

Bulletin of the Southern California Academy of Sciences

Volume 116 | Issue 3

Article 5

2017

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Recommended Citation

Creley, Carly M. and Muchlinski, Alan E. (2017) "Distribution of the Eastern Gray Squirrel (*Sciurus carolinensis*) within California as of 2015," *Bulletin of the Southern California Academy of Sciences*: Vol. 116: Iss. 3.

Available at: <https://scholar.oxy.edu/scas/vol116/iss3/5>

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Cover Page Footnote

We would like to thank all of the individuals and organizations who submitted data and provided the information that makes citizen science work. Thanks to: Dr. Frasier Schilling at the University of California, Davis and the California Roadkill Observation System, along with David Waetjen (UC Davis) for creating the California Roadkill Observation System; Janel Ortiz; the California Department of Public Health West Nile Virus Surveillance Program System – especially Leslie Foss, Vicki Kramer, and Kerry Padgett; Gold Country Wildlife Rescue; Lindsay Wildlife Experience; Peninsula Humane Society; Society for Prevention of Cruelty to Animals, Monterey County; Shasta Wildlife Rescue; Sonoma County Wildlife; Stanislaus Wildlife Care Center; Sulphur Creek Nature Center; Tehama Wild Care; WildCare; and the Wildlife Center of Silicon Valley. Maps were created using ArcGIS software by Esri. ArcGIS and ArcMap are the intellectual property of Esri and are used herein under license. Copyright Esri. All rights reserved

Distribution of the Eastern Gray Squirrel (*Sciurus carolinensis*) within California as of 2015

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Abstract.—The goals of this study were to map the distribution of the invasive eastern gray squirrel, *Sciurus carolinensis*, in California as of 2015 and to assess range expansion since the first documented sightings within the state. Range maps exist, but the last update by the California Department of Fish and Wildlife was in 2007. An assessment of the rate of range expansion over time has not been conducted, but comparisons between the locations of initial sightings and the current distribution are included. Location data were obtained from museum specimens, wildlife rehabilitation centers, a roadkill database, and research-grade citizen observations. Range maps were produced with ArcGIS software. Populations of eastern gray squirrels are currently concentrated around Sacramento and Davis, the western side of San Francisco Bay, within as well as north and east of Santa Cruz, within Monterey, north of the Golden Gate Bridge through Marin County as well as around Santa Rosa, and around the Bellota/Stockton area. Isolated populations on the eastern side of San Francisco Bay occur around Berkeley, Hayward, and Pleasanton. Observations extend into the foothills of the Sierra Nevada Mountain Range from north of the American River to south of the San Antonio River. We suggest that the eastern gray squirrel might become more damaging to the two native diurnal species of tree squirrels in California, *Sciurus griseus* and *Tamiasciurus douglasii*, than the introduced eastern fox squirrel (*Sciurus niger*).

The eastern gray squirrel, *Sciurus carolinensis* (EGS), is a medium sized tree squirrel with a total length of 380–525 mm, and adult body mass from 300 to 700 g (Barkalow and Shorten 1973; Hall 1981). Its congeners are the eastern fox squirrel, *Sciurus niger* (EFS), which is greater than 20% larger in body size (McGrath 1987), and the western gray squirrel, *Sciurus griseus* (WGS), which is slightly longer in total length (Koprowski 1994). The EGS has a gray dorsal pelage and white tipped guard hairs that are never tawny, brown, or orange (Koprowski 1994). Unlike the WGS, which has a uniformly gray body and pure white underside, the EGS may have a cinnamon wash on the hips, feet and head, buff to gray to white on the ears, and gray to buff to cinnamon underside (Flyger and Gates 1982).

The EGS is native to the deciduous forests of the eastern United States and southern Canada from Saskatchewan to North Dakota, south to eastern Texas, east to Florida, and throughout Quebec and Maine (Koprowski 1994). The EGS's original native range consists of mature, continuous woodlands over 40 ha in size, with diverse woody understories and tree species such as oak (*Quercus*), hickory (*Carya*) and walnut (*Juglans*). However, the EGS can also live in urban and suburban environments, even with relatively few mature trees (Thorington et al. 2012).

