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Distributions of eastern and western red bats in western North America

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Abstract.—The known distributions of eastern red bats and western red bats in western North America have changed greatly over the past 2 decades, resulting in inaccurate range maps and uncertainty regarding the presence or probable absence of these species within states and provinces. We obtained capture and specimen records from the western United States and Canada for 276 eastern red bats and for 863 western red bats. We documented the expansion of the range of eastern red bats in northwestern Canada and clarified the northern and eastern limits of western red bat distribution in the United States. We found that the eastern red bat and western red bat exhibit a mostly allopatric distribution, with western red bats mainly inhabiting warmer, drier forested ecoregions at lower latitudes than those inhabited by eastern red bats. A small zone of overlap between the species was identified only in far western Texas, although it is possible that sympatry may be more widespread due to errors on museum specimen labels and misidentification of captured red bats.

Resumen.—Las distribuciones del murciélago colorado y el murciélago rojo del desierto en el oeste de América del Norte han cambiado mucho en las últimas 2 décadas, lo que ha generado mapas de distribución imprecisos e incertidumbre sobre la presencia o la probable ausencia de estas especies en los diferentes estados y provincias. Obtuvimos registros de captura y registros de especímenes colectados de 276 murciélagos colorados y 863 murciélagos rojos del desierto del oeste de Estados Unidos y Canadá. Documentamos la expansión de la distribución de murciélagos colorados en el noroeste de Canadá y clarificamos los límites de distribución norte y este de los murciélagos rojos del desierto en los Estados Unidos. Encontramos que los murciélagos colorados y los murciélagos rojos del desierto mostraron una distribución principalmente alopátrica. Los murciélagos rojos del desierto habitan principalmente ecorregiones de bosques más secos y con temperaturas más altas, en latitudes más bajas, que los murciélagos colorados. Se identificó una pequeña zona de superposición entre las 2 especies en el extremo oeste de Texas, aunque es posible que la simpatría sea mayor debido a errores en la identificación de los especímenes del museo y de los murciélagos capturados.

North American red bats were once considered a single species, *Lasiurus borealis*, comprising an eastern (*L. b. borealis*) and a western (*L. b. teliotis*) subspecies (Shump and Shump 1982). Molecular phylogenetic examination (Baker et al. 1988) elevated these subspecies to species status: the eastern red bat, *L. borealis*, and the western red bat, *L. blossevillii*. Over the past 2 decades, capture records have expanded the known distribution of eastern red bats (e.g., Patriquin 2004, Lausen and Player 2014), while record clarification has largely reduced the distribution of western red bats in western North America (Nagorsen and Paterson 2012). However, these changes are not widely recognized and are not yet included on range maps (e.g., the IUCN Red List of Threatened Species, Bat Conservation International, NatureServe, the Smithsonian National Museum of Natural History) or in written species descriptions by international and regional wildlife organizations (e.g., the Western Bat Working Group). Uncertainty regarding the presence or probable absence of species can be problematic when making decisions for species conservation and land management. Here, we consolidate current knowledge of the known occurrences (i.e.,

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distribution) of eastern red bats and western red bats by using capture and specimen records to establish updated distribution maps for these species throughout the western United States and Canada. We also compare the species' distributions relative to ecological regions (hereafter, ecoregions; Omernik 1987, Omernik and Griffith 2014) of western North America to examine how occurrence of these species may be associated with broad biogeographical patterns and landscape features.

