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*).

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ABSTRACT

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*).

By

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The fox squirrel (*Sciurus niger rufiventer*) was introduced into Los Angeles County from the Mississippi Valley circa 1904 and has greatly increased its numbers and distribution since that time. After the initial introduction, numerous range-expanding introductions have taken place. The fox squirrel is now thriving in areas of high human population densities and is considered a pest species causing significant damage to property. Researchers are also concerned that range expansion by the non-native fox squirrel may be displacing the native western gray squirrel (*Sciurus griseus*) from less populated foothill habitats. To better understand and subsequently control the growing fox squirrel population in the Greater Los Angeles Metropolitan Area, the current and historic distributions of the fox squirrel in Los Angeles, Orange, and Ventura Counties were examined. Address data for the current range of the fox squirrel were collected through questionnaires, personal observations, specimen records, and submissions by residents to an online data collection form. More than 800 address points were collected, and subsequently Geo-coded and mapped using GIS software. Results suggest the distribution of the fox squirrel in Southern California has expanded at rates ranging from

0.68 km/yr to 6.84 km/yr during varying time periods over the past 100 years. A field study was also conducted in an area where fox squirrel and gray squirrel distributions overlap. Behaviors of squirrels were documented twice weekly for a period of one year, with gray squirrels initiating 43 of 57 (75 percent) of aggressive encounters with fox squirrels. Both species used the same trees for nesting sites and consumed many of the same food items. Additional studies are needed to conclude if the fox squirrel can displace gray squirrels in certain habitats or if habitat loss and/or mange are the primary factors leading to gray squirrel decline in Southern California.

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CHAPTER 1

Introduction

A species or subspecies of animal inhabiting California is typically considered to be native or indigenous to a particular area if it originated in that area or came to the area under natural conditions prior to European settlement. Our knowledge of what organisms are native to a locale is primarily based on historical reports, museum records, natural history surveys, as well as paleontological and archeological studies. Species or subspecies that are not native are those that have evolved elsewhere and have been purposely or accidentally relocated to areas outside their natural range. These species are labeled interchangeably as: non-native, alien, exotic, non-indigenous, invasive, or introduced. Wild-bred offspring of these exotic animal species are also not considered to be native, since they originated from imported genetic stock of non-natives (Devine 1998; Jurek 1992).

Urban ecosystems such as those found in Southern California are generally complex mixtures of native and non-native organisms. While some species have invaded habitats on their own, human exploration and colonization have dramatically increased the diversity and scale of invasions by exotic species. Non-native organisms typically access new habitats through accidental introduction, escape after importation for a limited purpose, or deliberate introduction. These exotic species often find no natural enemies in their new habitat and therefore spread easily and quickly, often outnumbering native species in urban and suburban areas (Levin 1989). Examples of such non-native species include the house sparrow, European starling, Norway rat, eastern gray squirrel, fox squirrel and Virginia opossum.

The California Department of Fish and Game identifies California as one of three states "having the most severe problems with exotic species," listing 22 (12%) of 183 species of breeding terrestrial mammals as non-native (http://www.dfg.ca.gov). The eastern fox squirrel (*Sciurus niger*) serves as a prime example of one of the twenty-two exotic mammal species now successfully breeding in California. The fox squirrel is native to the eastern half of the United States, with the subspecies *S. niger rufiventer* inhabiting much of the Midwest along the Mississippi Valley between southern Illinois and central Tennessee (Hall and Kelson 1959). It has since been successfully introduced into many western states such as California, Washington, Oregon, Idaho, Montana, Wyoming, Colorado, and New Mexico, as well as into British Columbia and Ontario, Canada (Flyger and Gates 1982; Jordan and Hammerson 1996).

Since the introduction of the fox squirrel into Los Angeles circa 1904, the fox squirrel has generally remained restricted to areas of human habitation throughout Southern California. With continued range expansion however, the fox squirrel has become sympatric in many foothill areas with the native western gray squirrel *Sciurus griseus anthionyi* (Hoefler and Harris 1990; Ingles 1954).

Sciurus niger rufiventer, the smallest of the ten *S. niger* subspecies, can be identified by grizzled dorsal coloration with buff to orange, accompanied by a tan to rufous venter and bright orange-brown ears. The fox squirrel, often incorrectly referred to as the red squirrel by residents of Southern California, is visually distinguishable from the native western gray squirrel by the gray's slightly larger size, silver-gray fur with creamy white underparts, and notably bushier tail (Koprowski 1994).

Historically, fox squirrels were common at the interface of the deciduous forests and the prairie in the eastern United States, while gray squirrels were found in interior forest habitat, chiefly associated with the oaks of the Upper Sonoran and Transition Life Zones (Allen 1943; Ingles 1954; Smith & Follmer 1972). Today, fox squirrels are common inhabitants of urban and suburban areas throughout eastern North America (Steele and Koprowski 2001; Wolf and Roest 1971). Even though the fox squirrel has been introduced to many parks, campuses, and suburbs in California (Becker and Kimball 1947; Byrne 1979; Ingles 1954), there has been limited research on this animal in this state.

Within the past 20 years, Los Angeles County residents have noticed a decline in the number and range of western gray squirrels coinciding with an increase in the number of fox squirrels (Byhower 2002; Byhower and Lokitz 2000; Sue et. al. 2002). This may indicate competitive exclusion, however, the observation is confounded by an increase in suburban development and forest fragmentation. Continued land development is seen in areas such as the Santa Susana Mountains of Los Angeles and Ventura Counties where prime gray squirrel habitat is being replaced at a rate of approximately 1,400 acres per year by highways, strip malls, housing tracts and golf courses (Polakovic 1999). Gray squirrels appear more sensitive to habit fragmentation than fox squirrels as long-term trends from the Midwest have shown population declines in eastern gray squirrels (*S. carolinensis*) and increases in fox squirrel numbers as forest cover is reduced (Allen 1943; Nixon et al. 1978). Research by Barnum (1975) documented the presence of gray squirrels "only in stands with ≥ 5 acres of mature oaks and ≤ 430 yards from water." Areas supporting <5 acres of oak with no conifers therefore may be inadequate habitat to support western gray squirrels in Southern California. Research by Nupp and Swihart (2000) by contrast identified *S. niger rufiventer* as having little sensitivity to habitat fragmentation and was often associated positively with isolation of forest patches. Suburban development therefore should be advantageous to the fox squirrel and promote its future range expansion in the Greater Los Angeles Metropolitan Area.

Gray squirrel population decline in Southern California may alternately be the result of a multi-year drought and the susceptibility of gray squirrels to mange. Mange results from parasitism by mange mites from the genera *Notoedres, Sarcoptes,* or *Cnemidoptes*. Notoedric mange begins with small red spots on the head and neck, with sores developing and the hair falling out, first over the chest and shoulders, then progressing over the entire body. Affected animals become weak and emaciated due to the interference with vision and feeding caused by the formation of scabs around the eyes. They often perish from exposure as a result of hair loss (Allen 1943; Bryant 1926; Laviopierre 1964; www.michigan.gov/dnr).

Mange greatly reduced the western gray squirrel population throughout much of its range between 1913 and 1921 in California (Bryant 1926; Ingles 1947; Shannon 1922). During January through March 1931, gray squirrels were also reported to be dying in great numbers in Los Angeles and Santa Barbara Counties as a "result of the disease coccidiosis as well as the presence of mites" (Moffitt 1931). Coccidiosis and mange reached epidemic proportions again in the Newhall/Placerita Canyon areas of Southern California during the mid 1970s, decimating the local gray squirrel population (F. Havore, personal communication October, 2003). Although mange has been prevalent in nearly 50% of fox squirrels admitted to several Northern California wildlife rehabilitation centers in recent years (P. Nave, personal communication June 18, 2004), Southern California fox squirrels admitted to five rehabilitation centers within Los Angeles and Ventura Counties during the past 13 years have not been documented as having mange (S. Baird, personal communication June 18, 2004).

Meffe and Carroll (1994) state that the highest concentrations of exotic species are often found in the habitats that have been most altered by human activity. Exotic species such as the fox squirrel therefore may be better suited to take advantage of disturbed conditions than the native western gray squirrel and consequently invade areas that were once inhabited by the gray squirrel before the habitat was altered by development. Fox squirrels exhibit many characteristics that would classify them as successful invaders. They have high reproductive rates (2 litters per year), high dispersal rates, broad native range and diet, are habitat generalists, and are human commensal. Los Angeles County can be considered an ideal invadable community for the fox squirrel given the mild climate and year-round food supply offered by exotic plant species, accompanied by the absence of the native western gray squirrel throughout most of the Los Angeles Basin. In the foothill areas however, where the expanding range of the fox squirrel has overlapped with that of the gray squirrel, the fox squirrel is both morphologically and ecologically similar to this native species, thus providing an opportunity for interspecific competition in areas of niche overlap (Meffe and Carrol 1994).

Interspecific competition is believed to be of limited importance in determining squirrel distributions in the Midwest where the fox squirrel and eastern gray squirrel (S. *carolinensis*) coevolved, however, that may not hold true for fox and western gray squirrels in California (Armitage and Harris 1982; Brown and Batzli 1985; Brown and Yeager 1945). In Southern California, the western gray squirrel (*S. griseus)* evolved in the absence of a conspecific arboreal squirrel species. For that reason, the introduction of a comparable sized tree squirrel with similar food and nesting site preferences may create high levels of interspecific competition between *S. niger* and *S. griseus*.

Niche theory assumes that only one species can occupy a niche space, and that competitive exclusion takes place in areas of overlap. If competition is taking place, we should see one of two outcomes over time at locations supporting both *S. niger* and *S.*

griseus. If the niche of *S. niger* contains the niche of *S. griseus* and *S. niger* is competitively superior, *S. griseus* will be excluded over time from its preferred feeding and nesting sites. Relegation to substandard sites could result in a relative decrease in fitness of *S. griseus* in that area. If *S. griseus* is competitively superior, it will eliminate *S. niger* from the part of the niche space *S. niger* occupies. The two species should then coexist within the same fundamental niche as some niche space is shared and some is exclusive (Feldhamer et. al. 1999).

The research described in this thesis was initiated in 2002 to determine: 1) the current distribution of the non-native eastern fox squirrel (*Sciurus niger*) in the Greater Los Angeles Metropolitan Area from its introduction point at the Sawtelle Veterans' Home, 2) the rate and method of this expansion, 3) the nature of the interaction between *S. niger* and the native western gray squirrel (*S. griseus*) in areas where their ranges now overlap, and 4) the timing of litter production by both species. By determining the periphery of the current fox squirrel distribution and their rate of expansion, wildlife managers in surrounding communities may be able to anticipate the locations where future range expansions may occur. With this knowledge, they can develop preemptive management strategies for pest control thus avoiding future damage.

Aggressive interaction between the two squirrel species was assumed to stem from competition over nesting sites and food availability. Therefore, tree species selected for nesting as well as food items eaten by both *S. niger* and *S. griseus* were compared at one suburban Southern California park where the ranges of both squirrel species have overlapped since about 1994. It was predicted that the generalist fox squirrel should utilize a wider variety of nest trees and food items than the native gray squirrel. Similarly, the fox squirrel should initiate and “win” significantly more aggressive interspecific interactions over feeding and nesting sites. Prior research by Brown and Yeager (1945), Byrne (1979) and Moore (1957) suggests that the fox squirrel is capable of producing two litters annually in times of abundant food resources, so it was anticipated that the fox squirrel would consistently produce two litters per year in Southern California, while the native western gray squirrel would continue producing only a single litter. The gray squirrel, therefore, would be outcompeted by sheer numbers in locations where populations come into contact with *S. niger*.

CHAPTER 2

Methods and Materials

Mapping the Current Fox Squirrel Distribution

Initial boundaries of the fox squirrel distribution were obtained though community responses to a mailed questionnaire. One hundred thirty-three questionnaires were sent to golf courses, cemeteries, arboretums and regional parks throughout Los Angeles, Ventura, Orange, Riverside, and San Bernardino Counties in Southern California. Each questionnaire displayed a color photograph of both the fox squirrel (*Sciurus niger)* and the western gray squirrel (*Sciurus griseus)* and was accompanied by a brief physical description of the species below its photograph. Recipients were asked if either species had been observed at the receiving facility and were encouraged to place a check mark in the yes or no boxes provided below each photograph. The questionnaire (Figure 1) was accompanied by a brief description of the project, contact information in case of questions, and a self-addressed stamped envelope to encourage the return of their responses.

While awaiting the return of questionnaires, numerous parks, neighborhoods, and potential undeveloped locations considered to exhibit suitable tree squirrel habitat were visited throughout Los Angeles, Orange, Ventura, San Bernardino and Riverside counties. Photographs of *S. niger* and *S. griseus* were shown to individuals encountered at these locations and they were subsequently asked to confirm the presence of either

Are either one of these tree squirrel species present at your facility? Please place a check mark next to the appropriate answer.

Western Gray Squirrel –gray body with white undersides and large bushy tail (above)

Yes____________ **No__________________**

Fox Squirrel- body is brownish-gray with rust or tan underparts.
Tail is a mixture of cinnamon and black hairs.

