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Cover Page Footnote
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Recent Decline of Lowland Populations of the Western Gray Squirrel in the Los Angeles Area of Southern California

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Abstract.—We provide an overview of the distribution of lowland and otherwise isolated populations of the western gray squirrel (*Sciurus griseus*) in the Los Angeles area of southern California, an area that has experienced a recent and ongoing invasion by the non-native eastern fox squirrel (*Sciurus niger*), an urban-adapted species introduced a century ago. Away from its strongholds in the western Santa Monica Mountains, San Gabriel Mountains, and Santa Ana Mountains, the western gray squirrel is resident locally in both the Santa Susana and the Verdugo Mountains, in Griffith Park, in low hills at the eastern periphery of the San Gabriel Valley and in Claremont, and along the Santa Ana River canyon near Yorba Linda. It also persists east of the Los Angeles area in residential areas of Redlands and Yucaipa, which as of 2014 are still outside the range of the eastern fox squirrel. Here we document several gray squirrel extirpation events within its lowland range, and discuss factors influencing its persistence and its extirpation.

The western gray squirrel (*Sciurus griseus*) is a large tree squirrel native to forests of the western United States and extreme northwestern Mexico, with the subspecies *S. g. anthonyi* common and widespread in oak- and pine-dominated areas of the hills and mountains of southern California (Wilson and Reeder 2005). In the Los Angeles area, a region we define as extending from eastern Ventura County east through Claremont and south through the coastal plain into Orange County to the base of the San Joaquin Hills, it also occurs in human-modified habitats, including large city parks and golf courses, where scattered trees, particularly conifers, provide year-round food and shelter. It is one of two tree squirrels in the Los Angeles area, the other being the eastern fox squirrel (*Sciurus niger*), a non-native introduced in the early 1900s, and now abundant throughout much of the Los Angeles area of southern California (Jameson and Peeters 1988, King et al. 2010).

As discussed by Linders and Stinson (2007) western gray squirrels are closely tied to oak and evergreen woodland, and serve two main roles in maintaining native woodlands: they harvest and bury acorns throughout the woodland, and disperse the seeds and fruit of various oak woodland component tree and shrub species, such as California bay (*Umbellaria californica*). They also forage heavily on truffle-like mycorrhizal fungi found in leaf litter and loose soil, which aid oaks in fixing nitrogen and retaining water through dry months. During foraging, western gray squirrels deposit the spores of these fungi through their droppings, thus spreading them throughout the oak woodland and promoting the health of its trees. Because of this close association with oaks, the presence

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of western gray squirrels may serve as an indicator of oak woodland health. By contrast, the eastern fox squirrel is highly generalist in its food sources, requires a much smaller home range (becoming super-abundant in urban settings), and occurs in a much wider array of habitats than *S. griseus* away from the major mountain ranges in the region (Gatza 2011, Ortiz 2014).

The history and origin of western gray squirrel populations on the floor of the Los Angeles Basin are poorly understood. Today, most lowland populations of *S. griseus* are strongly associated with planted pines and other conifers, which may now be crucial habitat elements for the species. It was presumably naturally present at lower elevations when oak woodland (mostly *Quercus agrifolia*) once covered large areas of now-urbanized places like the San Gabriel Valley, a pattern shared by numerous lower montane plant and wildlife species that are able to persist locally at lower elevations in suitable areas of canyons and woodlands (Cooper 2011). Later, as the region developed, populations of *S. griseus* may have retreated to large urban parks and more wooded residential areas, where it persisted through most of the 1900s, including those at the base of the San Gabriel Mountains foothills from Pasadena east into Claremont (an area referred to as the ''mesa'' by early naturalists, e.g., Grinnell 1898). It is also possible that they colonized these areas later by moving down from the surrounding foothills, or that both patterns occurred, with isolated lowland populations ''winking'' out periodically, replenished by animals from surrounding highlands. Whatever the history, in the years between the late 1990s and the mid-2000s, *S. griseus* became scarce or altogether absent within many of these same neighborhoods. Clear instances of its extirpation and subsequent replacement – directly or indirectly – by the non-native eastern fox squirrel are now well documented (e.g., Muchlinski et al. 2009, Guthrie 2009, King et al. 2010).