Capture and specimen records for eastern and western red bats were obtained from these state and provincial agencies (n = 646 records): Alberta Environment and Parks, Alberta Fish and Wildlife Management Information System, Arizona Game and Fish Department, California Bat Conservation Plan, California Department of Fish and Wildlife, Colorado Division of Wildlife, Colorado Natural Heritage Program, Colorado Parks and Wildlife, Montana Natural Heritage Program, Nevada Department of Wildlife, Nevada Natural Heritage Program, Utah Division of Wildlife Services, Utah Natural Heritage Program, and the Wyoming Natural Diversity Database. Museum records (n = 317) were found using the Arctos Collaborative Collection Management Solution online museum database. Additional records came from literature sources (n = 122), personal communications with biologists (n = 27), and publicly available wind energy facility fatality data (n = 27). Each record corresponds to an individual animal. Bat location data were provided as shapefiles, Universal Transverse Mercator coordinates, latitude and longitude coordinates, or written location descriptions (e.g., county, city, wind energy facility, park), and were synthesized into a final digital data layer using ArcGIS 10.4. (ESRI, Redlands, CA). The most precise location information available was used for each record to create each point location on the final map. We used records for both sexes and from all times of year, though eastern red bats are long-distance migrants and western red bats exhibit more local movements but have different summer ranges for males and females (Shump and Shump 1982, Cryan 2003). Cryan (2003) provides monthly distribution maps for both species that indicate that eastern red bats migrate from the southeastern United States to the Midwest and Canada, while western red bats appear to be year-round residents in California and move between Mexico and Arizona seasonally.

Eastern and western red bats are physically similar, and are typically distinguished based on geography: red bats captured east of the Rocky Mountains are eastern red bats, and red bats captured west of the Rocky Mountains are western red bats (Morgan et al. 2019). In areas of potential overlap, captured western red bats are distinguished from eastern red bats based on the lack of white-tipped hairs in the dorsal pelage and a sparsely furred lower third of the tail membrane (Bogan and Williams 1970). Misclassification of living red bats is possible, and in areas of potential sympatry, these classifications should be treated with caution. Western red bats have significantly smaller cranial measurements than eastern red bats do (Schmidley and Hendricks 1984) and are less likely to be confused in areas of sympatry (Genoways and Baker 1988). These species produce echolocation calls with similar shapes, but with slightly different characteristic frequencies. Eastern red bats are slightly lower in pitch (29 kHz–49 kHz) than western red bats (36 kHz–53 kHz; Szewczak 2011a, 2011b). We did not include acoustic records in this study given the high degree of overlap in characteristic frequencies between these species and the high degree of intraspecific variation inherent to bat echolocation in general (Barclay 1999).

Prior to 2012, the known distribution of western red bats extended from southern British Columbia to Mexico, with absence only in the Great Basin Desert region of the western United States (Shump and Shump 1982). This distribution was erroneously based on a red bat specimen collected in southern British Columbia in 1905 and labeled as *L. b. teliotis*, the western subspecies, based on its location west of the Rocky Mountains (Nagorsen and Brigham 1993). However, DNA sequencing and examination of this specimen (Nagorsen and Paterson 2012) revealed that the genetic profile, along with pelage coloration and a heavily furred interfemoral membrane, matched that of *L. borealis*. Despite the 2012 revision, inaccurate distribution maps of *L. blossevillii* extending into Canada persist (e.g., the IUCN Red List of Threatened Species).

To determine the current distribution of western red bats, we obtained and mapped 863 capture and specimen records of *L. blossevillii*