Yes______________ **No_____________________**

Figure 1. Questionnaire sent to golf courses, parks, cemeteries and Arboretums throughout the Greater Los Angeles Metropolitan Area.

species. The addresses of parks and residences where fox squirrels and/or gray squirrels had been observed were documented. Fifteen undergraduate students attending California State University Los Angeles (CSULA) who were enrolled in an upper division mammalogy class also assisted in gathering address data throughout the cities of Fullerton, Brea and Long Beach during two weekend field trips. The students drove or walked through neighborhoods in groups of four to five students repeating the previously described process whenever they encountered residents outside involved in activities such as walking their dog or washing their car. All addresses associated with the presence of *S. niger* or *S. griseus*, as well as those addresses described as "neither" were documented.

A website, http://instructional1.calstatela.edu/amuchli/squirrelform.htm was established in January 2003 in anticipation of greatly increasing the level of community involvement with the data collection process. Individuals viewing the website were able to enter information pertaining to either fox or gray squirrels seen in their neighborhood. The website provided a brief history of the introduction of the fox squirrel into Los Angeles County as well as a preliminary map of Los Angeles County showing 250 fox squirrel locations created using Geographic Information Systems (GIS). Individuals were asked to submit information such as their street address, the number of fox or gray squirrels seen at the reported location, squirrel interactions, and the year they first saw either species at that location. A comments section was also available where additional information could be provided in their own words. Once submitted, the data form was sent electronically to a Biological Sciences Department email account at CSULA where it could later be printed and entered in GIS format (Figure 2a, Figure 2b).

If left to chance encounter through web browsing, the number of community members discovering the webpage and subsequently submitting responses would have been inadequate. Publicity was needed in order to increase community awareness of the website. The Office of Public Affairs at CSULA therefore was contacted and agreed to assist in establishing a relationship with local publications that would be interested in writing an article featuring the newly named Southern California Fox Squirrel Project website. Several publications agreed, resulting in articles being published in the Los Angeles Times (February 8, 2003), Cal State University Reports (Fall 2003), Cal State LA Today (Fall 2003), and Scrawl of the Wild: a Southern California wildlife rehabilitators' newsletter (February 2003). Each publication was circulated among thousands to millions of individuals throughout Los Angeles, Orange, and Ventura counties. The articles included a photograph of a fox and gray squirrel, information pertaining to the introduction of the fox squirrel in Southern California, and a request for community assistance in reporting the locations of both species to the website.

The address data collected from mailed questionnaires, student collection, personal observation, and website form submittal, were entered into a database and imported into ArcGIS where each address was mapped through a process called geo-coding or geo-referencing. Geo-coding is a GIS procedure of matching addresses to a GIS database that contains a database relationship between addresses and geographic

Date of sighting:

<Month> <Day> <Year>

Location/Address of sighting
(e.g. 1234 Oak St., Los Angeles, CA, 90032 or Pinecrest Blvd and La Cieniga Ave, Los Angeles)

How many fox squirrels were observed?:

<quantity>

How many gray squirrels were observed?:

None

Did you observe any interactions between tree squirrels? (Check all that apply):

- [ ] No interactions observed
- [ ] Aggressive interactions between 2 fox squirrels
- [ ] Aggressive interactions between 2 gray squirrels
- [ ] Aggressive interactions between a fox squirrel and a gray squirrel
- [ ] Playful interactions between 2 fox squirrels
- [ ] Playful interactions between 2 gray squirrels
- [ ] Playful interactions between a fox squirrel and a gray squirrel

Figure 2a –Data Collection Form from Southern California Fox Squirrel Webpage.

Environment:

- (•) Single Family Residence
- ( ) Commercial or Business Establishment
- ( ) School, College or University Campus
- ( ) Farmland
- ( ) Vacant Lot
- ( ) Apartment/Condo/Townhouse
- ( ) Cemetery
- ( ) Local or State Park
- ( ) Zoo, Arboretum or Botanical Garden

Are there raptors (e.g. hawks), cats and/or dogs present at the area?

Raptors	( ) None	( ) Low	( ) Medium	( ) High
Dogs:	( ) None	( ) Low	( ) Medium	( ) High
Cats:	( ) None	( ) Low	( ) Medium	( ) High

When did you first observe the presence of fox squirrels in this particular location?:

- ( ) within the past year
- ( ) within the past 5 years
- ( ) within the past 10 years
- ( ) within the past 20 years
- ( ) over 20 years ago
- ( ) not sure

How did you find this web page?

<select below > Other:

Please enter any additional comments you may have in the space provided below

Figure 2b. Continuation of Southern California Fox Squirrel website submission form. http://instructional1.calstatela.edu/amuchli/squirrelform.htm features. Geo-coding software (ArcGIS version 8.0) links records in the two databases by matching street names and addresses. When the database records are successfully matched to a reference street map, the records are tagged with the correct map positions, typically longitude and latitude coordinates. Once the geo-coding is completed, the database table carries its own position information and can be mapped without the reference street map or address dictionary (Ormsby et al. 2001; Schlosser 2001).

Reference layer maps used in geo-referencing fox squirrel locations in each county included Los Angeles County Roads, Ventura County Roads, and Orange County Roads. These layers, made publicly available for free downloading by Environmental Systems Research Institute (ESRI), are based on Census 2000 TIGER/Line Data produced by the U.S. Bureau of the Census. All addresses representing a fox squirrel location were entered into the database, geo-coded, and subsequently plotted on the Roads Layer for each of the three counties, thus generating a new map: 2004 Fox Squirrel Distribution in Los Angeles, Orange and Ventura Counties. Each address submitted was represented by a diamond-shaped colored symbol on the map generated through the geo-coding process.

In order to determine if members of the community submitting address data to the website were able to accurately identify and thereby distinguish the fox squirrel from the gray squirrel or California ground squirrel (*Spermophilus beecheyi*), 50 addresses, roughly 10 percent, were randomly selected from all 473 addresses submitted via the website and visited to visually confirm the report. Fox squirrels seen within two residential blocks of the given address were considered to also occur at the reported address. Leaf nests observed in trees lining the designated street were documented, while residents seen outside within the two block radius were shown photographs of the 3 squirrel species and were asked to confirm or deny the presence of the fox squirrel at that location.

A second map was created to show the historical range expansion of the fox squirrel from its introduction point at the Sawtelle Veterans' Home in 1904, to the current distribution in 2004. The boundaries of the fox squirrel distribution during the years of 1904, 1920, 1930 and 1947, were defined in an article written by Elmer Becker, the Los Angeles Agricultural Commissioner during the 1940s (Becker and Kimball 1947). The street boundaries described by Becker were considered reasonably accurate and confirmed through specimen collection dates and locations for fox squirrels in the mammal collection at the Los Angeles County Museum of Natural History. This information was used to define the boundaries for the fox squirrel in Los Angeles County from 1904 through 1947. Information pertaining to fox squirrel distribution in Ventura County during 1970 was obtained from Wolf and Roest (1971). No later publications have described the range expansion of the fox squirrel, so subsequent distributional data used in this study were collected from the 354 submissions to the website which provided a precise year that fox squirrels were first seen at the residences indicated.

Behavioral Interactions Between Fox Squirrels and Gray Squirrels

Study Area

The city of San Dimas, located in Southern California is characterized by a Mediterranean climate having short wet winters and long hot summers with most of the yearly precipitation (<10 inches) occurring between the months of November and April. Average daily temperatures typically range between 55 and 95 degrees Fahrenheit.

San Dimas Canyon Park (SDCP) has supported a breeding population of both *S. niger* and *S. griseus* for a minimum of 10 years and was selected as the study area for the collection of nesting and behavioral data associated with both *S. niger* and *S. griseus*. The 138-acre park is located at approximately 1080 feet elevation at the intersection of Sycamore Canyon Road and San Dimas Canyon Road in the city of San Dimas (34N 08'00", 117W 47' 43"). This suburban park is bordered by the Angeles National Forest to the north, residential homes to the east and west, and a flood control channel to the south of San Dimas Canyon Road. A chain-link fence and dirt pathway run East/West the length of the park, separating the 12.8 southernmost acres of suitable tree squirrel habitat from the remaining 125 acres of what may be considered unsuitable habitat. All observations of nests and squirrels therefore took place in this southern area between the fence and San Dimas Canyon Road (Figure 3).

North of the fence, open fields of black mustard (*Brassica nigra*), jimson weed (*Datura wrightii*), and foxtail (*Setaria sp.*) gradually ascend into chaparral-covered foothills. Gray and fox squirrels coexist together in this coast live oak transitional zone at the base of the foothills. The northern end of the park is bordered by National Forest Service land and quickly changes from coast live oak and western sycamore to a coastal sage scrub ecosystem, supporting such plant species as prickly pear cactus (*Opuntia littoralis*), bush monkey flower (*Mimulus aurantiacus*), poison oak (*Toxicodendron diversilobum*), white sage (*Salvia apiana*), coyote brush (*Baccharis pilularis sp*.), and sugar bush (*Rhus ovata*).

Within the study area, the tree species most commonly represented in order of abundance were: coast live oak (*Quercus agrifolia)*, blue gum eucalyptus (*Eucalyptus globules*), red gum eucalyptus (*Eucalyptus camaldulensis*), western sycamore (*Platanus racemosa*), Chinese elm (*Ulmus parvifolia*), and casuarina (*Casuarina equisetifolia*). The majority of mature oaks were in excess of 100 years of age and produced considerable mast each fall. The park's understory vegetation was comprised of a well-manicured lawn, which was trimmed weekly, and all acorns not buried by squirrels or avian species such as scrub jays and acorn woodpeckers were raked and disposed of by greenskeepers. Very few shrubs were present, thus scarcely contributing to the understory vegetation layer utilized by either squirrel species.

Figure 3. Aerial photograph of the southern portion of San Dimas Canyon Park study site. Image taken 01 June 1994, courtesy of the
US Geologic Survey. ©2004 Microsoft Corporation

Location and Use of Nests in San Dimas Canyon Park

All trees growing south of the bisecting fence were counted while walking along 10m transect lines from north to south. This process was then repeated in the east to west direction for numerical comparison. Trees were identified as one of eight species: coast live oak, eucalyptus, maple, Chinese elm, magnolia, pine, sycamore or fruitless mulberry and their relative frequency of occurrence calculated. All cherry trees and saplings of the eight species were excluded due to small tree size and were not considered to be used by either *S. niger* or *S. griseus* as a potential source of food or nesting site.

Leaf and cavity nests of both species were tallied in SDCP each month between September 2002 and September 2003. Due to the difficultly in accurately differentiating between active and inactive nests, only those nests with a general tight spherical shape and large enough to hold an adult squirrel were counted. A detailed description of nest location, tree species in which the nest was found, unique identifying nest number, and observation date, was assigned to each tree squirrel leaf or cavity nest viewed during nest searches. In order to locate potential nests throughout the study area, each tree was visited and the canopy visually scanned while standing underneath or circling the tree. A squirrel observed crawling into a nest and remaining there for a minimum of five minutes was considered to be utilizing that nest and was matched with the nest unique identifying number. All squirrels were identified to species, sex, and age-class whenever possible. All nests linked to a particular squirrel species were subsequently marked as waypoints and mapped using a Garmin 76S Global Positioning System (GPS) unit. Nest locations identified as waypoints were then uploaded into Garmin MapSource US Topo Software and mapped at 200-foot zoom for analysis.

Scan Sampling of Squirrel Behaviors

Scan sampling was the method used to identify the daily activity patterns of both *S. niger* and *S. griseus* throughout the year at SDCP. Upon arrival at the study site, a visual scan of the park using 7x42 power binoculars was made. The number of fox and/or gray squirrels seen at that time was noted, and their behavior at that instant was documented. This procedure was repeated every ten minutes for the duration of the day's observation period. Observations of gray squirrels and fox squirrels within SDCP took place on average 6 times per month between October 2002 and September 2003 during peak hours of squirrel activity. In order to cover the entire diurnal period for activity throughout the year, yet avoid observer fatigue by observing sunrise to sunset, the day was broken up into more manageable subunits of 4-7 hour increments, with an average of 4 hours 40 minutes spent per observation day. For example, day one may have entailed making observations from 6am to 10am or 6am to 12pm, while observations on day two encompassed the hours of 10am to 2pm or 10am to 5pm. This allowed for all periods to be evenly covered without the single observer being present at SDCP during all daylight hours once or twice weekly.