Sciurus niger became established in the neighborhoods surrounding the eastern Santa Monica Mountains in the western Los Angeles Basin during the decades following its introduction in 1904, it only arrived in the San Gabriel Valley around 1990, the east San Gabriel Valley around 1998, and the Claremont area and Orange County in the early 2000s (Guthrie 2009, King et al. 2010). In recent years, *S. niger* has also colonized much of urbanized Santa Barbara County (P. Collins, pers. comm.) and portions of San Diego County, the latter also following an early introduction (King et al. 2010). Now virtually ubiquitous throughout the Los Angeles area from the San Fernando Valley east to San Bernardino County and south through Orange County, *S. niger* appears to still be absent at several urban-edge locations at the margins of the Los Angeles area, including parks and neighborhoods in Redlands and Yucaipa, San Bernardino Co. (Ortiz 2014); canyons in the lower San Gabriel Mountain foothills from the Sunland-Tujunga area east through Claremont (Gatza 2011), and along the Santa Ana River at Gypsum Canyon, near Yorba Linda, Orange Co. (AEM, unpubl. data).

Only a handful of local naturalists have noticed this turnover, and few published data exist on the range *of S. griseus* in the Los Angeles area prior to the arrival of *S. niger*. Today, only a few populations of *S. griseus* remain away from the larger mountains [typically below around 457 m (1500') a.s.l.], with only a handful, at the far eastern periphery being free of *S. niger*. To ensure the ecological integrity of these remaining populations of *S. griseus* – and of their habitat patches – particularly in areas where *S. niger* has not yet invaded (or at least where it is not completely dominant), it is important that remaining populations of *S. griseus* be identified and recognized by conservation agencies and organizations. Since the late 1990s, we (DSC and AEM) have been making notes on the occurrence of *S. griseus* in the Los Angeles area, as described

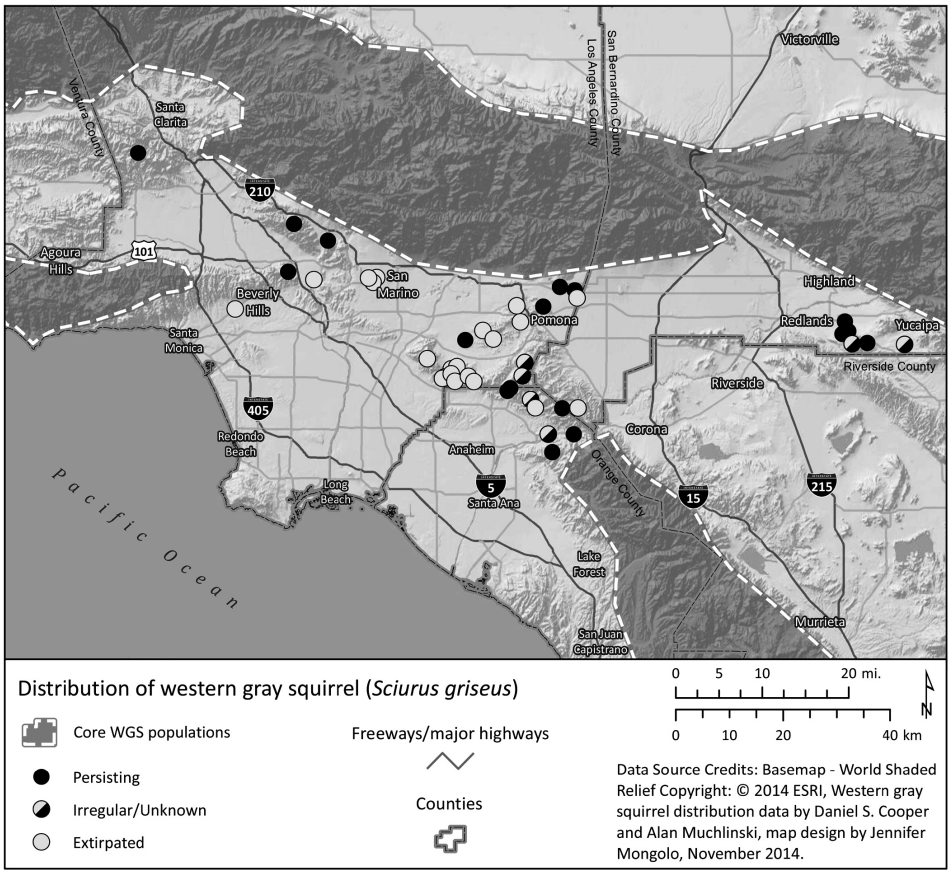

Fig. 1. Map showing current (2012–2014) range of western gray squirrel in the Los Angeles area.

below. This paper synthesizes findings from each of these efforts and provides detail on a dramatic and ongoing ecological replacement of a native species by a non-native one.

