

New records for Douglas's squirrel (*Tamiasciurus douglasii*) in two mountain ranges of the Great Basin

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ABSTRACT.—New records of Douglas's squirrel (*Tamiasciurus douglasii*) document the species in 2 mountain ranges of the Great Basin where tree squirrels have not been previously reported, including 2 sites in the White Mountains, California, and 1 site in the Desert Creek Mountains, Nevada. In the White Mountains, squirrels were photographed by a camera trap on 9 different dates in winter and spring 2016–2017 at a site on the east side of the range crest near the Crooked Creek Field Station of the White Mountain Research Center (3125 m). In early winter 2018, two Douglas's squirrels were observed and photographed 25 km distant and 716 m lower in Leidy Canyon (2409 m) on the lower east side of the White Mountains, 3.5 km west of the Nevada state line. In the Desert Creek Mountains, Douglas's squirrels were observed on 4 days in autumn 2017 and winter 2018 along Desert Creek from 2005 m to 2307 m. We present evidence to suggest that at least the White Mountains records represent recent colonization(s) and, as such, call into consideration the question of how montane mammals are able to migrate into isolated mountain ranges of the Great Basin during warm Holocene climates.

RESUMEN.—Nuevos registros de la ardilla de Douglas (*Tamiasciurus douglasii*) documentaron a la especie en dos cadenas montañosas de la Gran Cuenca (the Great Basin), donde no habían sido reportadas previamente, incluyendo dos sitios en White Mountains en California, y uno en las Montañas Desert Creek, Nevada. En White Mountains, del lado este de la cresta de la cordillera y cerca de la Central de Investigación Crooked Creek del Centro de Investigaciones White Mountain (3125 m), las ardillas fueron fotografiadas mediante una cámara trampa, en nueve fechas distintas durante el invierno y la primavera del 2016 y 2017. A principios del invierno del año 2018, dos ardillas de Douglas fueron observadas y fotografiadas a 25 km de distancia y a 716 m más abajo, en Leidy Canyon (2409 m), en la parte baja del este de White Mountains, a 3.5 km al oeste de la frontera con Nevada. A lo largo de las montañas Desert Creek desde los 2005 a los 2307 m, fueron observadas ardillas de Douglas durante cuatro días de otoño del año 2017 y de invierno del año 2018. En este estudio, presentamos evidencia que sugiere que, al menos los registros de White Mountains representan colonizaciones recientes, que llaman a reconsiderar cuestionamientos acerca de cómo los mamíferos de montaña fueron capaces de migrar a las cadenas montañosas aisladas de la Gran Cuenca, durante los climas cálidos del Holoceno.

Douglas's squirrel (*Tamiasciurus douglasii*) is a common tree squirrel of the Pacific states, with its range extending from southern British Columbia through south central California (Fig. 1). The squirrel occurs primarily in coniferous forests of the coastal mountains and the Cascade Range–Sierra Nevada cordillera (Steele 1999). Three subspecies are recognized (Hall 1981): *T. d. douglasii* in coastal Washington and Oregon; *T. d. mollipilosus* of British Columbia, the Cascade Range of Washington, and the Coast Range of Oregon and California; and *T. d. albolimbatus* in the Oregon Cascade Range and Blue Mountains and the Sierra Nevada of California. Diurnal and nonhibernating behavior and distinctive markings and

calls make this species easily recognizable and familiar to many forest visitors. Douglas's squirrel is dependent on coniferous and angiosperm forests due to its diet of tree parts (Steele 1999). Favored forage items include reproductive structures of conifers and angiosperms and, especially in winter and spring, pine cambium obtained from tips of branches. Fruiting bodies of fungi are also important in their diet. Douglas's squirrels have solitary habit and aggressively defend territories centered on larderhoards, which typically comprise conifer cones (Steele 1999).

In California, *T. d. albolimbatus* occurs commonly on both sides of the Cascade Range and the Sierra Nevada (Steele 1999) where the

