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Cover Page Footnote

We would like to acknowledge the following entities and individuals for help in gathering data for this project. We thank the California Department of Public Health West Nile Virus Surveillance Program System – especially Leslie Foss, Vicki Kramer, and Kerry Padgett, along with the California Roadkill Observation System (CROS), and David Waetjen (UC Davis) for creating the California Roadkill Observation System. We thank Ruby Alvidrez, Carly Creley, Lauren Zameito, Gina Navia, Chris DeMarco and all of the volunteers who contributed observations. The following wildlife rehabilitation centers provided data used in this study: California Living Museum, California Wildlife Center, Critter Creek Wildlife Station, Gold Country Wildlife Rescue, Lindsey Wildlife Museum, Peninsula Humane Society, SPCA Monterey County, Sonoma County Wildlife Rescue, Squirrelmender Wildlife Rehabilitation, Stanislaus Wildlife Rehabilitation Center, Suisun Wildlife Rescue Center, Sulphur Creek Nature Center, Wetlands and Wildlife Care Center, WildCare, and Wildlife Center Silicon Valley. We also thank the many individuals who utilized iNaturalist, CROS, or other sources to submit observations of the eastern fox squirrel within California.

Distribution of the Eastern Fox Squirrel (*Sciurus niger*) within California as of 2015

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Abstract.—The eastern fox squirrel, *Sciurus niger*, has been introduced to many areas outside of its native range. Once introduced to a new region the species has generally expanded its geographic range and is considered to be an invasive species, causing both ecological and economic harm. While some information is available on where introductions have occurred, detailed information is not available on the current geographic distribution of the species within California. Since invasive species tend to be under-represented in specimen collections at museums, new methods for obtaining location data were needed. We used a time period of 1995 through 2015 for observations so that location data would be most up-to-date. A majority (51%) of location data used in this study came from wildlife rehabilitation centers, approximately 31% came from citizen-science type sources such as the California Road-Kill Observation System, a previously published journal article, and research-grade submissions to iNaturalist, 10% came from the California Department of Public Health West Nile Virus Surveillance Program, and 8% came from the authors and trained student observers. Maps are presented to show the current geographic distribution of the species indicating a broader range than what was previously known.

The eastern fox squirrel, *Sciurus niger*- hereafter EFS, is native to the eastern and central United States and the southern prairie provinces of Canada, south of approximately 48°N latitude (Koprowski 1994) where they are known to live in forests, woodlands, agricultural landscapes and urban areas (Kleiman et al. 2004). In the native range, the EFS is most often found in deciduous and mixed forests and ideal habitats are small stands of large trees separated by agricultural land (Allen 1982). Ten subspecies of EFS are recognized based on size, coat color, and geographic location (Wilson and Reeder 2005). While four subspecies of the EFS are listed as threatened or endangered: *S. n. avicennia*, *S. n. cinereus*, *S. n. niger*, and *S. n. shermani* (Loeb and Moncrief 1993), it is thought that the subspecies present within California is *S. n. rufiventer* (Moncrief et al. 2010; Claytor et al. 2015). *Sciurus niger rufiventer* is the most wide-ranging subspecies within the native range of the species (Koprowski 1994; Wilson and Reeder 2005) and is characterized by a brown with buff or orange coloration on the back and sides, the abdomen being orange, cinnamon, or white in color (Koprowski 1994). It has been noted (AEM) that most EFS individuals observed within California have a cinnamon or orange colored abdomen but some individuals found around Sacramento and Davis have white fur on the abdomen.

Eastern fox squirrels have been intentionally introduced from portions of their native range of the mid-western United States to many urban and suburban areas within the western United

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States including areas within Arizona (Brady et al 2017), California, Idaho, Montana, Oregon, and Washington (Koprowski 1994). The species has reached the state of Colorado through natural range expansion (Geluso 2004; Hoover and Yeager 1953) and New Mexico through introductions (Frey and Campbell 1997). The species has also been observed in Laramie, Wyoming (AEM personal observation).

