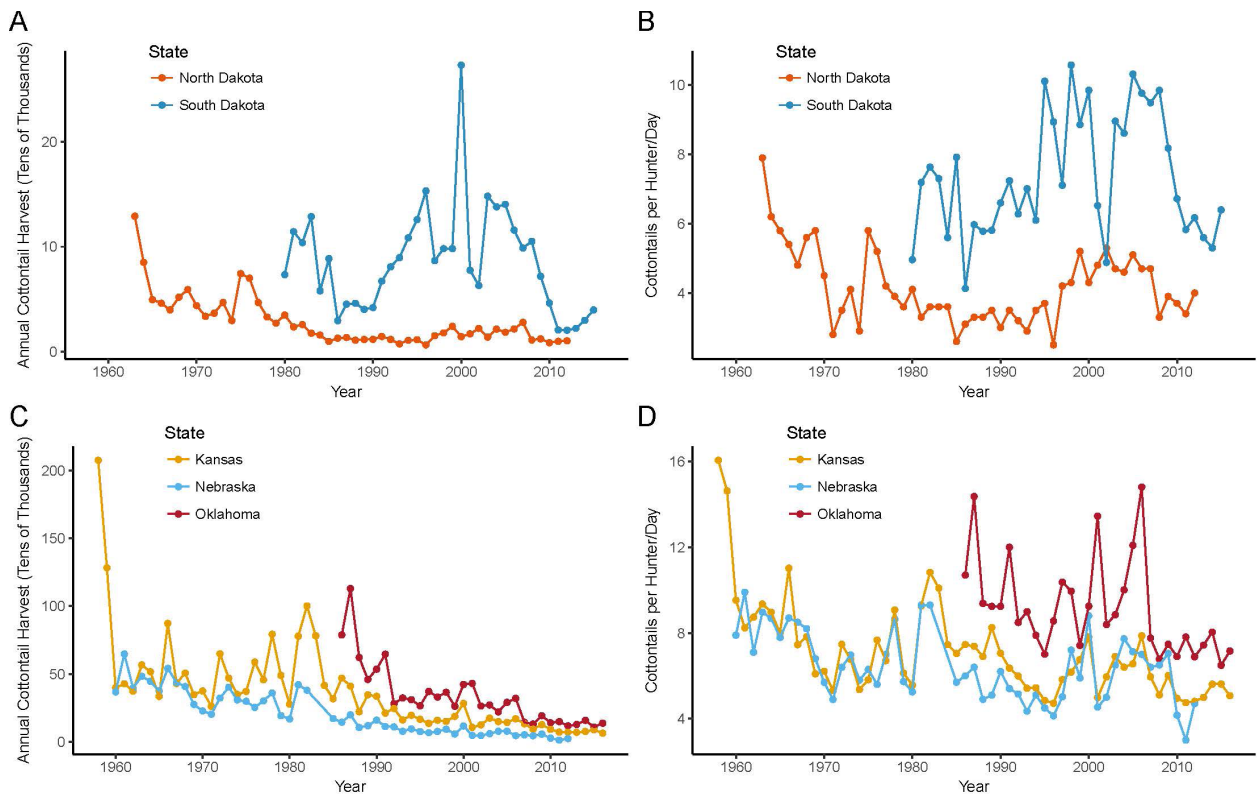
Figure 9. Annual cottontail hunt information from North Dakota, South Dakota, Nebraska, Kansas and Oklahoma. (A) Cottontail harvest trends for North Dakota and South Dakota; (B) Cottontail hunter success trends (cottontails per hunter) for North Dakota ($r = -0.31$; $t = 3.10$; df = 48; $P < 0.010$), 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
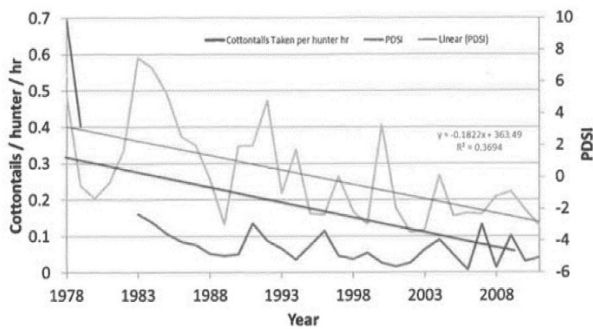
Figure 10. Cottontail hunt success at Oracle Junction, Arizona, compared with the Palmer Drought Severity Index for Southeast Arizona, 1979–2012 (from Levi Heffelfinger et al., unpubl. data).

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 ectoparisites, 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.

LITERATURE CITED

Adams, H.B., and L. Adams. 1959. Black-tailed Jackrabbit carcasses on the highways in Nevada, Idaho, and California. Ecology 40:718–72.

Amacher, A.J., R.H. Barret, and S.L. Stephens. 2011. Observations on Black-tailed Jackrabbits (*Lepus californicus*) increase within forests treated with prescribed fire. Southwestern Naturalist 56:115–118.

Anderson, J.E., and M.L. Shumar. 1986. Impacts of Black-tailed Jackrabbits at peak population densities on sagebrush-steppe vegetation. Journal of Range Management 39:152–156.

Applegate, R.D. 1997. Distribution and relative abundance of Black-tailed Jackrabbits in Kansas, 1975–76 — 1995–96. Transactions of the Kansas Academy of Science 100:159–161.

Applegate, R.D., and C.K. Williams. 1998. Results from 30 years of Kansas April rural mail carrier surveys. Transactions of the Kansas Academy of Science 101:95–100.

Applegate, R.D., B.E. Flock, and E.J. Fink. 2003. Changes in land use in eastern Kansas, 1984–2000. Transactions of the Kansas Academy of Science 106:192–197.

Arizona Game and Fish Department (AGFD). 2014. Hunt Arizona 2014 Edition. Arizona Game and Fish Department, Phoenix, Arizona.

Armstrong, D.M. 1972. Distribution of mammals in Colorado. University of Kansas Museum Natural History Monograph 3:1–415.

Bacon, M., and C.H. Drake. 1958. Bacterial infections in wild rabbits of eastern and central Washington. Northwest Science 32:124–131.

Bahre, C.J., and M.L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southern Arizona. Journal Biogeography 20:489–504.

Bartel, R.A., F.F. Knowlton, and L.C. Stoddart. 2008. Long-term patterns in mammalian abundance in

northern portions of the Great Basin. Journal of Mammalogy 89:1170–1183.

Becker, P.A., and S.M. DeMay. 2016. Re-introduction of the Columbia Basin Pygmy Rabbit in central Washington, USA. Pp. 195–199 *In* Global Re-introduction Perspectives: 2016. Soorae, P.S. (Ed.). International Union for Conservation of Nature/Species Survival Commission Re-introduction Specialist Group and Environment Agency-Abu Dhabi, Abu Dhabi, United Arab Emirates.

Bednarz, J. and J. Cook. 1984. Distribution and numbers of the White-sided Jackrabbit (*Lepus callotis gaillardi*) in New Mexico. Southwestern Naturalist 29:358–360.

Beever, E., and J. French. 2018a. *Sylvilagus nuttallii* Bachman, 1837; Mountain Cottontail. Pp. 147–149 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Beever, E., D.E. Brown, and C. Lorenzo. 2018b. *Lepus californicus* Gray, 1837; Black-tailed Jackrabbit. Pp. 170–173 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Beever, E., D.E. Brown, and J. Berger. 2018c. *Lepus townsendii* Bachman, 1839; White-tailed Jackrabbit. Pp. 218–220 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Berger, J. 2008. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. Oryx 42:139–142.

Berger, J., K.M. Berger, P.F. Brussard, R. Gibson, J. Rachlow, and A.T. Smith. 2005. Where have all the rabbits gone? Wildlife Conservation Society, New York, New York.

Best, T.L. 1996. *Lepus californicus*. Mammalian Species 530:1–10.

Best, T.L., and T.H. Henry. 1993a. *Lepus callotis*. Mammalian Species 442:1–6.

Best, T.L., and T.H. Henry. 1993b. *Lepus alleni*. Mammalian Species 424:1–8.

Bock, C.E., Z.F. Jones, and J.H. Bock. 2006. Abundance of cottontails (*Sylvilagus*) in an exurbanizing southwestern savanna. Southwestern Naturalist 51:352–357.

Bierregaard, R.O., Jr., A.B. David, L. Gibson, R.S. Kennedy, A.F. Poole, M.S. Scheibel, and J. Victoria. 2014. Post-DDT recovery of osprey (*Pandion haliaetus*) populations in southern New England and Long Island, New York, 1970-2013. Journal of Raptor Research 48:361-374.

Boutin, S., and H.D. Cluff. 1989. Coyote prey choice, optimal or opportunistic foraging? A comment. Journal of Range Management 53:663–666.

Bowen, R.E., K.J. McMahon, and R.W. Mitchell. 1960. Infectious diseases in a Black-tailed Jackrabbit (*Lepus californicus melanotis mearns*) population in southwestern Kansas. Transactions of the Kansas Academy of Sciences 63:276–284.

Bronson, F.H., and O.W. Tiemeier. 1958. Notes on crop damage by jackrabbits. Transactions of the Kansas Academy of Science 61:226–229.

Brooks, M. 1999. Effects of protective fencing on birds, lizards, and black-tailed hares in the western Mojave Desert. Environmental Management 23:387–400.

Brown, D.E. 1979. Factors influencing reproductive success and population densities in Montezuma Quail. Journal of Wildlife Management 43:522–526.

Brown, D.E. 2012. Bringing Back the Game: Arizona Wildlife Management: 1912–1962. Arizona Game and Fish Department, Phoenix, Arizona. 489 p.

Brown, D.E., and N.B. Carmony (Eds.). 2009. Wildlife in Arizona Territory, 1865–1912. Arizona Game and Fish Department, Phoenix, Arizona. 446 p.

Brown, D.E., and E. Makings. 2014. A guide to North American Grasslands. Desert Plants 29:1–159.

Brown, D.E., R.D. Babb, C. Lorenzo, and M.M. Altemus. 2014. Ecology of the Antelope Jackrabbit (*Lepus alleni*). Southwestern Naturalist 59:577–589.

Brown, D.E., C.L. Cochran, and T.E. Waddell. 1978. Using call-counts to predict hunting success of Scaled Quail. Journal Wildlife Management 42:281–287.

Brown, D.E., C. Lorenzo, and Altemus, M. 2018a. *Lepus alleni* Mearns, 1890; Antelope Jackrabbit. Pp. 159–162 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Brown, D.E., C. Lorenzo, and M.B. Traphagen. 2018b. *Lepus callotis* Wagler, 1830; White-sided Jackrabbit. Pp. 173–176 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Brown, L. 1940. The distribution of the White-tailed Jackrabbit (*Lepus townsendii campanius* Hollister) in Kansas. Transactions of the Kansas Academy of Science 43:385–389.

Brown, L. 1947. Why has the White-tailed Jackrabbit (*Lepus townsendii campanius*) become scarce in Kansas? Transactions of the Kansas Academy of Science 49:455–456.

Burnett, W.L. 1926. Jack rabbits of eastern Colorado. Technical Report of Office of State Entomologist, Circular 52:1–18.

Caro M., J.A. Shargel, and C.J. Stoner. 2000. Frequency of medium-sized mammal road kills in an agricultural

landscape in California. American Midland Naturalist 144:362–369.

Carter, F.L. 1939. A study in jackrabbit shifts in range in western Kansas. Transactions of the Kansas Academy of Science 42:431–435.

Cervantes, F.A. 1993. *Lepus flavigularis*. Mammalian Species 423:1–3.

Chapman, J.A. 1975. *Sylvilagus nuttalli*. Mammalian Species 56:1–3.

Chapman, J.A., and J.E.C. Flux. 1990. Rabbits, Hares and Pikas. Status Survey and Conservation Action Plan. International Union for Conservation of Nature, Gland, Switzerland.

Chapman, J.A., and G.R. Willner. 1975. *Sylvilagus auduboni*. Mammalian Species 106:1–4.

Chapman, J.A., J.G. Hockman, and M.M. Ojeda-C. 1980. *Sylvilagus floridanus*. Mammalian Species 136:1–8.

Christensen, E.M., and M.A. Hutchinson. 1965. Historical observations on the ecology of Rush and Toole valleys, Utah. Proceedings of the Utah Academy of Science, Arts, and Letters 42:190–205.

Clanton, C.W., and M.L. Johnson. 1954. White-tailed Jackrabbit in Washington. Murrelet 35:15.

Clark, F. 1972. Influence of jackrabbit density on Coyote population change. Journal of Wildlife Management 36:343–356.

Clark, W.R., and F.H. Wagner. 1984. Role of livestock and Black-tailed Jackrabbits in changing abundance of *Kochia americana*. Great Basin Naturalist 44:635–646.