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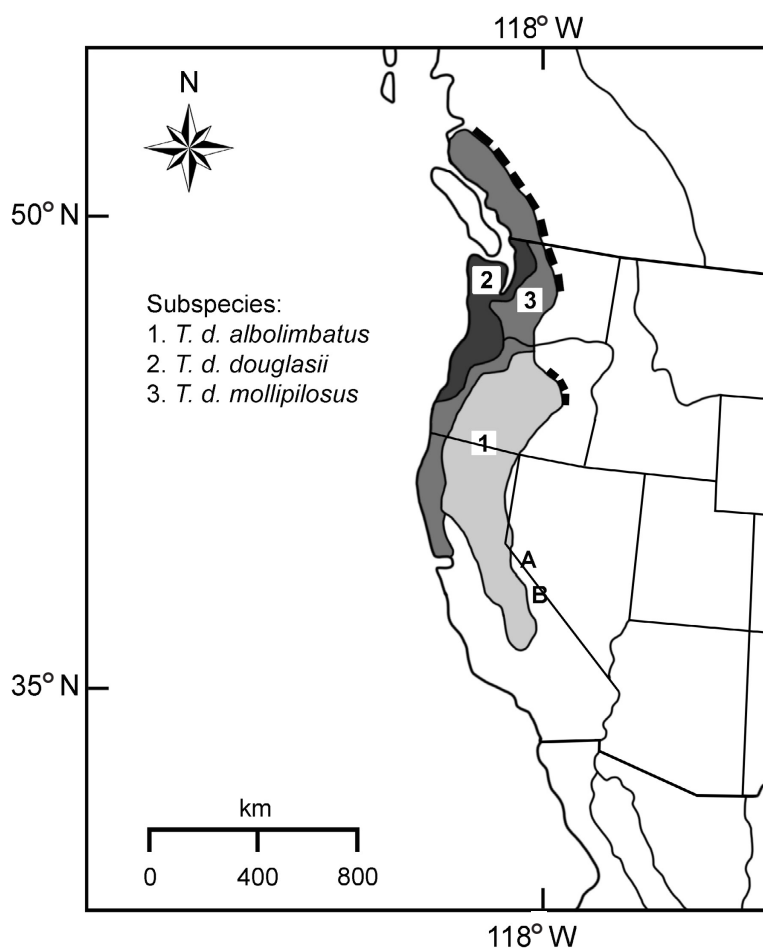


Fig. 1. Distribution of Douglas's squirrel (*Tamiasciurus douglasii*) in western North America showing 3 subspecies and 2 zones of parapatry (bold dashed lines) with the red squirrel (*T. hudsonicus*). Ranges with new records (see Fig. 2) are indicated: A. Desert Creek Mountains; B. White Mountains. Modified from Steele (1999).

species extends across a broad elevation range following forest occurrence from the foothills into the subalpine zone (Jameson and Peeters 2004). East of the Sierra Nevada, a handful of records document the species in the Glass Mountains (1 record, 1942, Arctos database, accessed 1 February 2018; all Arctos records cited herein are from the University of California, Museum of Vertebrate Zoology; 2012–2013 camera trap images, KH unpublished) and the southern Sweetwater Range (7 records, 1946, Arctos database, accessed 1 February 2018). The species is recorded in Nevada only in the Carson Range (39 records, Natural Diversity Database, Nevada Department of Wildlife, accessed 24 January 2018), a spur range of the Sierra Nevada.

The only congener that Douglas's squirrel contacts is the red squirrel (*T. hudsonicus*), whose range overlaps Douglas's squirrel in a zone that extends from southern British Columbia to northeastern Washington and a small disjunct area in the Blue Mountains of Oregon (Steele 1998, 1999; Fig. 1). The western gray squirrel (*Sciurus griseus*), another native tree squirrel, overlaps Douglas's squirrel in California west of the Sierra Nevada crest at elevations below 2000 m (Carraway and Verts 1994, Jameson and Peeters 2004). The western gray squirrel is known east of the Sierra crest only in the Tahoe Basin (Carson Range) and a few points in the vicinity of Reno, Nevada (*iNaturalist* database, accessed 14 March 2018).

METHODS AND RESULTS

We encountered Douglas's squirrel beyond its known distribution in 2 previously undocumented Great Basin mountain ranges of California and Nevada. Our observations are serendipitous in that we made no systematic searches for the species. We documented occurrences of the species through 3 methods: camera trapping, handheld-camera photographs, and indirect sign, each of which is adequate for species identification in these regions (J. Patton, University of California, personal communication). A camera trap set at one location documented Douglas's squirrel(s) on 9 different dates over an 8-month period. In another location we photographed Douglas's squirrels with a handheld camera. In addition to directly observing individuals, we also discovered indirect sign of Douglas's squirrel in regions where their range does not overlap with those of other tree squirrels (Steele 1999). These include distinctive vocalizations and piles of remnant conifer parts below trees where the squirrels are feeding. Conifer remnants include scales and chewed cores of cones and clipped branch tips lying directly below tree crowns. No other bird or animal leaves such sign in this location and abundance.

Our observations document 3 new locations: 2 point sites in the White Mountains of California and 1 band that extends from the Desert Creek Mountains into the northern tip of the Sweetwater Mountains, Nevada. The following are details about each site.

Crooked Creek, White Mountains,
Mono County, California

Douglas's squirrel was documented by camera trap at 37.49749, -118.17015, 3125 m elevation, in a gully 220 m southeast of Crooked Creek Station (Figs. 2B, 3A). The camera trap was one of 4 set around Crooked Creek Station during winter and spring 2016–2017 as part of a coyote study, and the only camera trap to document Douglas's squirrels. The gully is a short, seasonal side drainage to Crooked Creek, with strewn boulders and scattered bristlecone pines (*Pinus longaeva*) and limber pines (*Pinus flexilis*). The camera was mounted on the trunk of a limber pine, pointing down the gully (Fig. 3B). At the top of the gully, the pines are no longer present and the area flattens and changes to sagebrush scrub. In the broader

region, scattered individuals of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*) have been reported.