Extant populations of the EGS are located in central California, with populations spreading and growing since their introduction. The earliest recorded sighting of the EGS in California

occurred in 1900 at Golden Gate Park in San Francisco. Specimens were collected in 1921 at Stanford University in Palo Alto. The first specimen collected from the city of Santa Cruz was in 1938. By 1940 the species had spread west from Palo Alto to the eastern edge of the Santa Cruz Mountains and by 1946 specimens were collected within the Santa Cruz Mountains. The species had also spread north from Palo Alto to Redwood City by 1948. The species was introduced to the Capitol Mall in Sacramento in 1973, and populations were identified in Pleasanton, as well as in a region called Bellota, an area within San Joaquin County along the Calaveras River, in 1974 (Byrne 1979).

The species may have been introduced to large estates as early as the 1860s in an effort to create park like grounds similar to those found on the east coast (Byrne 1979). Specimens from California are probably underrepresented in museum collections because of the species' recent colonization of the state. The California Department of Fish and Wildlife last updated its range map for the EGS in California in 2007. The existing data is insufficient to complete a study on the rate of range expansion of the EGS in California, but a general assessment is made of the species' spread over time.

Invasive populations of the EGS have been associated with negative ecosystem effects including the decline of native species and damage to forests in the United Kingdom, Ireland, Italy, and parts of western North America (Benson 2013; Bertolino 2008; Bertolino and Lurz 2013; Gurnell et al. 2004). The EGS threatens native species and habitats because of its ability to live and reproduce in a wide range of urban, suburban, and natural habitats, its broad diet (Bertolino 2008), its high reproductive rate, and its ability to establish a population from a small number of founders (Wood et al. 2007). External effects that are occurring simultaneously with the invasion, such as habitat fragmentation, changes in forest structure, the spread of other invasive species, and the species' favorable public perception (Bertolino and Genovesi 2003) contribute to its invasive ability.

Materials and Methods

Location data gathered from within California between January 1900 and the end of August 2015 were used for this study. Museum records were collected from iDigBio, the Global Biodiversity Information Facility (GBIF), and Vertnet. Since specimens of invasive species such as the EGS are very limited in museum collections, other sources of location data were needed for this study. Of the 3,633 observations of EGSs, 78% were obtained from wildlife rehabilitation centers. Some rehabilitation centers were able to provide detailed intake records from 2005 through 2015, while other centers could only provide records for a more limited number of years. Records from wildlife rehabilitation centers are concentrated around the area of their geographic locations, and this may lead to an overrepresentation of location records from residential areas surrounding the center. Intake records from these centers show the location from which the squirrel was collected by the person who dropped the squirrel off at the rehabilitation center. Geographical bias related to records from wildlife rehabilitation centers would come from most centers being located in urban/suburban areas. We used only records that included information that could be traced to a specific street address or intersection within a specified city.

Additional sources of data included: The California Department of Public Health's West Nile Virus Surveillance Program; the California Roadkill Observation System, operated through the University of California, Davis; research grade human observations from iNaturalist; and observations by Alan Muchlinski and graduate research students from California State University, Los Angeles. Research grade iNaturalist data include a date of observation, photo, as well as latitude and longitude coordinates, and the species has been corroborated by at least one additional user.

Since some misidentifications were likely to be present in all of the sources of data, field surveys were conducted in selected regions of California and observation reports of the EGS outside of the previously reported distribution were scrutinized for accuracy. Field surveys were conducted in parts of the Santa Cruz Mountains, the Central Valley, and southern California. Records from areas where the species was not thought to occur currently or historically were investigated, and if the species was not found, the records were expunged from this study. Biodiversity databases are constantly changing as records are added from existing databases and erroneous records are erased. The location data from iDigBio, GBIF, and Vertnet used in this paper were accessed on 31 August 2015. Although use of multiple databases may result in some redundancy of location points, this does not change the overall distribution of the species.