The first successful introduction of the EFS into California probably occurred to Golden Gate Park in San Francisco before 1890, although specific details related to this introduction are not known (Byrne 1979). The species was introduced to the city of Fresno from Missouri in 1900 or 1901 (Storer Papers). The first specimen recorded on the campus of Stanford University in Palo Alto, CA, which is 56 km south of Golden Gate Park in San Francisco, was in 1921 (Byrne 1979). Animals were also moved from Golden Gate Park in San Francisco to Sacramento in 1921 (Byrne 1979; Storer Papers) and animals appeared on the campus of the University of California, Berkeley circa 1926 (Boulware 1941). Animals, most likely from the east bay area of San Francisco, were moved to Mount Diablo in Clayton in 1960 (King 2004). The EFS was introduced to the Veteran's Hospital in Yountville within the Napa Valley at some early date, since they had spread significantly before the 1970s, and to Vacaville, which lies between San Francisco and Sacramento, as early as the 1930s (Byrne 1979).

Individuals from Fresno were used to establish a population at Mieke's Grove Park, located between Lodi and Stockton (Byrne 1979), making Fresno the most likely source of the current population around Stockton. Animals currently located in Merced may have come from Fresno as the species is not found in the City of Modesto, which lies between Merced and Stockton.

Eastern fox squirrels were released or escaped from captivity at the Veteran's Hospital in West Los Angeles in 1904. The source for this population was suggested as some region of the Mississippi Valley (Becker and Kimball 1947). Individuals also escaped from captivity at the San Diego Zoo in 1920 (Staff Writer 1929), establishing the current population within that city. The EFS was first observed in Santa Barbara in 2006 (personal records of Paul Collins, Curator of Vertebrates, Santa Barbara Museum of Natural History). Although the source population for Santa Barbara is not known, the EFS was found in Ventura 50 km to the southeast by the late 1960s (Wolf and Roest 1971). Animals were moved from Fresno to Bakersfield in 1985 (King 2004) and the EFS appeared in Kernville, which is located 84 km northeast of Bakersfield and adjacent to the Sequoia National Forest, from an unknown location prior to the late 1970s (S. Anderson, pers. comm.). An isolated population of the EFS has been present in the Wood Streets area of the City of Riverside, CA for at least the last 40 years (G. Garcia, pers. comm.). Information regarding the source of this population is unavailable.

With the exception of the introductions to Bakersfield, Sacramento, Stockton, and to Los Angeles, very little is known regarding the source populations of the founding animals, the number of founding animals to any specific area within California, or the number of separate introductions to any area over time. Molecular genetic techniques such as analysis of mitochondrial haplotypes could help sort out more details regarding transfers of animals within the state, and possibly source populations from outside the state. What is known is that the species has greatly expanded its range within California over the past ~125 years (Byrne 1979; King et al. 2010). This paper documents the range occupied by the EFS within California as of 2015 and provides some estimates of range expansion for the species with California.

In California, animals have dispersed from original points of introduction through natural dispersal and through intentional movement of animals by humans. For example, since the original introduction to Los Angeles, the EFS has expanded its range at rates up to 3.44 km/yr (King et al. 2010) although rates of about 1.50 km/yr may be more realistic within suburbanized habitats (Garcia and Muchlinski 2017). King (2004) reported many cases of

intentional relocation of EFSs by residents of Los Angeles County where squirrels are often considered pests. Squirrels are often live trapped and released into parks and golf courses where the species was not present, thereby facilitating range expansion beyond what would occur through natural dispersal. The EFS has been hypothesized to compete with native western gray squirrels (*Sciurus griseus* – hereafter WGS) for resources such as nesting sites, space, and food, and the EFS has actively replaced the WGS within certain habitats in southern California (Muchlinski et al. 2009; Cooper and Muchlinski 2015). The EFS is considered a game species by the California Department of Fish and Wildlife with open seasons for hunting in parts of the state by use of gun, bow and arrow, or falcon. The Department of Fish and Wildlife also allows, but regulates, the intake and release of juvenile or injured EFSs by rehabilitation facilities throughout the state.