The camera, a Moultrie model m880, documented Douglas's squirrel on 9 different dates over the 8-month period (15 September 2016, 29 September 2016, 12 October 2016, 5 November 2016, 14 December 2016, 19 December 2016, 10 March 2017, 15 March 2017, and 12 May 2017; Fig. 4). In Fig. 4B a Douglas's squirrel can be seen with a limber pine cone in its mouth. The camera also documented bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), yellow-bellied marmot (*Marmota flaviventris*), golden-mantled ground squirrel (*Callospermophilus lateralis*), chipmunks (*Neotamias* spp.), and mice (*Peromyscus* spp.).

Leidy Canyon, White Mountains,
Mono County, California

Douglas's squirrel was observed at 37.70249, -118.21809, 2409 m elevation, in Leidy Canyon, an east-facing canyon of the White Mountains, California and Nevada (Fig. 2B). Extending to the crest of the range, the Leidy watershed originates north of White Mountain Peak (4333 m), the high point of the range. Leidy Creek is intermittent in its upper reaches but attains perennial condition where Cabin Creek joins it. Leidy Creek drains into Fish Lake Valley, Nevada, which is a large evaporative basin with base elevations of ~1500 m. The upper slopes of Leidy Canyon (above 2500 m) support forests of bristlecone pine and limber pine while foothill slopes contain pinyon pine–Utah juniper woodlands. A rare stand of lodgepole pine (*Pinus contorta*) occupies subalpine elevations (above 3100 m) along Cabin Creek, north of Leidy Canyon.

Two Douglas's squirrels were observed on 5 January 2018 in the riparian zone of Leidy Creek, 3.5 km west of the Nevada state line and coincident with the first crossing (in the upstream direction) of the dirt track that climbs the canyon (Fig. 5). The winter drought of 2018 resulted in a lack of snow on the ground although the creek was frozen, but daytime temperatures were below freezing on the day of the observation. The squirrels brought their presence to attention by alarm calls, the first alerting from downed branches of a mature black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) directly adjacent to

