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SPATIAL AND TEMPORAL PATTERNS IN POPULATION TRENDS AND BURROW USAGE OF BURROWING OWLS IN NORTH AMERICA

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ABSTRACT.—Many researchers have suggested that abundance of Burrowing Owls (*Athene cunicularia*) has declined in many portions of their breeding range, but a thorough review of their population trends over time is lacking. Published population trends from the North American Breeding Bird Survey program suggested that Burrowing Owl populations in the US have declined over the past 60 yr, but the declines were not considered significant until 2014. However, accurate trend estimates and the statistical significance of those estimates were hampered by low relative abundance of owls. Moreover, many authors have suggested that eradication of burrowing animals is a major cause of Burrowing Owl declines, because burrows dug by burrowing animals are a critical resource for Western Burrowing Owls (*A. cunicularia hypugaea*). Despite this, we currently lack a range-wide summary of the burrowing animals on which Western Burrowing Owls depend. To help fill these two information gaps, my objectives were to: (1) use Breeding Bird Survey (BBS) data to examine geographic patterns in population trends of Burrowing Owls throughout their breeding range in the USA, and (2) use past studies to provide the first summary of the spatial extent to which Western Burrowing Owls rely on the suite of burrowing animals throughout their breeding range. Significantly more BBS routes in the US show declining counts of owls than show increasing or stable counts, and the declines were most apparent prior to 1995. Counts of Burrowing Owls declined most precipitously on the northern edge and southern edge of the owl's US breeding range. Western Burrowing Owls primarily use black-tailed prairie dog (*Cynomys ludovicianus*) burrows in the eastern portion of their breeding range, whereas the diversity of burrowing species on which the owls depend is much greater in the western and central portions of their breeding range. Burrowing owl declines have been most apparent in portions of their range where they rely primarily on Richardson's ground squirrels (*Urocitellus richardsonii*), California ground squirrels (*Otospermophilus beecheyi*), black-tailed prairie dogs, and American badgers (*Taxidea taxus*).

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *Breeding Bird Survey*; *burrowing*; *burrows*; *distribution*; *fossorial*; *grasslands*; *population trend.*

PATRONES ESPACIALES Y TEMPORALES EN TENDENCIAS POBLACIONALES Y USO DE MADRIGUERAS DE *ATHENE CUNICULARIA* EN AMÉRICA DEL NORTE

RESUMEN.—Numerosos investigadores han sugerido que la abundancia de *Athene cunicularia* ha disminuido en varias partes de su área de cría; sin embargo, se hace necesario un análisis meticuloso de sus tendencias poblacionales a través del tiempo. Las tendencias poblacionales publicadas por el Censo de Aves Reproductoras de América del Norte sugieren que las poblaciones de esta especie en los Estados Unidos han disminuido durante los últimos 60 años, pero estas disminuciones no fueron consideradas como significativas hasta el 2014. Sin embargo, las estimaciones precisas de las tendencias poblacionales y la significancia estadística de dichas estimaciones se han visto obstaculizadas por la baja abundancia relativa de los búhos. Además, muchos autores han sugerido que la erradicación de animales que excavan madrigueras es una de las principales causas de las disminuciones poblacionales de *A. cunicularia*, debido a que las

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madrigueras excavadas por otros animales son un recurso crítico para la subespecie *A. c. hypugaea.* A pesar de esto, actualmente no existe un resumen de los animales que excavan madrigueras a lo largo del área de distribución completa de *A. c. hypugaea* de los cuales depende esta especie. Para ayudar a completar estos vacíos de información, mis objetivos fueron: (1) utilizar datos del Censo de Aves Reproductoras (CAR) para examinar patrones geográficos en las tendencias poblacionales de *A. cunicularia* a lo largo de su área de cría en los Estados Unidos y (2) utilizar estudios previos para proporcionar el primer resumen de la extensión espacial de la que depende *A. cunicularia* a lo largo de su área de cría, basado en el conjunto de animales que excavan madrigueras. Un número significativamente mayor de transectos del CAR en los Estados Unidos muestran disminución en los conteos de *A. cunicularia* que conteos con crecimiento o poblaciones estables, y las disminuciones fueron más evidentes antes de 1995. Los conteos de *A. cunicularia* disminuyeron fuertemente en los límites boreal y austral del área de cría de la especie. *A. cunicularia* principalmente utiliza madrigueras de *Cynomys ludovicianus* en la parte este de su área de cría, mientras que la diversidad de especies excavadoras de madrigueras de las que *A. cunicularia* depende es mucho mayor en las zonas occidentales y australes de su área de cría. Las disminuciones poblacionales de *A. cunicularia* han sido más evidentes en las zonas de su área de distribución en las que dependen principalmente de *Urocitellus richardsonii, Otospermophilus beecheyi, C. ludovicianus,* y *Taxidea taxus.*

[Traducción del equipo editorial]