Observations obtained through iNaturalist are utilized under a Creative Commons By Attribution Non-Commercial License or from observations that are in the Public Domain. The Global Biodiversity Information Facility is an international open data source. VertNet is a National Science Foundation funded project that makes museum-curated biodiversity data free and available on the web. Names of contributors to GBIF and iNaturalist can be obtained through a search using the data posted at DOI: 10.13140/RG.2.2.21869.59367. Data used in this manuscript are available for use by others under a Creative Commons By Attribution Non-Commercial 4.0 International License.

The mapped results are presented at different landscape levels, including various regions of the state. Individual sighting data that were submitted as addresses or location descriptions were converted to geographic coordinates using Google Maps. The coordinates and corresponding information related to species identification, the date of the observation, and additional information were saved as a comma-delimited file. Location data for the EGS were added to ArcMap 10.3.1 and projected to the NAD 1983 California (Teale) Albers (Meters) data frame coordinate system because that is the preferred projection of the California Department of Fish and Wildlife.

Inconsistent data recording and collection over time make it impossible to calculate the rate of spread of the EGS in California. Data were collected in bursts from different sources. For example, from 1900 to 1969, most records are from museums. In the 1970s a large number of Vertnet records were provided by Sheila Byrne (Byrne 1979). From 2004 – 2015 most of the records are provided by wildlife rehabilitators (Table 1).

Results

The overall distribution of the EGS within California is depicted in Fig. 1. One population of EGSs is located on the southern peninsula of San Francisco Bay, from San Francisco south to areas around Gilroy and Santa Cruz (Fig. 2). Sightings have not been reported that directly connect animals in Gilroy with animals in Santa Cruz, without heading north to the main body of the distribution near San Jose. The population is highly concentrated within urban and suburban areas of San Francisco, San Mateo, Santa Cruz and Santa Clara Counties, and the population follows developed areas along the Highway 101 corridor to the southern edge of Santa Clara County. The species has been observed in forested mountain habitat away from urban/suburban areas (Fig. 2), and could be more widely distributed within large tracts of redwood forests in areas such as Big Basin Redwoods State Park and Henry Cowell Redwoods State Park. EGSs were observed within both parks by co-author AEM so more investigation of the distribution of the EGS in these areas is warranted. This population is positioned to expand north into developed areas along the eastern side of San Francisco Bay by wrapping around the bay from the areas near San Jose.

Table 1. Sources of observations of the EGS, *Sciurus carolinensis*, within California from 1900 through 2015.

Sources of observations from 1900 - 2015	Records
California Department of Public Health	154
California State University, Los Angeles	27
Global Biodiversity Information Facility	39
iDigBio	17
iNaturalist	209
Lindsay Wildlife Experience	23
Peninsula Humane Society	756
Society for the Prevention of Cruelty to Animals, Monterey County	7
Sonoma County Wildlife	1
Stanislaus Wildlife Care Center	7
Sulphur Creek Nature Center	6
UC Davis, California Roadkill Observation System	122
Vertnet	239
WildCare Rehabilitation Center	334
Wildlife Center of Silicon Valley	1,692
Total observations in California	3,633

Another large area occupied by EGSs is present within the city of Sacramento, west to Davis, east to areas around Placerville, south along the foothills of the Sierra Nevada Range, and then west to areas around Modesto and areas west of Stockton (Fig. 3). Sightings on the eastern edge of the distribution range along California Highway 49 from south of the town of San Andreas on the south to near Interstate Highway 80 on the north, while the western edge runs from around Manteca on the south to Davis on the north. Sightings along the northern edge of the distribution follow Interstate 80 from Davis, through Sacramento, past Roseville north of Folsom Lake State Recreation area, along U.S. 50 through Folsom, into the El Dorado Hills and into areas around and north of Placerville. Whether there is a continuous connection to form one single population or whether there are separate northern and southern populations within this overall area (Fig. 3) is uncertain at this time. Animals in the northern part of this region may have originated from the population established at the Capitol Mall in Sacramento while animals in the southern part of the region may have originated from the population established around Bellota.