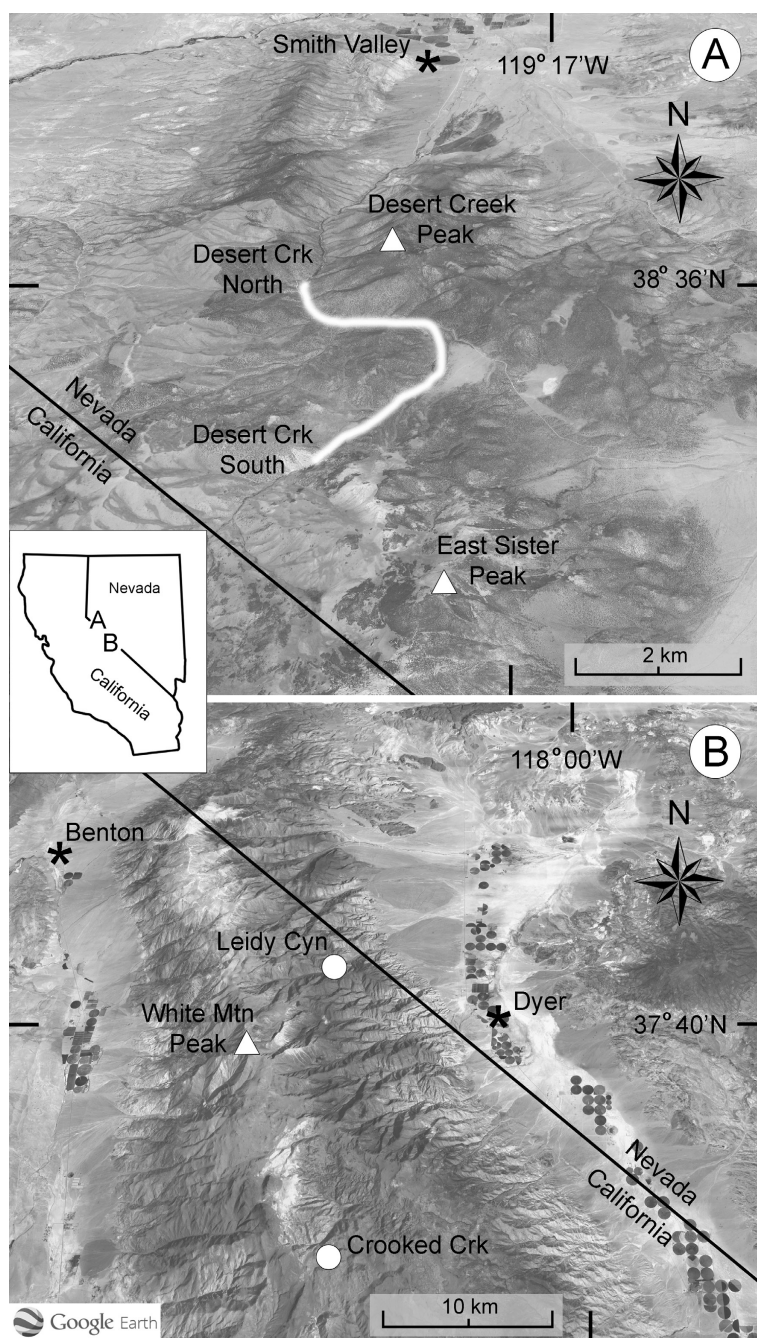


Fig. 2. New record locations of Douglas's squirrel. Asterisks indicate towns, and triangles indicate mountain peaks. **A.** Desert Creek Mountains and northern Sweetwater Mountains: the broad white line indicates a riparian zone of occupied habitat characterized by animal sightings, vocalizations, and indirect sign. Record locations are at the ends of the white line. **B.** White Mountains: white circles indicate record locations at Crooked Creek and Leidy Canyon.

the creek. This individual was observed and photographed (hand-held camera) at 11:15 (11:15 AM). Soon thereafter a second individual

was observed and photographed on downed cottonwood branches on the north side of the creek ~100 m upstream (Fig. 6). On

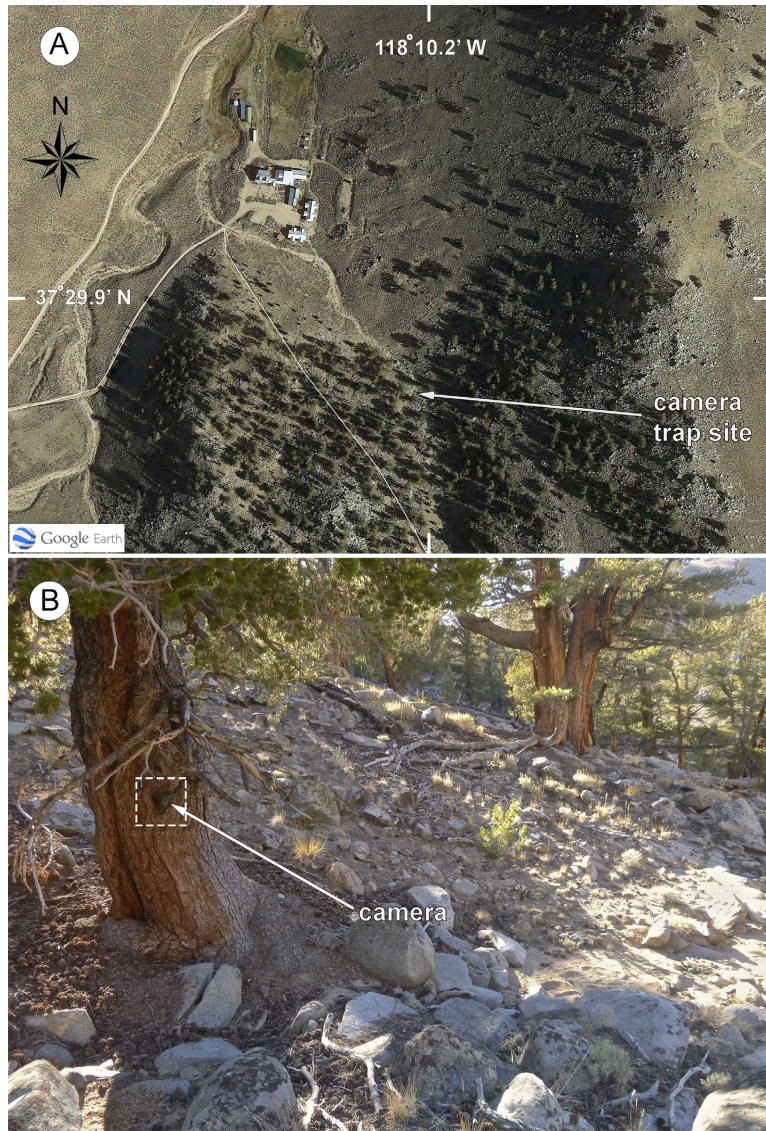


Fig. 3. Crooked Creek, White Mountains, California. **A.** Location of the camera trap and its proximity to the Crooked Creek Field Station of the University of California's White Mountain Research Center. **B.** Position of the camera trap on a limber pine above the field station.

return down-canyon later the same day at 15:30 (3:30 PM), 2 Douglas's squirrels were observed at the same location chasing one another near the ground. The riparian zone at this location is dominated by a cottonwood overstory with willow (*Salix* sp.) in the mid-canopy. Scattered pinyon pines extend into the riparian community while a few solitary individuals of limber, bristlecone, and lodgepole pines occur in the riparian zone down-

stream from the observation. The only indirect sign of Douglas's squirrel was tracks in the icy snow of the frozen creek.

Desert Creek, Desert Creek Mountains,
and Sweetwater Mountains,
Lyon County, Nevada

The site extends from 38.60096, -119.33624 , 2005 m elevation along Desert Creek to 38.54864, -119.31972 , 2307 m elevation.