Burrowing Owls (*Athene cunicularia*) were once common breeders in grasslands throughout North America. Abundance of Burrowing Owls has declined sharply in Canada and the species is listed as endangered under the Canadian Species at Risk Act (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2006). The population trajectory of Burrowing Owls in the US has been less clear and has been a topic of debate for decades (Haug et al. 1993, Sheffield 1997, Klute et al. 2003, Poulin et al. 2011). Burrowing Owls are listed as a Species of National Conservation Concern in the US and in every US Fish and Wildlife Service Region in which they occur (US Fish and Wildlife Service 2008), and have experienced population declines in at least some portions of their US breeding range (Smith et al. 1997, Dechant et al. 1999, Desmond et al. 2000, Wellicome and Holroyd 2001, Klute et al. 2003, Conway and Pardieck 2006, DeSante et al. 2007, but see DeSante et al. 2004, Bartok and Conway 2010). Moreover, Burrowing Owls are listed as endangered, threatened, or a species of concern in nine states (Klute et al. 2003) and several articles have documented a contraction in the spatial extent of their breeding range (Wellicome and Holroyd 2001, Macías-Duarte and Conway 2015). However, we lack a thorough examination of the available data regarding population trends of Burrowing Owls (especially in the US) and how those trends vary spatially across the species' range. To address this need, I aimed to use data from the North American Breeding Bird Survey program (Ziolkowski et al. 2010) to examine the temporal and spatial patterns in Burrowing Owl population trends during the past 60 yr.

Documenting population trajectories of imperiled species is useful, but such information, alone, does not provide guidance on causes of declines or management actions that may help reverse declines. Many potential factors have been mentioned as causes of population declines in Burrowing Owls, but reductions in numbers of burrowing mammals is often included as one of the likely causes (Zarn 1974, Desmond and Savidge 1996, Sheffield 1997, Desmond et al. 2000, Conway et al. 2006, Conway and Pardieck 2006, Poulin et al. 2011). Burrows are a critical resource for Western Burrowing Owls (*A. cunicularia hypugaea*; Coulombe 1971, Zarn 1974) because they do not dig burrows themselves; they depend on the abandoned burrows of burrowing animals (in contrast, Florida Burrowing Owls, *A. cunicularia floridana*, dig their own burrows). Hence, persistence of the burrowing animals that dig the burrows on which Western Burrowing Owls depend likely influences population trends and persistence of the owls. Yet, no current literature summarizes the relative importance of the different burrowing species on which Western Burrowing Owls depend throughout their breeding range. To fill this data gap, I aimed to create the first summary of the symbiotic relationship between Western Burrowing Owls and the suite of species of burrowing animals on which they depend throughout their breeding range. I used range maps of burrowing animals in North America to develop a map that depicts the primary burrowing species on which Western Burrowing Owls depend throughout their range, and I

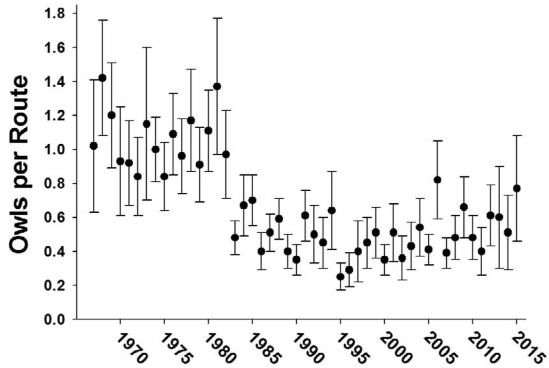

Figure 1. The average number of Burrowing Owls detected per BBS route per year (for the routes that detected ≥1 Burrowing Owl during ≥1 yr) based on the 168 BBS routes in the US that were initially surveyed prior to 1970. Error bars indicate ± 1 SE.

consulted the Burrowing Owl literature to validate the map. This map (and future revisions of it) should provide a more informed discussion of the importance of revised policies for managing the burrowing animals upon which Western Burrowing Owls depend. I then used this map to examine whether population trends of Western Burrowing Owls differed among portions of the owl's breeding range where they rely on different species of burrowing animals.

METHODS

Trend Analysis from Breeding Bird Survey Data. I summarized the annual estimates of Burrowing Owl population trends over nearly 20 yr (1996–2015) from the archived results from the US Geological Survey's North American Breeding Bird Survey (BBS) program website (http://www.mbr-pwrc.usgs.gov/bbs/bbs.html; Sauer et al. 2014). The BBS is a continent-wide avian monitoring program initiated in 1966 in which qualified surveyors record the number of individual birds detected each year for all species at pre-selected points along survey routes throughout North America (Robbins et al. 1986). Each BBS survey route consists of 50 survey points at 0.8-km intervals along secondary roads and the routes are randomly chosen within grid blocks throughout North America.

Low relative abundance is one of the deficiencies that can cause bias in BBS trend estimates. The BBS credibility measures suggest that trend estimates have a "deficiency" that affects credibility of the trend estimate when based on species with regional abundance <1.0 bird/route (low abundance), and they have an "important deficiency" when based on species with relative abundance <0.1 bird/route (very low abundance). Breeding density of Burrowing Owls is relatively low in most portions of their range; the relative abundance of Burrowing Owls on BBS routes is <1.0 bird/route on 74.3% of the BBS routes that have detected owls. To understand how low relative abundance can affect trend estimates, consider a region or BBS route where the relative abundance of Burrowing Owls was initially 0.5 owls/route and after 10 yr owls were extirpated from the region (i.e., relative abundance became 0 owls/route). With each passing year of zero counts beyond those initial 10 yr, the estimated trend in that region would become flatter and flatter (i.e., the trend estimate would approach zero). Because of the problems associated with trend estimates based on BBS data when average counts are <1 bird/route, I obtained the raw count data from the BBS and used linear regression to calculate a route-level trend estimate for all of the BBS routes that detected at least one Burrowing Owl and was surveyed in at least 2 yr between 1966–2015. That is, I computed separate linear regressions for each BBS route where ≥1 owl was detected during ≥1 yr and the route was surveyed for ≥2 yr.