Materials and Methods

Location data from California were gathered over the time frame of January 1995 through August of 2015. Since specimens of invasive species such as the EFS in museum collections are very limited, other sources of location data were needed for this study. Of the 7,307 observations mapped for this study (Table 1), most location data (51%) were obtained from wildlife rehabilitation centers situated throughout the state of California. Some rehabilitation centers were able to provide detailed intake records from 1995 through 2014 while other centers could only provide records for 2014 and a few previous years.

Additional sources of data included the California Department of Public Health West Nile Virus Surveillance Program, the California Roadkill Observation System operated through the University of California - Davis, the Global Biodiversity Information Facility (GBIF) – searched on October 25, 2015 for museum specimens and iNaturalist Research Grade Human Observations from January 1995 through August 2015, a thesis produced by King (2004), information obtained through personal observations (AEM and graduate research students) and information obtained via a web-based survey form. Observations through iNaturalist are utilized here under a Creative Commons Non-Commercial License. Name attribution to contributors of information can be obtained through a search on GBIF¹.

Mapping results are presented at different landscape levels including the entire state of California and various regions of the state. Location addresses were converted to geographic coordinates by finding the latitude and longitude coordinates of each individual sighting through Google Maps. The coordinates were saved as a text file along with corresponding information related to species type, year observed, specific date seen if given, and additional information if given. The location information was added to ArcMap 10.2.2 for display purposes and projected to 1984 California State Plane (Albers).

Results

A state-level view of the current distribution of the EFS within California is shown in Fig. 1. From this landscape level, as well as in more detailed landscape levels, the vast majority of observations are located in urban and suburban areas of the state. This result is not surprising as (1) the original introductions took place in what are now highly urbanized/suburbanized areas, and (2) observations would tend to occur most frequently in areas inhabited by large numbers

¹https://www.researchgate.net/publication/313241828_Location_data_for_eastern_fox_squirrel_Sciurus_niger_within_California_from_1995-2015

Table 1. Sources of observations of the Eastern Fox Squirrel, *Sciurus niger*, from 1995 through 2015 within California.

Data source	Area	Location points
Alan Muchlinski and Students ¹	Statewide	329
California Department of Public Health ²	Statewide	722
California Roadkill Observation System ³	Statewide	703
Emails (Web Survey) ¹	Statewide	255
Julie King Thesis ¹	Los Angeles Area	757
Wildlife Rehabilitation Centers ⁴		3714
California Living Museum	Bakersfield, CA	6
California Wildlife Center	Los Angeles Area	136
Crittter Creek Wildlife Station	Fresno, CA	51
Gold Country Wildlife Rescue	Auburn, CA	29
Lindsey Wildlife Museum	Walnut Creek, CA	1995
Peninsula Humane Society	Burlingame, CA	15
SPCA Monterey County	Monterey County	88
Sonoma County Wildlife Rescue	Petaluma, CA	40
Squirrelmender Wildlife Rehabilitation	Ventura County	34
Stanislaus Wildlife Rehabilitation Center	Hughson, CA	11
Suisun Wildlife Rescue Center	Suisun, CA	127
Sulphur Creek Nature Center	Hayward, CA	361
Wetlands & Wildlife Care Center	Orange County	172
WildCare	San Rafael, CA	301
Wildlife Center Silicon Valley	San Jose, CA	348
Online Geodatabases		548
Global Biodiversity Information Facility ⁵	Statewide	548
Grand Total		7307

¹ Location information and species identification from these sources were by observations of live animals in the natural environment.

² Location information was through coordinates of latitude and longitude, and species identification was by in-hand observation of deceased animals sent to the California Department of Public Health.

³ Location information was through coordinates of latitude and longitude, and species identification was through observations of photographs.

⁴ Location information was gathered from intake forms and species identification was by trained individuals who worked at the rehabilitation center.

⁵ Location information and species identification from this source was through data from museum specimens or through observations, with photographs, by individuals using iNaturalist.

of people. However, it will be pointed out later in this section that the EFS is also found in areas with much lower human population density, ranging from rural to unpopulated areas.