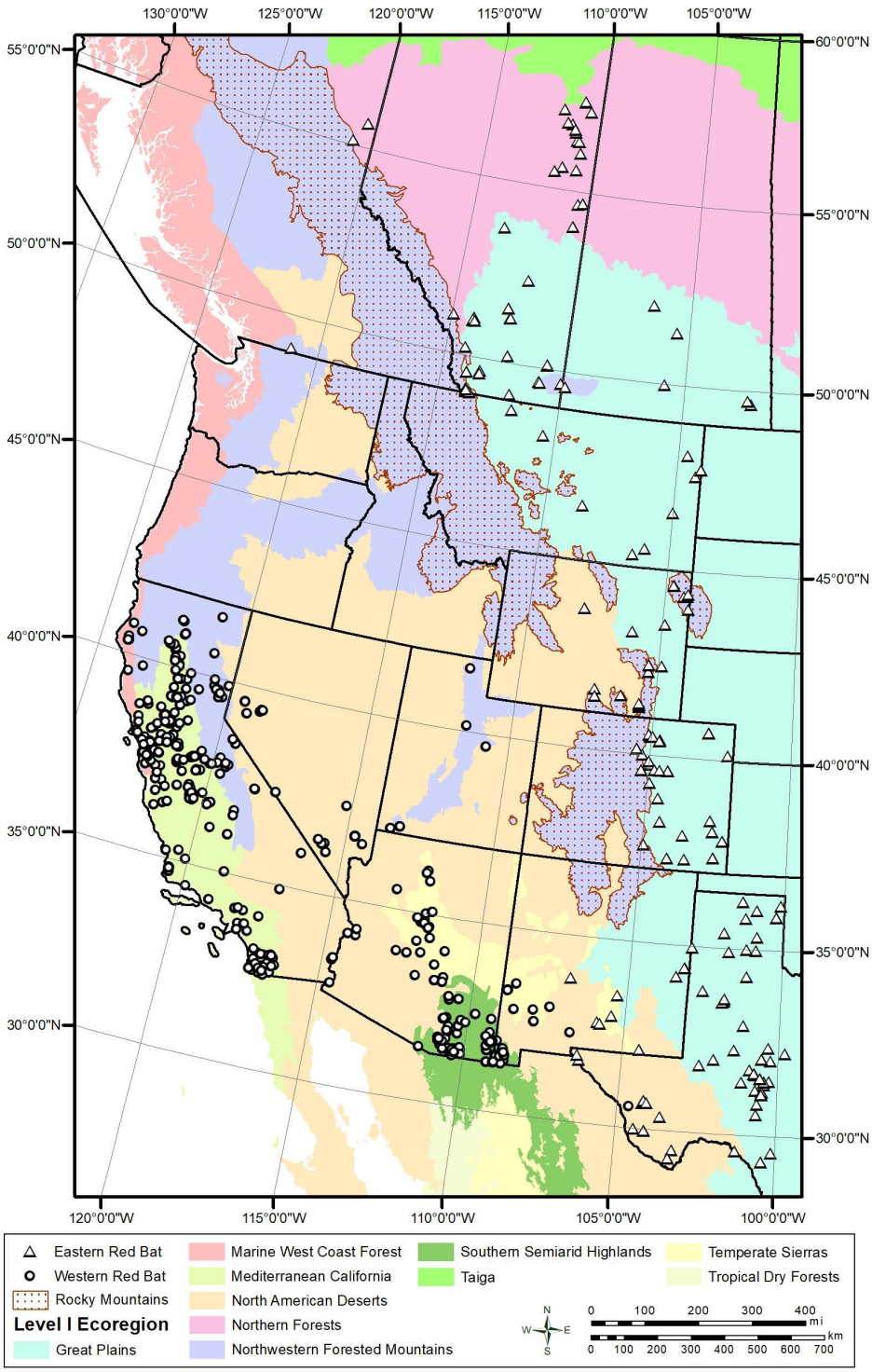

Fig. 1. Records for eastern red bats and western red bats captured or collected in the western United States and Canada, in relation to ecological regions and the Rocky Mountains. Data points represent individual records. Data source: ESRI Base Layers. Projection: Contiguous USA Albers NAD 1983; North American States and Provinces, Ecological Regions of North America Level 1 (CEC 2010a), and Ecological Regions of North America Level III (CEC 2010b).

(Fig. 1). Most of these records (72.4%) documented bats from north-central and coastal California and southeastern Arizona, corresponding to the Mediterranean California (n = 385) and the Southern Semi-Arid Highlands (n = 240) ecoregions, respectively (Fig. 1). A smaller number of western red bat records were also reported in the Temperate Sierras (n = 44) and Northwestern Forested Mountains (n = 32) ecoregions (Fig. 1). All of these regions include forests and are characterized by warm, semiarid climates (mean summer temperatures range from 12 °C to 20 °C; CEC 1997). The western red bat is a foliage-roosting species associated with riparian habitats, particularly willow (*Salix* spp.), cottonwood (*Populus* spp.), and sycamore (*Platanus* spp.; Pierson et al. 2006, Andersen and Geluso 2018). In California, these bats have been found roosting in fruit and walnut orchards (Constantine 1959), and reproductive females appear to be associated with lower-elevation riparian habitats, whereas males and nonreproductive females are found at higher elevations (Pierson et al. 2001). Fewer records for western red bats were from the North American Deserts ecoregion (n = 126), and 60.3% of these were recorded within 8 km of major rivers and streams.