Materials and Methods

Little published information exists on the current or historical distribution of the western gray squirrel, so we relied on a variety of sources, including online museum databases for specimen records (www.vertnet.org, last search conducted 21 October 2014), and field notes and recollections of a network of environmental professionals and colleagues in the Los Angeles area. DSC conducted surveys of birds and vegetation in the Puente and Chino Hills on the east side of the Los Angeles Basin for two years in the late 1990s (1997–1998; see Cooper 2000), and kept field notes of all sightings of *S. griseus* from this area. AEM collected data on observations of *S. griseus* through an online survey form (http://instructional1.calstatela.edu/amuchli/squirrelform2.htm), which has received over 9000 visits since January 23, 2007, through field studies by four graduate students (Lewis 2009, Gatza 2011, Erkabaeva 2013, Ortiz 2014), and through his own observations within and east of the San Gabriel Valley.

DSC initiated a volunteer-based tree squirrel survey of Griffith Park in summer 2010; with ten observers each searching up to five of 40 similarly sized survey blocks in and

around the park. The following year, DSC and volunteers spent 25 days in the park between 8 August and 21 November 2011, gathering observations on foraging, breeding, aggression displays and other behavior, and from 5 August 2011 to 11 July 2012, DSC conducted a region-wide search for any remaining *S. griseus* populations in the lowland Los Angeles area away from known occupied habitat. During this period, DSC posted short articles and requests for information on local listserves (e.g., Pasadena Audubon Society; various neighborhood ''Patch'' websites). Also, DSC and colleagues made site visits (30 min – 2.5 hrs in duration) on 21 dates to 32 different locations in the eastern Santa Monica Mountains, the west San Gabriel Valley, and in the Verdugo Mountains and San Rafael Hills north of Glendale following up on reports and checking all accessible lowland areas with appropriate habitat. To supplement these surveys, DSC and colleagues installed motion-activated cameras during the same time period at Descanso Gardens in the San Rafael Hills west of Pasadena (two near the upper portion of the property bordering open space) and in the Verdugo Mountains (nine within canyons in three areas: La Tuna Canyon, Cedarbend Canyon, and Whiting Woods; *ibid*).

Results

Within its core range in mountains at the periphery of the Los Angeles area, *Sciurus griseus* is a conspicuous resident in canyons and oak groves, and appears to have little contact with *S. niger* except at the immediate urban-wildland interface zone (Gatza 2011). Below around 457 m (1500') a.s.l., numerous subpopulations of *S. griseus* persisted into the 1990s in areas between these major mountain ranges, and in some cases, well onto the floor of urbanized areas, as summarized below, and in Figure 1 and Table 1.

Eastern Santa Monica Mountains/Griffith Park

Griffith Park, at the far eastern end of the Santa Monica Mountains, appears to support the only large remaining population of the species in this range east of Sepulveda Pass/Interstate 405, with approximately 25–50 individuals largely confined to two main drainages (Western Canyon and Vermont Canyon). During intensive searches of potential habitat in 2011 and 2012, no observations of *S. griseus* were made between Sepulveda Pass and Cahuenga Pass (U.S. 101), an area that includes significant open space at Franklin Canyon Park and elsewhere. However, we remain hopeful that *S. griseus* may persist here, as we were unable to obtain access into the large Stone Canyon Reservoir open space (Los Angeles Dept. of Water and Power) just east of Sepulveda Pass near Bel Air, which supports apparently suitable habitat.

Santa Susana Mountains/Simi Hills

Located on the northwestern edge of the San Fernando Valley, these generally arid ranges are dominated by low-growing chaparral and coastal sage scrub, with a small number of permanent streams and oak woodlands, best developed in the former range. Ecologically, the Simi Hills are more similar to the Santa Monica Mountains immediately to the south than the San Gabriel and Sierra Madre ranges to the north, while the Santa Susana Mountains reach higher elevations and feature more montane elements such as bigcone douglas-fir (*Pseudotsuga menziesii*) and extensive savannah dominated by annual grassland and valley oaks (*Quercus lobata*). Based on field notes of local naturalists, *S. griseus* is absent from the Simi Hills, but persists in the Santa Susana Mountains at Browns Canyon and Devils Canyon (S. Bernal, 2012, in litt.), and possibly at O'Melveny Park (sight record on 20 April 2014, CSULA web survey). Its historical status in either

Table 1. Distribution of "lowland" populations of western gray squirrel in Los Angeles area (i.e., away from major mountain ranges/foothills), 2014. Status: P = Persisting population; E = Extirpated; EFS = Eastern fox squirrel.