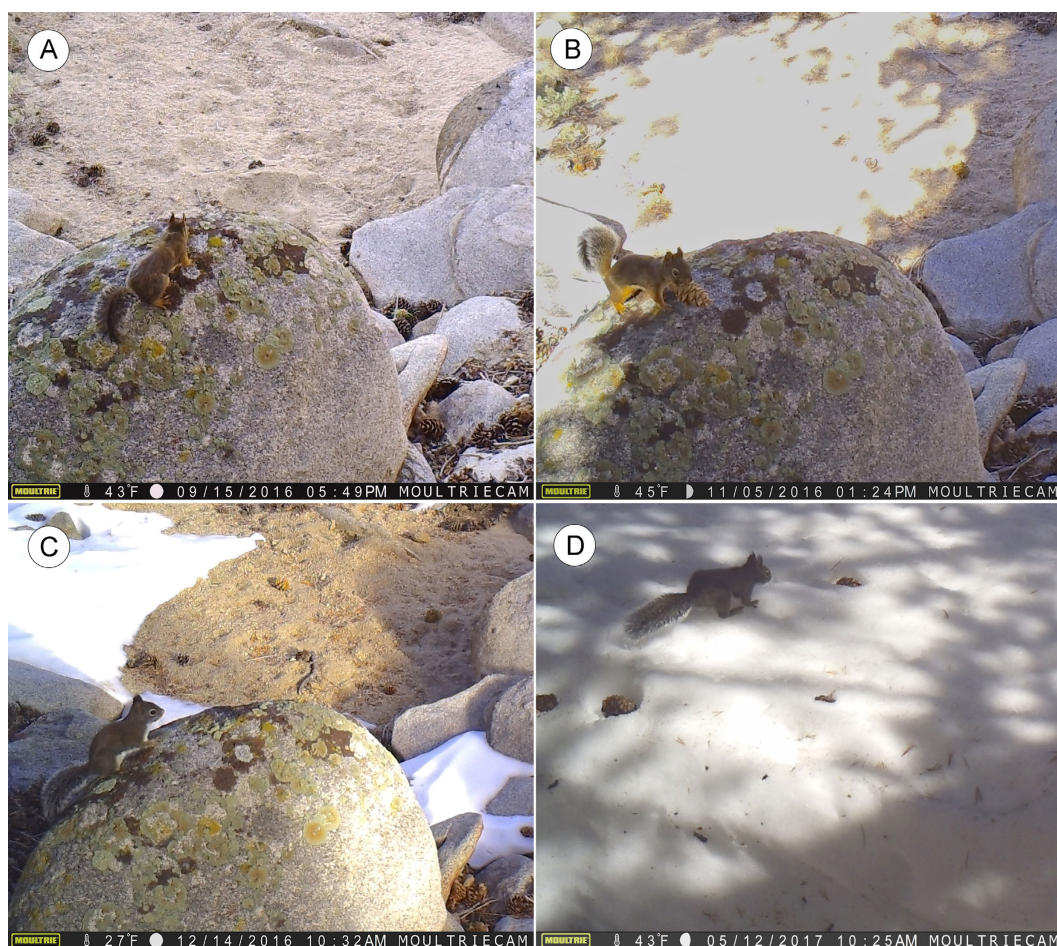


Fig. 4. Douglas's squirrels photographed by camera trap at Crooked Creek, White Mountains, California. A. 15 September 2016. B. 5 November 2016. C. 14 December 2016. D. 12 May 2017.

Desert Creek is a north-flowing perennial stream that originates on the west slopes of the Sweetwater Mountains. It passes the range-terminus north of East Sister (3172 m) and continues northward into the foothills of and along the west side of the Desert Creek Mountains (high point is Desert Creek Peak, 2732 m; Fig. 2A). Limber pine is the primary conifer on subalpine slopes of the north Sweetwater Mountains. Pinyon pine and Utah juniper form woodlands on low slopes of the Sweetwater Mountains and at all elevations of the Desert Creek Mountains. The riparian zone of Desert Creek in the reach where tree squirrels were observed supports black cottonwood, willows, and aspen (*Populus tremuloides*), as well as an old-growth forest of Jeffrey pine (*Pinus jeffreyi*) with scattered indi-

viduals of lodgepole pine and Sierra juniper (*Juniperus grandis*; Fig. 7). Two forest roads, Risue Road and Desert Creek Road, parallel Desert Creek in the squirrel habitat.

Douglas's squirrel was heard and observed at multiple locations along Desert Creek on several dates (21 October 2017, 22 October 2017, 3 February 2018, and 6 February 2018); photographs of individuals of the species, however, were not successfully obtained. During the October visits, squirrels were much more active than in winter. In autumn they were observed on branches of Jeffrey and pinyon pines, as well as on the ground, and they were heard along the reach of Desert Creek described, especially in the vicinity of large Jeffrey pines. Indirect sign of chewed scales and cores of Jeffrey pine cones and clipped



Fig. 5. Leidy Canyon, White Mountains, California. **A.** Overview of Leidy Canyon facing west to the squirrel observation site. **B.** Leidy Creek, the Douglas's squirrel observation site.