Activity Patterns of *S. niger* and *S. griseus*

Instantaneous sampling was conducted during 10-minute observation periods in conjunction with scan sampling during each visit to SDCP. Instantaneous sampling, a form of one-zero sampling, allowed the observer to score whether a behavior occurred (1) or did not occur (zero) at predetermined "points" in time. In each case, a single subject animal, *S. niger* or *S. griseus* was selected from the park and its behavior was recorded. The squirrel seen upon arrival at the park was the first subject selected. Each additional animal sampled was selected *ad libitum*, yet typically represented the next animal of the opposite species able to be located at the opposite end of the park where the previous animal was sampled. Data were recorded on check-sheets containing 10 columns denoting 10 different possible categories of behavior, and 40 rows denoting successive 15-second sampling intervals. The 10 categories established were: 1) travel in/up tree 2) scavenging for food in tree or on ground 3) still: no movement 4) lying/sleeping on branch 5) walking/running on ground 6) eating 7) grooming 8) building nest 9) burying acorns 10) interacting with another individual: fox or gray. A pocket watch with a visible second hand was used to determine the timing of each record. All behaviors exhibited by the subject animal at the instant the second hand landed on the 12, 3, 6, or 9 (beginning of each 15-second sample interval) were recorded in the interval block in which they occurred and were considered a sample point (Altmann 1974; Lechner 1979). Standard information such as date, time, weather, species, sex, age-class, physical description, types of food eaten, and location of subject within the park, were all documented at the top of each check sheet.

The relative time spent by each species in major out-of-nest activities was determined. The original 10 categories were too narrow in scope, and thus several were either combined into 4 primary categories: Foraging, Traveling, Agonistic and Resting or were eliminated from the analysis due to lack of data. Proportions of time spent in each activity by season were compared using pie charts similar to those displayed by Ryan and Carey (1995).

Aggressive Interactions

Aggressive interactions occurring between two or more individual squirrels were documented using behavior sampling, also referred to as “conspicuous behavior recording”. This method of sampling has mainly been used for “recording rare but significant types of behavior such as fights or copulations, where it is important to record each occurrence” (Martin and Bateson 1994). During weekly data collection, two squirrels seen in close proximity (<10’) to one another on the ground were observed for signs of behavioral interaction. Displays of aggression often escalated from one squirrel standing upright on its hind legs looking directly at the other individual, to teeth chattering, violent tail wagging, and finally a charge and chase in which the initiator would bite at the tail and hind quarters of the targeted animal while in close pursuit.

Submissive behavior displayed included running across the ground and up the nearest tree in an effort to escape the biting of the aggressor. The submissive individual would often be chased for less than 30 seconds, whereby the initiator would terminate the pursuit, descend the tree, and return to the area where the chase began to resume its prior activity. All interactions occurring between two squirrels whether interspecific or intraspecific in nature were documented. The species of squirrels involved, the date, time, initiator, winner, loser, sex, age-class, and a written description of what occurred were documented whenever witnessed. A Chi-square test was used to compare the number of interspecific aggressive interactions initiated and won by *S. niger* as compared to those of *S. griseus*.

Yearly Litter Production By *S. niger* and *S. griseus*

Mating chases between conspecifics were distinguished from aggressive interactions by the males of either species slowly yet relentlessly following females on the ground or in the trees. This behavior was generally accompanied by the sniffing of the female genitalia, a slow wagging of the tail and a general disinterest by the pursued female. If the casual following erupted into a chase, it typically moved to a tree where the two squirrels would playfully circle the tree trunk, often stopping and waving their tails. These chases would often last several minutes or more in duration and would occasionally involve multiple males pursuing a single female. The dates of such occurrences between two or more fox squirrels or gray squirrels were recorded in order to identify the approximate breeding season(s) of each species.

In order to compare the timing of the breeding seasons and number of litters each species produce annually with what was witnessed at SDCP, wildlife rehabilitation centers within Los Angeles, Ventura, and Orange Counties that accept *S. niger* and/or *S. griseus* were contacted. The three centers willing to participate were asked to submit the specific dates during 2002 and 2003 in which they had received litters of nestling tree squirrels. For both species, they were asked to provide the age (in weeks) of each litter at the time the nestlings were brought to the rehabilitation center if this had been documented. Due to the small number (n=15) of gray squirrel litters accepted at wildlife centers as compared to fox squirrel litters (n=135), the number of gray squirrel litters born in each month were converted into a percentage of the total number of gray squirrel litters born. Assuming the total number of gray squirrel litters was equal to the total number of fox squirrel litters, the percentages for each month were multiplied by 135, allowing for the projected number each month of gray squirrels to be based upon the same total number of litters as the fox squirrel. The relative numbers of litters per month for both species were subsequently graphed to show the peaks of litter production for each species during the year.

CHAPTER 3

Results

<u>The Current Distribution of *S. niger*</u>

<u>Geo-Coding</u>

A total of 831 addresses from Los Angeles County along with 24 addresses from Orange County and 49 addresses from Ventura County were geo-coded (Appendix 1). Four-hundred-twenty seven of the 831 addresses from Los Angeles County were obtained through website submission, while 79 addresses were the result of returned questionnaires sent to area golf courses, cemeteries, parks and arboretums. Eighty six addresses were contributed as a result of two CSULA Mammalogy class field trips and 163 addresses were provided by two participating wildlife rehabilitation centers: Wildlife on Wheels and California Wildlife Care Center. The remaining addresses were collected through personal observation (n=21), contacting residents walking in neighborhoods (n=28), 23 twelfth-grade student responses after an in-class presentation at Bravo Medical Magnet High School, and 4 from specimens at the Los Angeles County Museum of Natural History.

Locations of fox squirrels occurring throughout Orange County (n=24) were gathered via the website (n=13), returned questionnaires (n=5), and personal contact with individuals at their residence (n=6). Similarly, a total of 49 addresses were recorded in Ventura County, with the majority coming from website response (n=33). The remaining addresses were collected via wildlife rehabilitation centers (n=6), returned questionnaires (n=7), and personal observations (n=3) (Figure 4).

Fifty of the 473 total addresses obtained for the three counties via the website were randomly selected and personally visited to establish the validity of the community's responses to the data form. The presence of *S. niger* was visually confirmed at 49 of 50 (98 percent) visited locations. A single residence in the city of Walnut believed to have incorrectly reported the presence of *S. niger*, supported multiple colonies of *S. beecheyi* on the hill above the home. The home was built less than a year earlier in a new housing development considered as unsuitable habitat due to the absence of large trees. Contacting multiple residents walking outside in the surrounding area, confirmed the absence of *S. niger* at this location.

The current distribution of the fox squirrel in Los Angeles, Orange, and Ventura Counties is shown in Figure 5. As of June 2004, the current distribution of the fox squirrel in Los Angeles County was found to encompass the majority of West Los Angeles and Santa Monica; extending along the coastal cities of Malibu and most communities ranging between Pacific Palisades south to Rancho Palos Verdes, San Pedro and Long Beach. Heading in the northeast direction from Long Beach, the fox squirrel distribution follows the Los Angeles County border with Orange County where it has been reported to occur in the cities of Whittier, Walnut, and West Covina. The fox squirrel was reported being seen for the first time in 2003 in the cities of Claremont and

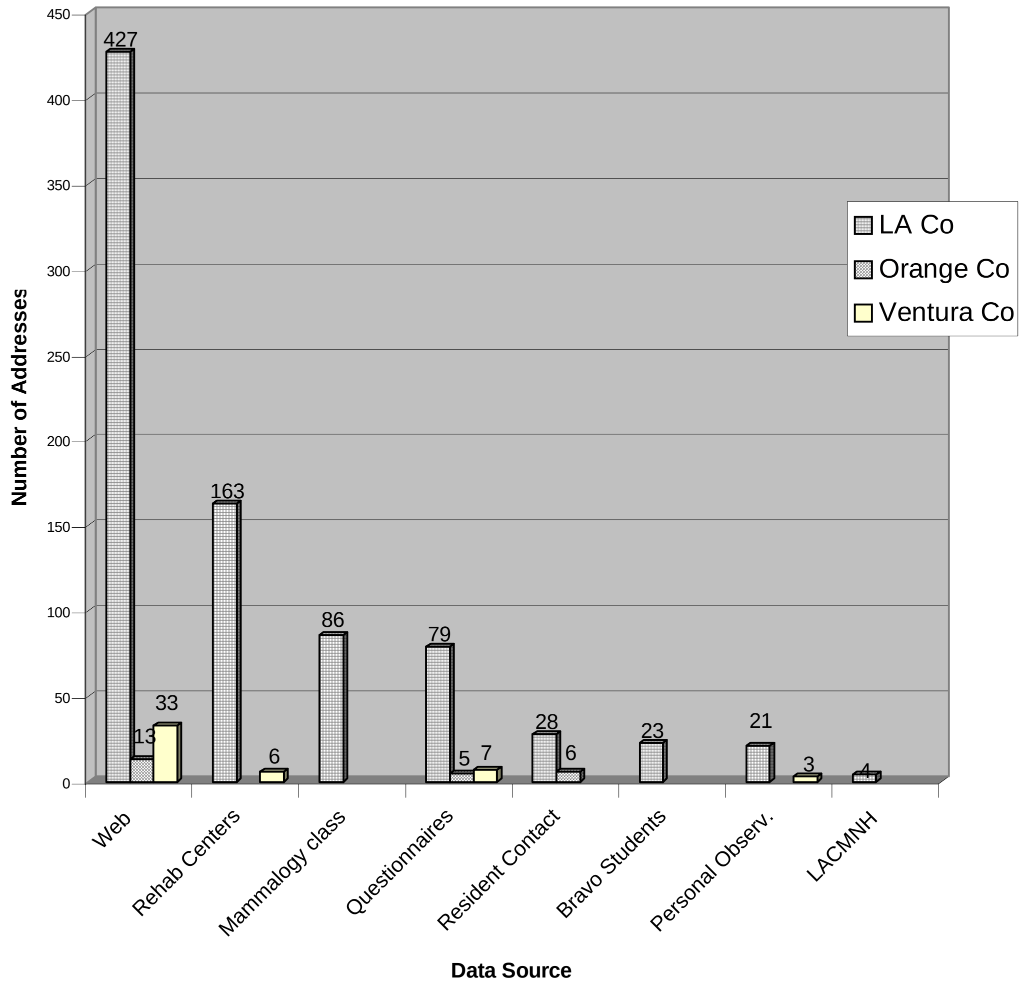

Figure 9 Sources of address data using in mapping the distribution of S. griseus in Los Angeles, Orange & Ventura Counties

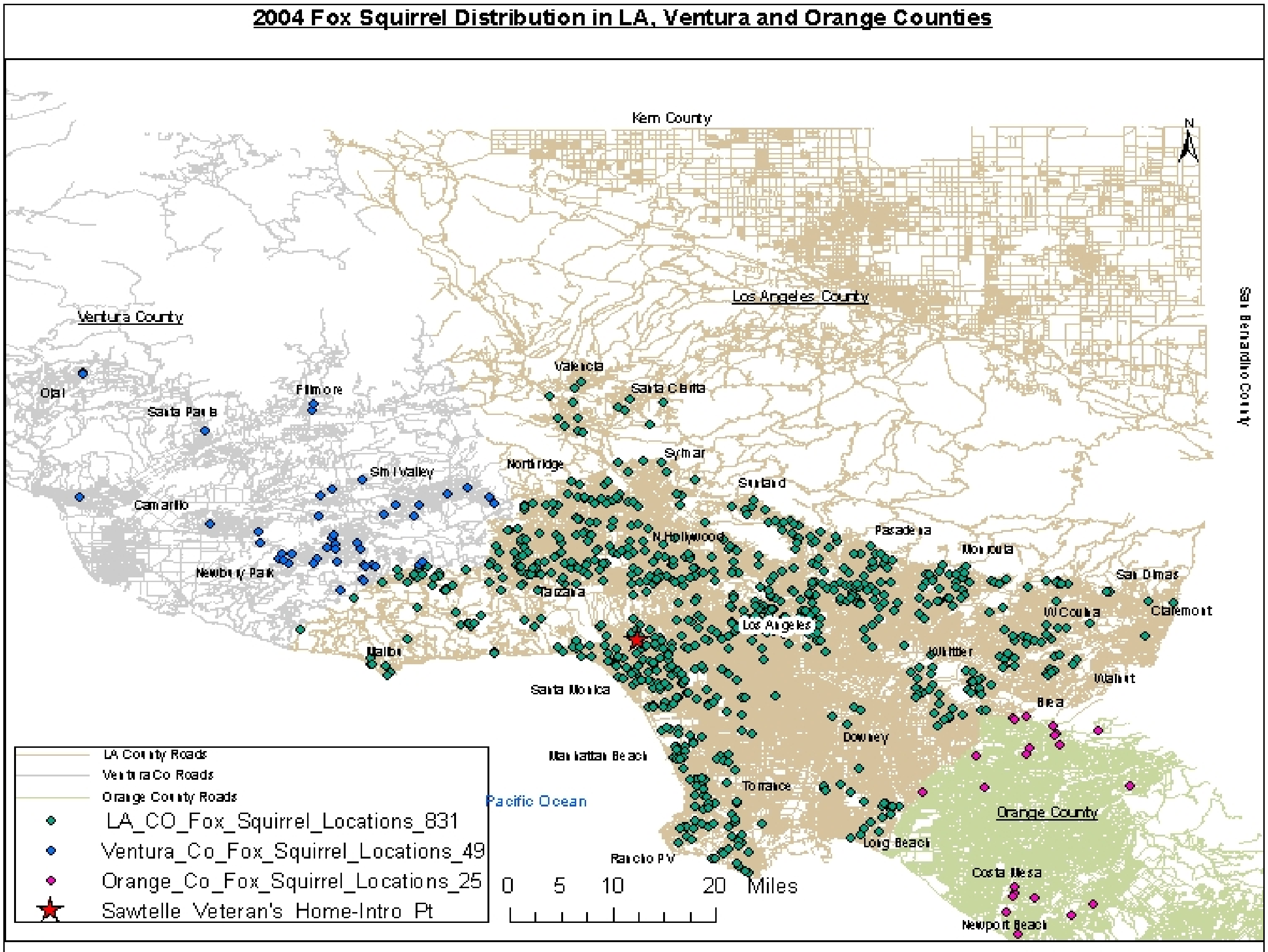

Figure 5: 2004 Distribution of S. niger in the Greater Los Angeles Metropolitan Area

Pomona, which have come to represent the easternmost boundary of their distribution in Los Angeles County thus far.