Region	Subarea	Location, as applicable	Elevation	Status	EFS?	Date of last record (Source)
East Santa Monica Mountains						
	Beverly Hills		<1200'	E	Yes	1975 (specimen, LACM 60617)
	Griffith Park		<1200'	P	Yes	2014
Santa Susana Mountains			1400'	P	Yes	2014[1,2]
West San Gabriel Valley						
	Verdugo Mountains		1800'	P	Yes	2012 (DSC, unpubl. data)
	San Rafael Hills		1300'	P	Yes	2014 (Erkabaeva 2013)
	San Marino					
		Huntington Library	600'	E	Yes	2010 (CSULA database)
		Lacy Park	600'	E	Yes	1976 (specimen, LACM 90234)
		Mission Canyon[3]	600'	E	Yes	2012 (CSULA database)[4]
Northeast Los Angeles (Forest Lawn Glendale)			600'	E	Yes	1997 (DSC, unpubl. data)
East San Gabriel Valley						
	San Jose Hills					
		Industry Hills	600'	P	Yes	2014 (AEM, unpubl. data)
		Bonelli Park area[5]	1000'	P	Yes	2014 (AEM, unpubl. data)
		Walnut Creek Park	800'	E	Yes	2012 (DSC, AEM, unpubl. data)
		Galster Park	600'	E	Yes	1998 (DSC, unpubl. data)
		Cal Poly Pomona	800'	E	Yes	2009 (AEM 2009)
		Via Verde Country Club	800'	E	Yes	~2000 (AEM, unpubl. data)
	Western Puente Hills[6]					
		Whittier/Hacienda Heights	800'	E	Yes	1998 (DSC, unpubl. data)
		Powder Canyon	800'	E	Yes	2005 (R. Erickson, unpubl. data)
	Eastern Puente Hills/Chino Hills					
		Tonner Canyon	600–800'	P	Yes	2014 (R. Hamilton, L. Schmahl, via email)
		Chino Hills State Park	1200'	P	Yes	2014 (A. Ing, pers. comm.)
Pomona Valley/Claremont						
		RSABG[7]	1200'	P	Yes	2014 (AEM, unpubl. data)
		Pomona College	1200'	E	Yes	2012 (AEM, unpubl. data)
		Arlington Dr.	1200'	P	Yes	2012 (CSULA database)
Redlands/Yucaipa						
	North of I-10					
		Univ. of Redlands/ Sylvan Park	1500'	P	No	2014 (Ortiz 2014)
		3rd St., Yucaipa	2600'	?	No	2011 (CSULA database)
	South of I-10					
		Ford Park	1600'	P	No	2014 (Ortiz 2014)
		Prospect Park	1600'	P	No	2014 (Ortiz 2014)
		Rossmont Dr.	2000'	?	No	2009 (CSULA database)
		Hilltop Dr.	2200'	P	No	2012 (CSULA database)

Table 1. Continued.

Region	Subarea	Location, as applicable	Elevation	Status	EFS?	Date of last record (Source)
Orange County						
	Anaheim Hills					
		Oak Canyon Nature Center	800'	P	Yes	2013 (CSULA database)
	Santa Ana River Canyon					
		Yorba Reg. Park	400'	P	Yes	2014 (B. Leatherman, via email)
		Canyon RV Park	400'	P	No	2014 (AEM, unpubl. data)

[1] Includes sight record from O'Melveny Canyon Park in 2014 (CSULA web survey).
[2] S. Bernal, unpubl. data.
[3] Includes oak woodland patches along Kewen, Canon and Encino Dr. at San Marino/Pasadena border.
[4] This population was seen continuously through 2010; the 2012 report was likely a dispersing individual from elsewhere.
[5] Includes Mountain Meadows Golf Course.
[6] We use State Route 57 as the east/west dividing line.
[7] Rancho Santa Ana Botanic Garden, Claremont.

range is not known (a single specimen exists from "Oat Mountain" from 1969, LACM 47332), nor is the size of the extant population in the Santa Susana Mountains. A recent (2014) observation of a roadkill *S. griseus* on U.S. 101 at Las Virgenes Canyon Rd. (C. DeMarco, via email) suggests that colonization north from the Santa Monica Mountains might be a possibility without the freeway and associated development as a barrier. *Sciurus niger* is common in the Simi Hills, particularly at the urban periphery (DSC, pers. obs.).

Verdugo Mountains/San Rafael Hills

Populations of *S. griseus* in both the Verdugo Mountains and the adjacent San Rafael Hills are isolated from the San Gabriel Mountains to the north by Interstate 210 and by dense residential development along Foothill Blvd. Despite searching promising areas such as La Tuna Canyon Rd., Crescenta Valley Park and the Whiting Woods neighborhood on the north slope of the Verdugos, and Descanso Gardens and Scholl Canyon in the San Rafaels, we could not locate any individuals during observational surveys in 2011–12. However, in approximately three months operating motion-activated cameras in 2012, we detected single individual *S. griseus* at two sites, one in Cedarbend Canyon and one near Whiting Woods, confirming that the species persists in the Verdugo Mountains. In the San Rafael Hills, Erkabaeva (2013) observed four *S. griseus* in a group on one occasion at Descanso Gardens in La Cañada, as well as several lone individuals here during 2012. Later, a motion-activated camera that had been placed at Descanso Gardens since 2012 recorded a single *S. griseus* in July 2014, indicating the persistence of at least a small population here. *Sciurus niger* is very common throughout both the Verdugo Mountains and San Rafael Hills, including within seemingly pristine habitat far from development (DSC, pers. obs.).