Eastern fox squirrels introduced to Golden Gate Park in San Francisco have undergone significant range expansion to the south (Fig. 2). The species is currently found in an uninterrupted distribution to the south of San Francisco along the western side of San Francisco Bay, through San Jose and further south to the Cities of Gilroy, and Salinas, within the Santa Cruz Mountains, and in the City of Santa Cruz. A population of EFSs exists within the Cities of Monterey, Pacific Grove, and Carmel. Range expansion of the EFS also occurred from south to north along the southeastern portion of San Francisco Bay where animals met conspecifics undergoing range expansion from Berkeley south through Oakland, San Leandro, Hayward, and Fremont. The EFS has a continuous distribution along the eastern side of San Francisco Bay.

The EFS was first cataloged at WildCare Rehabilitation Center in the City of San Rafael, Marin County, CA, which lies north of the Golden Gate Bridge, in 2002 (Fig. 3). Possible

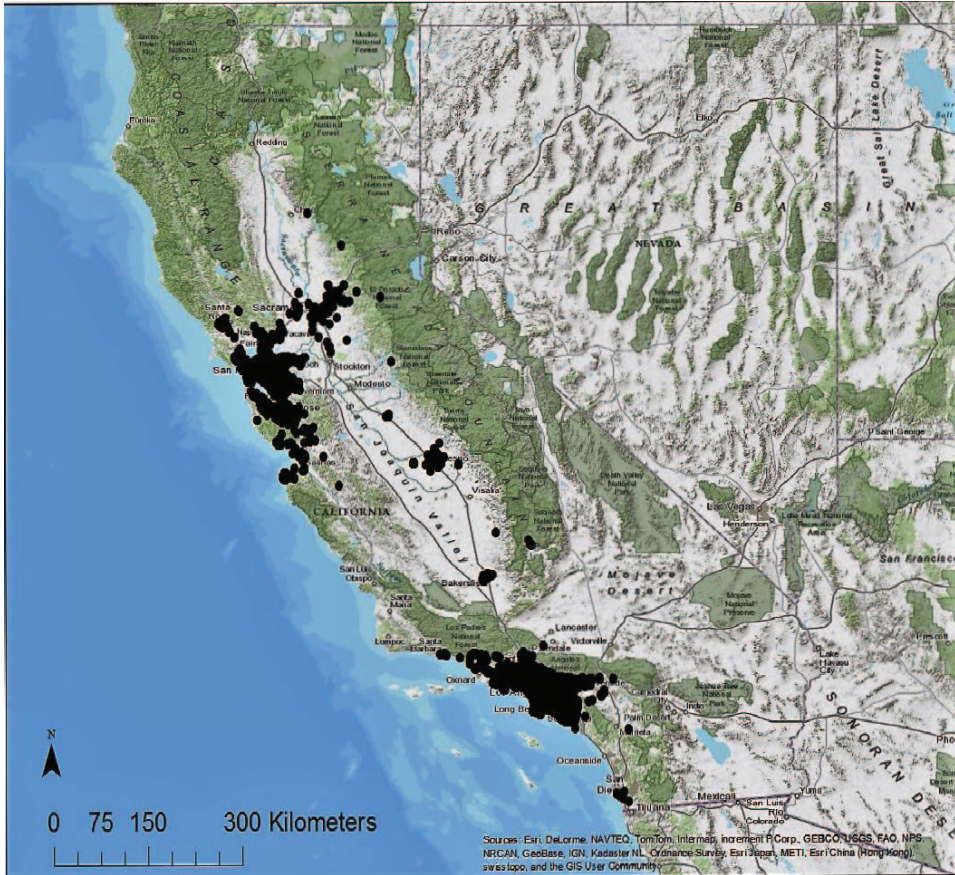


Fig. 1. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in California over the time period 1995 through 2015. Maps throughout this paper were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved.

scenarios by which the species appeared in San Rafael could involve movement through human activity north of the Golden Gate Bridge into Marin County or movement south from the City of Santa Rosa where the species was found in the 1970s. Because the vast majority of collected observations are on the more southern end of the corridor, in Marin County, we believe it is most likely that the EFS was transferred across the Golden Gate Bridge sometime prior to the year 2000. The species now exists northward through San Rafael, San Anselmo, and Fairfax, north along the Highway 101 corridor through Petaluma, Rohnert Park, and Santa Rosa, and west to Sebastopol. The species is also present within the full range of the Napa Valley from Napa northward to Calistoga.