Because of the potential bias discussed above and because I wanted to use linear regression of BBS count data for individual routes, I merely summarized the regressions for each route as to whether the slope was positive, negative, or zero. Examination of BBS count data in this way overcomes the potential bias caused by low abundance discussed above. Estimating trends from BBS count data has other potential biases as well, but data for Burrowing Owls has fewer of these problems (compared to other species) for several reasons: (1) nearly 100% of Burrowing Owls detected during roadside point-count surveys like the BBS are detected visually rather than aurally (Conway and Simon 2003); (2) Burrowing Owls breed almost exclusively in very flat areas with little vegetation so the surveyors' visibility is typically excellent when they are in Burrowing Owl habitat; (3) Burrowing Owls routinely spend morning hours standing on a visible mound or perching on a post or wire near their nest burrow during the breeding season (Thomsen 1971); (4) most detections during the morning BBS surveys are of owls that are at or very close to their nest burrows; (5) detection probability of Burrowing Owls at known nest sites is high (often >60%) during morning spring-time surveys (Conway and Simon 2003, Conway et al. 2008); and (6) misidentification is less likely compared to other birds (Conway and Simon 2003, Conway and Pardieck 2006). Hence, after addressing the bias associated with low abundance, I believe that summaries of simple linear regressions from BBS count data are informative for Burrowing Owls (even though they may not be for species that do not share the qualities above; also see Sheffield 1997).

I used a Pearson's chi-square test to examine whether the number of BBS routes with negative trends was greater than the number of BBS routes with positive trends. I also plotted the change over the past half-century (from 1966–2015) in the average number of Burrowing Owls detected per occupied BBS route for the 168 routes in the US that were first surveyed prior to 1970. I also conducted a binary logistic regression with the BBS trend (negative or positive) as the response variable and latitude and longitude as explanatory variables to examine the spatial pattern of Burrowing Owl population trends in the US. I also included a quadratic term for both latitude and longitude to account for nonlinear patterns. I summarized BBS routes in Canada separately because we already know that Burrowing Owls in Canada have declined significantly over the past 50 yr. I used SPSS (2016) to perform statistical analyses.

Symbiotic Relationship Between Burrowing Animals and Burrowing Owls throughout their Breeding Range. I obtained shape files of the range maps for the 15 species of burrowing animals that I knew to be primary nest burrow providers for Western Burrowing Owls throughout their range in North America. I included the Florida Burrowing Owl for analyses of trend (above), but Florida Burrowing Owls excavate their own burrows, so I only examined burrow providers for Western Burrowing Owls. I obtained shape files from the International Union for Conservation of Nature (IUCN; http://maps.iucnredlist.org/) for the ranges of the primary species that dig burrows used by Western Burrowing Owls. I obtained the shape file for the range map of desert tortoise (*Gopherus* spp.) from the US Fish and Wildlife Service (www.fws.gov/Nevada/desert_tortoise/dtro/index.html). I overlaid the range maps of the burrowing animals on top of a shape file of the Western Burrowing Owl distribution (Wellicome and Holroyd 2001) that I obtained from T. Wellicome, Environment Canada. In portions of the Western Burrowing Owl's breeding range where the range maps of burrowing animals overlapped, I inferred the primary burrow type based on the degree of coloniality (higher weight given to more colonial burrow excavators), the frequency with which the species is mentioned as a burrow provider in Burrowing Owl publications, and my own field observations. For example, I assumed that Western Burrowing Owls primarily used burrows dug by black-tailed prairie dogs (*Cynomys ludovicianus*) as nests, even in areas where the range of other burrowing animals overlapped that of black-tailed prairie dogs. I assumed the following hierarchy in areas where more than one burrowing animals' ranges overlapped: black-tailed prairie dog, Mexican prairie dog (*Cynomys mexicanus*), Gunnison's prairie dog (*Cynomys gunnisoni*), Utah prairie dog (*Cynomys parvidens*), white-tailed prairie dog (*Cynomys leucurus*), California ground squirrel (*Otospermophilus beecheyi*), round-tailed ground squirrel (*Xerospermophilus tereticaudus*), desert tortoise (*Gopherus agassizii, Gopherus morafkai,* and *Gopherus evgoodei*), banner-tailed kangaroo rat (*Dipodomys spectabilis*), Nelson's kangaroo rat (*Dipodomys nelsoni*), Merriam's kangaroo rat (*Dipodomys merriami*), yellow-bellied marmot (*Marmota flaviventris*)/American badger (*Taxidea taxus*), rock squirrel (*Otospermophilus variegatus*), Richardson's ground squirrel (*Urocitellus richardsonii*)/American badger, and American badger.