The northern border of the range for fox squirrels includes the southern foothill communities of the San Gabriel Mountains including such cities as San Dimas, Monrovia, Arcadia, Altadena, La Canada, Tujunga, and Lakeview Terrace as well as Valencia, Santa Clarita, Canyon Country, and Saugus. Fox squirrels have not been reported to occur north of these communities in the undeveloped forested areas of the San Gabriel Mountains aside from occasional riparian canyon corridors leading up out of housing developments.

The distribution of the fox squirrel along the Ventura County border includes the cities of Northridge, Chatsworth, West Hills, Agoura Hills, Calabasas, and West Lake Village. In Ventura County, *S. niger* is found throughout the Simi Valley, as well as in Thousand Oaks, Newbury Park, Moorpark, Camarillo, Fillmore, Ventura and Santa Paula. The fox squirrel has occupied many of these areas in Ventura County since the mid-1960s.

Unlike what is seen in Los Angeles and Ventura Counties, *S. niger* has only been documented in several isolated pockets of Orange County. Through human involvement, *S. niger* is believed to have been intentionally introduced into several parks and surrounding neighborhoods within the cities of Irvine, Costa Mesa and Newport Beach circa 1998. Also, within the last five years, juvenile dispersal has allowed *S. niger* to naturally extend its distribution southward from Los Angeles County into the bordering Orange County cities of Brea and La Habra.

The distribution of the fox squirrel within Los Angeles, Orange, and Ventura counties was found to overlap with that of the gray squirrel (*S. griseus*) in less developed foothill areas supporting substantial numbers of mature coast live oaks. These areas of distributional overlap between the two species include pockets within the cities of San Dimas, Whittier, La Habra, Claremont, and much of the Santa Monica Mountains National Recreation Area, as well as the Puente Hills (Figure 6). *Sciurus griseus* and *S. niger* are also found together in several isolated localities such as Industry Hills Golf Course where they both may have been introduced.

Sciurus griseus is the only tree squirrel species, however, found in the undeveloped public lands of the Los Angeles, Los Padres and Cleveland National Forests. In suburban areas where it occurs alone, *S. griseus* typically inhabits less developed locales such as golf courses and parks situated along the base of the foothills (Figure 7). Neither *S. niger* nor *S. griseus* has been reported within Los Angeles County north of the San Gabriel Mountains, in cities such as Lancaster and Palmdale. This absence is attributed to a lack of suitable habitat. Both squirrel species are likewise believed to be absent from the urban industrial inner cities of south central Los Angeles County, which include the cities of Lynwood, Compton, and Carson. Several trips to parks within this geographic area produced no confirmed sightings, while returned

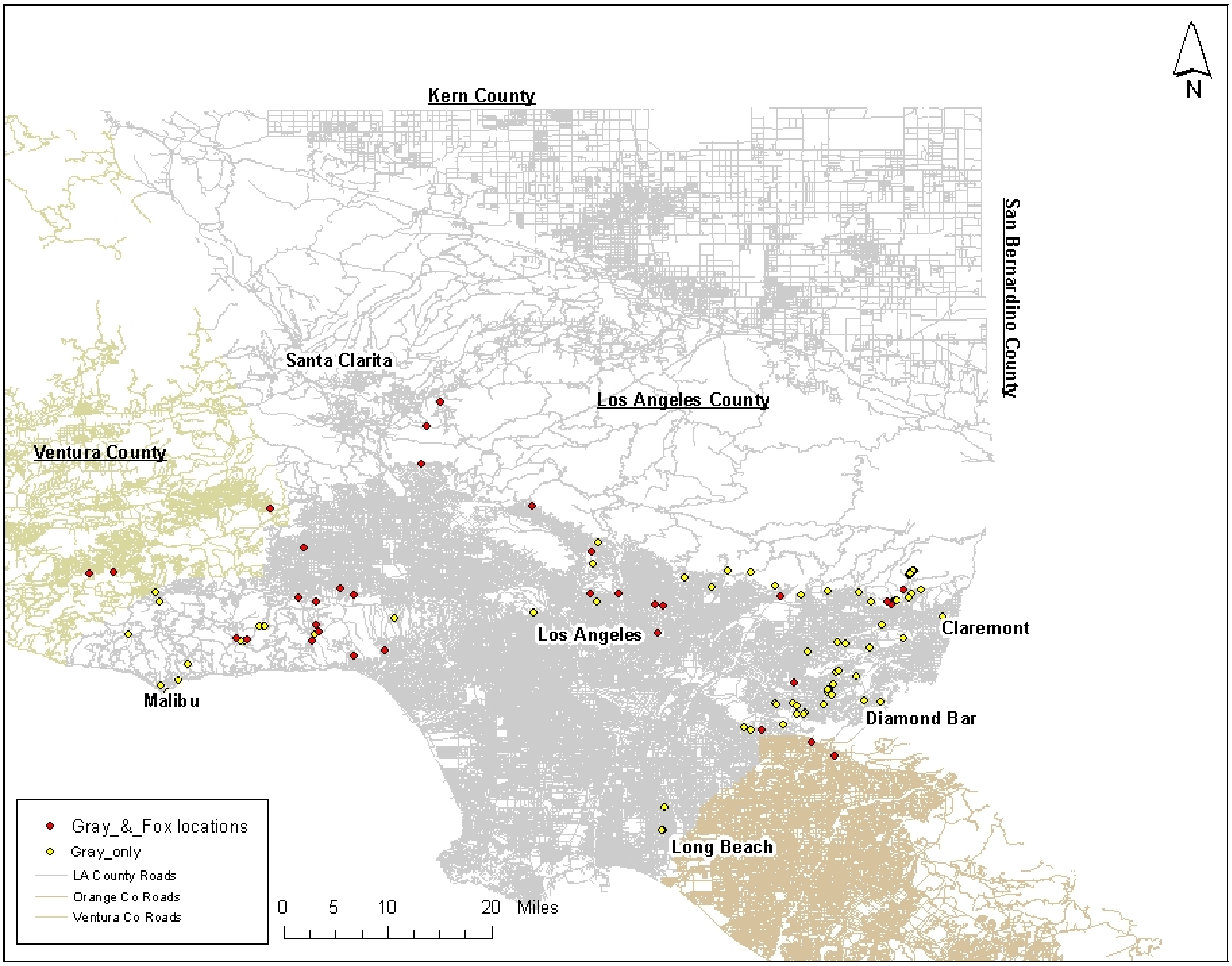

Figure 6. Locations where only *S. griseus* were reported and locations where both S. griseus and *S. niger* occur together.

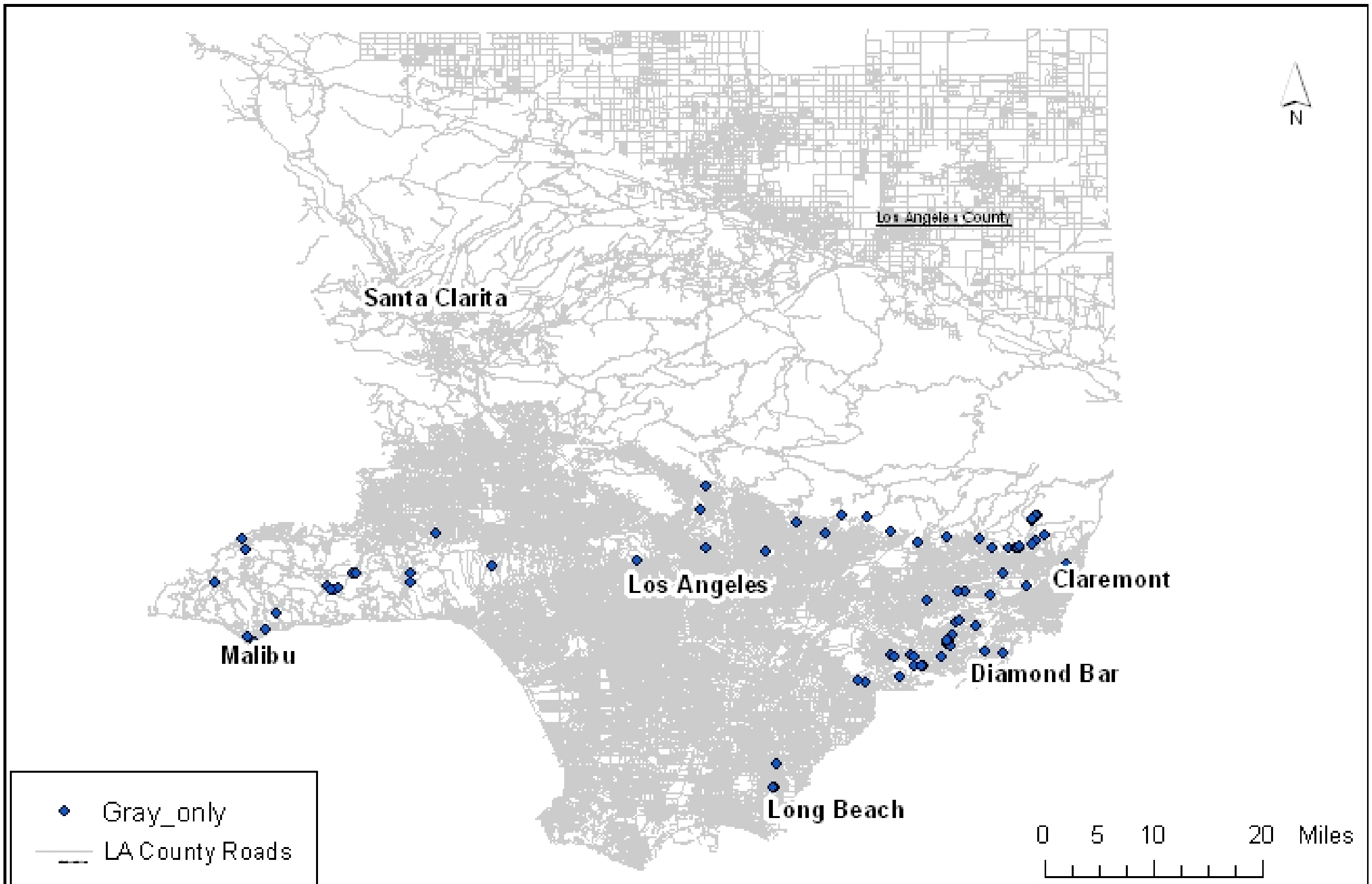

Figure 7. Locations of western gray squirrels reported in developed areas of Los Angeles County.

questionnaires and website submissions similarly provided no accounts of either squirrel species.

Historical Movement of *S. niger*

The distribution and average expansion rate was determined for *S. niger* in the Greater Los Angeles Metropolitan Area. The squirrel advanced most rapidly from Sawtelle eastward to Claremont, a straight-line distance of 41.26 miles (66.34 km) in 99 years (0.68 km/yr), and northwest to Ventura, a distance of 47.2 miles (75.86 km) in 22 years (3.44 km/yr). Movement southward to the city of San Pedro represents a distance of 25.4 miles (40.9 km) in 6 years (6.84 km/yr), while expansion northward extended 26.9 miles (43.25 km) to Saugus by 1975 (1.5 km/yr) (Figure 8). The dispersion pattern was not equal in all directions due to the Pacific Ocean to the west, and the coniferous forests of the San Gabriel Mountains to the north. The expansion has been primarily to the northwest and to a lesser degree, eastwardly. This movement rate therefore ranges from 0.68 km/yr to 6.84 km/yr (0.42-4.25 miles/yr) over varying periods of time.