In 1979, the population of the EFS around the east bay area of San Francisco and the population around Sacramento were separate populations; although the population in Sacramento had been founded by animals from San Francisco. By 2015 the two populations seem to have merged, or are very close to merging, forming one metapopulation from near Monterey north through the San Francisco Bay Area, then east through Davis and Sacramento to cities such as Auburn, Coloma and Grass Valley in the foothills of the Sierra Nevada Mountains (Fig. 3).

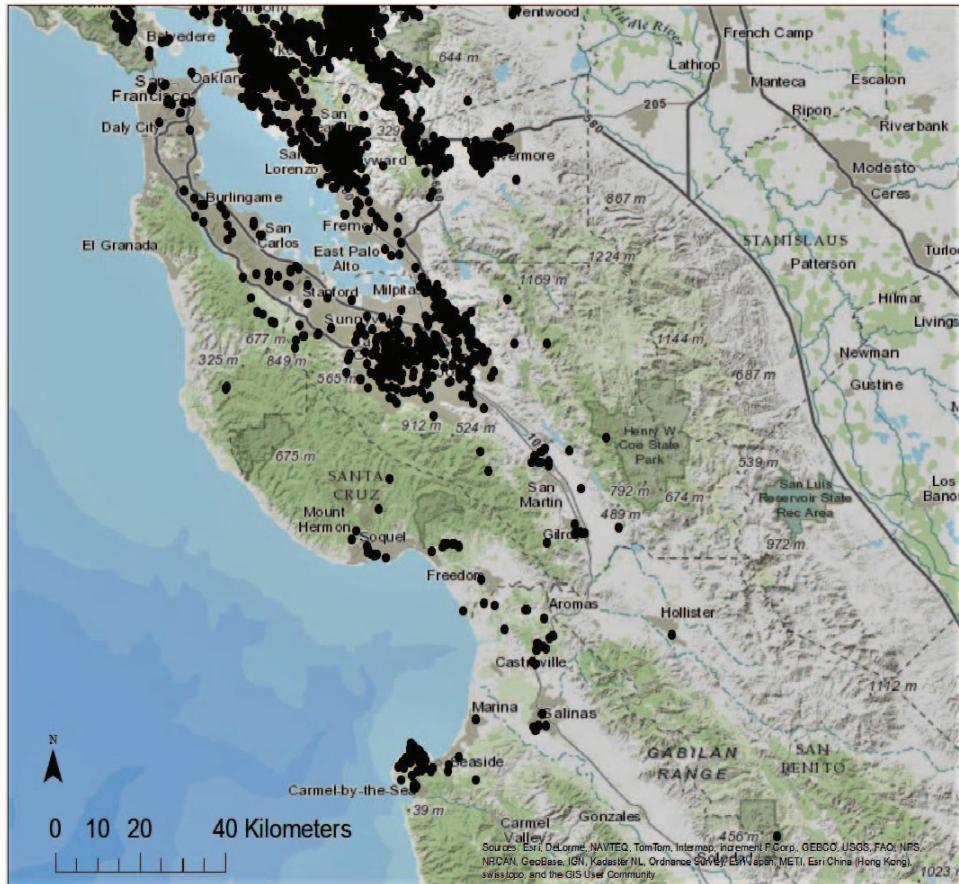


Fig. 2. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in the area of the San Francisco Bay south to Monterey/Carmel and San Benito over the time period 1995 through 2015.

The distribution of the EFS around Fresno is not as closely linked to the urban/suburban areas of the city as it is in other parts of the state (Fig. 4). The agricultural area surrounding Fresno is rich in orchards of almond, peach, nectarine, and cherry trees. The EFS is found in almond orchards at least 30 km west of Fresno, including orchards west of the small town of Kerman, and it is also found 30 km east of Fresno along branches of the King River. Fruit orchards are fairly contiguous east of Fresno and Clovis to the foothills of the Sierra Nevada Mountain Range.