Clemons, C., L.G. Rickard, J.E. Kierans, and R.G. Botzler. 2000. Evaluation of host preferences by helminths and ectoparasites among Black-tailed Jackrabbits in northern California. Journal of Wildlife Diseases 36:555–558.

Conover, M.R., and D.J. Decker. 1991. Wildlife damage to crops: perceptions of agricultural and wildlife professionals in 1957 and 1987. Wildlife Society Bulletin 19:46–52.

Couch, L.K. 1927. Migrations of the Washington Black-tailed Jackrabbit. Journal of Mammalogy 8:313–314.

Cypher, B.L., K.A. Spencer, and J.H. Scrivner. 1994. Food-item use by Coyotes at the Naval Petroleum Reserves in California. Southwestern Naturalist 39:91–95.

Cypher, B. L., G. D. Warrrick, M. R. M. Otten, T. P. O'Farrell, W. H. Berry, C. E. Harris, T. T. Kato, P. M. McCue, J. H. Scrivner and B. W. Zoellick. 2000. Population dynamics of San Joaquin Kit Foxes at the Naval Petroleum Reserve in California. Wildlife Monographs No. 145:1–43.

Dalquest, W.W. 1948. Mammals of Washington. Washington Agricultural Experiment Station Technical Bulletin 62:1–131.

Daniel, A., J. Holechek, R. Valdez, A. Tembo, L. Saiwana, M. Fusco, and M. Cardenas. 1993. Jackrabbit densities on fair and good condition Chihuahuan Desert range. Journal of Range Management 46:524–528.

Desmond, M.J. 2004. Habitat associations and co-occurrence of Chihuahuan Desert hares (*Lepus californicus* and *L. callotis*). American Midland Naturalist 151:414–419.

Dice, L.R., 1926. Notes on Pacific Coast rabbits and pikas. Occasional Papers Museum of Zoology, University Michigan No. 166. 28 p.

Donoho, H.S. 1971. Dispersion and dispersal of White-tailed and Black-tailed Jackrabbits, Pawnee National Grasslands. US/International Biological Program Technical Report No. 96:1–52.

Dunn, J.P., J.A. Chapman, and R.E. Marsh. 1982. Jackrabbits: *Lepus californicus* and allies. Pp.124–145 *In* Wild Mammals of North America: Biology, Management and Economics. Chapman, J.A., and G.A. Feldhamer (Eds.). John Hopkins University Press, Baltimore, Maryland.

Eberhardt, L.E., and P. Van Voris. 1986. Historical wildlife dynamics on the Dugway Proving Ground: population and disease trends in jackrabbits over two decades. PNL-5967, UC-11, Pacific Northwest Laboratories, Battelle Memorial Institute, Utah. 56 p.

Evans, J., P.L. Hegdal, and R.E. Griffith, Jr. 1970. Methods of controlling jackrabbits. Pp. 109–116 *In* Proceedings of the 4th Vertebrate Pest Conference. Dana, R.H. (Ed.). University of Nebraska, Lincoln.

Fedy, B.C., and K.E. Doherty. 2011. Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: Greater Sage Grouse and cottontail rabbits. Oecologia 165:915–924.

Ferguson, H.L., and M. Atamian. 2012. Habitat connectivity for White-tailed Jackrabbit (*Lepus townsendii*) in the Columbia Plateau ecoregion. Appendix A.4 In Washington Connected Landscapes Project: Analysis of the Columbia Plateau Ecoregion. Western Wildlife Habitat Connectivity Working Group (WHCWG) (Compilers). Washington Department of Fish and Wildlife, and Washington Department of Transportation, Olympia, Washington.

Fisher J.L. 2012. Shifting prehistoric abundance of leporids at Five Finger Ridge, a central Utah archeological site. Western North American Naturalist 72:60–68.

Fitch, H.S. 1947. Ecology of a cottontail (*Sylvilagus auduboni*) population in central California. California Fish and Game 33:159–184.

Fitcher, E. 1953. Control of jackrabbits and prairie dogs on rangelands. Journal Range Management 6:16–24.

Fitzner, R.E., and R.H. Gray. 1991. The status, distribution and ecology of wildlife on the U.S. DOE Hanford Site: a historical overview of research activities. Ecological Monitoring and Assessment 18:173–202.

Flinders, J.T., and J. A. Chapman. 2003. Black-tailed Jackrabbit (*Lepus californicus* and allies). Pp. 126–

146 *In* Wild Mammals of North America: Biology, Management and Economics. Chapman, J.A., and G.A. Feldhamer (Eds.). John Hopkins University Press, Baltimore, Maryland.

Flinders, J.T., and R.M. Hansen. 1975. Spring population responses of cottontails and jackrabbits to cattle grazing shortgrass prairie. Journal of Range Management 28:290–293.

Foster, B.E. 1932. Annual report of rodent control in Arizona for the period July 1, 1931 to June 30, 1932. U.S. Department of Agriculture, Bureau of Biological Survey and Agricultural Extension Service, University of Arizona, Tucson. 11 p.

French, N.R., R. McBride, and J. Detmer. 1965. Fertility and population density of the Black-tailed Jackrabbit. Journal of Wildlife Management 29:14–26.

Frey, J.K., and J.L. Malaney. 2006. Snowshoe Hare (*Lepus americanus*) and Mountain Cottontail (*Sylvilagus nuttallii*) biogeography at their southern range limit. Journal of Mammalogy 87:1175–1182.

Fritzell, P. (compiler). 2016. Trends in Iowa wildlife populations and harvest 2012. Iowa Department of Natural Resources, Conservation and Recreation Division, Des Moines, Iowa Game Summary. p. 135–164.

Ganskopp, D., B. Myers, and S. Lambert. 1993. Black-tailed Jackrabbit preferences for eight forages used for reclamation of Great Basin rangelands. Northwest Science 67:246–250.

Gilcrease, K., K. Inman, A. Preston and G. Bolinger. 2016. The decline of the White-tailed Jackrabbit (*Lepus townsendii*): carbohydrate and soil texture analysis. European Journal of Biological Research 6:74–81.

Germano, D.J., R. Hungerford, and S.C. Martin. 1983. Responses of selected wildlife species to the removal of mesquite from desert grassland. Journal of Range Management 36:309–311.

Gerow, K., N.C. Kline, D.E. Swann, and M. Pokorny. 2010. Estimating vertebrate mortality on roads at Saguaro National Park, Arizona. Human-Wildlife Interactions 4:283–292.

Gibson, L. 2006. The role of lethal control in managing the effects of apparent competition on endangered species. Wildlife Society Bulletin 34:1220–1224.

Gilchrist, D.A. 1930. Report of operations in Arizona during the period July 1, 1929 to June 30, 1930. U.S. Department of Agriculture, Bureau of Biological Survey, Phoenix, Arizona. 38 p.

Gray, J.P. 1977. Population studies of Sonoran Desert lagomorphs. M.S. Thesis, University of Arizona, Tucson. 40 p.

Grayson, D.K. 1977. On the Holocene history of some Great Basin lagomorphs. Journal of Mammalogy 58:507–513.

Gross, J.E., L.C. Stoddart, and F.H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildlife Monographs 40:3–68.

Gruell, G. 1996. Influence of fire on Great Basin wildlife habitats. Transactions of the Western Section of the Wildlife Society 32:55–61.

Gunther, K.A., R.A. Renkin, J.C. Halfpenny, S.M. Gunther, T. Davis, P. Schullery, and L. Whittlesey. 2009. Presence and distribution of White-tailed Jackrabbits in Yellowstone National Park. Yellowstone Science 17:24–32.

Hayden, P. 1966a. Seasonal occurrence of jackrabbits on Jackass Flat, Nevada. Journal of Wildlife Management 30:835–838.

Hayden, P. 1966b. Food habits of Black-tailed Jackrabbits in southern Nevada. Journal of Mammalogy 47:42–46.

Henke, S.E., and F.C. Bryant. 1999. Effects of Coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

Hernández, L., J.W. Laundré, K.M. Grajales, G.L. Portales, J. Lopez-Portillo, A. Gonzalez-Romero, A. Garcia, and J.M. Martinez. 2011. Plant productivity, predation and the abundance of Black-tailed Jackrabbits in the Chihuahuan Desert of Mexico. Journal Arid Environments 75:1043–1049.

Hernández, L., R.R. Parmenter, J.W. Dewitt, D.C. Lightfoot, and J.W. Laundré. 2002. Coyote diets in the Chihuahuan Desert, more evidence for optimal foraging. Journal Arid Environments 51:613–625.

Howell, A.B. 1923. Periodic fluctuations in the numbers of small mammals. Journal of Mammalogy 3:149–155.

Hoffman, S.W., and J.P. Smith. 2003. Population trends of migratory raptors in western North America. Condor 105:397–419.

Huey, L.M. 1942. A vertebrate faunal survey of the Organ-pipe Cactus National Monument. Transactions San Diego Society Natural History 9:353–375.

Humphrey, R.R. 1957. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review 24:193–252.

Hungerford, C.R., C.H. Lowe, and R.L. Madsen. 1974. Population studies of the Desert Cottontail (*Sylvilagus audubonii*), Black-tailed Jackrabbit (*Lepus californicus*) and Allen's Jackrabbit (*Lepus alleni*) in the Sonoran Desert. US/International Biological Program, Desert Biome Research Memo 74:1–22.

Jaksic, F.M., and J.L. Yanez. 1983. Rabbit and fox introductions in Tierra del Fuego: history and assessment of the attempts at biological control of the rabbit infestation. Biological Conservation 26:367–374.

Keane, R.E., J.K. Agee, P. Fulé, J.E. Keeley, C. Key, S.G. Kitchen, R. Miller, and L.A. Schulte. 2008. Ecological effects of large fires on US landscapes: benefit or

catastrophe? International Journal of Wildland Fire 17:696–712.

Kelly, P.A. 2018. *Sylvilagus bachmani* (Waterhouse, 1839); Brush Rabbit. Pp. 122–124 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Kline, P.D. 1963. Notes on the biology of jackrabbits in Iowa. Proceedings of Iowa Academy of Science 70:196–204.

Knetter, J.M. (Compiler). 2014. Statewide Report, Upland Game, Study II, Job1, July 1, 2011 to June 30, 2012. Idaho Department Fish and Game, Boise, Idaho. 140 p.

Knick, S.T. 1990. Ecology of Bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:3–42.

Knick, S.T., and D.L. Dyer. 1997. Distribution of Black-tailed Jackrabbit habitat determined by GIS in southwestern Idaho. Journal of Wildlife Management 61:75–85.

Kochert, M.N., K. Steenhof, L.B. Carpenter, and J.M. Marzluff. 1999. Effects of fire on Golden Eagle territory occupancy and reproductive success. Journal of Wildlife Management 63:773–780.

Krebs, C.J., and D.L. Murray. 2018. *Lepus americanus* Erxlebern, 1777; Showshoe Hare. Pp. 163–165. *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Laundré, J.W. 2018. *Sylvilagus audubonii* (Baird, 1857); Desert Cottontail. Pp. 120–122 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Lavazza, A., and B.D. Cooke. 2018. Diseases of lagomorphs. Pp. 18–21 *In* Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Lechleitner, R.R. 1958. Movements, density, and mortality in a Black-tailed Jackrabbit population. Journal of Wildlife Management 22:371–384.

Lightfoot, D.C., A.D. Davidson, C.M. McGlone, and D.G. Parker. 2010. Rabbit abundance relative to rainfall and plant production in northern Chihuahuan Desert grassland and shrubland habitats. Western North American Naturalist 70:490–499.

Lim, B.K. 1987. *Lepus townsendii*. Mammalian Species 288:1–6.

Link, S.O., C.W. Keeler, R.W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. International Journal of Wildland Fire 15:113–119.

Linsdale, J.M. 1932. Further facts concerning losses to wild animal life through pest control in California. Condor 34:121–135.

Lochmiller, R.L., D.G. Pietz, S.T. McMurray, D.M. Leslie, Jr., and D.M. Engle. 1995. Alterations in conditions for cottontail rabbits (*Sylvilagus floridanus*) on rangelands following brush management. Journal of Wildlife Management 48:232–239.

Lombardi, J.V., C.E. Comer, D.G. Scognamillo, and W.C. Conway. 2017. Coyote, fox, and Bobcat response to anthropogenic and natural landscape features in a small urban area. Urban Ecosystems 20:1239–1248.

Longland, W.S. 1991. Risk of predation and food consumption by Black-tailed Jackrabbits. Journal of Range Management 44:447–450.

Lord, R.D., Jr. 1961. Mortality rates of cottontail rabbits. Journal of Wildlife Management 25:33–40.