Data establishing the historical distribution of the fox squirrel in Los Angeles County between the years of 1904 to 1947 were obtained from detailed descriptions provided by Becker and Kimball (1947). They reported that *Sciurus niger rufiventer* had

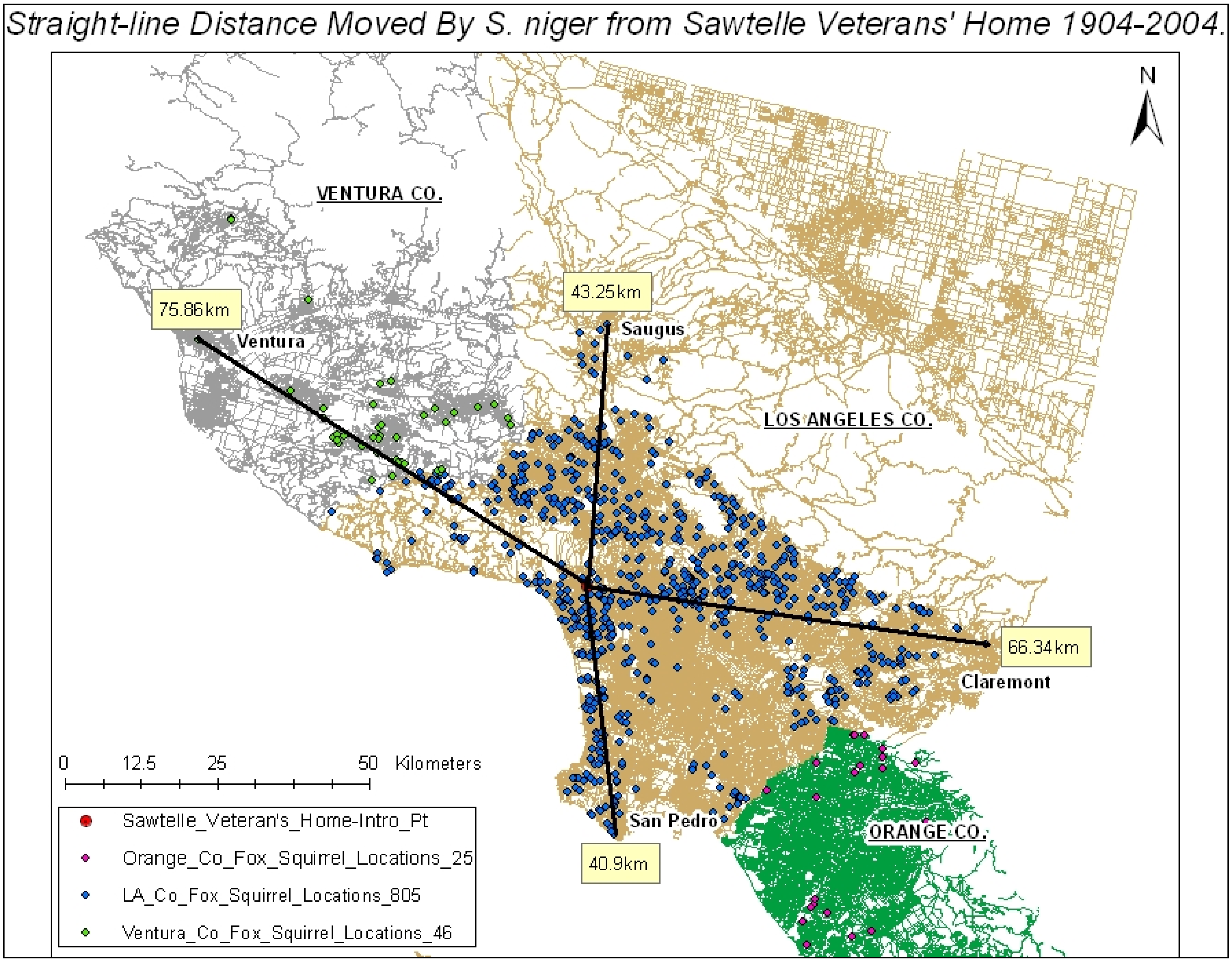

Figure 8. Straight-line distance moved by *S. niger* from Sawtelle Veterans' Home 1904-2004.

been introduced into Los Angeles County from the Mississippi Valley just prior to 1904, presumably by veterans residing at the Sawtelle Veterans' Home on Sepulveda and Wilshire Boulevards. The earliest Southern California specimens of this subspecies in the Los Angeles County Museum of Natural History, however, were collected from the city of Encino in 1942 (Jim Dines, personal communication 2003). Numerous introductions into Southern California surely took place later; however detailed records have not been kept. According to Becker and Kimball (1947), between 1904 and 1920, the fox squirrel expanded its range from Sawtelle into:

> *"the trees just north of the Veterans' Hospital near the old walnut orchard that used to be immediately west of Sepulveda and south of Sunset Blvd." They undoubtedly had reached areas of Santa Monica and Westwood as well. "They took to the Santa Monica Hills and their numbers increased by leaps and bounds. By the middle 1930s it was not uncommon to see them in the wind breaks of walnut orchards along Ventura Blvd from Sepulveda Blvd, westward to Calabasas. By 1947 they had spread "eastward through the Santa Monica Mountains to directly north of the Los Angeles City Hall, a distance of 18 or 20 miles. How far westward into the Conejo country no one knows. They have traveled northward into and across the San Fernando Valley over Santa Susana Pass into the walnut sections of Simi Valley. Eastward they've covered the valley and are probably already in the San Gabriel Mountains."*

George Willet similarly reported the presence of the fox squirrel at "several localities in the San Fernando Valley region" as of 1944 (Willet 1944). Subsequent estimations of their distribution had not been made until 1971 when Roest and Wolf described the distribution of the fox squirrel in Ventura County. They described the fox squirrel as inhabiting:

> *"the coastal plain from near Oxnard north to the mouth of the Santa Clara River and eastward to the vicinity of Camarillo; the Simi Valley as far east as the town of Simi; and the Santa Clara River Valley as far as Fillmore. There are unconfirmed reports of fox squirrels at Lake Casitas and Lion Canyon Campground and in Santa Barbara County near Carpinteria".*

Successive historical distribution data for *S. niger* were obtained from 354 website submissions making specific reference to the first year *S. niger* was observed at the reported location and typically included additional details in the comments sections.

In Los Angeles County, responses to the website data form indicated that *S. niger* occupied cities such as Woodland Hills, Santa Monica and Van Nuys during the 1950s and 1960s and had expanded its range by 1970 to include the cities of Sunland, Playa Del Rey, La Canada, Agoura Hills and Calabasas. These dates and locations were consistent with museum specimens at the Los Angeles County Natural History Museum collected during these time periods.

By 1980 *S. niger* had naturally extended its northern distribution into the cities of Valencia, Santa Clarita and Newhall, while simultaneously moving southward into Pacific Palisades and Topanga. During this time, circa 1980, the fox squirrel was assisted with expanding its range into new areas by being intentionally introduced into the city of Long Beach by unknown citizens. The fox squirrel was subsequently observed in Long Beach's El Dorado Park no earlier than 1990. By 1993, *S. niger* had dispersed northward from the park into the city of Downey and westward into Torrance. As this newly introduced population became established in the Long Beach region, the primary fox squirrel population continued its Los Angeles County eastward colonization, and had established populations in the communities of Monrovia, Duarte, Whittier, Temple City and Hacienda Heights by 1990.

Continued natural dispersal was representative of the fox squirrel movements into West Covina, Walnut, the City of Industry, and La Puente by 1998. Their intentional introduction in 1998 by unknown sources additionally resulted in their presence at several golf courses and parks on the Rancho Palos Verdes Peninsula. That same year, intentional introductions were also made into the city of Manhattan Beach in Los Angeles County as well as into the city of Costa Mesa in Orange County. Today, six years later, *S. niger* is know to inhabit most areas of the Palos Verdes Peninsula and is well established in both Manhattan Beach and Costa Mesa.

By 2002, natural range expansion southward from Los Angeles County resulted in populations of *S. niger* becoming established in the Orange County cities of Brea, La Habra Heights, Fullerton and Buena Park. That same year, *S. niger* was intentionally introduced in similar fashion as in previous examples, into the cities of Newport Beach and Irvine in Orange County.

Detailed accounts submitted to the website that included dates, together with the boundaries detailed by Becker and Kimball (1947) and Wolf and Roest (1971), were used to create an historical movement map depicting fox squirrel expansion at approximately 5,10, and 20-year intervals (Figure 9).

Behavioral Interactions

Location and Use of Nests

A total of 425 trees in the southern 12.8 acres of San Dimas Canyon Park exceeded 7" diameter at breast height (dbh), and were therefore categorized as large enough to serve as possible nest trees. Coast live oak comprised 59% of those trees available, while 26% were represented as blue or red gum eucalyptus. These two tree species, oak and eucalyptus, account for a combined total of 85% of all available nest trees in the park. In those 425 available trees, a total of 90 individual leaf nests were identified throughout the year, indicating that nesting space was not a limited resource in which to compete. Only 46 of the 90 nests however, were positively linked to either a fox squirrel (n=23) or gray squirrel (n=23). A single cavity nest in a sycamore tree was identified as being used by a female fox squirrel and her offspring, while all other nests were identified as "leaf nests." Many additional cavities with chew marks at the entrance indicating squirrel use were observed, yet they could not be classified as active, nor were they distinguishable from cavities being actively used by acorn woodpeckers, Nuttall's woodpeckers, or northern flickers.

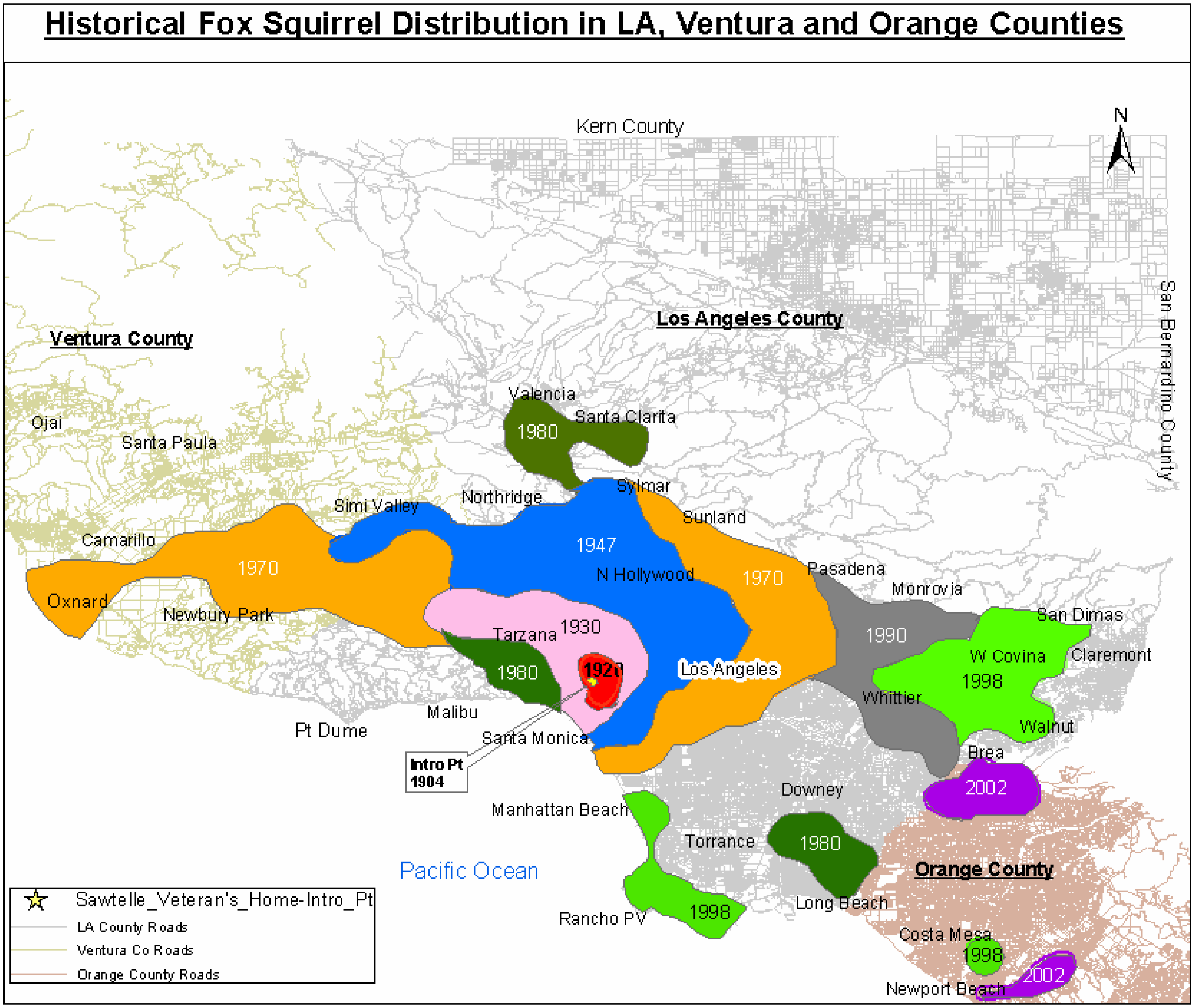

Figure 9. Historical movement of the fox squirrel from 1904 to 2003 in Los Angeles, Orange, and Ventura Counties.