Northeastern Los Angeles

The hilly residential neighborhoods of Los Angeles just south of the San Rafael Hills (including Eagle Rock and Highland Park) appear to have also lost at least one lowland population of western gray squirrels. Several individuals were observed in planted pines in the upper portions of Forest Lawn Glendale on the Eagle Rock border in 1997 (DSC,

pers. obs.), but a check in 2011 (this study) revealed only *S. niger*. Lack of records from considerable time afield in this region and no sightings by naturalists based at the Debs Park Audubon Center in Highland Park (J. Chapman, pers. comm.) suggest that no current population of *S. griseus* persists in this area, which includes the lowermost portion of the Arroyo Seco.

Pasadena/West San Gabriel Valley

Small numbers of western gray squirrel occur at the northern/urbanized edge of Pasadena/Altadena (c. 457 m a.s.l.), where *S. niger* is now abundant. One was observed in 2011 (DSC) in the courtyard of an abandoned U.S. Forest Service facility adjacent to Hahamongna Watershed Park near the Pasadena/La Cañada border, and according to a local resident, up to four individuals, including a probable family group (in January 2011), have been recorded here in recent years (L. Paul, via email). *Sciurus griseus* is occasional in the more wooded residential neighborhoods along the northern tier of Altadena at the base of the mountains (e.g., near Eaton Canyon and Kinneloa Canyon), but has apparently abandoned locales slightly downslope in denser residential areas, including a former retirement facility (''The Scripps Home'' at 2212 N. El Molino Ave.) that had its mature trees removed prior to a redevelopment effort in summer 2011 (an action which apparently drove out *S. griseus*, *fide* L. Paul). More significantly, a population of *S. griseus* that once occurred in remnant oak-walnut woodland amid residential estates along Mission Canyon at the border of San Marino and Pasadena (including Lacy Park) persisted to around 2012, with the last records (each of a single individual) being along Kewen Drive in San Marino on several dates in 2010 (J. Garrett, via email), and again in 2012 (M. Nakamura, CSULA web survey form). We also last received reports from the nearby Huntington Library around the same time (three separate sightings; T. Allison, CSULA web survey forms in 2008 and 2010; S. Claytor, photograph in 2008). We know of no remaining population of *S. griseus* here or along the lower Arroyo Seco south of Hahamongna/Devil's Gate Dam.

East San Gabriel Valley/San Jose Hills

As in the west San Gabriel Valley, western gray squirrels occur widely in canyons and locally in residential areas in the foothills on the northern tier of the east San Gabriel Valley (e.g., above Monrovia, San Dimas and La Verne, >305 m a.s.l.). South of here, the low range of hills in the eastern San Gabriel Valley referred to as the San Jose Hills apparently serves as an ecological connection between the San Gabriel Mountains and the Puente-Chino Hills, which then connect to the much larger Santa Ana Mountains to the south (see Cooper 2000). Here, the species persists only at Bonelli Park (San Dimas) and in the ''Industry Hills'' near La Puente, and several extirpations have been very recent (e.g., observed by DSC at Walnut Creek Park in Covina in 2011 but not since; *fide* AEM).

Puente-Chino Hills

Western gray squirrels occurred in multiple canyons and open space areas from Diamond Bar and Rowland Heights west into Whittier and La Habra Heights, and south into Brea, and Chino Hills State Park during the late 1990s (DSC, unpubl. data). A population in Turnbull Canyon in the Whittier Hills (far western Puente Hills) was apparently extirpated in the late 1960s following a major fire that burned many mature oaks (J. Schmidt, in litt.), indicating that even by then some loss had occurred. By the late 2000s they had been extirpated west of Harbor Blvd., with replacement by *S. niger*,

including along Powder Canyon in Rowland Heights/La Habra Heights, where *S. griseus* was present in late 2005 (1, R. Erickson, unpubl. data) yet absent by 2007 (DSC, unpubl. data; *fide* L. Longacre). The latter location is particularly notable, as the canyon is directly contiguous to hundreds of acres of natural habitat, has been protected as part of the Puente Hills Landfill Conservation Authority, and has seen little if any land use change in the past 20 years. A devastating fire in 2008 that burned most of Chino Hills State Park resulted in the immediate loss of most western gray squirrel populations there, with only a very small number of individuals persisting in oak woodland in the remote center of the park, north of San Juan Hill (A. Ing, pers. comm.).