Lorenzo, C., P. Cortés-Calva, G. Ruiz-Campos, and S. Ticul Alvarez-Castañeda. 2013. Current distributional status of two subspecies of *Sylvilagus bachmani* on the Baja California Peninsula, Mexico. Western North American Naturalist 23:219–223.

Lorenzo, C., T.M. Rioja, A. Carillo, and F.A. Cervantes. 2008. Population fluctuations of *Lepus flavigularis* (Lagomorpha: Leporidae) at Tehuantepec Isthmus, Oaxaca, Mexico. Acta Zoológica Mexicana 24:207–220.

Lusk, J. F. 2016. 2016 April rural mail carrier survey. Federal-Aid in Wildlife Restoration Project No. W-15-R, Wildlife Division, Nebraska Game and Parks Commission, Lincoln. 7 p.

MacCracken, J.G., and R.H. Hansen. 1962. Herbaceous vegetation of habitat used by Black-tailed Jackrabbits and Nuttall Cottontails in southeastern Idaho. American Midland Naturalist 107:180–184.

Mankin, P.C., and R.E. Warner. 1999. A regional model of the Eastern Cottontail and land-use change in Illinois. Journal of Wildlife Management 63:956–963.

Marín, A.I., L. Hernández, and J.W. Laundré. 2003. Predation risk and food quantity in the selection of habitat by Black-tailed Jackrabbit (*Lepus californicus*): an optimal foraging approach. Journal of Arid Environments 55:101–110.

Marzluff, J.M., S.T. Knick, M.S. Vekasy, L.S. Schueck, and T.J. Zarriello. 1997. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. Auk 114:673–687.

Matchett, M.R., and B.W. O'Gara. 1987. Methods of controlling Golden Eagle depredation on domestic sheep in southwestern Montana. Journal of Raptor Research 21:85–94.

McAdoo, J.K., W.S. Longland, G.J. Cluff, and D.A. Klebenow. 1987. Use of new rangeland seedings by Black-tailed Jackrabbits. Journal of Range Management 40:520–524.

McAdoo, J.K., L.T. Vermeire, and W. Gilgert. 2004. The other grazers. Rangelands 26:30–37.

McCarty, K.M., K.L. Lisence, and K.V. Jacobson. 2013. Arizona Golden Eagle Nest Survey 2013. Arizona

Game and Fish Department Nongame Branch, Technical Report 277, Phoenix, Arizona. 30 p.

McClure, M.F., N.S. Smith, and W.W. Shaw. 1996. Densities of Coyotes at the interface of Saguaro National Monument and Tucson, Arizona. Southwestern Naturalist 41:83–86.

Meslow, E.C., and L.B. Keith. 1968. Demographic parameters of a Snowshoe Hare population. Journal of Wildlife Management 32:812–834.

Miller, R.F., S.T. Knick, D.A. Pyke, C.W. Meinke, S.E. Hanser, M.J. Wisdom, and A.L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pp. 145–184 In Greater Sage-grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology, Volume 38. Knick, S.T., and J.W. Connelly (Eds.). University of California Press, Berkeley, California.

Mohr, W.P., and C.O. Mohr. 1936. Recent jackrabbit populations at Rapidan, Minnesota. Journal of Mammalogy 17:112–114.

Mutze, G., J. Kovaliski, K. Butler, L. Capucci, and S. McPhee. 2010. The effect of rabbit population control programmes on the impact of Rabbit Haemorhagic Disease in southeastern Australia. Journal of Applied Ecology 47:1137–1146.

Nelson, J., L. Holechek, R. Valdez, and M. Cardenas. 1997. Wildlife numbers on late and mid-seral Chihuahuan Desert rangelands. Journal of Range Management 50:593–599.

Nielson, C.K, and L.K. Berkman. 2018. Sylvilagus floridanus (J. A. Allen, 1890); Eastern Cottontail. Pp. 137–140 In Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Palmer, T.S. 1897. The jack rabbits of the United States. U.S. Department of Agriculture, Biological Survey Bulletin 8:1–88.

Phillip, C.B., J.F. Bell, and C.L. Larson. 1955. Evidence of infectious diseases and parasites in a peak population of Black-tailed Jackrabbits in Nevada. Journal of Wildlife Management 19:225–233.

Phillips, W.S. 1963. Vegetational changes in northern Great Plains. University of Arizona Agricultural Experiment Station Report 214:1–174.

Pitman, N.J. 2013. Rural mail carrier survey report 2012. Kansas Department of Wildlife, Parks and Tourism, Federal-Aid in Wildlife Restoration W-39-19, Pratt, Kansas. 20 p.

Portales-Betancourt, G.L., L. Hernández, J.W. Laundré, and F.A. Cervantes. 2012. Reproducción y densidad de la Liebre Cola-negra (Lepus californicus) en relación a factores ambientales, en la Reserva de la Biosfera Mapimí, Desierto Chihuahuense. Therya 3:171–183.

Rachlow, J.L., P.A. Becker, and L.A. Shipley. 2018. Brachylagus idahoensis (Merriam, 1891); Pygmy Rabbit. Pp. 87–90 In Lagomorphs: Pikas, Rabbits, and Hares of the World. Smith, A.T., C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Rice, B.L., and M. Westoby. 1978. Vegetation responses of some Great Basin shrub communities protected against jackrabbits and domestic stock. Journal of Management 31:28–34.

Rickard, W.H., and L.D. Poole. 1989. Terrestrial wildlife of the Hanford Site: past and future. Northwest Science 63:183–193.

Roberts, N.M., and S.M. Crimmins. 2010. Bobcat population status and management in North America: evidence of large-scale population increase. Journal Fish and Wildlife Management 1:169–174.

Rosasco, M.E. 1957. Seasonal abundance of the tick Dermocentor parumapertus on the Black-tailed Jackrabbit, with notes on other ectoparasites. Journal of Mammalogy 38:485–490.

Roundy, B.A., G.J. Cluff, J.K. McAdoo, and R.A. Evans. 1985. Effects of jackrabbit grazing, clipping, and drought on Crested Wheatgrass seedlings. Journal of Range Management 38:551–555.

Sauer, J.R., and W.A. Link. 2011. Analysis of the North American breeding bird survey using hierarchical models. Auk 128:87–98.

Sauer, J.R., J.E. Fallon, and R. Johnson. 2003. Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. Journal of Wildlife Management 67:372–389.

Saunders, G., B. Cooke, K. McColl, R. Shine, and T. Peacock. 2010. Modern approaches for the biological control of vertebrate pests: an Australian perspective. Biological Control 52:288–295.

Schaible, D.J., C.D. Dieter, R.D. Neiger, and M.B. Hildreth. 2011. Calodium hepaticum in White-tailed Jackrabbits in South Dakota. Prairie Naturalist 43:56–58.

Schmitt, D.N., D.B. Madsen, and K. Lupo. 2002. Small-mammal data on Early and Middle Holocene climates in the Bonneville Basin, USA. Quaternary Research 58:255–260.

Simes, M.T., K.M. Longshore, K.E. Nussear, G.L. Beatty, D.E. Brown, and T.C. Esque. 2015. Black-tailed and White-tailed Jackrabbits in the American west: history, ecology, significance, and survey methodologies. Western North American Naturalist 75:491–521.

Smith, A.T, C.H. Johnston, P.C. Alves, and K. Hackländer (Eds.). 2018. Lagomorphs: Pikas, Rabbits, and Hares of the World. Johns Hopkins University Press, Baltimore, Maryland.

Smith, G.A., and J.R. Murphy. 1979. Breeding responses of raptors to jackrabbit density in the eastern Great Plains Desert of Utah. Journal of Raptor Research 13:1–14.

Smith, D.G., J.R. Murphy, and N.D. Woffinden. 1981. Relationships between jackrabbit abundance and Ferruginous Hawk reproduction. Condor 83:52–56.

Smith, G.W. 1990. Home range and activity patterns of Black-tailed Jackrabbits. Great Basin Naturalist 50:249–256.

Smith, R.H., and S. Gallizioli. 1965. Predicting hunter success by means of a spring call count of Gambel Quail. Journal of Wildlife Management 29:806–813.

Sosa Burgos, L.M. 1991. Ecology of two coexisting populations of lagomorphs in the Mojave Desert, *Lepus californicus* and *Sylvilagus audubonii*. Ph.D. Thesis, University of California, Los Angeles, California. 118 p.

Sowls, L.K. 1957. Reproduction in the Audubon Cottontail in Arizona. Journal of Mammalogy 38:234–243.

Stahlecker, D.W., D.G. Mikesic, J.N. White, S. Shaffer, J.P. Delong, M.R. Blackmore, and C.E. Blackmore. 2009. Prey remains in nests of Four Corners Golden Eagles, 1998–2008. Western Birds 40:301–306.

Steenhof, K., and M. Kochert. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. Journal of Animal Ecology 57:37–48.

Steenhof, K., M.N. Kochert, and T.L. McDonald. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. Journal of Animal Ecology 66:350–362.

Stoddart, L.C. 1970. A telemetric method for detecting jackrabbit mortality. Journal of Wildlife Management 34:501–507.

Stoddart, L.C. 1985. Severe weather related mortality of Black-tailed Jackrabbits. Journal of Wildlife Management 49:696–698.

Taylor, W.P., C.T. Vorhies, and P.B. Lister. 1935. The relation of jack rabbits to grazing in southern Arizona. Journal of Forestry 33:490–498.

Teixeira, F.Z., A.V.P. Coelho, I.B. Esperandio, and A.Kindel. 2013. Vertebrate road mortality estimates: effects of sampling methods and carcass removal. Biological Conservation 157:317–323.

Tiemeier, O.W. 1965. Study area, reproduction, growth and development, age distribution, life span, censusing, live trapping and tagging, crop damage, predation and habits. Pp. 5–39 *In* The Black-tailed Jackrabbit in Kansas. Kansas State University Agricultural Experimental Station Technical Bulletin 140:1–75.

Turner, F.B., R.H. Rowland, and R.A. Wood. 1966. Nuclear engineering and wildlife: radioactivity in jackrabbits after the Sedan Test. Journal of Wildlife Management 30:433–443.

Turner, R.M., R.H. Webb, J.E. Bowers, and J.R. Hastings. 2003. The Changing Mile Revisited. University of Arizona Press, Tucson, Arizona.

Van Auken, O.W. 2000. Shrub Invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

Verts, B.J., and L.N. Carraway. 1998. Land Mammals of Oregon. University of California Press, Berkeley, California.

Vorhies, C.H., and W.P. Taylor. 1933. The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* ssp. in relation to grazing in Arizona. University of Arizona, College of Agriculture Technical Bulletin No. 49:467–510.

Wagner, F.H., and C. Stoddart. 1972. Influence of Coyote predation on Black-tailed Jackrabbit populations in Utah. Journal of Wildlife Management 36:329–342.

Watkins, L.C., and R.M. Nowak. 1973. The White-tailed Jackrabbit in Missouri. Southwestern Naturalist 18:352–354.

Washington Department of Fish and Wildlife (WDFW). 2008. Priority habitat and species list. Washington Department of Fish and Wildlife, Olympia, Washington. 295 p.

Weddell, B.J. (Compiler and Editor). 2001. Restoring Palouse and Canyon grasslands: putting back the missing pieces. Fire in steppe vegetation of the Northern Intermountain Region. BLM Technical Bulletin No. 01-15, Idaho Bureau of Land Management, Cottonwood, Idaho. 11 p.

Westoby, M., and F.H. Wagner. 1973. Use of Crested Wheatgrass seeding by Black-tailed Jackrabbits. Journal of Range Management 26:349–352.

White, J.A. 1991. North American Leporinae (Mammalia: lagomorpha) from Late Miocene (Clarendonian) to Latest Pliocene (Blancan). Journal of Vertebrate Paleontology 11:67–89.

Williams, C.S., and M.C. Nelson. 1939. Highway mortality of rabbits in Idaho. Journal of Mammalogy 20:380–382.

Williams, D.F. 1986. Mammalian species of special concern in California. California Department Fish and Game, Sacramento, California. 111 p.

Williams, D.F., P.A. Kelly, L.P. Hamilton, M.R. Lloyd, E.A. Williams, and J.J. Youngblom. 2008. Recovering the endangered Riparian Brush Rabbit (*Sylvilagus bachmani riparius*): reproduction and growth in confinement and survival after translocation. Pp. 349–361 *In* Lagomorph Biology: Evolution, Ecology, and Conservation. Alves, P.C., N. Ferrand, and K. Hackländer (Eds.). Springer, Berlin, Germany.

Wills, C.A., and W.K. Ostler. 2001. Ecology of the Nevada Test Site: an annotated bibliography. DOE/NV/11718-59. Bechtel Ecological Services, Las Vegas, Nevada. 386 p.