The northernmost records of western red bats were from near the northern borders of California and Utah. To our knowledge, neither species of red bat has ever been captured or otherwise confirmed in Oregon, despite extensive bat surveys in the state (Pat Ormsbee, personal communication). An individual captured and released during a 2016 workshop by J. Szewczak and J. Tyburec in northeastern California, and a 1994 capture by B.J. Lengas and E. Owens in Cache County, Utah (Oliver 2000), are the northernmost records for this species. In Utah, only 15 western red bats have been captured, 8 of which were 2 adults with 3 young each that were found in the southwestern corner of the state (Presnall and Hall 1936). None have been reported in Utah in the past 25 years; the 2 most recent records were a specimen collected in north-central Utah, near Provo in 1991 (Oliver 2000) and the Cache County capture in 1994.

To determine the current distribution of eastern red bats, we obtained and mapped 276 capture and specimen records of *L. borealis* (Fig. 1). The current distribution for eastern red bats extends in a line from the North American Deserts ecoregion of southwestern Texas through the Northern Forests ecoregion of northeastern British Columbia, largely following the eastern edge of the Rocky Mountains (Fig. 1). The range of eastern red bats also extends into the eastern United States and Canada (Shump and Shump 1982), where they are common, and south into Mexico (Ceballos 2014). In this study, we have not included records for eastern red bats east of a line from the border of Saskatchewan and Manitoba south through central Texas.

Eastern red bats are considered rare in the western United States (Adams 2003, Hester and Grenier 2005, Neubaum 2005). In western Canada, prior to 2000, only 6 eastern red bats had been captured in southern Alberta (Saunders 1990, Hill 1993) and eastern Saskatchewan (Willis and Brigham 2003). These records were believed to be wayward migrants. In 2001, 2 female eastern red bats were captured in Cypress Hills Provincial Park, an isolated forest habitat in southwest Saskatchewan, representing a 300-km range extension of the species (Willis and Brigham 2003). That same summer, a female eastern red bat was captured in the boreal mixed-wood forest of northeast Alberta (Patriquin 2004), extending the range north approximately 800 km. Over the next decade, dozens more eastern red bats were captured in northeastern (Grindal et al. 2011, Lausen and Player 2014) and southern (e.g., Lausen 2012) Alberta, and 15 eastern red bats were found as fatalities at a wind facility in southwestern Alberta (Baerwald and Barclay 2011, Baerwald personal communication). Formerly considered extralimital, Alberta records now seem to be firmly within the limits of eastern red bat distribution. Similar range expansions have recently been documented for other species of North American bats (*L. seminolus*, Perry 2018; *Nycticeius humeralis*, Andersen et al. 2017; *Tadarida brasiliensis*, McCracken et al. 2018). It is unknown whether the increased numbers of eastern red bats documented after the turn of the century in Canada result from increased survey effort by biologists (Grindal et al. 2011, Lausen and Player 2014), expansion of deciduous forest across the western prairies (Neubaum 2005), and/or a warmer climate causing northern latitudes to become more favorable to this species (Willis and Brigham 2003). The 1905

specimen from southern British Columbia remains the westernmost record for eastern red bats in Canada. However, because the conditions under which this specimen was collected were not included on the museum tag, it is unknown whether this bat was a resident or a wayward migrant. Eastern red bats are capable of long-distance movement, and have been documented landing on ships approximately 210–240 km offshore in the Atlantic (Norton 1930, Brown 1953) and occurring well north of tree line in Nunavut (64° N; van Zyll de Jong 1985). Three fatalities found at Bear Mountain Wind Park ($n = 2$; Nagorsen and Paterson 2012) and the Quality Wind Farm ($n = 1$; Hemmera 2013) in northeastern British Columbia are the only other physical records for this species in this province, though this species may have been detected acoustically in southern and western British Columbia (Fenton et al. 1983; Lausen, personal communication).