Pomona Valley/Claremont

While still present at Rancho Santa Ana Botanic Gardens and along the San Gabriel foothills through the northern portion of Claremont (e.g., San Dimas Canyon, Marshall Canyon, *fide* AEM), western gray squirrel has been recently extirpated from several areas, and replaced by *S. niger*, within the city of Claremont to the south, including the Claremont Colleges area (Guthrie 2009). There are apparently no historical or recent records of *S. griseus* from the eastern Pomona Valley nor along the lower Santa Ana River Valley upstream of Prado Dam.

Redlands/Yucaipa (San Bernardino County)

Western gray squirrels are widespread and conspicuous residents of the San Bernardino Mountains. However, lowland populations away from the lower foothills persist (as of 2014) at University of Redlands, Sylvan Park, Ford Park, and Prospect Park (Ortiz 2014). The species has also been reported in the "Sunset Hills" area of Redlands just south of Interstate 10 and in an apparently small area of Yucaipa (including Third St.), where they are found in mature pines in a residential area (CSULA web survey). These populations do not appear to be in contact with *S. niger* as of 2014, and are much higher in elevation than other lowland sites discussed. However, because they are persisting away from the main mountain ranges in what is still obviously lowland (non-montane or foothill) habitat, we have included them here.

South Orange County

In contrast to the report by Pequegnat (1951) that the western gray squirrel was not found in the Santa Ana Mountains, the species is present in several oak-filled canyons in the Santa Ana Mountains (e.g., Trabuco Canyon, CSULA web survey and J. Ortiz, via email; Modjeska Canyon/Tucker Wildlife Sanctuary, CSULA web survey; Whiting Ranch Wilderness Park, R. Hamilton, via email). Additional reports to the CSULA web survey locate western gray squirrels at the suburban-wildlands interface west of Lake Elsinore. Whether they are recent (post-1950s) arrivals to this range is not known.

Away from the Santa Ana Mountains, two small populations are known from Oak Canyon Nature Center in the Anaheim Hills, and along the "Santa Ana River canyon" where the Chino Hills meet the northern Santa Ana Mountains (AEM, unpubl. data; B. Leatherman, via email). We know of no records from the San Joaquin Hills, where *S. niger* has been present in residential areas since around 2010 (R. Erickson, via email). Like much of San Bernardino (and Riverside) County, *S. niger* has only recently (late 1990s) penetrated Orange Co., but it is now widespread and common into Irvine (D. Willick, via email).

Other Areas

DSC (unpubl. data) observed a small number of what appeared to be western gray squirrels in pines at the golf course at the Palos Verdes Country Club near Malaga Cove on the Palos Verdes Peninsula in the 1990s; in this same area in roughly the same time period, a local naturalist observed what appeared to be a single individual in the same area (R. Melin, via email). A recent visit to this area (October 2014) revealed that it still supported a dense forest of coast live oak, toyon (*Heteromeles arbutifolia*), many mature planted conifers and eucalyptus, and a riparian strip running through the golf course (DSC, pers. obs.). And, whereas the eucalyptus plantation here has apparently been established for more than a century (Gales 1988), due to the extreme isolation of this area from any other known S. *griseus* populations, its coastal location, and the possibility that this population derived from deliberately introduced individuals (or pertains to the eastern gray squirrel, *Sciurus carolinensis*), we consider a Palos Verdes population to be ''hypothetical'' for now until more information is uncovered that would support its inclusion in the current range of the species.

Discussion

Our investigation into the distribution of the western gray squirrel in the Los Angeles area elucidates its status as essentially a foothill species that is now rare and declining below around 457 m elevation, particularly in areas where it has come into contact with the eastern fox squirrel. Away from its main strongholds in the western Santa Monica Mountains, the San Gabriel Mountains, and the Santa Ana Mountains, small, isolated populations persist only in the Santa Susana Mountains, Griffith Park, the Verdugo Mountains and San Rafael Hills, the San Jose Hills, the Chino Hills, at Rancho Santa Ana Botanic Gardens in Claremont, and in Redlands/Yucaipa. Based on local naturalists' observations, several lowland populations appear to have declined in the past five years, including that in Bonelli Park, the San Rafael Hills, Chino Hills State Park, and along the Santa Ana River Canyon near Yorba Linda. Invariably, extirpations have occurred concurrently with colonization by the ubiquitous *S. niger*.