Several more apparently isolated populations exist within the state. One apparently isolated population exists on the Monterey Peninsula (Fig. 2). This population ranges from the northern tip of the Monterey Peninsula south to the Carmel River and inland to Salinas, although it is unknown if there is a direct connection between animals around Monterey and those within Salinas (Fig. 2). The lack of sightings directly between Santa Cruz and Gilroy as well as between Monterey and Salinas could be because the land is largely agricultural and unsuitable for tree squirrels, or because the area is highly rural and no sightings have been reported.

Isolated populations now exist north of the Golden Gate Bridge within Marin and Sonoma Counties. The first EGS reported by WildCare Rehabilitation Center, approximately 16 km north of the bridge, was in 2005, indicating the species most likely arrived in the area within a decade prior to 2005. One population occupies an area from Sausalito on the south, along the Highway 101 corridor, through San Rafael, to around Novato on the north, while the second population is located within the city of Santa Rosa, west to Sebastopol, and south to Rohnert Park. It is uncertain if these two populations have merged into one population at this time.

Isolated populations of the EGS are now found on the eastern side of San Francisco Bay in two locations. One population, first recorded in 1974, is located around Pleasanton, a city located

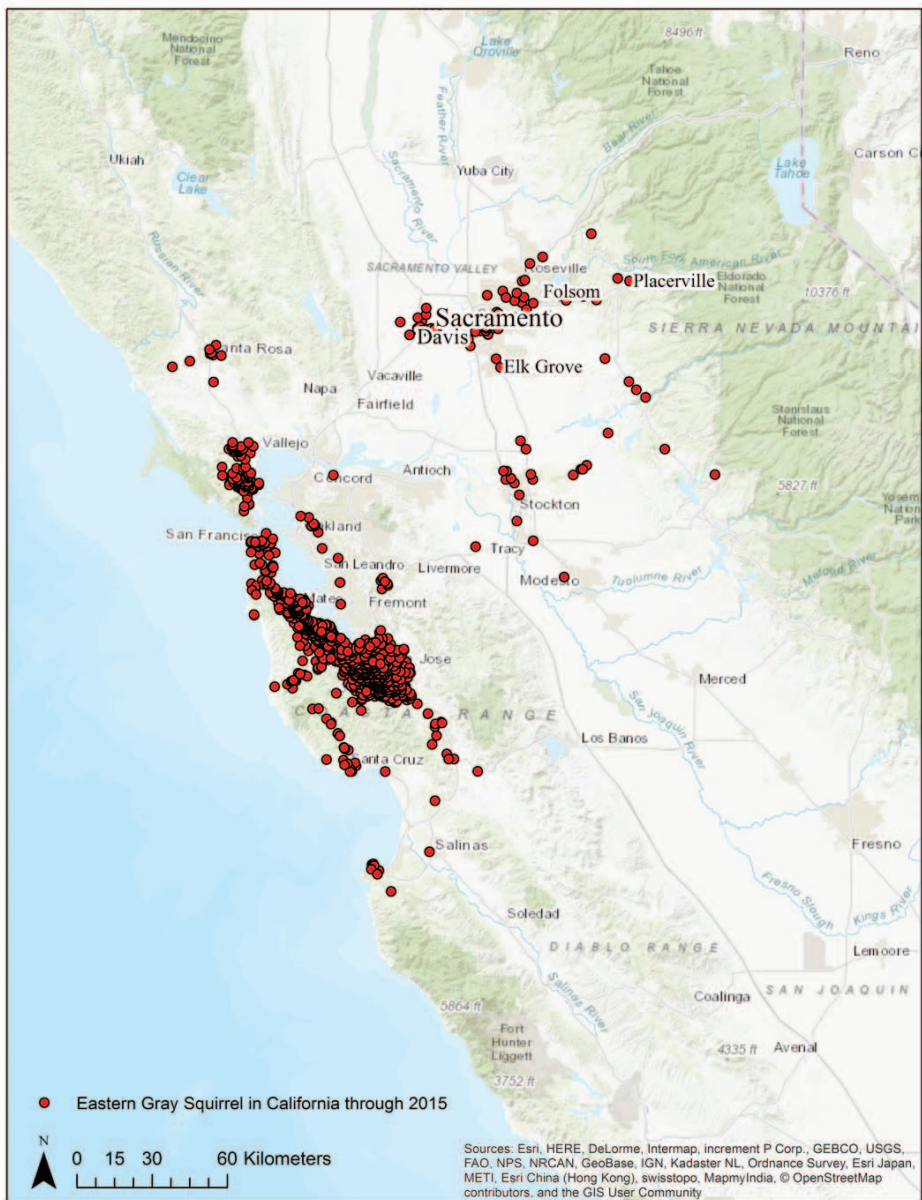


Fig. 1. Range Map of the eastern gray squirrel within California as of 2015. Reported observations of eastern gray squirrels are shown as points.

east of the Coastal Range and west of Livermore, CA. A second population appears to occupy an area from Berkeley south to Hayward, mostly along the edge of the bay (Fig. 2). The first intake records for EGSs from Sulphur Creek Nature Center (SCNC) in Hayward are from 2009, indicating relatively recent occupation of habitat south of Oakland on the western side of the Coastal Range. The full extent of the population in and around Hayward is not known as SCNC