Twenty-three nests utilized by *S. niger* were located in 5 of 14 tree species found within the study area. These nests were observed in tree species in the following relative abundances: Coast Live Oak (n= 12, 52%), Eucalyptus (n= 6, 26%), Casuarina (n=3, 13%), Chinese Elm (n=1, 4%), and Western Sycamore (n=1, 4%). Fox squirrels built these nests in 4 of the 5 tree species according to the proportion of availability of the tree species. Only the Cassuarina tree was used significantly more than expected (X^2= 14.02, $p<0.005$, df=1).

Gray squirrels by contrast, were observed to have built nests in only two of the 14 tree species found within the park, yet gray squirrels also used these two species according to their availability. Of the 23 nests linked to *S. griseus*, 16 (70%) were built in Coast Live Oak, while the remaining 7 (30%) were built in Eucalyptus (Figure 10).

Multiple leaf nests were often observed in the same tree, however no trees were identified to have both a gray and fox squirrel nest in the same tree. Aside from one gray squirrel leaf nest located along the park's western parking lot, gray squirrel nests were primarily clumped in the park's interior, furthest from the roads and ball field. Fox squirrel nests by contrast, tended to be located in trees along the park boundary and nearest to residential homes (Figure 11).

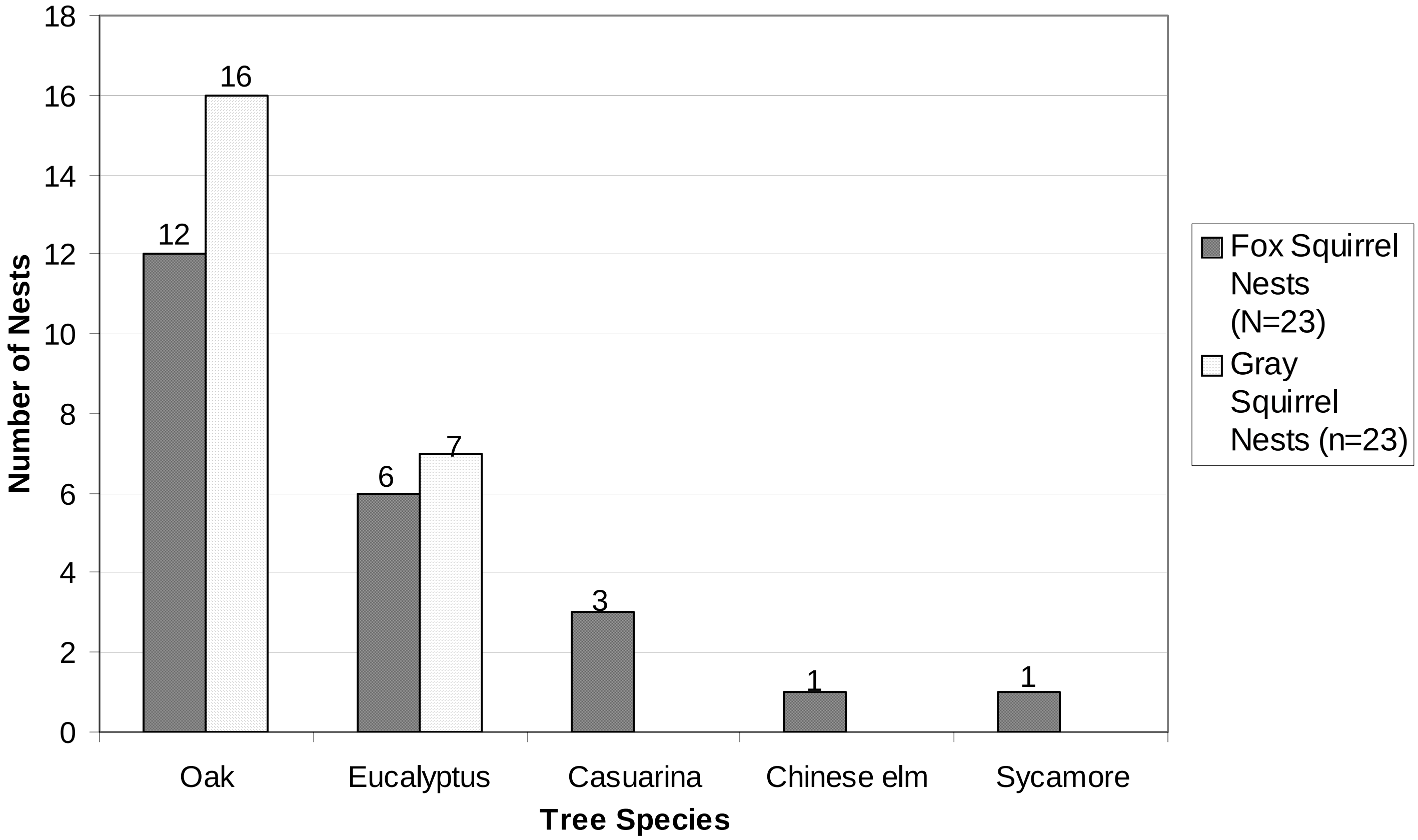

Figure 10. Number of fox squirrel and gray squirrel nests observed in each tree species in San Dimas Canyon Park, 2002-2003.

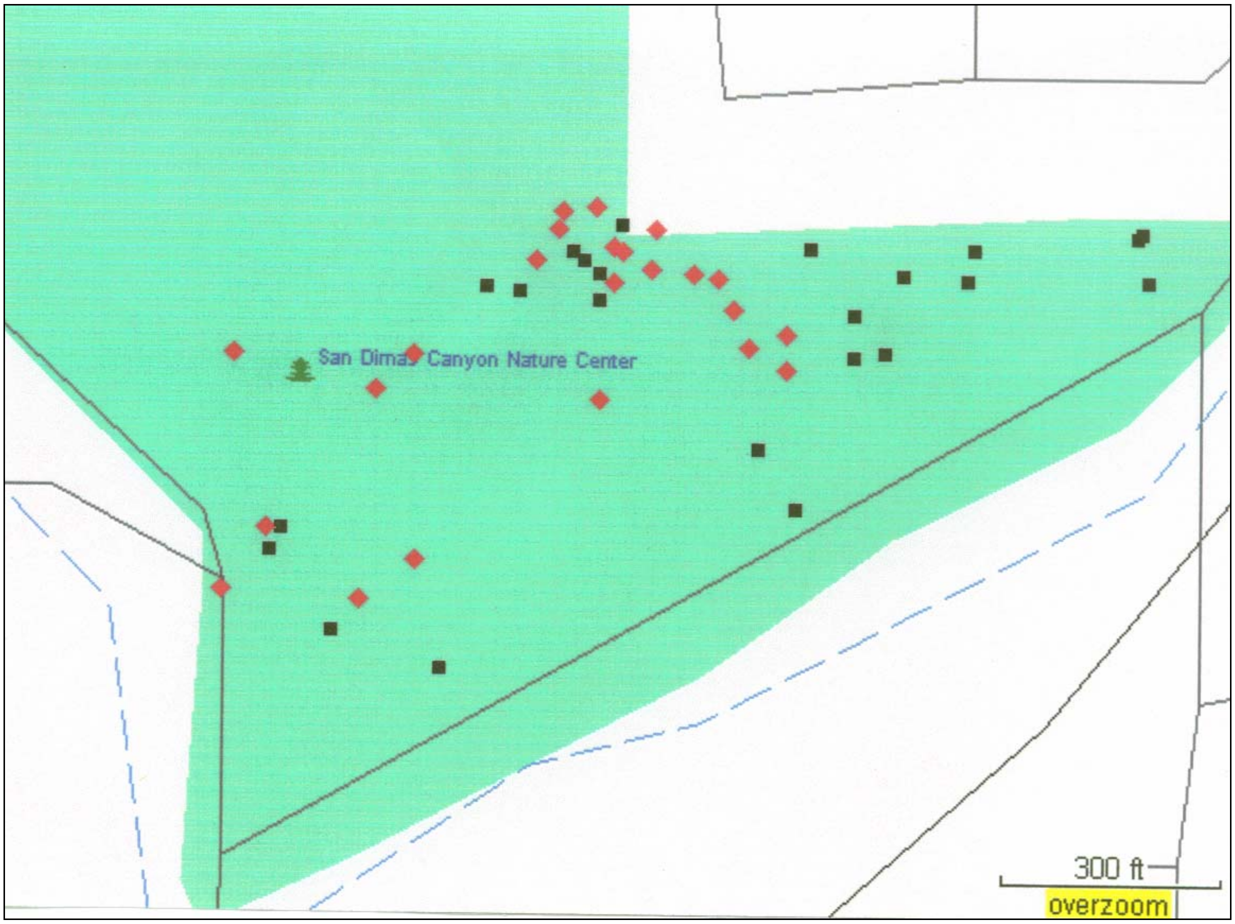

Figure 11. GPS waypoint locations of 23 gray squirrel nests represented by red triangles and 23 fox squirrel nests represented by black squares in San Dimas Canyon Park. Park image courtesy of Garmin MapSource US Topo Version 4.0.

Activity Patterns

A total of 66 visits were made to SDCP between October 2002 and September 2003, with an average of 6.4 visits per month. The duration of each visit averaged 4 hours 41 minutes. A total of 260 ten-minute observation periods took place, during which time 148 periods were spent documenting fox squirrel behavior while 112 periods were spent recording gray squirrel behavior. The average number of unique fox squirrels seen daily ranged from 4 and 5 individuals in December and July respectively to highs of 7 to 8 fox squirrels during the autumn months of October and November. Fewer gray squirrels were seen during all months of observation. Lowest average numbers of gray squirrels were seen in September (0.5 squirrels/day), with a high of 4.7 in April (Figure 12).

Individual squirrels were observed for up to 10 minutes at a time and primary-out-of-nest activities were documented. No statistical tests were conducted to quantitatively compare the time spent by both species in out-of-nest activities; however, pie charts were constructed to illustrate seasonal differences in activity patterns. Primary activities varied seasonally for both *S. niger* (Figure 13) and *S. griseus* (Figure 14). Seasons were identified by the following dates: Winter= December 21-March 20, Spring= March 21-June 20, Summer= June 21-September 20, Fall= September 21-December 20. Throughout the entire year, both species spent most of their out-of-nest activity time foraging for acorns or traveling through the trees or along the ground in search of acorns

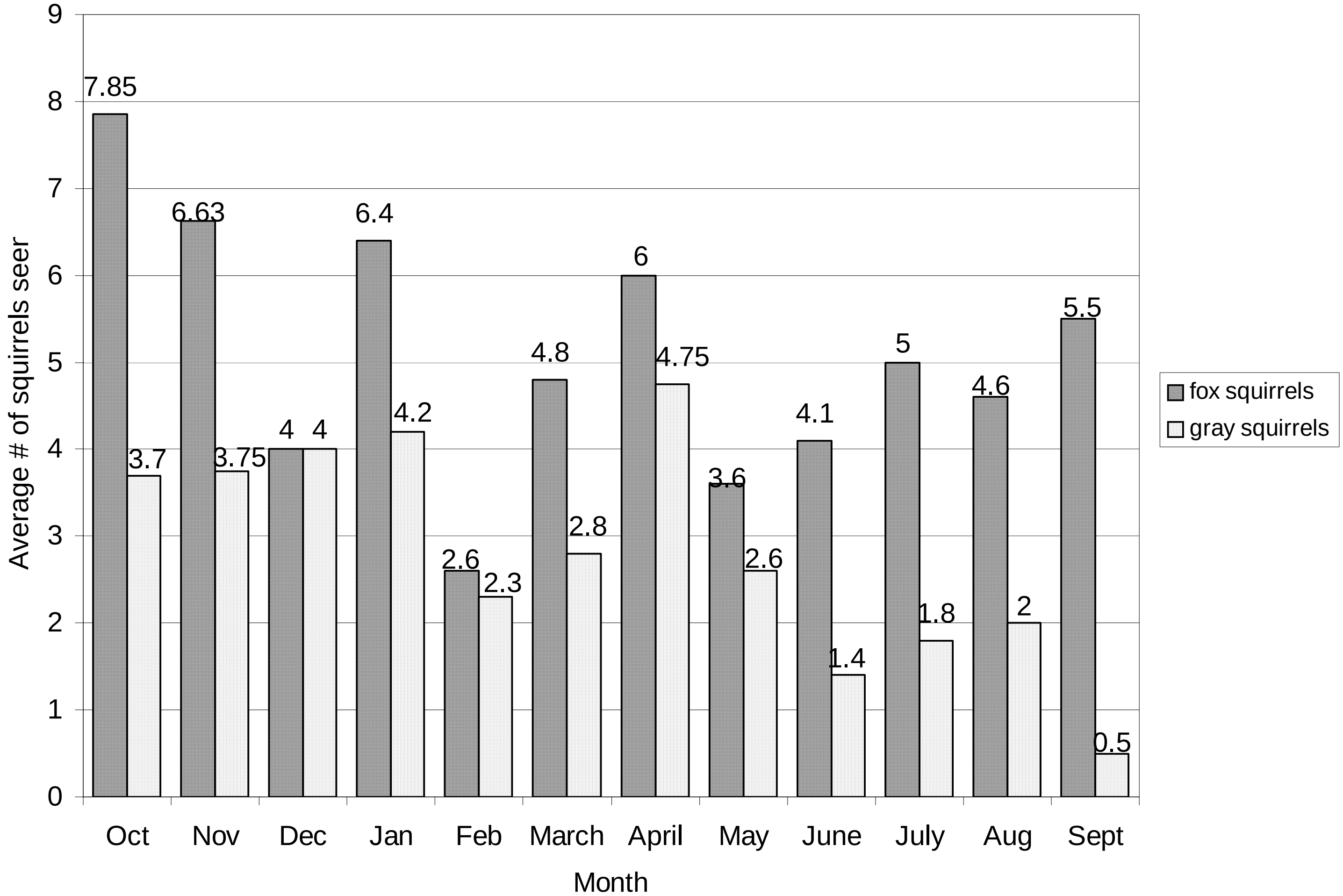

Figure 12. Daily average number by month of unique fox squirrel and gray squirrel individuals seen at San Dimas Canyon Park, 2002-2003.