Following introduction to Los Angeles in 1904, range expansion has occurred in all directions so that the species is now found not only in Los Angeles County but also in Orange, Riverside, San Bernardino, Santa Barbara, and Ventura Counties (Fig. 5). It is unknown when range expansion to Santa Barbara County occurred but the species is now common throughout urban and suburban areas around Santa Barbara and Montecito; indicating rapid range expansion in the last couple of decades. Range expansion by the EFS has come at the expense of populations of native western gray squirrels at locations such as Ganna Walska Lotusland in Montecito and Rocky Nook Park in Santa Barbara (AEM personal observations). There appears to be a break between the population in the area around Santa Barbara and the population in the area around

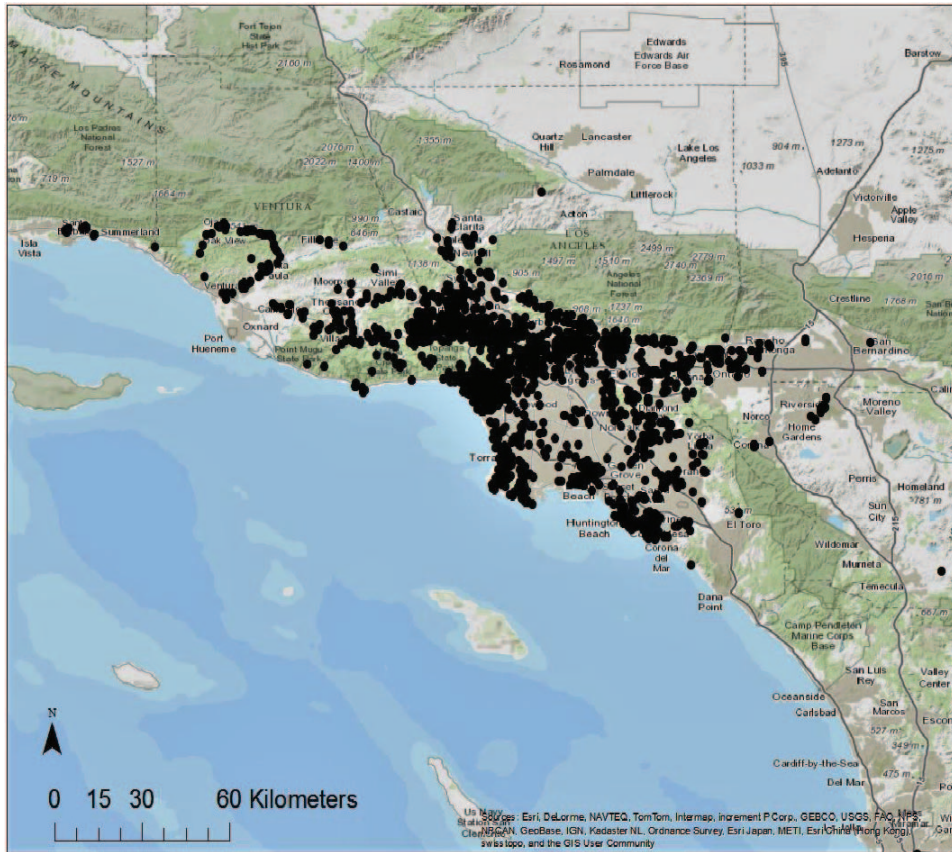


Fig. 5. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in the Los Angeles metropolitan area north to Santa Barbara over the time period 1995 through 2015.

while a MSLD of 64 km from Sacramento to Placerville gives a rate of 0.7 km/yr. Using 1890 as an introduction date to Golden Gate Park in San Francisco, although the introduction may have been before 1890, the MSLD to Salinas of 145 km gives an expansion rate of 1.2 km/yr. The MSLD from Stanford University (introduction 1921) to Salinas is 95 km giving a rate of 1.0 km/yr.