The map was intended to identify the primary (most common) type of burrow used by nesting Western Burrowing Owls in each portion of the owl's breeding range, recognizing that they use more than one type of burrow in most areas. I assumed that yellow-bellied marmot and Richardson's ground squirrel were of similar importance to badgers in areas where their ranges overlapped with badgers. Marmots are uncommon and very patchily distributed throughout their range, so most Burrowing Owls use badger burrows in the areas where badger and marmot ranges overlap, but I included marmots as co-primary burrow providers in those areas because the owls seem to prefer marmot burrows in areas where marmots are indeed present. I then reviewed >200 articles on Western Burrowing Owl nesting biology for information regarding the primary type of burrow that the owls used for nesting (i.e., the burrowing species that originally excavated the burrow). I plotted the location of those studies on the range map of the presumed primary burrowing animal used by Western Burrowing Owls as a way to validate the map. I also examined whether population declines differed spatially based on the

Table 1. Estimates of population trend for Burrowing Owls in the US and Canada from the North American Breeding Bird Survey Program.

1966-YEAR[a]	US			CANADA	
	TREND ESTIMATE	P VALUE	95% CI	TREND ESTIMATE	95% CI
1994[a]	−0.5%				
1996	+0.9%	0.710	(−3.7, 5.4)		
1998	+0.4%	0.830	(−3.4, 4.3)	−11.8%	(−18.5, −5.1)
1999	−0.7%	0.830	(−7.3, 5.9)	−12.0%	(−18.5, −5.4)
2000	−1.6%	0.560	(−6.9, 3.8)	−11.6%	(−18.3, −4.8)
2001	−1.5%	0.570	(−6.5, 3.6)	−12.1%	(−18.4, −5.9)
2002	−1.4%	0.570	(−6.2, 3.4)	−13.1%	(−19.7, −6.5)
2003	−1.2%	0.630	(−6.1, 3.7)	−13.2%	(−19.7, −6.7)
2004	−2.2%	0.500	(−8.5, 4.1)	−13.3%	(−20.0, −6.7)
2005	−2.2%	0.500	(−8.7, 4.3)	−13.4%	(−20.0, −6.8)
2006	−1.5%	0.650	(−8.0, 5.0)	−13.5%	(−20.1, −6.9)
2007	−1.4%	0.640	(−7.5, 4.6)	−12.7%	(−18.7, −6.7)
2008[b]	−1.0%		(−2.7, 0.0)		
2009	−1.5%	0.650			
2010	−1.4%	0.640			
2011	−1.0%		(−2.3, −0.1)	−8.0%	(−13.4, −2.4)
2012	−1.0%		(−2.3, −0.1)	−6.9%	(−12.4, −1.3)
2013	−1.0%		(−2.1, −0.1)	−6.0%	(−10.6, −1.3)
2015	−0.9%		(−2.1, −0.05)	−6.4%	(−11.1, −1.8)

[a] Trend estimate for 1966 through year listed based on archived BBS results (Sauer et al. 2014). Trend for 1994 is from Sheffield (1997). Archived BBS trends for 1997 and 2014 are not available.
[b] Only survey-wide estimate available (not US and Canada separately) and no P value given.

primary burrow provider by summarizing the percent of BBS routes with negative trends within each portion of the owl's range based on the map of the primary burrow provider.

RESULTS

Burrowing Owls in Canada have declined dramatically over the past 50 yr (6.0–13.5% annual rate of decline) and the BBS trend estimates for Canada have been significant since at least 1998 (Table 1). In contrast, the estimates of long-term population trends for Burrowing Owls in the US reported by the BBS program were negative but not deemed statistically significant from 1999–2010 despite the fact that the point estimate suggested a decline of –0.7% to –2.2% annually since 1999 (Table 1). The long-term trend estimate for Burrowing Owls in the US was significant for the first time in 2011 (i.e., the confidence interval for the trend no longer overlapped zero in the years 2011–2015; Table 1). However, population declines in the US are most apparent prior to 1995; the average number of Burrowing Owls detected per occupied BBS route declined from 0.80–1.40 owls per route during 1966–1983 to 0.20–0.70 owls per route during 1995–2014 (for the 168 routes that were initiated prior to 1970; Fig. 1).

When I examined the proportion of BBS routes with negative slopes, Burrowing Owls in the US seem more clearly to be declining (compared to inferences from an overall linear trend). More BBS routes in the US with Burrowing Owls had a negative slope than a positive one ($\chi^2 = 14.53$, df $= 1$, $P < 0.001$): 257 BBS routes had positive slopes (42%), 351 BBS routes had negative slopes (57%), and 4 routes had slopes of zero. In comparison, 9 BBS routes had positive slopes (31%) and 20 BBS routes had negative slopes (69%) in Canada ($\chi^2 = 4.17$, df $= 1$, $P = 0.041$). The percentage of BBS routes that had negative slopes varied nonlinearly with latitude, but not longitude (Table 2, Fig. 2).