Wilson, D.E., and S. Ruff (Eds.). 1999. The Smithsonian Book of North American Mammals. Smithsonian Institution Press, Washington, D.C.

Wing, L.W. 1960. Scattered reports and latitudinal passage in rabbit and rodent cycles. Journal of Cycle Research 9:51–66.

Woffinden, N.D., and J.R. Murphy. 1977. Population dynamics of the Ferruginous Hawk during a prey decline. Great Basin Naturalist 37:411–425.

Woffinden, N.D., and J.R. Murphy. 1989. Decline of a Ferruginous Hawk population: a 20-year summary. Journal of Wildlife Management 53:1127–1132.

Woodbury, A.M. 1955. Ecology of the Great Salt Lake Desert: I. An annual cycle of the desert jackrabbit. Ecology 36:353–356.

Woodgerd, W. 1952. Food habits of the Golden Eagle. Journal of Wildlife Management 16:457–459.

Woolf, A., D.R. Shoemaker, and M. Cooper. 1993. Evidence of tularemia regulating a semi-isolated cottontail rabbit population. Journal of Wildlife Management 57:144–157.

Woolsey, N.G. 1956. The vanishing Antelope Jackrabbit. Arizona Wildlife Sportsman November: 24–27.

Wooster, L.D. 1935. Notes on the effects of drought on animal populations in western Kansas. Transactions of the Kansas Academy of Science 38:351–353.

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THE BIOLOGY AND ECOLOGY OF THE AMARGOSA VOLE
(MICROTUS CALIFORNICUS SCIRPENSIS)

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Abstract.—Obtaining detailed biological data from field studies of small mammals is challenging, yet these data are crucial for management. We discuss data on sexual dimorphism, molt patterns, morphometrics, dietary habits, and behavior of the endangered Amargosa Vole (*Microtus californicus scirpensis*). These data are from our captive colony and field studies, but also include comparisons to data from other studies. Male voles had significantly larger body mass, longer total length, and longer tail length. Molt progression in 11 captive-reared individuals began at the dorsal mid-line, creating a strip of juvenile hair from head to rump that disappears around eight weeks of age. These traits allow for better characterization of age classes of voles captured in the wild. Captive voles initially rejected fresh cuttings of native Olney's Three-square Bulrush (*Schoenoplectus americanus*), the dominant plant in the wild Amargosa Vole diet, although they consumed all portions of the plant when it was provided erect in planted cups. We captured images of voles in the wild on camera twice consuming plants other than Olney's Three-square Bulrush. This information is essential to link management actions with species biology, including habitat management, disease work, and population biology.

Key Words.—behavior; captive-breeding; conservation; food habits; Mojave Desert; natural history; recovery plan; species description

INTRODUCTION

Detailed biological data from field studies of small mammals are crucial for understanding the natural history of these animals and for developing management plans. Sources of such data may include published data, gray literature, museum field notes, and observations of captive breeding. The Amargosa Vole (*Microtus californicus scirpensis*) is a highly specialized desert rodent that is endemic to the Amargosa River valley and associated isolated springs near Tecopa in Inyo County, California (U.S. Fish and Wildlife Service [USFWS] 1997; Cudworth and Koprowski 2010). After Bailey (Bailey 1900) first described the vole over 100 y ago, few studied the vole until the State of California listed it as endangered in 1980 and the federal government listed it in 1984 (USFWS 1997). An early physical description of the animal indicated that whiskers of Amargosa Voles were white terminally and black basally, noses were black, tail was short and bicolored, dorsal pelage varied from bright brown to cinnamon-colored with neutral gray color ventrally, and that this vole was distinct from other voles in California by virtue of their small skull with comparatively wide zygomatic arch (Kellogg 1918).

After a status review (USFWS 1997), field studies focused on distribution, persistence, genetic status, and ecology (Neuwald 2010; Ott-Conn et al. 2014, 2015; Poulsen et al. 2017). The species is dependent on Olney's Three-square Bulrush (*Schoenoplectus americanus*) for both habitat and nutrition (Klinger et al. 2015). In 2016, the population estimate for all Amargosa Voles was just 66–425 individuals (unpubl. report). While the species was probably never abundant or widely distributed, it is now completely absent from its type locality in Shoshone, California. A railroad grade, roads, parks, and alkali flats separate remaining habitat patches in Tecopa but it is not known how important such barriers might be.

Despite an improved understanding of this species, empirical data needed to inform recovery planning were still lacking. In fact, the Recovery Plan for the Amargosa Vole stated that it could not establish criteria for delisting due to a lack of biological data specific for Amargosa Voles (USFWS 1997). In the absence of detailed information on key biological attributes, such as reproduction, behavior, and ontogeny, biologists surmised that biological characteristics of the Amargosa Vole were the same as more common and not desert-adapted subspecies of *Microtus californicus* (USFWS 1997). As part of recovery efforts, we established a captive breeding colony in 2014. In this paper, we present detailed biological data from our captive colony and summarize discoveries about the biology and ecology of the Amargosa Vole from a combination of colony and field data.

METHODS

Study area.—We studied wild Amargosa Voles near Tecopa, California, in southeastern Inyo County. This area of the Mojave Desert experiences temperature fluctuations from a mean low of 3.2° C to high of 41° C and mean annual rainfall of 12.3 cm (National Oceanic

and Atmospheric Administration 2010). Amargosa Vole habitat is characteristically patchy with spring-fed marshes dominated by Olney's Three-square Bulrush (*Schoenoplectus americanus*; hereafter bulrush) separated by minimally vegetated alkaline playa and salt scrub.

Field sampling.—We collected data on wild Amargosa Voles as part of ongoing population assessments conducted by the California Department of Fish and Wildlife, the University of California, Davis, School of Veterinary Medicine, and the United States Geological Survey. We placed Sherman live traps (H.B. Sherman, Tallahassee, Florida, USA) in established grids near Tecopa Hot Springs, California, as previously described (Klinger et al. 2015; Foley et al., unpubl. report). Trap bait varied across trapping periods but included either peanut butter, four-way horse feed (corn, barley, oats, and wheat with molasses), and apples; or peanut butter and oats. We added apples for moisture. We handled Amargosa Voles when they were awake and typically recorded sex, body mass, age, reproductive status (males: position of the testes; females: condition of vaginal opening and size of mammae), body condition (Ullman-Cullere and Foltz 1999), and health, including trauma or evidence of ectoparasites. We tagged all voles with a uniquely numbered ear tag (1005-1 Monel, National Band and Tag Co., Newport, Kentucky, USA) and we secondarily tagged some individuals with subcutaneous passive integrated transponders (PIT).

To examine natural behavior in the wild, we deployed camera traps in 21 marshes. Typically, we placed three NatureView 11-9740 CAMHD (Bushnell Overland Park, Kansas, USA) or Reconyx PC900 (Holmen, Wisconsin, USA) cameras per marsh, which we fastened with bailing wire to metal U-posts and angled them downward in the direction of vole sign. We modified cameras by placing black duct tape over half of the LED lights to minimize overexposure and we attached a 600 mm lens for close-range photographs. We baited cameras by distributing approximately 200 g of oats, peanut butter, alfalfa, and four-way horse feed in a pile in front of each camera on the day the camera was armed, and we programmed these cameras to take five photographs when triggered with no delay between images. Cameras remained active for approximately six weeks, although full memory cards at some sites resulted in fewer than six weeks of data being collected; we considered this 4–6 week period a primary period.

Trained personnel reviewed images and when voles were observed on camera, the date, time, and number of voles were recorded. Events of aggression included biting, chasing, or fighting. Analysis of activity used a presumed number of independent observations of voles per hour based on Sanderson's AllPictures method (Sanderson and Harris 2013) assuming that events separated by at least 15 min were independent (Rendall

et al. 2014). We analyzed the first five days from each primary period. The software summarized the number of events into four seasons: winter (December-February), spring (March-May), summer (June-August), and fall (September-November). Daytime was any hour after the time of sunrise and before sunset on the mid-day of the 5-d sampling period. Nighttime was any time after sunset but before sunrise as reported by the National Oceanic and Atmospheric Administration.

Museum data.—We reported descriptive characteristics and measurements of Amargosa Voles using specimens submitted to the Museum of Vertebrate Zoology at the University of California Berkeley from 2013-2016.

Captive colony sampling.—*Colony management:* A captive breeding colony of Amargosa Voles lived at the University of California, Davis, in both indoor and outdoor caging (Allan et al. 2018). Briefly, indoor environments consisted of 1–3 Amargosa Voles kept in polycarbonate cages (Bellmore, New York, USA) topped with wire lids with a thick layer (15 cm) of rice or wheat straw for bedding and fresh water daily. Technicians spot-cleaned bedding daily to remove wet or soiled straw, and transferred animals to sterilized cages with new straw monthly. We kept rooms at 18.3–23.9° C with a 12-h light cycle. Initially, we fed Amargosa Voles Harlan rodent chow #2018 (Teklad Diets, Madison, Wisconsin, USA) augmented with fresh bulrush grown in a greenhouse and occasionally fresh greens, fruits, seeds, root vegetables, or alfalfa, but we later transitioned them to a high-fiber, lower fat rabbit chow (LabDiet 5326-3, Stewart's Feed Service, Lawrenceville, Georgia, USA).

Outdoor environments consisted of 1–3 Amargosa Voles housed in mesocosms under a large, chain-link structure reinforced with 1.3 cm mesh hardware cloth to exclude small predators. Mesocosms were structural foam planters (139.7 × 100.0 × 63.5 cm) with potting soil and a bulrush clone from Tecopa. We provided water in large glass bowls and offered chow supplementary to bulrush. An irrigation system kept bulrush plants and soil moist.

Breeding: We established the vole colony with 20 wild-caught founder individuals. In 2016, we brought an additional 12 wild voles into captivity. When pups reached sexual maturity, we selected individuals for breed pairs based on an electronically maintained pedigree to minimize average relatedness. For each indoor pairing, we placed a male and a female vole together in a guinea pig cage with food, water, and bedding. Although we conducted breeding in outdoor housing when the colony was first established, we later discontinued this because monitoring births was infeasible in mesocosm burrows and there was an incident of parent-offspring inbreeding. If we only desired one litter from a breed pair, we removed the male from the breeding cage 20

d after pairing, before the first litter was born. This ensured that the post-partum estrus of a female was not consummated, preventing a second litter. If we desired more than one litter from a breed pair, we left the male in the breeding cage to assist with pup rearing and to allow for continued mating. If a pair did not produce a litter within approximately 60 d, we usually re-paired the male and female with new mates. Once pups were born, we left the breeding cage relatively undisturbed for the first 7–10 d except to provide fresh water and food. Twenty-one days after birth, we weaned pups, removed them from the parental cage, marked them with permanent ear tags, and housed them in groups of up to three same-sex litter-mates.

Ontogeny data collection: We based developmental progression on observations of 114 litters born in captivity. Although we checked pups daily, we rarely handled them prior to 10 d of age to avoid stressing the mother, which could result in offspring being abandoned or cannibalized. Following a molt study in California Voles (*Microtus californicus* ssp.; Ecke and Kinney 1956), we noted qualitative data on the coat color of live individual Amargosa Voles at least 10 d of age with a particular focus on the width and location of the dorsal stripe. Prior to weaning, we chose voles at random from each litter on each collection date because pups were too young to be ear-tagged and therefore could not be individually identified. After weaning, we randomly chose one individual from each litter and followed them for the duration of the study along with two additional voles that were litter mates of different sexes to improve sample size. In total, we assessed 11 individuals (six males, five females) for molt progression every 4 d from ages 10–56 d.

Statistical analyses.—We maintained data on every animal, including veterinary notes, birth dates, wean dates, death dates, and physical examination results, in an electronic spreadsheet in Excel (Microsoft, Redmond, Washington, USA) and the database FileMaker Pro Advanced 12.0v1 (FileMaker Incorporated, Santa Clara, California, USA). Initially, we managed colony lineages using the pedigree software PopLink 2.4, but these data were also moved to FileMaker. We conducted all analyses in R (Version 3.2.3; R Core Team 2017) and considered a *P*-value ≤ 0.05 to be significant. Where comparison of mean values was intended, we assessed differences using Welch's t-test. After assessing data for normality with a chi-square test, we used two-factor ANOVA to compare activity detected on cameras (as defined above) between day or night and season. We analyzed monthly distributions of aggression events with a chi-square and factors influencing breeding success using logistic regression. We defined breeding success as the birth of pups that were successfully weaned into the colony. An unsuccessful litter was one where we confirmed that pups were born but the dam did not successfully wean pups, either due to neonatal mortality, poor maternal care, or other reasons. We omitted attempted pairings from which pups were never born. We generated kinship coefficients to assess the impact of inbreeding on litter success from a kinship matrix of all pairs computed in the R package kinship2 (Therneau and Sinnwell 2015).