Discussion

As we have shown, the EFS has greatly expanded its range within California from points of initial introduction. Although the species is mainly observed at this time within urban and suburban areas of California, animals have also been observed in rural areas (west and east of Fresno) and in areas of native range of California (along the south fork of the American River near Coloma and in areas around Grass Valley in the foothills of the Sierra Nevada Mountains). The EFS is an agricultural pest in almond and fruit orchards west of Fresno and the dispersal of animals along major waterways such as the American, Kern, King, and Sacramento Rivers has allowed the species to occupy areas of native range away from human habitation. The EFS is now located in regions where invasion of habitats within the Sierra Nevada Mountains, as well

as other mountain ranges within the state is possible. An important question to ask is how far from urban and suburban areas the EFS will expand its range.

The EFS is a generalist species (Koprowski 1994) typically found within its native habitat in upland forested areas, open forests, riparian areas, residential areas, or areas neighboring open spaces such as agricultural lands and pastures containing trees. The EFS is able to live in large numbers in areas with high tree diversity (Nixon and Hansen 1987) and they are also more tolerant than some other species of low tree density (Wolf and Roest 1971). The EFS has a higher reproductive output than the WGS with adult females capable of producing litters twice per year with an average litter size of two to three pups (Koprowski 1994). Breeding generally occurs November-February and April-July (Brown and Yeager 1945; Moore 1957). The EFS is also more generalist than the native WGS in food choice (King 2004; Ortiz and Muchlinski 2015). The above referenced natural history traits may allow the EFS to displace the native WGS in certain habitats (Muchlinski et al. 2009; Cooper and Muchlinski 2015).

Some reasons for differences in the rate of range expansion by tree squirrels have been suggested by Signorile (2014) and include size of the founding population, genetic diversity and population structure. Larger sizes of founding populations were associated with greater genetic diversity, more dispersal, less local genetic differentiation and faster rate of range expansion rate in squirrels. The rates of long-term range expansion between 0.5 and 1.2 km/yr determined from this study are less than the 1.5 km/yr determined by Garcia and Muchlinski (2017) in highly suitable suburban habitat. As the EFS expanded its range over many decades it may have encountered habitats, which were not highly suitable at one time but highly suitable at a later date, thereby decreasing the long-term rate of range expansion in comparison to shorter term rates in highly suitable habitats.

It is very likely that the EFS will continue to expand its range within California, especially in human-developed areas and potentially into additional natural habitats. With continued range expansion of the EFS there may be additional impact on the native WGS, especially in lowland habitats (Cooper and Muchlinski 2015). However, in areas of California where the EFS is now sympatric with the invasive eastern gray squirrel, *Sciurus carolinensis* (EGS), or may become sympatric with the EGS, the EFS may experience contraction in geographic range or in population size (Creley and Muchlinski 2017). The EGS is spreading rapidly in many areas of central California so continued assessment of the relationship between the EFS, the WGS, and the EGS within California is warranted.

Acknowledgements

We acknowledge the following entities and individuals for help in gathering data for this project. We thank the California Department of Public Health West Nile Virus Surveillance Program System – especially Leslie Foss, Vicki Kramer, and Kerry Padgett, along with the California Roadkill Observation System (CROS), and David Waetjen (UC Davis) for creating the California Roadkill Observation System. We thank Ruby Alvidrez, Carly Creley, Lauren Zameito, Gina Navia, Chris DeMarco and all the volunteers who contributed observations. The following wildlife rehabilitation centers provided data used in this study: California Living Museum, California Wildlife Center, Critter Creek Wildlife Station, Gold Country Wildlife Rescue, Lindsey Wildlife Museum, Peninsula Humane Society, SPCA Monterey County, Sonoma County Wildlife Rescue, Squirrelmender Wildlife Rehabilitation, Stanislaus Wildlife Rehabilitation Center, Suisun Wildlife Rescue Center, Sulphur Creek Nature Center, Wetlands and Wildlife Care Center, WildCare, and Wildlife Center Silicon Valley. We also thank the many individuals who utilized iNaturalist, CROS, or other sources to submit observations of the eastern fox squirrel within California.

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