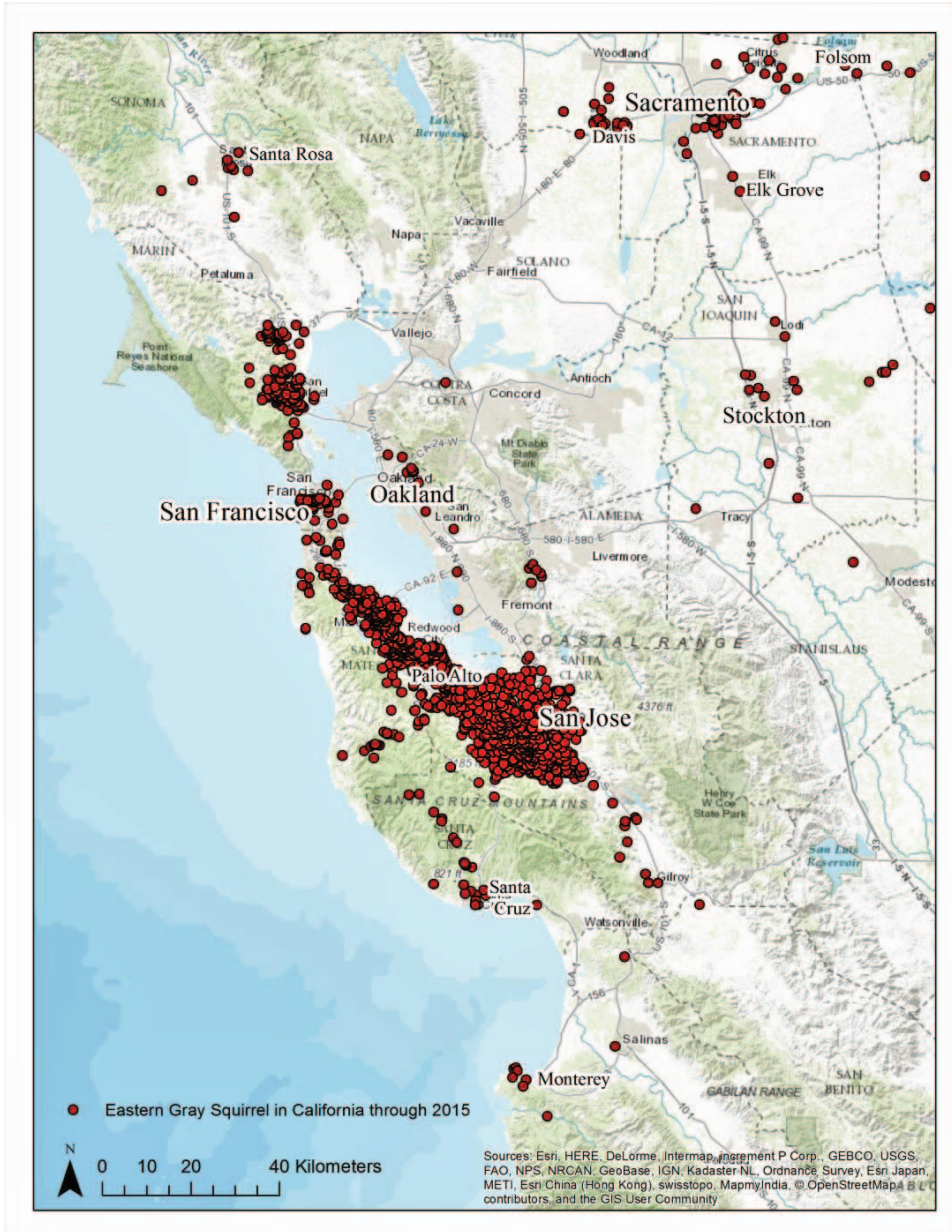


Fig. 2. Location map of the eastern gray squirrel on and around the San Francisco Bay as of 2015. Reported observations of eastern gray squirrel are shown as points.

is funded by the City of Hayward and only takes in animals from the immediate surrounding area. However, EGSs seem to be much less abundant in the area at this time than EFSs. While 173 EFSs were taken in by SCNC between 2009 and 2013, only 9 EGSs were taken in over the same time period. At this time the EGS is greatly outnumbered by the EFS on the eastern side of San Francisco Bay.