Of the Canadian records for eastern red bats west of Manitoba ($n = 75$), 53.3% are from the Northern Forests and Northwestern Forested Mountains ecoregions (Fig. 1). Throughout the eastern part of its range, this species is typically found in mixed hardwood and deciduous forests with open understories where it roosts in tall, living deciduous trees (Menzel et al. 1998, Hutchinson and Lacki 2000). However, shelterbelts in intensively farmed areas, and mature urban trees in wooded parks, residential areas, and riparian corridors provide habitat as well (Mager and Nelson 2001). From Montana to Colorado, 20.2% of records for eastern red bats are from the Northwestern Forested Mountains ecoregion, mainly along the eastern edge of the Rocky Mountains (Fig. 1). Most records for eastern red bats in western North America are from the Great Plains ecoregion ($n = 183$), a third of which (34.4%) were captured or collected within 8 km of major rivers and streams. To date, the northernmost range of eastern red bats appears to be the boundary between the Taiga and Northern Forests ecoregions in Canada. However, possible acoustic recordings and visual sightings of eastern red bats from the southwestern Northwest Territories (Lausen et al. 2014, Wilson et al. 2014) and the southern Yukon (T. Jung, personal communication; Slough et al. 2014) suggest that this species may occur farther north. We expect that eastern red bats could be found throughout the Northern Forests ecoregion of Saskatchewan as well, based on habitat similarities with northeastern Alberta.

The current geographic ranges of these 2 species appear to demonstrate distinct allopatry throughout western North America, with the Rocky Mountains providing a natural barrier between distributions in Canada and much of the United States. Only one eastern red bat has been found west of the Rocky Mountains: the 1905 specimen from British Columbia (Fig. 1). Based on our collected data, eastern red bats and western red bats only overlap in the Desert ecoregion of western Texas and potentially in south-central New Mexico (Fig. 1). The single western red bat specimen in Texas was collected in 1969 (Genoways and Baker 1988, Ammerman et al. 2012). Distribution maps for these species in Mexico (Ceballos 2014) also indicate a small area of potential overlap in northwest Chihuahua, just across the U.S. border (Bogan and Williams 1970, Anderson 1972).

It is unknown why the distributions of these ecologically similar species do not overlap to a greater extent. One possibility is that the species do overlap more than our distribution maps indicate due to museum or database errors, illustrated by the aforementioned British Columbia specimen. Indeed, a query for *L. borealis* using the Arctos online museum database returned 3 specimens (MSB 9465, 9466, and 10516) from the Glenwood Fish Hatchery in southwestern New Mexico, overlapping with the distribution of western red bats. Further investigation at the Museum of Southwestern Biology found that those specimens had been labeled *L. borealis teliotus* (the former name for western red bats) in 1960, and were later confirmed to be western red bats (E. Valdez, personal communication), but this was not reflected in the database.

It is also possible that some capture records of eastern red bats and western red bats in New Mexico and Texas, or elsewhere (e.g., northern Utah) were misidentified, and sympatry may be more widespread, as properly identifying red bats to species in hand is difficult. Indeed, as this manuscript was nearing completion, genetic analysis of 3 bats found at wind facilities in Hidalgo County in far south Texas revealed them to be western red bats (A. Hale, personal communication). Two

eastern red bat specimens have also been collected in Hidalgo County (Mulaik 1943, Ammerman et al. 2012). The presence of an eastern red bat approximately 130 km west of the western edge of the Rocky Mountains in British Columbia and the presence of at least one western red bat in a region of Texas devoid of natural barriers (Fig. 1) indicate that care should be taken when identifying red bats in areas of potential sympatry, especially considering the migratory, wide-ranging behavior of these species (Shump and Shump 1982). Guidance beyond variable pelage characters, such as external measurements, would be useful for distinguishing eastern and western red bats in hand.

Lastly, allopatry between eastern red bats and western red bats throughout most of their ranges may indicate adaptations to different environmental conditions that are relaxed in the southern U.S. and northern Mexico. Wide differences in cranial measurements among individuals of the 2 species captured in west Texas suggest that these bats do not hybridize in this region (Genoways and Baker 1988). Morphological differences, together with slightly different ranges of frequencies used in echolocation suggest possible dietary niche separation, which may also influence foraging strategies, but these effects remain unstudied. The larger size and fully furred tail membrane of eastern red bats may also convey thermoregulatory benefits that allow it to survive at higher latitudes than western red bats. We hypothesize that differences in morphology and pelage explain why western red bats are largely restricted to the warmer, milder regions of the southwest, while eastern red bats are able to inhabit the cooler, more northern regions of western North America.

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