Western Burrowing Owls primarily use black-tailed prairie dog burrows in the eastern portion of their breeding range, whereas the diversity of burrowing species on which they depend is much greater in the northern and central portions of their breeding range (Fig. 3). Most (90%) of the study locations from published articles that mentioned the primary type of nest burrow used by Western Burrowing Owls corroborated the primary burrow usage map. The

Table 2. Relationship between Burrowing Owl population trajectory (increasing or decreasing) and latitude and longitude based on binary logistic regression of survey data from 1966–2015 along 612 BBS routes in the US. The quadratic term for latitude (latitude^2) was significant, indicating a significant nonlinear relationship between population trajectory and latitude. β is the beta coefficient from a binary logistic regression and Wald is the test statistic describing how the coefficient differs from zero.

VARIABLE	β	±SE	WALD	P value
Latitude	0.81	0.27	8.7	0.003
Latitude^2	−0.01	0.01	9.3	0.002
Longitude	−0.20	0.23	0.8	0.383
Longitude^2	−0.01	0.01	0.7	0.387
Constant	−26.2	11.3	5.4	0.020

primary burrow type used by Western Burrowing Owls differed from the one predicted on the map at only 8 of the 81 study sites in past studies (the orange squares in Fig. 3). Five of the eight incongruities were in New Mexico. Based on the burrow usage map, four species of burrowing mammals are the primary burrow provider within 61% of the Western Burrowing Owl's range: black-tailed prairie dog (35% of its range), yellow-bellied marmot (11%), Richardson's ground squirrel (10%), and American badger (26% of its range, including areas where badgers are considered co-primary burrow providers along with marmots and Richardson's ground squirrels). Other burrow providers are important in more localized areas: round-tailed ground squirrel (6% of the owl's range), rock squirrel (6% of the owl's range), Gunnison's prairie dog (5% of owl's range), California ground squirrel (5% of owl's range), and seven other species that were the primary burrow provider in <5% of Western Burrowing Owl's range (Fig 3).

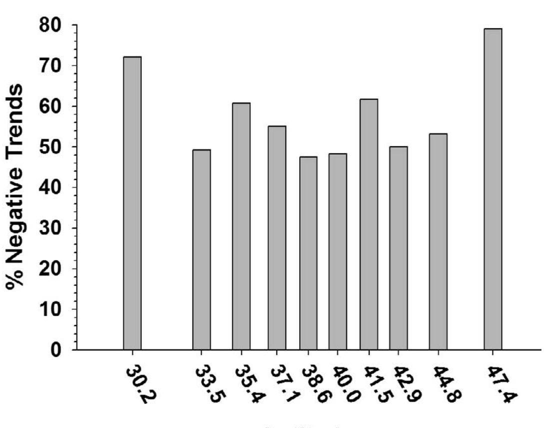

Figure 2. The relationship between latitude and the percent of BBS routes with negative trends (1966–2015) for 612 BBS routes in the US. To illustrate the relationship, the 612 routes were split into 10 latitudinal bins with equal numbers of BBS routes. The numbers on the x-axis are the mid-points of those 10 latitudinal bins.

The percent of BBS routes with negative population trends was highest in portions of the owl's range where the primary burrow provider was Richardson's ground squirrel, California ground squirrel, black-tailed prairie dog, and American badger (Table 3, Fig. 3). These regions were in the northernmost, westernmost, and easternmost portions of the Western Burrowing Owl's range.

DISCUSSION

Population trend estimates from the BBS program suggested nonsignificant trends for Burrowing Owls in the US for many years. The BBS program changed analytical methods in 2011 and the long-term trends for Burrowing Owls in the US were significantly negative for the first time in 2011. Most of the declines in Burrowing Owl abundance occurred in the 1970s, 1980s, and early 1990s, but the analytical methods used prior to 2011 did not detect a significant decline. However, population declines of the magnitude suggested by the point estimates even in years prior to 2011 (–0.7% to –2.2% annually) are substantial even though they are likely underestimates of the rates of decline and were not statistically significant. A 1% annual decline in abundance over a 49-yr period (e.g., 1966–2015) equates to a 39% decline in abundance over those 49 yr. Low relative abundance of Burrowing Owls likely affected the statistical power of the trend estimates from the earlier analytical method. Indeed, numerous local and regional studies have documented population declines of Burrowing Owls (Desmond et al. 2000, Klute et al. 2003, Conway and Pardieck 2006).