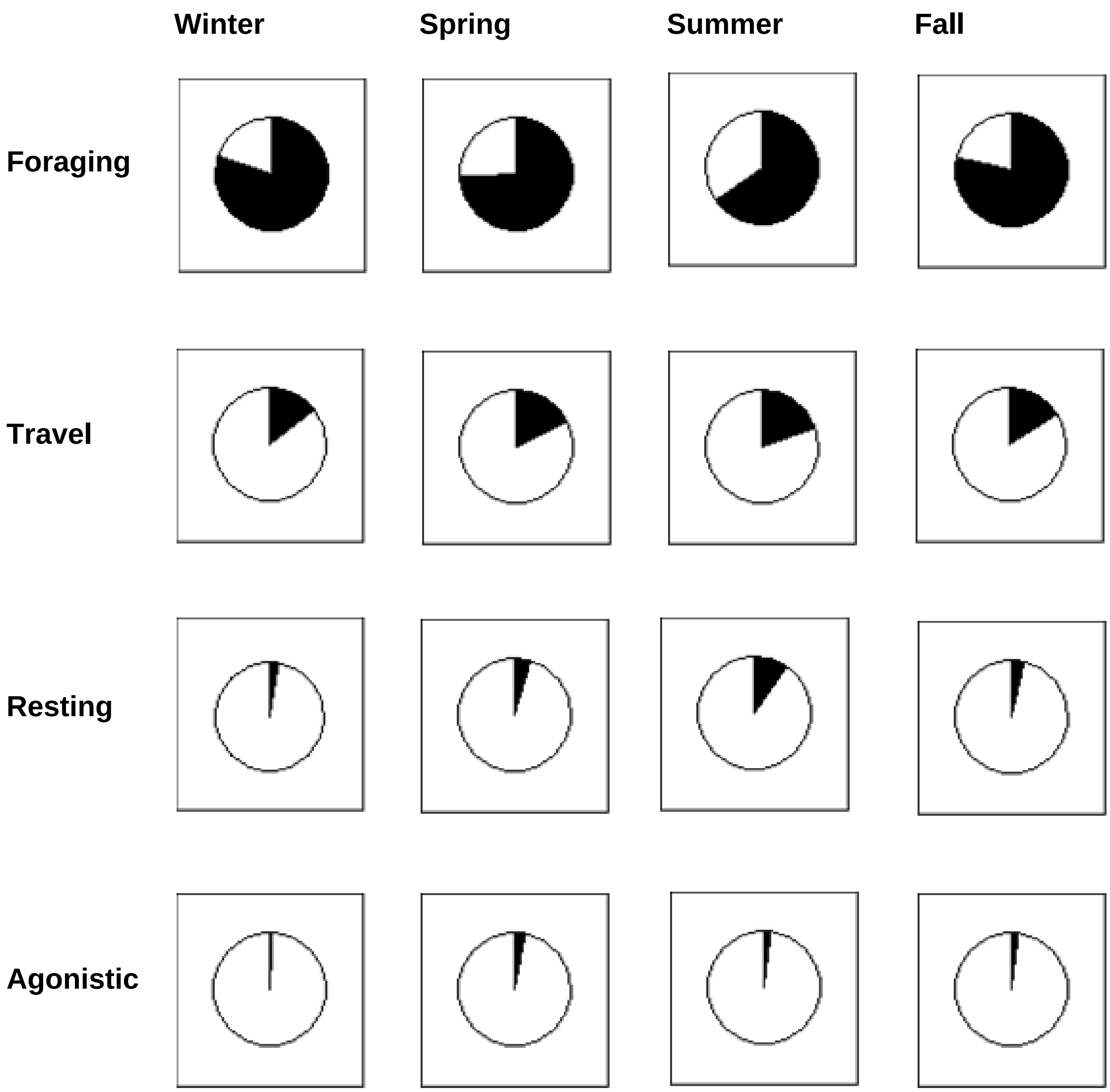

Figure 13. Relative time spent in major out-of-nest activities by the fox squirrel *Sciurus niger*, San Dimas Canyon Park, 2002-2003.

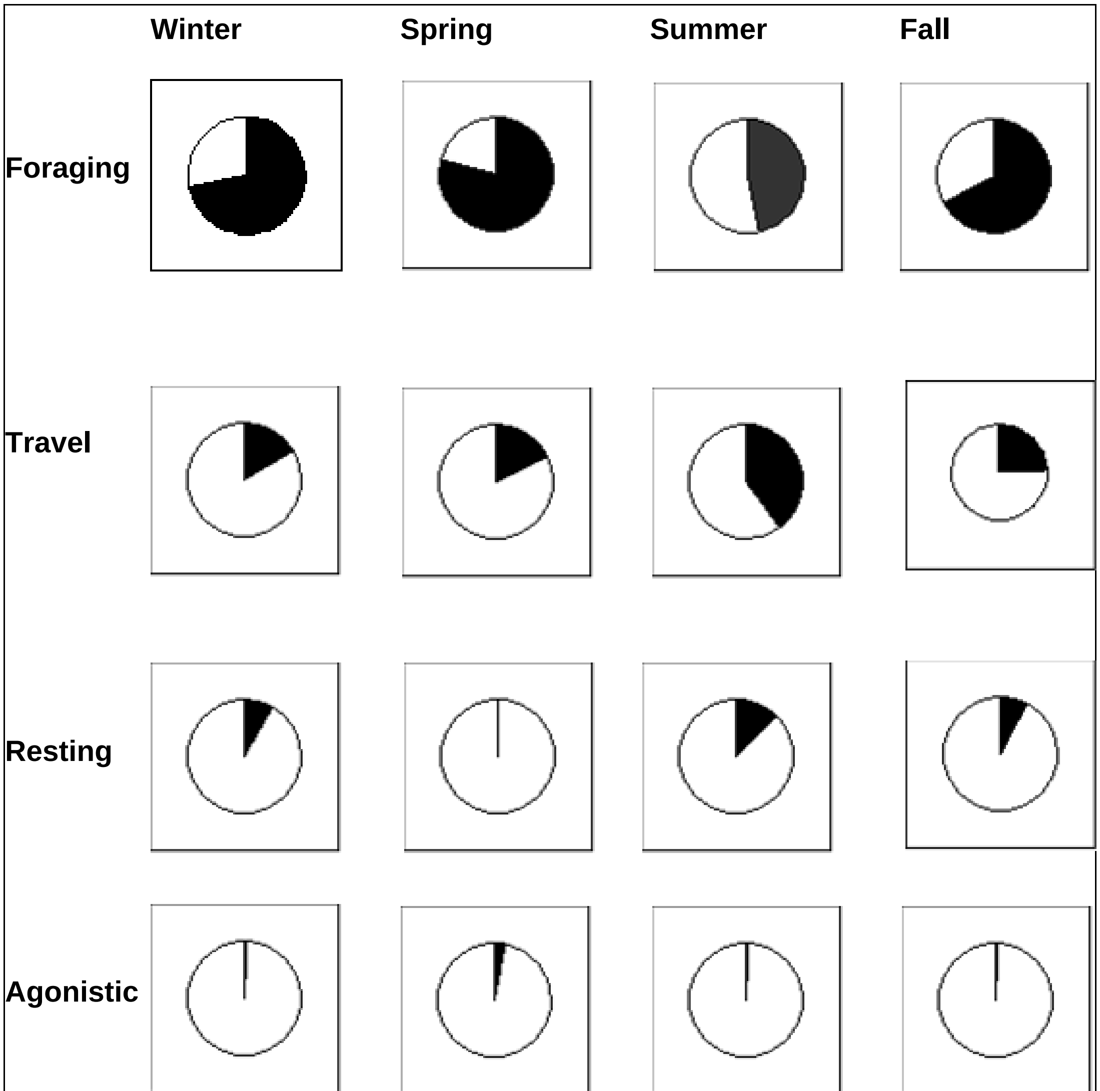

Figure 14. Relative time spent in major out-of-nest activities by the gray squirrel *Sciurus griseus,* San Dimas Canyon Park, 2002-2003.

or, in the case of the fox squirrel, eucalyptus pods as well. Foraging included such acts as eating, burying acorns, digging up acorns, and meticulously looking through the ends of the branches for new acorns or flower buds.

Sciurus griseus spent proportionally the least amount of time foraging during the summer months when there were very few acorns available, and therefore spent the greatest amount of time traveling in search of food during this season. The gray squirrel spent much more time traveling in search of food than did *S. niger* during the summer season as the fox squirrel was able to switch to eating the seed pods of the red and blue gum eucalyptus, thus decreasing its need for longer distance travel in search of food. The gray squirrel by contrast, was never observed eating eucalyptus pods or flowers, resulting in increased daily travel in search of buried acorns.

The time spent by both species in foraging activities increased from summer lows to higher levels during the fall as a result of acorn mast production. This surge in food production allowed for less time spent traveling by *S. griseus,* while the proportion of time spent traveling by *S. niger* remained constant throughout the year.

As fall transitioned into winter, foraging time for both species increased and shifted from burying acorns, to searching for and recovering the acorns buried during the previous season. Both red and blue gum eucalyptus bloom during winter, resulting in *S. niger* proportionally spending the greatest amount of time during the year foraging both for eucalyptus flowers and buried acorns during this season.

The onset of spring brought an abundance of new vegetation growth and the emergence of flowers in SDCP, resulting in the highest proportional levels of time spent foraging by *S. griseus*, while *S. niger* showed a slight decrease in amount of time foraging time and an increase in resting time. Time spent resting and participating in agonistic encounters, varied similarly between the two species throughout the year, with agonistic interactions occurring most frequently during the spring.

The onset and cessation of daily activity was not substantially different between the two species as had been anticipated. Morning activity exhibited by *S. griseus* began after sunrise and continued until approximately 8am when it decreased until 10am to coincide with the activity of park staff involved in noisy park maintenance duties such as leaf blowing, mowing and tree-trimming equipment. Activity by *S. griseus* resumed after park staff ceased working at approximately 11am with levels rising until 1pm. Activity typically ceased during the heat of the day between 2pm and 5pm then rose again during the evening hours of 5pm to 7pm. All squirrels returned to their nests for the night by sunset.

Sciurus niger showed similar activity patterns in the morning, including decreased levels during periods of park maintenance. Activity levels similarly reached lows between 1pm and 4pm and rose again after 5pm as evening approached (Figure 15).