It is probably unlikely that truly extirpated, isolated lowland populations in the area will re-develop on their own. Areas of recent extirpation (or near-extirpation, where *S. griseus* is no longer resident but may occur irregularly) are typically separated from the nearest presumed source population by more than a kilometer, and generally by dense residential or urban development. Multi-lane freeways now provide formidable barriers between these areas of extirpation and source populations of *S. griseus*. Remarkably, animals do persist in a handful of lowland areas with very limited habitat, including the Industry Hills in La Puente, which suggests that certain small, isolated subpopulations may act as ''refugia'', perhaps from pathogens that periodically sweep through larger and more intact populations. Of course, these same refugia are vulnerable to their own extinction events, and so are almost certainly temporary.

Erkabaeva (2013) demonstrated that the length of projected coexistence of the two squirrel species in a given habitat fragment depends upon both the size of the habitat fragment and the structure of the habitat within the fragment, with length of coexistence associated with a higher diversity of food bearing tree species and coniferous trees. *Sciurus griseus* had a high probability of going extinct within a relatively short period of time (10 to 40 years) in small to medium-sized habitat fragments. The presence of the *S. niger* in the same habitat brought about extinction in a shorter period of time.

Competition with other squirrel species has been suggested as a potential cause of *S. griseus* decline (or a contributor to its current patchy distribution) in the region, but the mechanisms involved in this relationship need further study. Extirpation sites generally support very high densities of *S. niger*, yet this species simply occurs at higher densities in general. *Sciurus niger* is highly urban-adapted, and occurs at all the sites where *S. griseus* has vanished, and we have not confirmed a site where *S. griseus* has been extirpated and where *S. niger* is completely absent. Still, King (2004) found few interactions among *S. niger*, *S. griseus*, and even California ground squirrel (*Spermophilus beecheyi*) in her study area where all three occur in San Dimas, California (eastern Los Angeles Co.), and Ortiz (2014) also observed very few aggressive interactions between *S. niger* and *S. griseus* in her local study areas. Regardless of the mechanism, the loss of *S. griseus* in these areas – and region-wide – may be associated with a profound ecological change and degradation of seemingly healthy oak woodland and other habitat, particularly in wildland areas where replacement has occurred (e.g., the Puente-Chino Hills).

Larger wildland areas where *S. griseus* is persisting in the presence of *S. niger* are of particular interest because these appear to offer the basic habitat needs of both species, at least for some period of time, and possibly in different areas of the landscape. The discovery of nests of *S. griseus* well into protected open space such as in the rugged Cedarbend/Whiting Woods area of the Verdugo Mountains (DSC, unpubl. data) and at San Dimas Canyon Park (King 2004) suggests a pattern of edge-avoidance, possibly related to increased competition with the eastern fox squirrel at the urban edge. However, this pattern breaks down at sites like Fern Dell in Griffith Park, where *S. griseus* occurs a few feet from houses and dense urbanization (DSC, unpubl. data). Here, supplemental feeding or food provisioning may simply be ''propping up'' the population of *S. griseus* which has also been aided by the abundance of planted trees providing additional food sources (fruits and nuts). Although we have made a few direct incidental observations of supplemental feeding (e.g., unshelled peanuts dropped at Fern Dell in Griffith Park being carried off by *S. griseus*), it probably occurs widely. Other vegetative characteristics that allow *S. griseus* to persist here include some amount of closed-canopy woodland (or woodland-like groves of trees) with an open understory rich in non-woody debris and leaf litter; older, mast-producing trees for food; and at least a few very tall trees for nest placement (Linders and Stinson 2007), characteristics that still apply to many parks in the region.

More proximate factors in the decline of *S. griseus* relevant in our study area include death from injury and disease. Mortality from roadkill has been shown to be a major (if localized) factor in squirrel deaths in studies in Washington state (Linders and Stinson 2007), and *S. griseus* is frequently detected as roadkill in the Los Angeles area (pers. obs.). Many sites at the urban-wildland interface, including sites with documented *S. griseus* extirpations have roads along a canyon bottom, making squirrels that live in low densities and that forage on the ground particularly vulnerable. Other important causes of death and/or population decline include necrotic mange (found in many populations of *S. griseus* but oddly, apparently undocumented in the introduced *S. niger* in California, *per* King 2004); habitat quality decline from removal or disruption of the forest canopy due to development, tree-cutting, or fire; soil trampling and compaction (which reduces the biomass of fungi and perhaps other foods); and extreme natural events such as prolonged drought, which work synergistically to wipe out small populations. However, considering how modified the current habitat of many lowland *S. griseus* populations is (e.g., planted pines on golf courses), habitat transformation would seem to be a relatively minor threat.