Our methods did not control for changes in BBS surveyors over time. Failure to include observer as a covariate when estimating linear trends in BBS counts usually results in a positive bias in trend estimates (Sauer et al. 1994), so the higher proportion of negative trends on BBS routes is likely real and may actually be higher than what is reported here. Why have Burrowing Owls at the northernmost and southernmost portions of their US breeding range declined more than owls in the central portion of their US range? One hypothesis is that there are fewer burrow excavators at these latitudes. For example, perhaps the abundance and distribution of Richardson's ground squirrels, American badgers, and black-tailed prairie dogs have declined more so than other burrowing animals on which Burrowing Owls depend in the central portion of their US range (Fig. 3). Indeed, burrow availability is considered a primary habitat feature in the northern portions of the owl's range (Uhmann et al. 2001, Lantz et al. 2007) and the owl's population trends were more likely to be negative in portions of their range where they rely on these three species compared to other portions of their range (Table 3). Robust estimates of the extent of population declines among the different species of burrowing animals are needed to more rigorously test this hypothesis, but such estimates are currently lacking. Abundance of American badgers has declined, especially in the northern part of their range and in portions of their range where prairie dogs were formerly more abundant (Reid and Helgen 2008), and marmots are frequently removed by landowners in the northern portions of the US (C. Conway unpubl. data). Alternatively, the higher rates of decline in the northernmost portion of the owl's range may not be related to latitudinal variation in the types of burrows used, but rather may reflect differential changes in migratory behavior for owls in northern latitudes (Macías-Duarte 2011, Macías-Duarte and Conway 2015) or differences in farming practices, urbanization, or the differential effects of climatic changes (e.g., drought) or sylvatic plague at different latitudes. Indeed, Burrowing Owls have substantial intraspecific variation in reproductive traits (Conway et al. 2012) and latitudinal variation in these traits may contribute to the latitudinal variation in population trend (and provide clues to its underlying cause).

BBS routes are roadside surveys, so the trend estimates derived from BBS count data represent population trends of Burrowing Owls near roads. This is less likely to bias trend estimates of Burrowing Owls compared to similar approaches based on data for other bird species because Burrowing Owls do not seem to avoid roads. Indeed, daytime space use by owls in Canada showed they preferred fences (which are often along roads) and gravel and dirt roads, but avoided paved roads with high-speed traffic (Scobie et al. 2014). Additionally, owls seem to preferentially nest and forage near roads in at least some portions of their range (Haug et al. 1993, Conway and Pardieck 2006, Poulin et al. 2011). Another bias associated with trend estimates from BBS count data (or any count data) is the first-time effect; an observer's skill level increases after his or her first year of surveys (Kendall et al. 1996). The first-time effect is likely small for Burrowing Owls compared to other birds for the reasons mentioned above, and it causes trend estimates to be positively biased (Kendall et al. 1996), so the rate of decline may be even greater if the first-time effect influences Burrowing Owl counts on BBS routes. Some of the biases associated with trend estimates from BBS counts could be ameliorated if range-wide surveys designed specifically for Burrowing Owls were conducted (Holroyd and Wellicome 1997, Conway and Simon 2003, Conway et al. 2008).

Western Burrowing Owls rely on burrows dug by burrowing animals for nesting, roosting, and escape from predators and thermal extremes. Western Burrowing Owls modify and expand existing burrows, but they rarely initiate new burrows. Hence, burrowing animals are a critical resource for Western Burrowing Owls, and the fate and protection of the burrowing animals that dig the burrows on which owls depend likely influence population trends and persistence of Western Burrowing Owls (Wellicome and Holroyd 2001). As such, preservation of colonial burrowing animals is often one of the most common recommendations regarding methods to help conserve Burrowing Owls (Zarn 1974, Holroyd et al. 2001). The map presented here is the first effort to summarize and map the primary burrow types used by Western Burrowing Owls throughout their breeding range in North America. The map proved to be quite accurate when validated against 81 studies that reported the primary type of burrow used by nesting Western Burrowing Owls. The one area where the map did not perform well was New Mexico: five of the six Burrowing Owl studies in New Mexico were conducted within the IUCN range of black-tailed prairie dogs but they reported that owls primarily rely on a species other