Results

Field observations.—Field observations tended to be limited to body measurements, assessment of coat color, records of longevity extremes, and observations of behavior inferred from camera traps. We assessed sexual dimorphism in mass using 2,343 (1,040 male, 1,303 female) adult wild voles captured between 2010 and 2017. Male mass ranged from 21–128 g (mean 81.4 g) and was significantly larger than female mass ($t = 6.89$, df = 1993.8, $P < 0.001$), which ranged from 23–109 g (mean 77.4 g; Table 1). Typically, voles in the

TABLE 1. Mean (± standard deviation: SD) body mass (g), total body length (mm), tail length (mm), and hind foot length (mm) of adult Amargosa Voles (*Microtus californicus scirpensis*) compared to body trait measurements of Sanhedrin Voles (*M. californicus eximius*). Sample sizes for traits are given parenthetically below mean values. Samples sizes for total length, tail length, and hind foot length are the same and given only for total length. Data for *M. californicus eximius* come from Cudworth and Koprowski 2010. Significant differences in trait means between males and females is indicated by superscript [a] and between captive and wild males with a superscript [b].

| | *M. californicus scirpensis* | | *M. californicus eximius* | |
| | Female | Male | Female | Male |
Trait	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Body mass (g)				
wild	77.4 ± 12.6 (1,303)	81.4 ± 14.7[a] (1,016)	43.4 ± 1.8 (9)	47.1 ± NA (9)
captive	78.8 ± 17.5 (96)	89.7 ± 15.7[b] (113)		
Total length	200.6 ± 9.1 (13)	208.9 ± 10.3[a] (19)	167 ± 2.0 (21)	174 ± 2.9 (19)
Tail length	62.1 ± 3.8	66.3 ± 4.1[a]	45 ± 0.9	49 ± 1.2
Hind foot length	23.1 ± 1.6	23.1 ± 0.98	22 ± 0.3	22 ± 3.8

Figure 1. Characteristics that are unique to modern day Amargosa Voles (*Microtus californicus scirpensis*) include (left) white markings on the upper and/or lower lip, sometimes forming a "white beard" (Photographed by Eliška Rejmánková), and (right) extremely dark juvenile pelage of *M. californicus scirpensis* (D) compared to M. californicus vallicola (A-C) and *M. oregoni adocetus* (E; Photographed by Chris Conroy).

wild were a dark mouse brown and most had a distinct white circum-oral beard. It was common to recapture individual voles over several months, but recaptures diminished thereafter. Exceptions included four female voles that we occasionally recaptured and survived at least 16–20 mo.

Cameras recorded numerous instances of voles consuming bulrush, but there were also two cases of consumption of other plants: once on Yerba Mansa (*Anemopsis californica*) and the other on Clustered Goldenweed (*Pyrrocoma racemosa* var. *paniculata*). Camera evidence also confirmed agonistic behaviors. We examined 1,220 baited camera-days and there were 1,603 independent camera events: these featured a vole and 30 independent aggression events. Most events were non-specific, with two or three animals in the same proximity with evidence of chasing and subsequent absence of one of the animals. Seven images clearly showed a vole being bitten or rolled over by another vole. There were from one to 23 aggression events per primary period, with on average 0.02 aggression events per day (Table 2). Considerably more vole sightings and significantly more aggression events were observed in May than other months ($\chi^2 = 20.85$, df = 6, $P < 0.001$). All aggression events occurred when cameras were baited. Three aggression events between a vole and a Desert Woodrat (*Neotoma lepida*) were consistent with a vole possibly initiating the interactions but in the end, each vole left the scene to the woodrat. Hourly activity was highest in spring (2.2 vole sightings per hour) and lowest in fall (0.5 sightings per hour). Although nighttime activity was significantly higher than daytime (1.5 vole sightings per

hour at night and 1.3 vole sightings per hour in day; $F_{1,1078}$ = 4.90, $P = 0.030$), we observed numerous voles during the day.

Colony results.—We assessed length and body mass dimorphism using museum specimens including 15 adult females (one brought into the colony from the field, eight colony F_1 generation, and six F_2) and 20 adult males (one from the field, 10 F_1, and nine F_2). We also had body mass data from 209 captive-reared voles (113 male, 96 female). Overall, Amargosa Voles were relatively large (Table 1) and males had larger body mass ($t = 4.70$, df = 192.57, $P < 0.001$), longer total length ($t = 2.42$, df = 28.01, $P = 0.022$), and longer tail length ($t = 2.92$, df =

Table 2. Summary of independent aggression events among Amargosa Voles (*Microtus californicus scirpensis*) detected during the first 5 d of camera trap deployment between November 2015 and September 2016 near Tecopa, California. Abbreviations are TAE = total number of aggressive events, NIS = number of independent vole sightings, and PEA = proportion of events that were aggressive.

Month	Day 1	Day 2	Day 3	Day 4	Day 5	TAE	NIS	PEA
Nov./ Dec.	0	1	0	0	0	1	52	1.9%
Jan.	1	0	0	0	0	1	208	0.5%
March	0	1	0	0	0	1	413	0.2%
May	1	4	7	6	5	23	459	5.0%
June	0	1	0	0	1	2	248	0.8%
Aug.	0	0	0	1	1	2	223	0.9%
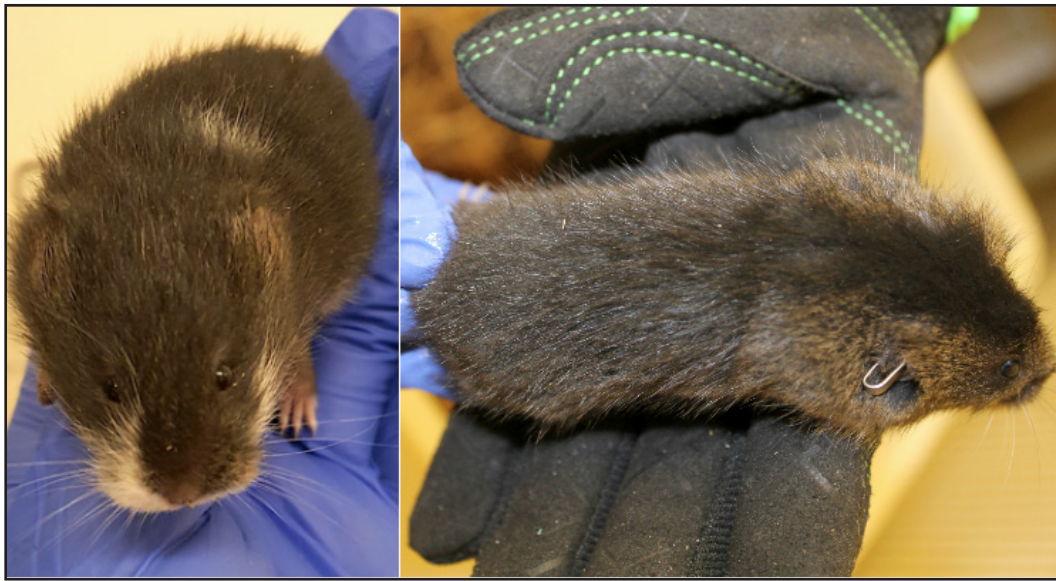
FIGURE 2. Left: Juvenile Amargosa Vole (*Microtus californicus scirpensis*) with irregular, exaggerated color markings consisting of sweeping white marks from nose to ear and a circular white patch behind the shoulder. (Photographed by Nora Allan). Right: Subadult Amargosa Vole exhibiting characteristic dorsal stripe of juvenile hair during molt. (Photographed by Risa Pesapane).

24.81, $P = 0.007$) than females, but hind foot length did not differ by sex (Table 1). Captive animals, particularly males, tended to be heavier than their wild counterparts ($t = 5.37$, df = 134.87, $P < 0.001$). Colony voles survived up to 34.5 mo in absence of medical conditions.

Whiskers were mostly white with a black base, tails were short and bicolored, and adult coat colors ranged from light to dark brown or cinnamon brown dorsally and gray ventrally. Amargosa Voles also occasionally had pink noses, typically exhibited areas of white above and/ or below the mouth that sometimes formed a white beard and had extremely dark black juvenile pelage (Fig. 1). Additional markings commonly observed in the colony included white toes on one or more feet and white-tipped tails. One colony individual developed a large beard consisting of sweeping white marks from chin to ear and a circular white patch on the dorsal body (Fig. 2).

Newborn vole pups were hairless, blind, and pink in color (Fig. 3), turning gray to black on day two. Dark juvenile pelage was fully developed by day four and pups opened their eyes and became highly mobile on day nine (Fig. 3). White markings on the face were also present by day nine. Juvenile Amargosa Voles began to consume solid food between weeks two and three but continued to suckle milk from their dams until weaning at day 20–21. They were independent at three weeks of age, but retained portions of their juvenile pelage. Molting of fine, dark black juvenile hair to coarser, dark brown adult pelage began at the dorsal mid-line, creating a strip of juvenile hair (Fig. 2) from head to rump that extended down past the shoulder blades and hips. The dorsal stripe progressively narrowed, and molting continued in the posterior to anterior direction until about eight weeks of age at which point young voles were indistinguishable from adults.

The youngest female known to conceive in captivity was 25 d old. Males in captivity were not given an opportunity to breed before eight weeks of age. Both males and females continued to produce young after 12 mo of age with one female giving birth at 455 d old. Amargosa Vole gestation period was 20 d and litters could be born every 21 d, meaning females were receptive to copulation on the same day as parturition. Litter sizes ranged from 1–6 pups with a mean of 2.96 ± 1.32 (SD) pups per litter. Based on 37 pups from 10 litters and six breed pairs, the mean mass of each pup in a litter at weaning was 34.7 ± 7.5 g.

Among 78 litters in the colony, 64 (82.1%) were successful and 14 (17.9%) were unsuccessful. Differences in success among litters born to wild sires and dams (generation = Parental), F_1, F_2, and $F_{1.5}$ crosses (e.g., $F_1 \times F_2$) were not significant (coefficient = 0.65, $Z = 0.81$, $P = 0.400$), nor was there any trend towards reduced success after multiple generations in the colony. However, having a wild sire was marginally associated with failure to produce a successful litter, with an odds ratio of 3.1 (95% C.I. = 1.5–6.2, $P = 0.090$). Primiparous dams had 79% litter success compared to 85% success if the mother had a previous litter, alive or not. Dams of successful litters were on average 197.2 ± 74.9 d old compared with unsuccessful dams, which were 200.6 ± 64.5 d old. There were significant differences in breeding success by month ($\chi^2 = 20.21$, df = 1, $P < 0.05$) ranging from 100% of litters successful in February, April, and November to just 20% in October.

Diet.—Captive Amargosa Voles housed indoors showed strong aversion to novel foods although adapting idiosyncratically to various foods. They were most willing to eat commercial rodent or rabbit chow, jicama,

Figure 3. Progression of Amargosa Vole (*Microtus californicus scirpensis*) pup development from day 1 (A) pups are born pink, hairless and blind, days 2-3; (B) skin of pup darkens as pigments deposit in the follicles, days 4–7; (C) juvenile pelage is present, and (D) days 9–11 eyes of pup are open and they are fully mobile. (Photographed by Risa Pesapane).

alfalfa hay, carrots, and sweet potatoes in spite of being offered fresh cuttings of native bulrush. They refused seeds of non-bulrush plants indefinitely. Initially, voles also rejected fresh cuttings of native bulrush although they consumed all portions of bulrush, including stalks, flowers, seeds, and rhizomes beneath the soil when bulrush was provided erect in planted cups. Amargosa Voles displayed a preference for upper stems over lower stems. To date, no captive voles have successfully maintained body mass on a diet of all bulrush. Voles engaged in allo- and autocoprophagia.

Behavior.—In cages with multiple individuals, we frequently observed mutual grooming. Both male and female parents groomed and retrieved pups and guarded the nest. Nest building efforts varied by individual and did not appear to be associated with sex, co-housing, age, or parental experience. Amargosa Voles regularly defecated, washed, and preened in the water bowls provided. Some individuals also clipped straw bedding and stacked clippings in water bowls.

In indoor housing, pairs of sibling males typically cohabitated indefinitely in rat cages without aggression with the exception of two cages where minor wounding was observed. In contrast, in outdoor housing, several pairs of sibling males demonstrated lethal aggression towards one another (so we discontinued cohabitation in outdoor pens). We only observed minor aggression between sibling females once in the colony. When

provided with fresh soil, all voles, regardless of housing or sex, became more active and in some cases more aggressive towards handlers than those provided only with straw.