Fig. 6. Douglas's squirrels at Leidy Canyon, White Mountains.

branch tips were commonly observed along the valley bottom under large pines (Fig. 8). The Jeffrey pine forest dwindles and ends above the southernmost location of squirrel observations, and this likely represents the local end of their range (squirrels perhaps recur at higher elevations in the subalpine forest), whereas squirrels likely inhabit the riparian zone farther downstream than indicated here as the Jeffrey pine forest continues in the canyon of Desert Creek for at least another 2.5 km.

DISCUSSION

Our observations represent important range extensions for Douglas's squirrel, not only because the reported locations include 2 previously undocumented mountain ranges but also because of Great Basin small mammal biogeography. The bioregion—with its archipelago of sky-island ranges set in a sea of low evaporative basins—has long challenged biologists to explain the patterns of upland species'

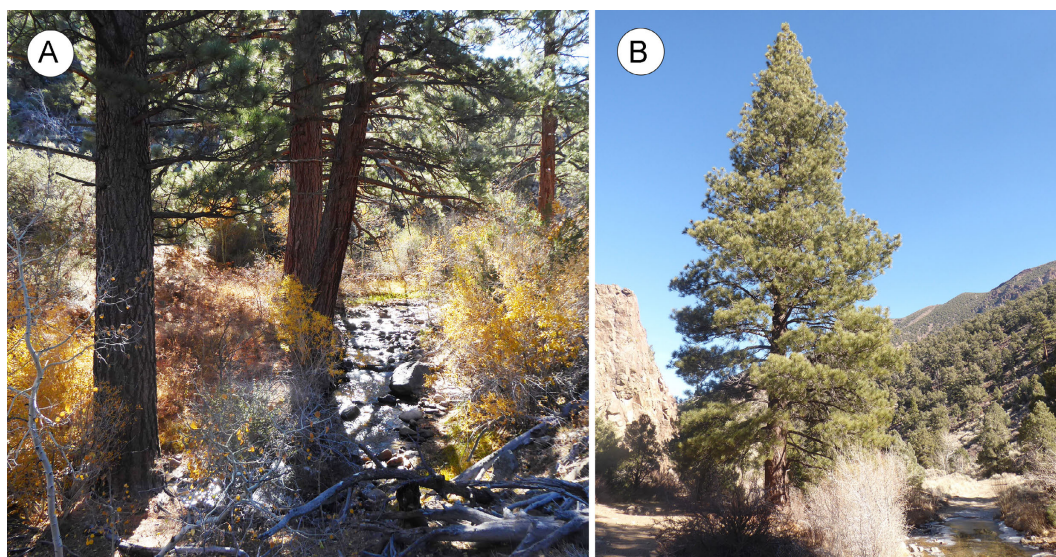


Fig. 7. Jeffrey pine habitat along Desert Creek in the Desert Creek Mountains and north Sweetwater Mountains, Nevada. **A.** Near the southern (upper) end of squirrel habitat. **B.** Middle of the squirrel habitat along Desert Creek.

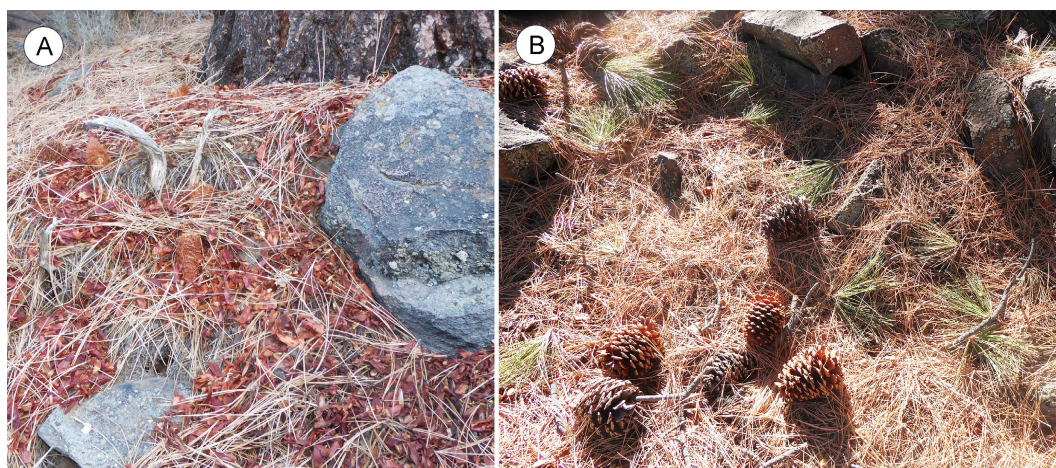


Fig. 8. Indirect sign of Douglas's squirrel occurrence at Desert Creek, Desert Creek Mountains. **A.** Chewed cores and scales of Jeffrey pine cones at the bases of trees (22 October 2017). **B.** Freshly clipped winter branches of Jeffrey pine below tree crowns (6 February 2018).