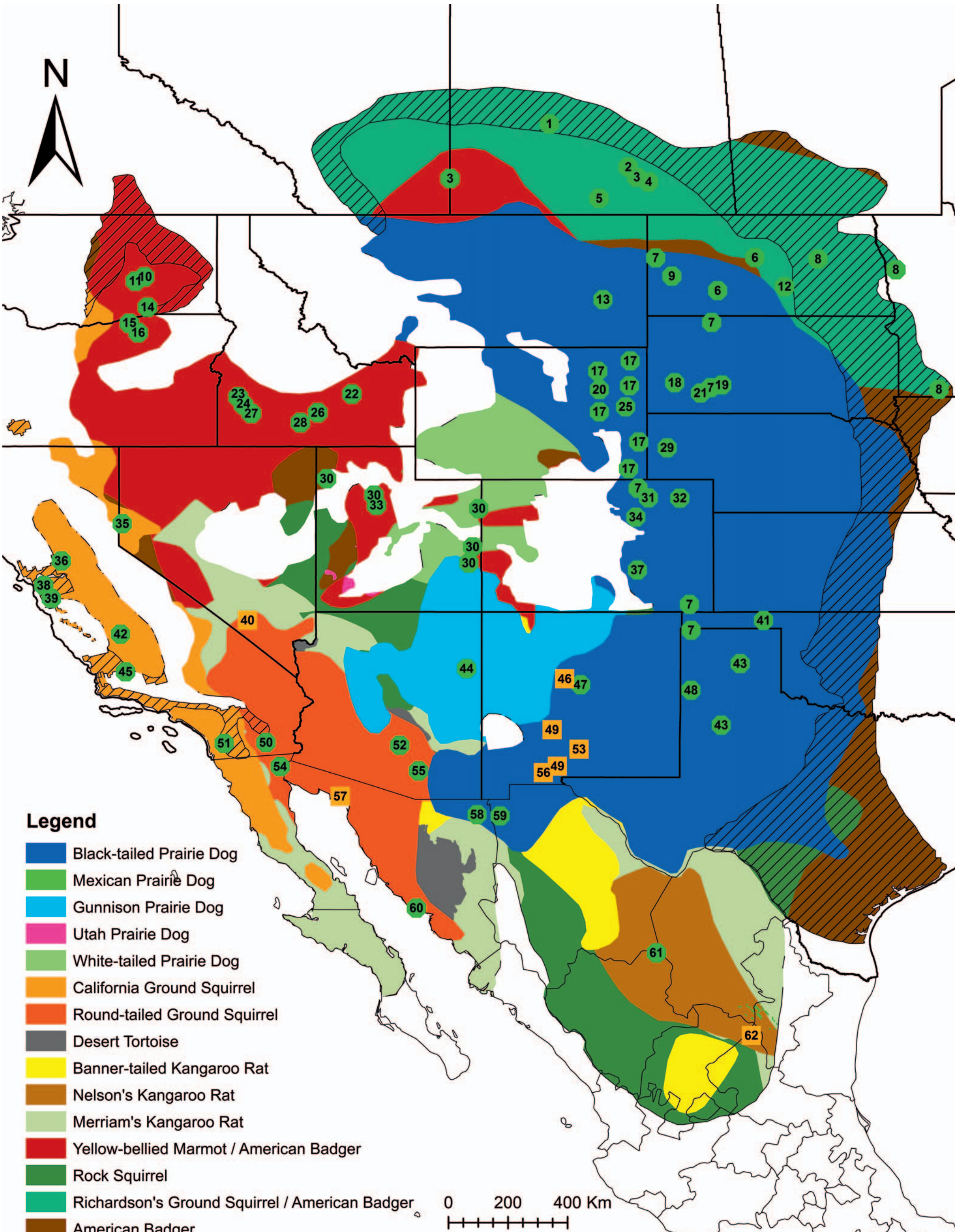

Figure 3. The Western Burrowing Owl uses abandoned burrows dug by burrowing animals for its nest burrow and the primary architect of the owl's nest burrows differs throughout the owl's breeding range in North America. The map is based on the overlap in the distribution of Western Burrowing Owls and the distributions of the burrowing animals that dig the burrows that the owls primarily use. White areas on the map indicate areas outside the Western Burrowing Owl's range and the hatched areas indicate portions of the owl's historical range where it no longer occurs (based on Wellicome and Holroyd 2001). The different colors represent the assumed species of burrowing animal on which the Western Burrowing (Figure caption continued on the bottom of the next page.)

Table 3. Percent of BBS routes with a negative trend (1966–2015) within portions of the Burrowing Owl's range that differ based on the primary burrower provider (i.e., the polygons in Fig. 3).

PRIMARY BURROW PROVIDER	BBS ROUTES WITH NEGATIVE TRENDS (%)	NO. OF BBS ROUTES
Richardson's ground squirrel/American badger	83.3	18
California ground squirrel	70.7	41
American badger	66.7	9
Black-tailed prairie dog	59.6	302
Yellow-bellied marmot/American badger	52.3	88
Round-tailed ground squirrel	53.3	30
Merriam's kangaroo rat	50.0	4
Gunnison prairie dog	44.4	27
White-tailed prairie dog	37.0	25
Rock squirrel	33.3	9
Total[a]	57.7	553

[a] Fifty-five routes were outside of the published range of the western Burrowing Owl and hence were excluded from this summary.

than black-tailed prairie dogs. This lack of congruence in New Mexico could reflect: (1) a lack of precision in the IUCN range maps in New Mexico, or (2) that black-tailed prairie dogs may have been eradicated in areas where Western Burrowing Owl studies have been conducted in New Mexico. For example, several studies in New Mexico reported that Western Burrowing Owls used rock squirrel, badger, or kangaroo rat burrows and that prairie dogs were not present in their area (despite being within the IUCN range).

With the exception of New Mexico, 67 of the 68 Western Burrowing Owl studies in the US and Canada corroborated the assumptions in the burrow usage map. I was not able to adequately validate the map in several portions of the Western Burrowing Owl range because I was unable to find studies in those areas that mentioned the primary burrow provider. I recommend that investigators who work in the following areas record the primary burrow provider to help further validate the map: Mexico, Nevada, northern Arizona, and southern Utah. The map suggests that conservation of black-tailed prairie dogs, American badgers, California ground squirrels, and round-tailed ground squirrels may be particularly important to the conservation and persistence of Western Burrowing Owls, as these four species are the primary burrow providers in the