Captive Amargosa Voles engaged in tunneling, chewing on bulrush plants, shredding bulrush stalks, building nests with straw, climbing cage structures, and digging when soil was available. When clusters of bulrush were available, voles climbed the stalks to reach the tips, flowers, and seeds. Both indoor and outdoor voles in captivity readily cached chow that they did not immediately consume.

DISCUSSION

For profoundly endangered species like the Amargosa Vole, biological details are critical for adequately linking species biology and ecology with management actions (Clark et al. 2002), and recovery plans that provide such linkage are more likely to improve population status (Boersma et al. 2001; Gerber and Hatch 2002). Our approach to Amargosa Vole conservation used both field and colony data to fill important gaps in knowledge. We report characteristics of Amargosa Vole biology and ecology that can now be included in recovery and captive release planning to more specifically address the needs of this subspecies.

Data from the field provided a snapshot of Amargosa Vole demography, behavior, and diet. Arguably, the

most important data collected were outcomes of vole-vole and vole-woodrat agonistic interactions, and the most important observations were that Amargosa voles consumed plants other than bulrush and wild individuals survived for nearly two years. The spike in aggression in May could have been due to changes in vole population size, breeding, changing food availability, or other factors. Amargosa Voles, like other microtine rodents, are locally important prey sources to a variety of predators and are *r*-selected to produce large numbers of offspring as long as resources support (Krebs 1966; Foley et al., unpubl. report). Investigations of the demography of the species are critical, but inference regarding population status is hindered by lack of ability to truly characterize age structure of the population because of lack of a series of individuals of known age with good data on size and coat color. Additionally, the Amargosa Vole has often been assumed to have a narrow niche breadth because of the extremely limited geographical range and obligate dependence on bulrush for food. However, even if unusual, consumption of other foodstuffs could provide flexibility for management and conservation of Amargosa Voles outside bulrush marshes of Tecopa.

Data from the captive colony served to fill in numerous answers to questions on the biology of the species that were previously only extrapolated from other California voles. This subspecies is considerably larger than most North American voles (Heske and Ostfeld 1990; Lidicker and Ostfeld 1991; Cudworth and Koprowski 2010), and we found that it has a molt progression and coloring of coat, whiskers, and tail similar to descriptions given previously (Kellogg 1918; Ecke and Kinney 1956). Categories of juvenile, subadult, and adult based on body mass can now be refined for Amargosa Voles. Our study suggests overlap among age categories in body mass, and that juveniles should be distinguished as individuals with a full pelage of dark, fine hair; subadults are individuals undergoing molt (i.e., with some portion of juvenile dorsal stripe present); and adults are individuals lacking all juvenile pelage. The white facial markings seen in field and colony, and larger swaths of white on some colony individuals, may be recently evolved characteristics given that earlier descriptions do not include these features. It is possible that the white beard was previously rare but during the period of the present study, it is present in almost all animals; this warrants further study to explore whether it is a result of a recent genetic bottleneck.

Colony data also informs the understanding of the reproductive strategy of this subspecies. Breeding as early as six weeks has been reported for California Voles (Hatfield 1935), whereas Amargosa Voles become sexually mature as early as one month of age and can continue producing successful litters lifelong. They have a periparturient estrous and can have litters of approximately four pups every 21 d, although somewhat lower fecundity was typical in the colony. Male and female tolerance and to some extent care of offspring was consistent with observations in the colony, although more research is needed to evaluate whether Amargosa Voles may be monogamous as is characteristic of Prairie Voles (*M. ochrogaster*; DeVries et al. 1995). Although survival in the wild is estimated to be just a few short months (Klinger et al. 2015), Amargosa Voles in captivity live up to 34.5 mo.

In contrast to reports that Amargosa Voles require bulrush for nutrition, other subspecies of California Voles typically consume grasses, sedges, forbs, seeds, and roots (Batzli and Frank 1971) and are often considered pests because they readily consume agricultural crops when available (Clark 1984; Baldwin et al. 2014). In addition to our few observations in the wild of Amargosa Voles consuming plants other than bulrush, colony data helped flesh out our understanding of food preference. Colony voles were initially averse to novel food items, including bulrush, wholly rejecting seeds from non-bulrush plants. Such fastidiousness could potentially hinder their response to shifts in their nutritional landscape, though their eventual acceptance of select root crops suggests they may adapt if palatable resources become available. Furthermore, the inability of captive Amargosa Voles to maintain body mass on bulrush suggests a complex strategy for acquiring sufficient nutrients in an environment where resources are extremely limited. Future research to explore the role of the gut microbiome in vole metabolism, particularly microbial fermentation of plant fibers to extract more energy from low-quality plants (Justice and Smith 1992; Morrison et al. 2009) is needed, and how captive conditions may shift the natural microbiome as has been shown in other species (Nakamura et al. 2011; Nelson et al. 2013; Clayton et al. 2016). Understanding Amargosa Vole nutrition will be critical to successful releases of captive individuals to native habitat.

Captive Amargosa Voles engaged in water-use, digging, and bulrush-scaling behaviors that align with wild vole behaviors observed by remote photography. Their preference for upper stems has been documented in other California Voles (Gill 1977). It is not known whether wild voles also cache their food, but this behavior may be valuable for voles if they can cache bulrush seeds when abundant for seasons when resources are scarce. In addition to feeding and drinking behaviors, the changes in aggression behavior in colony voles were interesting. Differences in aggression between voles housed indoors and outdoors and the more vigorous behavior of voles provided with soil suggest that conclusions drawn solely from animals housed indoors should be interpreted cautiously. Conversely, this difference suggests that our outdoor mesocosms are successfully replicating a more natural environment and are useful as way to prepare candidate individuals for release.

The establishment of captive breeding colonies of endangered species is commonly justified for insurance

against extinction in the wild, as sources for augmentation or reintroduction, or as means of maintaining genetic diversity. Captive breeding has played an integral role in effectively preventing extinction in California Condors (*Gymnogyps californianus*; Snyder and Snyder 1989), Black-footed Ferrets (*Mustela nigripes*; Miller et al. 1994), Mauritius Kestrels (*Falco punctatus*; Jones et al. 1995), and the Arabian Oryx (*Oryx leucoryx*; Spalton et al. 1999) among other species; however, captive breeding colonies are increasingly scrutinized for their overall modest success in serving proposed functions (Beck et al. 1994; Snyder et al. 1996). We propose that a critically important additional service of captive breeding colonies is the facilitation of the valuable study of biological and ecological species characteristics. Wildlife species that are highly secretive, like the fossorial Amargosa Vole, present unique challenges to adequately collecting detailed biological data using field techniques alone. This can be further compounded by the limitations of studying an endangered species where substantial disturbance or manipulation of individuals in the wild is inappropriate. Together, field studies and captive propagation can provide powerful resolution of biological characteristics that are imperative for linking management actions with species biology, protecting field populations from overly invasive sampling, and ultimately increasing the likelihood of successful species recovery.

Literature Cited

Allan, N., R. Pesapane, J. Foley, and D. Clifford. 2018. Successful care and propagation of the endangered Amargosa Vole (*Microtus californicus scirpensis*) in captivity. Zoo Biology 37:59–63.

Bailey, V. 1900. Revision of American Voles of the genus *Microtus*. Government Printing Office, Washington, D.C.

Baldwin, R.A., T.P. Salmon, R.H. Schmidt, and R.M. Timm. 2014. Perceived damage and areas of needed research for wildlife pests of California agriculture. Integrative Zoology 9:265–279.

Batzli, G.O., and A.P. Frank. 1971. Condition and diet of cycling populations of the California Vole, *Microtus californicus*. Journal of Mammalogy 52:141–163.

Beck, B.B., L.G. Rapaport, M.S. Price, and A.C. Wilson. 1994. Reintroduction of captive-born Animals. Pp. 265–286 *In* Creative Conservation. Feistner, A.T.C., G.M. Mace, and P.J.S. Olney (Eds.). Springer, Dordrecht, Netherlands.

Boersma, P.D, P. Kareiva, W.F. Fagan, J.A. Clark, and J.M. Hoekstra. 2001. How good are endangered species recovery plans? Bioscience 51:643–649.

Clark, J.A., J.M. Hoekstra, P.D. Boersma, and P. Kareiva. 2002. Improving US Endangered Species Act recovery plans: key findings and recommendations of the SCB recovery plan project. Conservation Biology 16:1510–1519.

Clark, J.P. 1984. Vole control in field crops. Pp. 5–6 *In* Proceedings of the Eleventh Vertebrate Pest Conference. Volume 9. Clark, D.O., R.E. Marsh, and D.E. Beadle (Eds.). University of California Davis, Sacramento, California.

Clayton, J.B., P. Vangay, H. Huang, T. Ward, B.M. Hillmann, G.A. Al-Ghalith, D.A. Travis, H.T. Long, B. Van Tuan, and V. Van Minh. 2016. Captivity humanizes the primate microbiome. Proceedings of the National Academy of Sciences 113:10376–10381.

Cudworth, N., and J. Koprowski. 2010. *Microtus californicus* (Rodentia: Cricetidae). Mammalian Species 42:230–243.

DeVries, A.C., M.B. DeVries, S. Taymans, and C.S. Carter. 1995. Modulation of pair bonding in female Prairie Voles (*Microtus ochrogaster*) by corticosterone. Proceedings of the National Academy of Sciences 92:7744–7748.

Ecke, D.H., and A.R. Kinney. 1956. Aging meadow mice, *Microtus californicus*, by observation of molt progression. Journal of Mammalogy 37:249–254.

Gerber, L.R., and L.T. Hatch. 2002. Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. Ecological Applications 12:668–673.

Gill, A. 1977. Food preferences of the California Vole, *Microtus californicus*. Journal of Mammalogy 58:229–233.

Hatfield, D.M. 1935. A natural history study of *Microtus californicus*. Journal of Mammalogy 16:261.

Heske, E.J. and R.S. Ostfeld. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. Journal of Mammalogy 71:510–519.

Jones, C.G., W. Heck, R.E. Lewis, Y. Mungroo, G. Slade, and T. Cade. 1995. The restoration of the Mauritius

Kestrel Falco punctatus population. Ibis 137:S173–S180.

Justice, K.E., and F.A. Smith. 1992. A model of dietary fiber utilization by small mammalian herbivores, with empirical results for *Neotoma*. American Naturalist 139:398–416.

Kellogg, R. 1918. A revision of the *Microtus californicus* group of meadow mice. University of California Publications in Zoology 21:1–42.

Klinger, R., M. Cleaver, S. Anderson, P. Maier, and J. Clark. 2015. Implications of scale-independent habitat specialization on persistence of a rare small mammal. Global Ecology and Conservation 3:100–114.

Krebs, C. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239–273.

Lidicker, W.Z. and R.S. Ostfeld. 1991. Extra-large body size in California Voles: causes and fitness consequences. Oikos 61:108-121.

Miller, B., D. Biggins, L. Hanebury, and A. Vargas. 1994. Reintroduction of the Black-footed Ferret (*Mustela nigripes*), Pp. 455–464 *In* Feistner, A.T.C., G.M. Mace, and P.J.S. Olney (Eds.), Creative Conservation. Springer, Dordrecht, Netherlands.

Morrison, M., P.B. Pope, S.E. Denman, and C.S. McSweeney. 2009. Plant biomass degradation by gut microbiomes: more of the same or something new? Current Opinion in Biotechnology 20:358–363.

Nakamura, N., K.R. Amato, P. Garber, A. Estrada, R.I. Mackie, and H.R. Gaskins. 2011. Analysis of the hydrogenotrophic microbiota of wild and captive Black Howler Monkeys (*Alouatta pigra*) in Palenque National Park, Mexico. American Journal of Primatology 73:909–919.

Nelson, T.M., T.L. Rogers, A.R. Carlini, and M.V. Brown. 2013. Diet and phylogeny shape the gut microbiota of Antarctic seals: a comparison of wild and captive animals. Environmental Microbiology 15:1132–1145.

Neuwald, J. 2010. Population isolation exacerbates conservation genetic concerns in the endangered Amargosa Vole, *Microtus californicus scirpensis*. Biological Conservation 143:2028–2038.

Ott-Conn, C., D. Clifford, T. Branston, R. Klinger, and J. Foley. 2014. Pathogen infection and exposure, and ectoparasites of the federally endangered Amargosa Vole (*Microtus californicus scirpensis*), California, USA. Journal of Wildlife Diseases 50:767–776.

Ott-Conn, C., L. Woods, D. Clifford, T. Branston, and J. Foley. 2015. Histopathology and impact on health of *Neotrombicula microti* infestation in the endangered Amargosa Vole (*Microtus californicus scirpensis*). Journal of Wildlife Diseases 51:680–687.