Based on the continuing trend of extirpation in the region, we consider all existing lowland populations of *S. griseus* to be highly imperiled throughout the Los Angeles area. We estimate one of the largest intact populations within the urban core of the region, that at Griffith Park, at well under 50 individuals, and even here it is geographically limited within the park itself, with most of the population in two adjacent canyons (DSC, unpubl. data). Smaller, more isolated populations such as that at Rancho Santa Ana Botanic Gardens and at various patches in the San Jose Hills are now "landlocked" by freeways and urbanization and are probably much more imperiled; populations here and the Chino Hills are now surrounded and infiltrated by *S. niger* (*fide* A. Ing), and they may not be able to resist continued invasion by this species. In the case of Redlands/Yucaipa, it is likely only a matter of time before *S. niger* colonizes and saturates the residential areas and parks where *S. griseus* currently occurs alone.

Should re-introduction of *S. griseus* to lowland areas be attempted, we recommend this be limited to large, protected areas of natural habitat; however, reintroduction into areas where *S. niger* has already saturated the surrounding landscape and *S. griseus* has disappeared, such as at Franklin Canyon Park in Beverly Hills or along the lower Arroyo Seco in Pasadena, seems unlikely to succeed in the long term. Another possibility might be the modification of large closed landfills that have trees with a significant amount of closed canopy and that produce appropriate food items. We refer readers to Gatza (2011) for information on a Habitat Suitability Model that would support *S. griseus* while not being conducive to *S. niger*. Landfills within large urban areas often cover hundreds of hectares, and modification of portions of these landfills with corridors between suitable habitat fragments could provide new habitat for "lowland" western gray squirrels. We would not recommend introducing individuals from outside into areas of continued occurrence, such as Griffith Park, which would have the potential to introduce an unknown pathogen into vulnerable, isolated populations.

Literature Cited

Cooper, D.S. 2000. Breeding birds of a highly-threatened open space: the Puente-Chino Hills, California. Western Birds, 31:213–234.

———. 2011. Rare plants of Griffith Park, Los Angeles, California. Fremontia, 38(4):18–24.

Erkabaeva, K. 2013. Habitat structure and extinction risk modeling of *Sciurus griseus* in long-term coexistence habitats of southern California. M.S. thesis, California State Univ., Los Angeles.

Gales, D. 1988. Handbook of Wildflowers, Weeds, Wildlife, and Weather of the South Bay and Palos Verdes Peninsula, Third Edition. FoldaRoll Company, Palos Verdes Peninsula, California.

Garrett, K. and J. Dunn. 1981. Birds of Southern California: Status and Distribution. Los Angeles Audubon Society, Los Angeles.

Gatza, B.P. 2011. The effects of habitat structure on western gray squirrels and invasive eastern fox squirrels. M.S. thesis, California State Univ., Los Angeles.

Grinnell, J. 1898. Birds of the Pacific Slope of Los Angeles County. Pasadena Academy of Sciences Publication No. 11.

Guthrie, D. 2009. Suburban Squirrels. Chaparral Naturalist, 49(1), September/October 2009.

Jameson, E.W. and H.J. Peeters. 1988. California Mammals. Univ. of California Press, Berkeley, CA.

King, J.L. 2004. The current distribution of the introduced fox squirrel (*Sciurus niger*) in the greater Los Angeles metropolitan area and its behavioral interaction with the native western gray squirrel (*Sciurus griseus*). M.S. thesis, California State Univ., Los Angeles.

———, M.C. Sue, and A.E. Muchlinski. 2010. Distribution of the eastern fox squirrel (*Sciurus niger*) in southern California. The Southwestern Naturalist, 55(1):42–49.

Lewis, S.A. 2009. Factors that allow the native western gray squirrel (*Sciurus griseus*) and the introduced eastern fox squirrel (*Sciurus niger*) to coexist in certain habitats within California. M.S. thesis, California State Univ., Los Angeles.

Linders, M.J. and D.W. Stinson. 2007. Washington State Recovery Plan for the Western Gray Squirrel. Washington Dept. of Fish and Wildlife, Olympia, 128+viii pp.

Muchlinski, A.E., G.R. Stewart, J. L King, and S.A. Lewis. 2009. Documentation of replacement of native western gray squirrels by introduced eastern fox squirrels. Bull. So. Calif. Acad. Sci., 108:160–162.

Ortiz, J.L. 2014. Behaviors of the native western gray squirrel (*Sciurus griseus*) and the invasive eastern fox squirrel (*Sciurus niger*) in Los Angeles and surrounding counties. M.S. thesis, California State Univ., Los Angeles.

Pequegnat, W.E. 1951. The biota of the Santa Ana Mountains. Journal of Entomology and Zoology. Nos. 3 and 4.

Wilson, D.E. and D.M. Reeder, Editors. 2005. Mammal species of the world: a taxonomic and geographic reference. Third Edition. Smithsonian Institution Press, Washington, D.C.