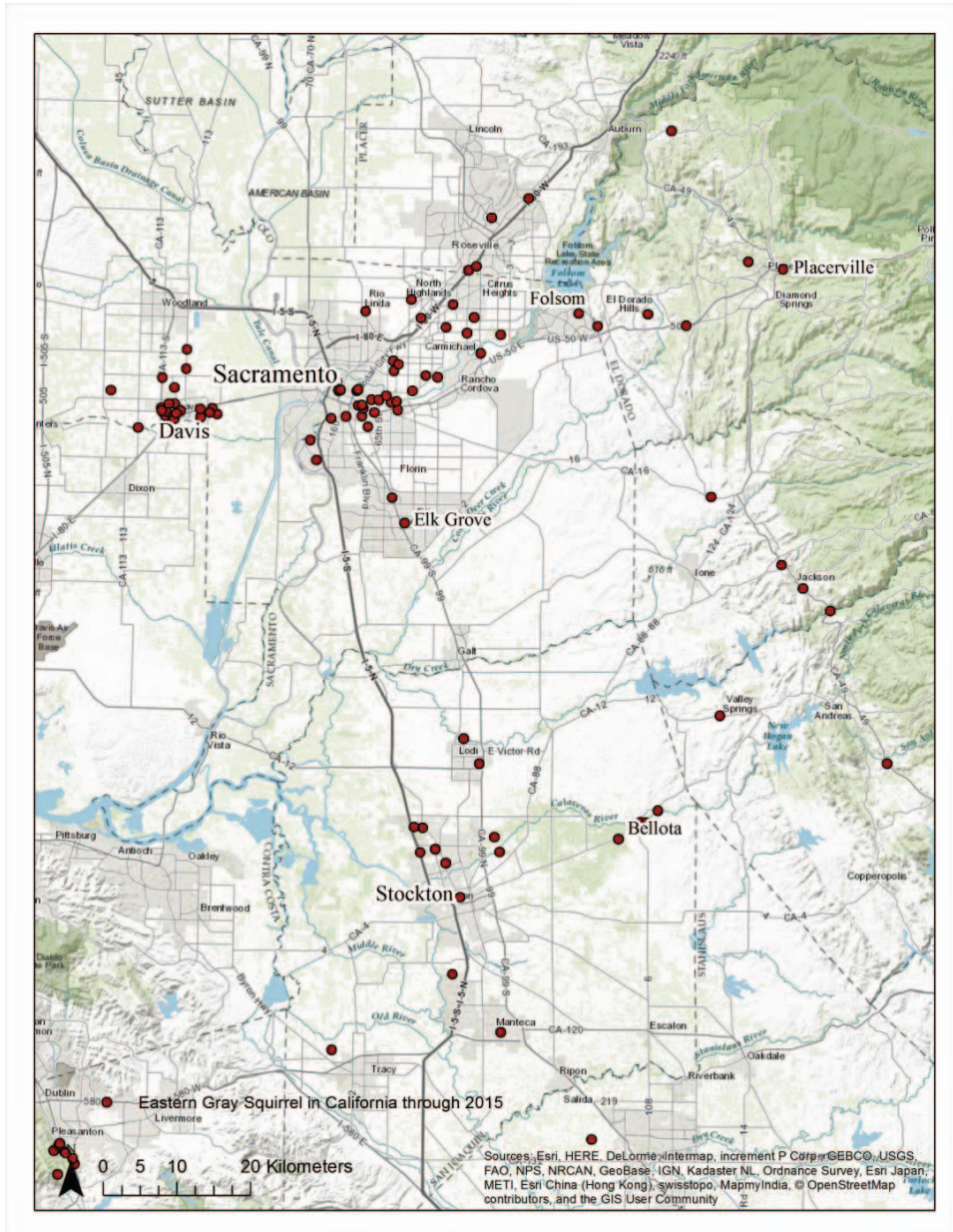


Fig. 3. Location map of the eastern gray squirrel around Sacramento and the Central Valley. Reported observations of the eastern gray squirrel are shown as points.

Discussion

The EGS is now well established in California and has expanded its range considerably since initial introductions. The EGS could affect populations of both native diurnal species of tree squirrels within California and it may be associated with changes in populations of the other introduced tree squirrel species in California, the EFS.

Populations of the Douglas squirrel, *Tamiasciurus douglasii*, (DS) are found in coniferous forests within the coastal mountain range in the northwestern region of California as well as at high elevations within the Sierra Nevada Mountains (Storer et al. 2004). Secondary habitats include hardwood and shrubby wetlands, conifer-hardwood forests and riparian habitats (Brown 1985, Zeiner et al. 1990). Replacement of the DS by the EGS in Vancouver, Canada has been in mixed hardwood habitat, not within coniferous forests (Hwang and Larivière 2006). Replacement of *Tamiasciurus hudsonicus* (American red squirrel) by the EGS on Vancouver Island, Canada has also been primarily in mixed-hardwood forests (Bruemmer et al. 1999). Coniferous forests dominated by pine, spruce and fir trees could be unsuitable habitat for the EGS in California. However, EGSs have been sighted by co-author AEM in redwood forests within Henry Cowell and Big Basin Redwoods State Parks between Santa Cruz and San Francisco. Future contact zones between the DS and the EGS near redwood forests should be monitored as should contact zones between the DS and EGS in mixed hardwood-conifer forests.