Poulsen, A., J. Foley, A. Roy, D. Clifford, H. Fritz, E. Glueckert, and P. Conrad. 2017. The prevalence and potential impact of *Toxoplasma gondii* on the endangered Amargosa Vole (*Microtus californicus scirpensis*). Journal of Wildlife Diseases 53:62–72.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project. org.

Rendall, A., D. Sutherland, R. Cooke, and J. White. 2014. Camera trapping: a contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. PLoS ONE, 9:1-10. https://doi. org/10.1371/journal.pone.0086592.

Sanderson, J., and G. Harris. 2013. Automatic data organization, storage, and analysis of camera trap pictures. Journal of Indonesian Natural History 1:6–14.

Snyder, N.F., and H.A. Snyder. 1989. Biology and conservation of the California Condor, Pp. 175–267 *In* Current Ornithology. Volume 6. Power, D.M. (Ed.). Springer, Boston, Massachusetts.

Snyder, N.F., S.R. Derrickson, S.R. Beissinger, J.W. Wiley, T.B. Smith, W.D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10:338–348.

Spalton, J.A., S. Brend, and M. Lawrence. 1999. Arabian Oryx reintroduction in Oman: successes and setbacks. Oryx 33:168–175.

Therneau, T.M. and J. Sinnwell. 2015. kinship2: Pedigree Functions. R package version 1.6.4. https://CRAN.R-project.org/package=kinship2.

U.S. Fish and Wildlife Service (USFWS). 1997. Recovery plan of the Amargosa Vole (*Microtus californicus scirpensis*). USFWS, Portland, Oregon.

Ullman-Cullere, M.H., and C.J. Foltz. 1999. Body condition scoring: a rapid and accurate method for assessing health status in mice. Laboratory Animal Science 49:319–323.

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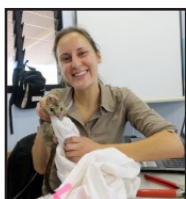
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NOTES

DIET AND NESTING TRENDS OF TWO SYMPATRIC TERNS BREEDING IN THE SAN FRANCISCO BAY

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Abstract.—The Hayward Regional Shoreline, located along the eastern side of the San Francisco Bay, provides nesting habitat for two sympatric terns. The endangered California Least Tern (*Sternula antillarum browni*) nests near a newly established Forster's Tern (*Sterna forsteri*) colony on a separate island. Their diets overlap slightly. Kleptoparasitism by the larger Forster's Terns on California Least Terns has been observed at this location. Diet trend data, gathered by us by collecting dropped fish at the colonies of species in 2015 and 2016, showed they forage on members of the Gobiidae, Engraulidae, and Atherinopsidae families. There was a significant difference between diets of the terns, with silversides (Atherinopsidae) making up a much larger proportion of the prey of California Least Terns than of Forster's Terns. To understand the effect of possible kleptoparasitism by Forster's Terns on California Least Terns, we collected reproductive success data at both colonies. This site-specific information on the California Least Tern nesting activities and diet choice during the breeding season supports recovery plan tasks that are consistent with preserving and managing habitat for this endangered species. There was no significant difference in nesting or fledgling success between these two colonies. Although kleptoparasitism may affect the individual fitness of a single bird in terms of time and energy spent avoiding parasitism, and the need for additional foraging attempts to make up for these losses, we found no evidence indicating aerial theft by Forster's Terns resulted in reduced food availability for California Least Tern chicks or affected California Least Tern productivity at this site.

Key Words.—California Least Tern; diet; Forster's Tern; reproduction

The California Least Tern (*Sternula antillarum browni*) is a migratory bird, which nests on beaches, bays, and lagoons from San Francisco Bay to Baja California (U.S. Fish and Wildlife 1980). The species was federally listed as endangered in 1970, and as endangered by California in 1971 (Massey 1974). The East Bay Regional Park District manages California Least Tern and Western Snowy Plover (*Charadrius alexandrinus nivosus*) nesting habitat at the Hayward Regional Shoreline (37°37'47''N 122°8'46''W) located along the eastern shore of San Francisco Bay (Riensche 2007; Riensche et al. 2015). A new colony of Forster's Terns (*Sterna forsteri*) established itself 300 m southwest of the California Least Tern colony on a separate island (Island Six) in 2013 (Riensche et al. 2012 a.). California Least Terns (Fig. 1) are the smallest of the tern species, averaging 22.8 cm in length, with a wingspan of 50.8 cm, an average bill length of 29.17 mm, and weighing approximately 42.5 g (Sibley 2003; Robinette 2003). Forster's Terns are medium-sized terns, averaging 33.0 cm in length, with a wingspan of 78.7 cm, an average bill length of 41.1 mm, and weighing approximately 170.0 g (Sibley 2003; Robinette 2003). Body size and bill length contribute to prey size selection (Robinette 2003) because larger species possessing longer bills typically choose larger prey items. Despite size and bill length differences between these two species, there is slight overlap in their diets and this overlap can increase in areas where these two species

FIGURE 1. Nesting California Least Tern (*Sternula antillarum browni*) at the Hayward Regional Shoreline, California. (Photographed by Daniel I. Riensche).

share breeding habitat (Robinette 2003). The size and type of prey captured can have a significant impact on the growth and development of chicks of California Least Terns (Riensche et al. 2012 b.). Competition for adequate prey sizes can result in kleptoparasitism in areas where these two species breed sympatrically. During the nesting season, kleptoparasitism by Forster's Terns on California Least Terns has been documented (Riensche et al. 2012a). This study investigates the diet overlap and its potential effects on reproductive success of these two sympatric terns breeding in the San Francisco Bay.
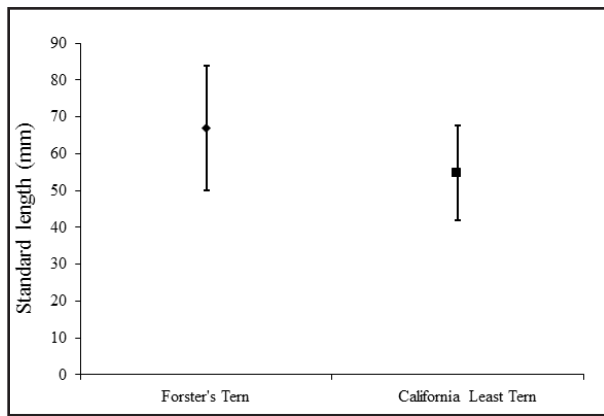
Figure 2. The mean (± 1 SD) standard lengths of fish dropped by Forster's Terns (*Sterna forsteri*) and California Least Terns (*Sternula antillarum browni*) at Hayward Regional Shoreline, California, 2015–2016.

We conducted the study on Island Five and Island Six at the Hayward Regional Shoreline, on the eastern side of San Francisco Bay of California. The habitat area on Island Five was established for the California Least Tern in 2001 and is 0.24 ha (0.6 ac) in size. Volunteers primarily built the island (Riensche 2007; Riensche et al. 2015). The area is off limits to the public. We obtained diet data by collecting fish dropped in the colony during the 2015 and 2016 breeding seasons. We stored collected specimens in plastic bags labeled with the gathering date. We soaked and cleaned fish samples with a fine artist's paintbrush and dried them in a laboratory convection oven. We gave all specimens a sample number, which was written with a fine tip marker on the specimen. For each sample, we recorded: species or lowest taxonomic group possible; total length (from the tip of the snout to the end of the caudal fin to 1 mm); standard length (from the tip of the snout to the end of the hypural bone to 1 mm); body depth (the widest part of the fish to 1 mm); and dry weight (to 1 g). Due to caudal fins being frequently broken, we used standard length as the testing measurement for size differences between the tern species. We used taxonomic families to compare prey composition between both species. To test for size differences in dropped prey between the two species (using all years and testing each year separately), we used the non-parametric Mann-Whitney U-test because the standard lengths of the fish dropped by Forster's Terns were not normally distributed (Shapiro-Wilk W test: $W = 5.098$, $P < 0.05$). We conducted a chi-square goodness-of-fit test to compare frequency of occurrence of the different prey groups in each tern species (using all years and each year separately).

During the breeding seasons of 2015 and 2016, we collected nesting and reproductive success data using the Type 1 Colony Survey Method (Marschalek 2005). In this method, permitted biologists entered the colonies twice a week to mark nests using numbered 5-cm diameter washers vertically cemented into a small plaster of Paris base. This type of intensive, in-colony monitoring yields data on clutch size, hatching and fledgling success, and evidence of any predation. We calculated hatching success as the total number of eggs producing chicks, and fledgling success as the number of fledglings produced per breeding pair. Based on our personal observations, we are assuming that the rate of kleptoparasitism is the same over the years (ranging from seven to 10 events each season and occurring only at the California Least Tern colony on Island Five). To compare the average hatching and fledgling success of the two colonies for both years combined, we used two-sample *t*-tests. For all tests, α = 0.05.

We analyzed 109 fish specimens during the nesting seasons of 2015 and 2016. We collected more dropped prey from the California Least Tern colony (n = 45 in 2015; n = 19 in 2016) than the Forster's Tern colony (n = 33 in 2015, n = 12 in 2016). In both years, the mean standard length of prey dropped by Forster's Terns was 67.0 mm (± 17.0 SD), while the mean standard length of prey dropped by California Least Terns was 54.7 mm (± 12.8; Fig. 2). The standard length of fish dropped by Forster's Terns was significantly longer than fish dropped by California Least Terns ($U = 3.64$, $P < 0.05$). We identified six families of dropped prey for both years and both tern species. We found significant difference in diet between the species ($\chi^2 = 31.27$, df = 5, $P < 0.001$). The difference in dropped prey between the species was attributed to a higher occurrence of silversides (Atherinopsidae) among California Least Terns, and higher occurrences of flatfishes (Paralichthyidae) and anchovy (Engraulidae) among Forster's Terns. Forster's Terns had a more diverse diet (prey from six families), but only prey from four families for California Least Terns (Fig. 3).

During 2015 and 2016, terns at both colonies produced high numbers of nestlings and fledglings (Tables 1 and 2). The number of California Least Tern chicks hatched in 2015 and 2016 were 120 and 152, respectively; the number of Forster's Tern chicks hatched in 2015 and 2016 were 94 and 83, respectively. There was no significant difference between the hatching success ($t = 2.80$, df = 2, $P = 0.218$) or the fledgling success ($t = 3.45$, df = 2, $P = 0.074$) of the colonies.

Kleptoparasitism is defined as the harassment of one bird species by another to force the victim to give up its food. Seabird species engaging in this behavior often obtain a significant portion of their diet through this aerial theft (Brockman and Barnard 1979; Furness 1987; Schnell et al. 1983) and tern species are frequently kleptoparasitized (Quintana and Yorio 1999). During the breeding season, interspecific kleptoparastism may result in negative effects on host species due to the reduction of food availability to chicks, time and energy spent avoiding parasitism, and loss of prey (Quintana and Yorio 1999).
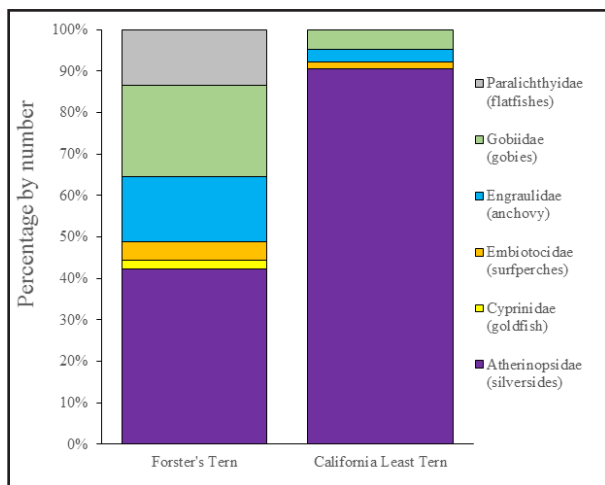
Although we found evidence of kleptoparasitism by Forster's Terns, it does not seem to be a significant factor affecting the breeding success of the California Least Terns at this location. We base this on several lines of evidence: both tern species had comparable number of nesting pairs, and (assuming kleptoparasitism rates were similar between years) California Least Terns hatched more chicks and produced more fledglings prior to and following the Forster's Terns arrival. According to Frost (2017), the ratio of fledging per pair of California Least Terns ranges from 0.35 to 0.50 statewide. The colony of California Least Terns at Hayward exceeded this state ratio of fledging per pair. Other factors (e.g., predation, protection from other species nesting nearby, types of prey available and consumed) may explain the lower breeding success of the Forster's Tern colony.

Further information will improve our knowledge on both kleptoparasitism, diet trends, and overall competition at breeding sites where terns co-occur. Study designs that compare diet and reproductive success at California Least Tern colonies in the presence of other tern species will likely contribute to their future conservation by helping to determine the site-specific factors affecting their choice of nesting, roosting, loafing, and feeding area during the breeding season. Such information will assist in developing management programs that identify special site protection plans and hopeful recovery of this endangered species.