distributions. For small montane animals that currently exist in Great Basin ranges, the question has been about how they arrived there. Dispersal across inhospitable basins into favorable habitat of adjacent mountain ranges seems highly unlikely under current climates. A solution to this conundrum was originally proposed by James Brown (1971) who invoked island biogeographic dynamics. His basic

premise was that Great Basin mountains received their montane (Brown called them “boreal”) mammalian faunas during the Pleistocene. This was a time when low-elevation valleys and basins were cool enough for mountain mammals to use them as dispersal corridors to reach other mountain ranges. With warming during the Holocene, the intermountain basins became unavailable as habitat and dispersal

corridors, so montane mammals migrated upslope. Since the Pleistocene, Brown argued, the mountains have seen differential extinction of montane mammal populations and no new colonizations.

Major challenges have undermined many interpretations of Brown's proposal in intervening years, especially regarding extinction dynamics (Grayson 2011). An important limitation, summarized by Lawlor (1998), is our incomplete knowledge of the historic distribution of small mammals due to the lack of original deposition and/or incomplete modern surveys (Grayson and Livingston 1993). Further, low-elevation records of a montane species (*Neotoma cinerea*) have documented mid-Holocene extinction followed by recolonization within the last 1000 years, thus revealing transbasin dispersal in the Late Holocene (Grayson and Madsen 2000).

Despite these challenges, Brown's basic premises still invoke key questions of how, when, and how often small montane mammals moved between and into isolated Great Basin mountain ranges during the Holocene. The situation with Douglas's squirrel has an added layer of complexity in that the species has been observed only at the far western edge of the Great Basin and in Nevada only in the Carson Range, which is continuous with the Sierra Nevada. Red squirrels occupy Great Basin ranges in the far eastern parts of the region and there only in Utah (Steele 1998). Questions arise about why Douglas's squirrel has not dispersed beyond the Carson Range in Nevada and whether this squirrel occurred in Nevada during prehistoric times. We can address the second question better than the first, given our knowledge of Quaternary mammal distributions. Douglas's squirrels have never been reported in late Pleistocene or Holocene faunal assemblages from the interior Great Basin (Grayson 1987; confirmed for intervening years by the Faunmap database, accessed 12 March 2018). Grayson included the species with 2 others also lacking in records (*Lepus americanus* and *Glaucomys sabrinus*) as likely candidates for occupancy during the last 12,000 years. By this he implied that records have not been found but that by expectations of species behavior and habitat, Douglas's squirrel could have dispersed into and occupied Great Basin mountain ranges in the past. A slightly different result came from the analy-

ses of Hope et al. (2016) who reconstructed Douglas's squirrel paleodistributions using bioclimatic envelopes. Although their projections for the mid-Holocene and Last Glacial Maximum extended potential habitat beyond the modern distribution in Nevada, these areas were limited to the southern and western fringes, with no habitat projected for the core of the Great Basin.

The possible existence of unfound prehistoric records bears on the discussion of our observations, including how Douglas's squirrel arrived at these Great Basin ranges and how long the species has been there. It is possible that Douglas's squirrel has long occupied but not been reported in the White Mountains and the Desert Creek Mountains. This seems probable for the Desert Creek Mountains because this range is little visited in general and even less visited by biologists. Notwithstanding, the single area in the range that is highly visited is in the squirrel habitat along Risue Road and Desert Creek Road where a U.S. Forest Service campground and numerous well-used undeveloped campgrounds are located along the creek. The extensive observed habitat of Douglas's squirrel, the likelihood of more habitat than described, the presence of many individuals of the species in this area, and the mid-20th century records of the species in the southern Sweetwater Mountains (documented by Ward C. Russell in 1946, Arctos, accessed 1 February 2018) suggest that the species has likely been in the Desert Creek Mountains for a long time. From a biogeographic standpoint, a dispersal path could link extensive cordilleran habitat in the Sierra Nevada through the Sweetwater Mountains and north into the Desert Creek Mountains. Because this is a relatively high-elevation—though sparsely forested—path, squirrels could have moved from the Sierra Nevada and/or Sweetwater Mountains into the Desert Creek Mountains at one or more times during the Holocene. The relative connectivity of these ranges removes the Desert Creek Mountains from the geographic context of severe isolation that applies to island ranges of the interior Great Basin.

The situation for the White Mountains is not as readily explained. In contrast to the Desert Creek Mountains, the White Mountains have been intensely studied by scientists for more than a century, although Leidy

Canyon is remote and little visited. That squirrels occurred and were overlooked for decades seems highly improbable, especially in the Crooked Creek vicinity adjacent to the heavily used University of California research facility (WMRC 2018). Intensive early surveys for mammals conducted by Joseph Grinnell and his team in the Crooked Creek area in summer 1917 documented no tree squirrels among 305 Rodentia specimens collected (MVZ 2018a). A search of all years, including 1917, returned a total of 656 specimens and 18 species of Rodentia for the Crooked Creek region and access roads, with no tree squirrels documented (MVZ 2018b).