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Owl primarily relies in that portion of its range (see text for rationale). The numbered symbols are the locations of studies that have reported the primary type of burrow used by nesting Western Burrowing Owls and whether the study corroborated (green circle) or did not corroborate (orange square) the assumptions of the map: (1) Haug 1985; (2) James et al. 1990; (3) Scobie 2015; (4) Wellicome et al. 1997; (5) Warnock and Skeel 2002; (6) Stewart 1975, Murphy et al. 2001; (7) Dominguez 2010; (8) Grant 1965; (9) Davies and Restani 2006; (10) Conway et al. 2006; (11) Climpson 1977; (12) Konrad and Gilmer 1984; (13) Restani et al. 2001; (14) Conway et al. 2006, Smith and Conway 2007, 2011; (15) Holmes et al. 2003; (16) Green and Anthony 1989; (17) Conway and Simon 2003; (18) Griebel 2000, Griebel and Savidge 2007; (19) MacCracken et al. 1985; (20) C. Conway unpubl. data, Conway and Simon 2003; (21) Martell et al. 1993; (22) Gleason 1978, Gleason and Johnson 1985; (23) Brady 2004, King and Belthoff 2001; (24) Belthoff et al. 1995; (25) Conway et al. 2005, Lantz et al. 2007, Lantz and Conway 2009; (26) Rich 1986; (27) Brady 2004; (28) Rich 1984; (29) Desmond et al. 2000; (30) C. Lundblad pers. comm.; (31) Conrey 2010; (32) Hughes 1993; (33) Smith and Murphy 1973; (34) Plumpton and Lutz 1993, Plumpton 1992; (35) Neel 1999; (36) Johnson 1997; (37) C. Conway unpubl. data; (38) Thomsen 1971; (39) Trulio 1997; (40) Hall et al. 2003, Steen et al. 1997, Greger and Hall 2009; (41) Butts 1972, Butts and Lewis 1982; (42) Gervais 2002, Gervais et al. 2003; (43) Ray et al. 2016, Teaschner 2005; (44) Bayless and Beier 2011; (45) Ronan 2002, Ronan and Rosenberg 2014; (46) Arrowood et al. 2001, Martin 1973; (47) Hawks Aloft 2003; (48) Ross 1974; (49) Berardelli et al. 2010; (50) Rosenberg and Haley 2004, Catlin 2004, Bartok and Conway 2010; (51) Unitt 2004; (52) Conway et al. 2007, Ogonowski and Conway 2009; (53) Johnson et al. 1997; (54) Itubarría-Rojas 2002; (55) Ogonowski and Conway 2009, Conway and Ogonowski 2005; (56) Best 1969; (57) A. Macías-Duarte pers. comm.; (58) Russell and Monson 1998; (59) Dominguez 2010, McNicoll 2005; (60) Macías-Duarte 2011; (61) Rodriguez-Estrella and Ortega-Rubio 1993; (62) Ruiz Ayma et al. 2016.

majority of the owl's range in the US and Canada. A broad-scale map like this cannot be 100% accurate in every location in North America because Western Burrowing Owls use a variety of burrow types in most portions of their range. For example, Burrowing Owls will also use the burrows of skunk, fox, coyote (*Canis latrans*), armadillo, other ground squirrel species (Townsend's [*Urocitellus townsendii*], etc.), and other burrowing animals not depicted on the map. Hence, this map is a simplified depiction of the burrowers that are important to Western Burrowing Owls, and conservationists or managers should not assume that, for a given area, only the species depicted in this map is important for Western Burrowing Owls. Indeed, in some instances, the primary burrow type may be in such low abundance that it is not the most commonly used burrow type. Despite these caveats, this map will provide a template for future refinement regarding the primary burrow providers for Western Burrowing Owls, and this map and future refinements of it will promote analyses regarding whether spatial patterns in declines in Western Burrowing Owl abundance are related to the burrowing species that dig the burrows on which they depend. This map can also be used to assess whether demographic traits and population viability vary among regions based on the primary burrowing species that provides burrows for Western Burrowing Owls. As such, this map may help future investigators generate and test hypotheses regarding the most likely cause(s) of observed population declines in Western Burrowing Owls.

What are the characteristics of underground burrows that make those created by one burrowing species more preferable to Western Burrowing Owls compared to those of another species? Diameter, depth, slope, number of turns, number of entrances, soil associations, longevity, and distance between adjacent burrows are some of the many burrow characteristics that likely vary among burrow providers and many of these traits affect use by Western Burrowing Owls (Belthoff and King 2002). Indeed, Western Burrowing Owls show preferences for some of these features (Smith and Belthoff 2001), but more research is needed to quantify how the burrows created by the different burrowing species differ from what Western Burrowing Owls prefer. Of the suite of burrowing animals that create burrows that are subsequently used by Western Burrowing Owls, some are likely more important to the conservation of owls than others. Some of the species depicted in the burrow usage map (Fig. 3) have experienced substantial declines in abundance and distribution (e.g., black-tailed prairie dogs, and American badgers). Other species have likely fared much better over the past century (e.g., round-tailed ground squirrels, white-tailed prairie dogs, and rock squirrels). Most Burrowing Owl publications do not state what species created the burrows used by owls in their study site. Those that do, often only state the primary species, and the few that describe all burrow types used by owls rarely state the proportions for each burrow type used or even rank their relative importance. This is surprising given the importance of burrowing animals to Western Burrowing Owls. I urge future authors to document and report the burrow types used by Western Burrowing Owls in their study area, so that more detailed versions of the map included here are possible. For example, future revisions of the burrower provider map should include "secondary" and "tertiary" species of burrowers used by owls in each portion of their range so that the map can better inform Western Burrowing Owl conservation efforts.

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