Replacement of the European red squirrel, *Sciurus vulgaris* by the EGS in mixed hardwood forests has occurred across most of Britain. However, the pattern of introductions of the EGS into and within California has been very different than introductions into and within Britain. Approximately eight introductions occurred into mainland areas of California, including areas around Bellota, Marin County, Monterey, Palo Alto, Sacramento, San Francisco, Santa Cruz, and Santa Rosa. Over 30 introductions and translocations of the EGS into and within Britain occurred mainly to large estates in rural areas between 1876 and 1930 (Middleton 1930). The mixed hardwood forests within these rural areas provided good habitat for the EGS. Other translocations within Britain likely occurred since 1930 along with rapid spread of the species across England, Scotland, and Wales in the mid-1900s (Shorten 1953). Continued range expansion by EGSs that now exist within Marin and Sonoma Counties into secondary habitats of the DS in the coastal mountain range could affect some populations of the DS in a manner similar to how the EGS has displaced *S. vulgaris* in parts of Great Britain. Therefore, monitoring of future contact zones is encouraged.

The EGS is a more generalist species than the WGS (Carraway and Verts 1994; Koprowski 1994), so it may pose a threat to the WGS as it continues range expansion within California. The EGS's original native range consists of mature, continuous woodlands over 40 ha in size, with diverse woody understories. However, EGSs can also live in urban and suburban environments, even with relatively few mature trees (Thorington et al. 2012). Habitat fragmentation poses a significant threat to WGSs but favors EGSs. WGSs can sometimes be found in cities or agricultural nut orchards, but are much more common farther from human development (Thorington et al. 2012), whereas the EGS is more tolerant of habitat fragmentation (Moore and Swihart 2007). In fragmented habitats, the EGS increases in density and reduces its home range, as long as it has a minimum patch size (Koprowski 2005). EGSs are capable of living in forested areas similar to those inhabited by the WGS. EGSs may pose a greater threat to the native squirrels than the EFS because although EFSs are similarly tolerant of habitat fragmentation (Moore and Swihart 2007) the EFS is more limited to areas with low ground cover (Gatza 2011). EGSs are capable of living in diverse habitats including forested mountains, so they may be capable of expanding to areas that EFSs cannot reach.

Finally, the EGS may be affecting populations of the invasive EFS within California. The EGS may be replacing the EFS along the western side of the San Francisco Bay in California. Although intake records have some geographic bias, an almost complete replacement of intake specimens of the EFS by specimens of the EGS submitted to two wildlife rehabilitation centers suggest that a replacement of the EFS by the EGS is occurring in these two locations. Intake records from Peninsula Humane Society Rehabilitation Center in Burlingame, California (approximately

half-way between San Francisco to the north and San Jose to the south) from 1975 show 0% (0) EGSs and 100% (152) EFSs. In 2013 intake records show 99.5% (405) EGSs and .5% (2) EFSs. Intake records from the Wildlife Center of Silicon Valley, located in San Jose, for 2004 show 60.5% (69), EGSs and 39.5% (45) EFSs, while in 2012 intake records show 87.2% (157) EGSs and 12.8% (23) EFSs. The EGS also replaced the EFS in the 1960s and 1970s in a new subdivision in St. Louis County, Missouri (Sexton 1990). As the EGS is positioned to invade the eastern side of San Francisco Bay from both the northern and southern sides, and isolated populations currently exist on the eastern side of the bay, there could be a decrease in the EFS population in this area and an increase of the EGS over time.

Conclusions

We suggest that the EGS might become more damaging to the two native diurnal species of tree squirrels in California (*Sciurus griseus* and *Tamiasciurus douglasii*) than the introduced EFS (*Sciurus niger*). The EGS currently occupies habitats within urban and suburban areas of the state and is encroaching into forests in California. Populations of the EGS are widespread throughout the southern peninsula of the San Francisco Bay, the northern peninsula of the San Francisco Bay, and San Jose. Smaller populations are located in Santa Cruz, spreading into the Santa Cruz Mountains, and on the Monterey Peninsula. In the Central Valley, populations exist in and around Sacramento, Davis, Placerville, Modesto, Stockton, and along the foothills of the Sierra Nevada Range. Populations have spread near undeveloped forested areas of the state as well as into additional human-developed regions. Careful attention should be paid to continued range expansion of this species.

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