Table 1. Breeding metrics of Forster's Terns (*Sterna forsteri*) at Hayward Regional Shoreline, California, 2015–2016. The abbreviation FPBP = fledglings per breeding pair.

Year	Nesting Pairs	Eggs	Chicks	Hatching Success	Fledglings	FPBP
2015	80	176	94	53%	51	0.63
2016	75	163	83	50%	25	0.33

Table 2. Breeding metrics of California Least Terns (*Sternula antillarum browni*) at Hayward Regional Shoreline, California, 2013–2016. The 2013 and 2014 data shown for comparison, which were the years prior to and following the arrival Forster's Terns (*Sterna forsteri*). The abbreviation FPBP = fledglings per breeding pair.

Year	Nesting Pairs	Eggs	Chicks	Hatching Success	Fledglings	FPBP
2013	83	170	155	91%	120	1.44
2014	85	167	150	90%	125	1.47
2015	71	136	120	88%	98	1.38
2016	84	174	152	87%	134	1.59

Literature Cited

Brockmann, H.J., and C.J. Barnard. 1979. Kleptoparasitism in birds. Animal Behaviour 27:487–514.

Frost, N. 2017. California Least Tern breeding survey, 2016 season. California Department of Fish and Wildlife, Wildlife Branch, Nongame Wildlife Program Report, 2017-03. California Department of Fish and Wildlife, Sacramento, California. 78 p.

Furness, R.W. 1987. Kleptoparasitism in seabirds. Pp. 77–100 *In* Seabirds: Feeding Ecology and Role in Marine Ecosystems. Croxall, J.P. (Ed.). Cambridge University Press, Cambridge, UK.

Marschalek, D.A. 2005. California Least Tern breeding survey, 2004 season. Habitat Conservation and Planning Branch, Species Conservation and Recovery Program Report, 2005-01. California Department of Fish and Game, Sacramento, California. 55 p.

Massey, B.W. 1974. Breeding biology of the California Least Tern. Proceedings of the Linnean Society of New York 72:1–24.

Quintana, F., and P. Yorio. 1999. Kleptoparasitism by Kelp Gulls on Royal and Cayenne terns at Punta Leon, Argentina. Journal of Field Ornithology 70:337–342.

Robinette, D. 2003. Partitioning of food resources by four sympatric terns (Aves: Laridae) breeding in southern California. M.S. Thesis, California State University, Long Beach, California. 86 p.

Riensche, D.L. 2007. California Least Tern habitat enhancement and nesting in the East Bay Regional Park District, California. Transactions of the Western Section of the Wildlife Society 43:62–71.

Riensche, D.L., S.C. Gidre, N.A. Beadle, and S.K. Riensche. 2015. Western Snowy Plover nest site selection and oyster shell enhancement. Western Wildlife 2:38–43.

Riensche, D.L., S. Dulava, E. Brownlee, D.A. Bell, S. High, M. Schynert, D. Wiley, S. Wiley and L. Vallee. 2012a. Kleptoparasitism by Forster's Tern on California Least Tern. Pacific Seabirds 39:55–56.

Riensche, D.L., M.L. Elliott, and S.H. Euing. 2012b. Breeding status, nesting densities and diet trends of two endangered California Least Tern colonies. Journal of Environmental Science and Engineering 1:1135–1145.

Schnell, G.D., B.L. Woods, and B.J. Ploger. 1983. Brown Pelican foraging success and kleptoparasitism by Laughing Gulls. Auk 100:636–644.

Sibley, D.A. 2003. The Sibley Field Guide to Birds of Western North America. Chanticleer Press, Inc., New York, New York.

U.S. Fish and Wildlife Service. 1985. California Least Tern Recovery Plan. U.S. Fish and Wildlife Service, Region 1. Portland, Oregon. 58 p.
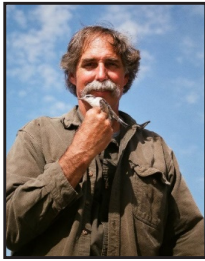
David L. Riensche is a Certified Wildlife Biologist and Wildlife Biologist for the East Bay Regional Park District, California, where he has worked for 30 y. For over 20 y he has been on the faculty of the Biology Department at Las Positas College where he teaches courses in Biology, Ecology, Vertebrate Natural History, and Field Biology. He is a recipient of The National Association for Interpretation (Region 9) - Outstanding Field Naturalist Award. David holds advanced degrees in both Natural Resource Management and Environmental Education and has an undergraduate degree in Biology (Wildlife). (Photographed by Sarah K. Riensche).

Meredith L. Elliott is a Senior Scientist at Point Blue Conservation Science, a non-profit science organization headquartered in Petaluma, California, where she has worked for 18 y. She earned her B.S. in Zoology from the University of California, Davis, and her M.S. in Marine Biology from San Francisco State University. Meredith researches marine food web dynamics by investigating the diets of marine predators (Brandt's Cormorants, *Phalacrocorax penicillatus*, California Sea Lions, *Zalophus californianus*, and California Least Terns) and identifying euphausiid species in zooplankton samples collected during at-sea surveys off the coast of north-central California as part of the partnership between Point Blue and the National Marine Sanctuaries called ACCESS (Applied California Current Ecosystem Studies; www.accessoceans.org). (Photographed by Mark McGinnis).

Sarah K. Riensche is a fifth-generation Californian who loves exploring and writing about the Golden State's many natural wonders. She has volunteered thousands of hours conducting bird and wildlife research and participating in habitat improvement projects for special status species. For over a dozen years, she has helped monitored nesting California Least terns, Western Snowy Plovers, and Black Skimmers (*Rynchops niger*). Her written contributions have appeared in *Western Wildlife*, *Outdoor California*, *California Waterfowl*, *Pheasants Forever*, and *Pointing Dog Journal*. She is pursuing a degree in Liberal Arts: Teacher Preparation and a career as an elementary school science teacher and outdoor journalist. (Photographed by David L. Riensche).

Rebekah E. Riensche is a fifth-generation Californian who loves exploring the outdoors and a training bird dogs. She has volunteered thousands of hours conducting bird and wildlife research and participating in habitat improvement projects for special status species. For over a dozen years, she has helped monitored nesting California Least terns, Western Snowy Plovers, and Black Skimmers (*Rynchops niger*). She is pursuing a degree in veterinary medicine and developing her own line of family and field-friendly German Shorthair Pointers. (Photographed by David L. Riensche).

The Western Section of The Wildlife Society

Strategic Plan

Preamble:

RESOLUTION ON TRANSPARENCY AND SECRECY IN THE WESTERN SECTION

Whereas, the Western Section of The Wildlife Society is a professional society and

Whereas, our mission is to serve the interests of our members and

Whereas, it is also our mission to advance the cause of wildlife conservation (*sensu* wise use) and

Whereas, the Western Section's Executive Board and chapter officers and volunteers are either elected or appointed per bylaws of the Section and

Whereas, these officers and volunteers therefore serve at the behest of the members and

Whereas, recognizing the mission and membership of the Western Section, secrecy has little place in such an organization and

Whereas, secrecy and lack of transparency can lead to deleterious situations and unintended consequences

Be it resolved, that a guiding principle of the Western Section shall be transparency in all its operations and functions, and its Executive Board and chapter officers and volunteers "shall endeavor to avoid even the suspicion of dishonesty, fraud, deceit, misrepresentation, or unprofessional demeanor," in accordance The Wildlife Society Code of Ethics.

Further, be it resolved, that the Western Section should maintain secrecy only under three circumstances – where personal information of employees and members is concerned, when negotiating with prospective donors or employees, and when a donor wishes to remain anonymous. Therefore, all Western Section business information available to the Western Section Executive Board (except the sensitive information described above) shall be available to any member of the Western Section upon request.

2018 ANNUAL MEETING REVIEW

Program Chair: **Jeff Davis**. Colibri Ecological Consulting, LLC.

Attendance: 634 participants including 130 students and 54 Early Career Professionals.

Plenary Theme: Communicating Science.

Plenary Speakers: **Randy Olson, Ph.D.**, Independent Filmmaker & Scientist; **Jon Hooper**, Professor Emeritus from the Department of Recreation, Hospitality, and Parks Management at California State University, Chico; **Mike Gil, Ph.D.**, is a National Science Foundation (USA) Postdoctoral Research Fellow (University of California, Davis), a TED Fellow, and a National Geographic Explorer; **Sarah ElShafie**, Doctoral Candidate in Integrative Biology at the University of California, Berkeley.

Keynote Address: **Kevin Hunting**, Chief Deputy Director for the California Department of Fish and Wildlife. The Wildlife Profession: Our Unintended Secret. A Career in Science, Policy, and the Business of Conservation.

Awards Bestowed

The Chapter of the Year Award went to the San Joaquin Valley Chapter. Accepting for the San Joaquin Valley Chapter was current Chapter President Larry Saslaw.

Raymond F. Dasmann Award for the Professional of the Year went to Kevin Hunting.

The Conservationist of the Year Award went to the Endangered Species Recovery Program (ESRP). Accepting for ESRP was Dr. Patrick Kelly, ESRP Director.

The Barrett A. Garrison Mentor of the Year Award went to Dr. Benjamin Sacks.

Student Presentation Awards

Oral Presentations:

1st Place: **Aviv Karasov-Olson**, *Habitat associations of small mammals along an elevation gradient in southern California*, University of California, Davis

2nd Place: **Brent Barry**, *Status of Fisher populations in Oregon*, Oregon State University

3rd Place: **Tierra Groff**, *Unexpected conspecific Leucocytozoon infection in Woodpeckers and Corvids*, San Francisco State University

Best Posters:

1st Place: **Michelle Harris**, *Wildlife mortalities in open top pipes in the South Fork Kern River Valley, Kern County, California*, Humboldt State University & Southern Sierra Research Station
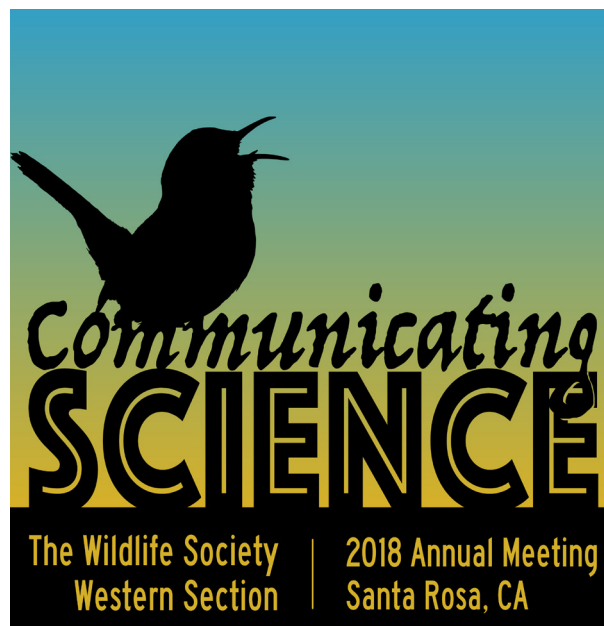
2nd Place: **Alex Single**, *Impact of nesting microhabitat and foraging habitat on colony locations of the Northern Black Swift (Cypseloides niger borealis)*, California State University, Fresno

3rd Place: **Alyssa Semerdjian**, *Evaluating the species distribution for the Giant Kangaroo Rat (Dipodomys ingens)*, Humboldt State University

2018 Western Section Membership

Regular: 604	Life-Full: 31
Student: 125	Life-Partial: 8
Early Career Professional: 96	Honorary: 1
Retired: 48	Supporting: 4

Total: 917

Life Members: Jeff Alvarez, Peter Bloom, Richard Botzler, Kurt Campbell, Lehong Chow, Laura Cockrell, Ginger Coleman, Randolph Coleman, Christopher Cummings, Brian Cypher, Amy Fesnock, David Germano, Elizabeth Gruenstein, Stephen Juarez, M. Dale Keyser, Patti Krueger, Andrew Loveall, Mark Mendelsohn, Cynthia Perrine, Don Rocha, Larry Saslaw, Janae Scruggs, Kathy Simon, Rachel Sprague, Karen Swaim, Dana Terry, Christine Van Horn-Job, Marshall White, Erin Whitfield, Donald Yasuda, Ryan Young.

Partial Life Members: Nicole Carpenter, Jeff Davis, Lisa Fields, Barry Nerhus, Susan Seville, Samuel Sosa, Jeffery Wilcox, Carie Wingert.

Honorary Members: Ralph (Rocky) Gutierrez

Supporting Members: David Lee, Lidia D'Amico, Sarah Allen, Virginia O'Rourke

TWS Western Section Board Members