Despite the lack of records over the past century, our observations of the species in 2 widely separated locations of the range suggest that squirrels have been there for some time. If only a single individual had been found at the Crooked Creek location, we would consider the likelihood of human introduction to the range. Cars and trucks do regularly travel to the White Mountain plateau, so it is possible that a squirrel “hitched a ride” in recent years. Such translocation events have been reported but are more common for ground squirrels than tree squirrels. At Crooked Creek, squirrels were documented by the camera trap over 9 months foraging cones and living through a record cold and snowy winter, suggesting that a well-established individual or population exists there. Translocation by vehicle seems especially unlikely for the Leidy Canyon location because the remote area is only accessible by a 4-wheel-drive track that is little used. At least in the Leidy Creek case, translocation by vehicle would have required either 2 individuals or a gravid female. Finally, our finding of multiple squirrels in a 9-month period living 25 km and 716 m in elevation apart would suggest multiple vehicle transports, which seems even more unlikely.

This leads to the suggestion that Douglas’s squirrels have migrated into the White Mountains in recent years or decades on their own, either in 1 event and then spreading within the range or in multiple events to reach disparate locations. Conceivably the species migrated into the White Mountains earlier in the Holocene but remained rare in the range due to inadequate habitat or environmental constraints. In contrast to the Desert Creek Mountains, the White Mountains qualify as

one of the Great Basin’s biogeographically isolated ranges (Brown 1971); dispersal into the range during the Holocene, especially during warm periods within the epoch, seems highly limiting. By any of the suggestions above, the dispersal route—presumably originally from the Sierra Nevada—is unclear. Montane habitat of the White/Inyo Mountains massif is isolated on the south, west, and east by barren low basins or desert hills, all hot and treeless. Without assistance of accidental transport, for instance by raptor, the most plausible dispersal route is from the north and west. Douglas’s squirrel was recorded in 2015 in the South Mono Craters (camera trap images; K. Hickman unpublished) and in 2018 in the North Mono Craters (indirect sign C. Millar personal observation) adjacent to the western end of the Glass Mountains. In the Glass Mountains, Douglas’s squirrel was recorded in 1942 in dense coniferous forests at Sawmill Meadows (Arctos, accessed 1 February 2018) and in 2012–2013 at Dexter and Wet Canyons (camera trap images; K. Hickman unpublished), all on the north slope. At least 2 other core Sierra Nevada small mammals are known from the Glass Mountains, including the lodgepole chipmunk (*Neotamias speciosus*) and Belding’s ground squirrel (*Urocitellus beldingi*; J. Patton personal communication). A pathway of relative uplands and coniferous forests—much of which, however, is sparse pinyon-juniper woodlands—extends east and north from the Glass Mountains across the Benton Range and into the Pizona uplands. Although Douglas’s squirrel is not known to favor pinyon-juniper woodlands, this route might provide a dispersal corridor enabling squirrels to enter the White Mountains from the north near Montgomery Pass. The distance from Montgomery Pass to Leidy Canyon, our northernmost Douglas’s squirrel location, is 32 km. The possibility of jump dispersal from the Glass Mountains across low, dry, and treeless Chalfant Valley to the only known stands of yellow pines (Jeffrey pine and ponderosa pine [*Pinus ponderosa*]) in the White Mountains at Jeffrey Mine and Lost Mine Canyons, 15 km southwest of Leidy Canyon is unlikely given the lack of tree squirrel evidence there (CIM personal observation, Jeffrey Mine Canyon, May 2018).

If, as our observations and interpretations allow, Douglas’s squirrel has entered the White

Mountains (and less likely the Desert Creek Mountains) only in recent years or decades and if by natural means, then these would represent additional exceptions to Brown's tenant that montane mammals have not (re)colonized Great Basin ranges since the Late Pleistocene. Whether by their own volition or by assisted migration (e.g., raptor, vehicle), the capacity of Douglas's squirrel to successfully inhabit White Mountain habitats corroborates the bioclimatic projections of Hope et al. (2016; Fig. 2), which include the White Mountains.

The questions of prior occupation in modern and prehistoric times, as well as the question of dispersal routes, prompt a call for widespread surveys of Douglas's squirrel not just in the 2 ranges studied but in other Great Basin ranges and for genetic analyses to trace phylogeography. The easily recognizable indirect sign and identifiable calls and the morphology of the species make surveys of contemporary occupancy of Douglas's squirrel easy, fast, and reliable without the need for trapping or advanced monitoring or identification methods. Molecular techniques could help discern the mode and source of migration into the range. If Douglas's squirrel has indeed dispersed to new GB ranges in recent decades, this may prompt further reconsideration of other montane mammal biogeography in the ecoregion.

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