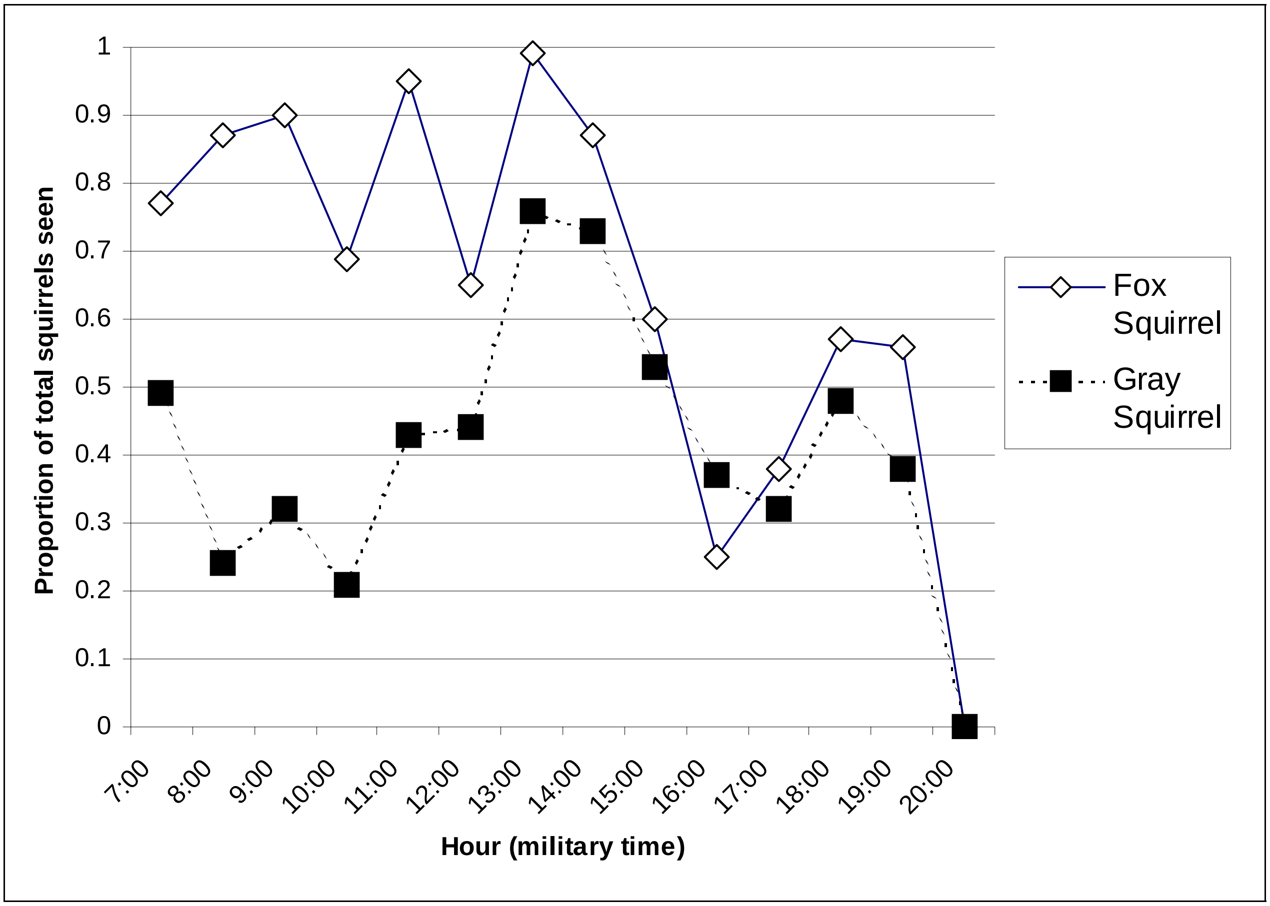

Figure 15. Onset and cessation of daily activity graphed as the proportion of fox squirrels and gray squirrels seen per hour throughout the year at San Dimas Canyon Park.

Food Item Consumed	**Fox Squirrel**	**Gray Squirrel**
Acorns *(Quercus agrifolia)*	X	X
Eucalyptus pods/flowers (*Eucalyptus spp.*)	X	
Maple Samaras (*Acer macrophyllum*)	X	
Clover *(Trifolium spp.)*		X
Black Walnut *(Juglans californica)*		X
Chinese elm flowers/samaras (*Ulmus parvifolia*)	X	
Mushrooms *(Amanita novinupta)*	X	
Lichen	X	
Insects (psyllids) (*Clycapsis brimbecombei)*	X	
Magnolia fruit (*Magnolia grandiflora)*	X	X
Shamrocks *(Oxalis spp.)*		X
Silk Oak flowers (*Grivellea robusta*)		X
Fruitless mulberry flowers *(Morus alba)*		X
Pine cones (*Pinus ponderosa*)		X

Table 1. Food items consumed by the fox squirrel (*S. niger*) and western gray Squirrel (*S. griseus*) at San Dimas Canyon Park.

Food Items

Fourteen unique food items consumed by either fox or gray squirrels were positively identified during 184 10-minute sampling periods (Table 1). Unlike many other urban parks, squirrels at SDCP were not observed at any point obtaining food from park visitors eating lunch, nor was either squirrel observed begging or approaching park visitors with the intent of obtaining food. Garbage cans within the park usually contained edible food, yet squirrels were never observed entering them to retrieve food or nesting material.

Gray squirrels were observed consuming acorns of the coast live oak (*Quercus agrifolia*) daily during each of the four seasons throughout the year. Acorns accounted for 89 percent of the 70 observation periods in which a food item being consumed by a gray squirrel could be accurately identified. Acorns therefore were considered to be the primary food source of *S. griseus* at SDCP. Green pinecones of the Ponderosa pine (*Pinus ponderosa*) produced during the spring and summer accounted for 3 percent of the total food item observations and were thus classified as the second most important food source to *S. griseus*. During the winter months, two single observations were made of a female on the ground eating clover flowers (*Trifoloim spp.)* and shamrocks (*Oxalis spp.)* a few weeks after heavy rains. Otherwise, only acorns were located and consumed during this winter season. Gray squirrels were observed consuming the widest variety of food items during the spring season. In addition to acorns that were dug up after being buried in the fall, *S. griseus* was witnessed on several occasions eating the flowers of the silk oak (*Grivellea robusta*), fruitless white mulberry (*Morus alba*) and magnolia (*Magnolia grandiflora*). The onset of summer signaled the beginning of acorn mast production and the maturation of pinecones. Both food items were consumed during this time. As autumn approached, the remaining acorns ripened and became the exclusive food choice of *S. griseus.*

The fox squirrel was observed to have a broader diet than that of the gray squirrel during three of the four seasons. Although acorns were consumed by the fox squirrel during 75 percent of the 114 observation periods throughout the year in which an identifiable food source being consumed was documented, the seed pods and flowers of the red gum eucalyptus (*Eucalyptus camaldulensis*) and blue gum eucalyptus (*Eucalyptus globules*) constituted the second most common food item consumed at 12 percent. Eucalyptus seed pods and flowers were eaten year-round, yet were much more important at the end of spring season and during most of the summer season when there were no acorns left on the ground and most of those that had been buried in the fall had been consumed during the winter. The young buds, flowers and samaras of the Chinese Elm (*Ulmus parvifolia*) accounted for 4 percent of observed food items, while maple samaras (*Acer macrophyllum*) as well as red gum lerp psyllids (*Clycapsis brimbecombei*), a pest insect of the eucalyptus each accounted for 2 percent of *S. niger's* observed diet. Single observations of *S. niger* eating clover, black walnuts, mushrooms (*Amanita novinupta*), and lichen probably translate into these items being supplemental food items, yet they do not represent high priority foods at SDCP.

Aggressive Interactions

Aggressive interactions were documented during each observational period if they occurred. Aggression was characterized by tail wagging and chattering at, or charging and chasing a second squirrel. A squirrel was considered dominant if it initiated the chase or held its ground. A submissive squirrel was one that was chased or did not hold its ground and fled the area. A total of 153 agonistic interactions were recorded throughout the year, with 57 interspecific encounters involving a gray and fox squirrel, 57 intraspecific fox squirrel confronting fox squirrel, and 39 intraspecific gray squirrel versus gray squirrel interactions. Contrary to initial predictions, the slightly larger gray squirrel initiated and won 43 of 57 (75 percent) of gray/fox aggressive interactions (Figure 16). Intraspecific interactions of both species followed a linear hierarchy of dominance, with males being dominant to females and adults dominating subadults and juveniles.

Two interspecific interactions were documented involving *S. niger* and the California ground squirrel (*Spermophilus beecheyi*). The first event (April 19, 2003) involved an adult *S. beecheyi* of unknown sex attacking and killing a juvenile (10-12 week-old) male fox squirrel while the juvenile scavenged for acorns on the ground. The

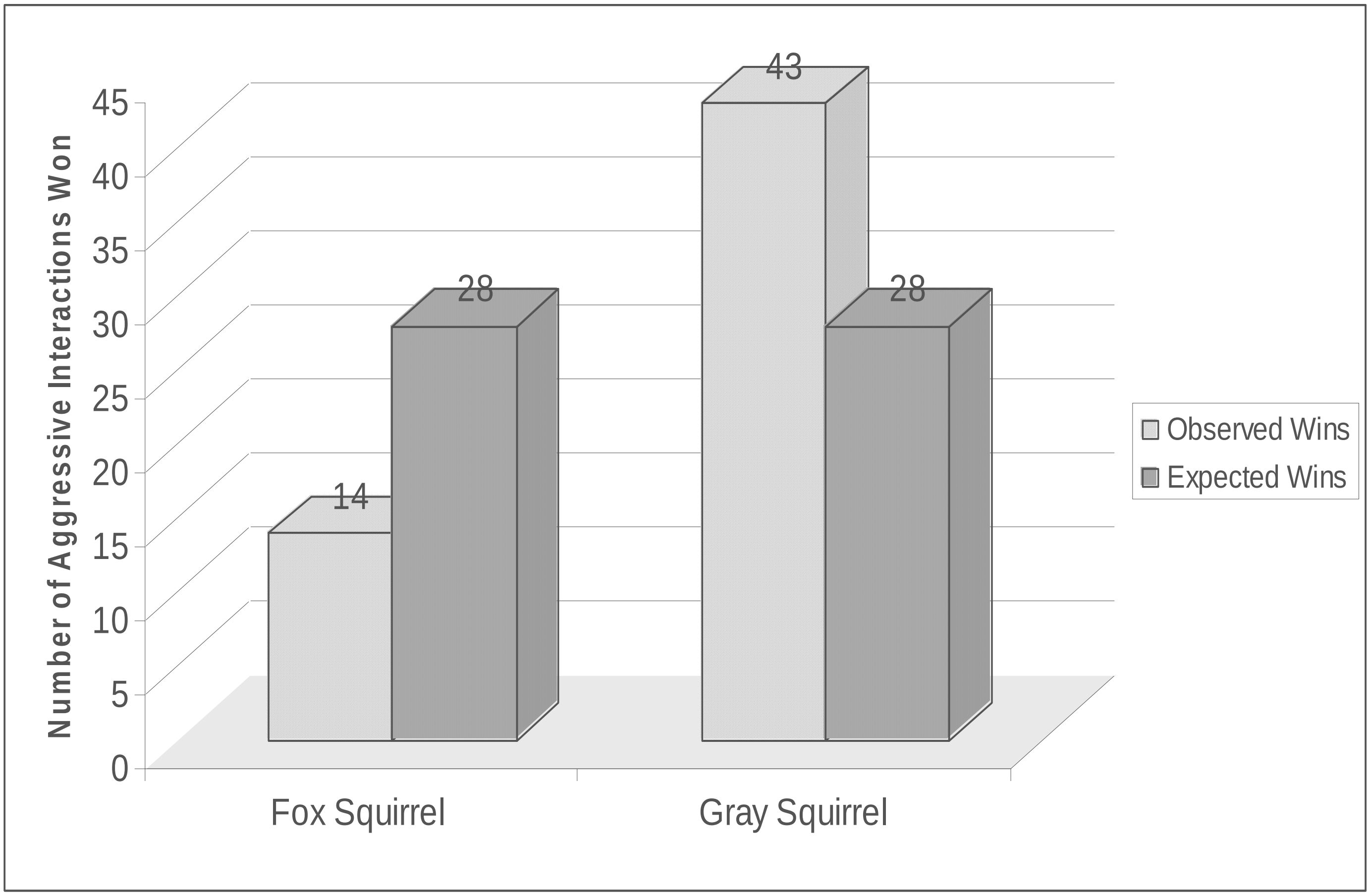

Figure 16: Number of observed verses expected aggressive interactions initiated and won per squirrel species.

fox squirrel approached within two meters of the *S. beecheyi* colony burrow, provoking the adult *S. beecheyi* to charge out of its burrow entrance and attack the fox squirrel, delivering lethal bites to the neck region. Once the young fox squirrel no longer resisted, the ground squirrel repeatedly thrust its front paws onto the chest of the dead squirrel before returning to its burrow.

The second occurrence (May 7, 2003) involved a single adult male fox squirrel and an adult California ground squirrel. The fox squirrel perched on the trunk of an oak above the ground squirrel's burrow. Upon emerging from its burrow at the base of the tree, the ground squirrel charged up the trunk after the fox squirrel and took the perch location as the fox squirrel quickly retreated down the trunk and across the grass to the next closest tree.

Yearly Litter Production

Three California wildlife rehabilitation centers (California Wildlife Care Center, Wildlife Fawn Rescue and Wildlife on Wheels) provided dates that 135 fox squirrel litters and 15 gray squirrel litters were admitted to their facilities during 2002. Only nestlings considered accurately aged to within one week upon admission were included in the data set. Birth dates for each litter were assigned for this study by subtracting the number of weeks the litter was aged at upon admission from their admission date. For example, if a litter of fox squirrel was admitted on Wednesday April 30, 2002 and the nestlings were aged at three weeks, then their birth date would be considered Wednesday April 9, 2002. The number of individuals comprising a litter upon admission was not considered to be indicative of true litter size since any number of individuals may have been rescued. All individual nestlings, whether there were one or four admitted by the same person on the same day were considered one litter. Often, multiple litters were admitted on the same day, yet by different members of the community.

The number of litters graphed by birth date showed the fox squirrel producing litters during two distinct seasons: spring and fall. Fifty-nine percent of *S. niger* litters reported were born during the months of February, March and April, with the highest monthly number (51 litters) being born during March. The second pulse of litter production occurred during the months of August, September and October.

The gray squirrel by contrast, exhibited a single spring breeding season beginning several weeks after that of the fox squirrel and lasting longer in duration than either of the two breeding seasons of *S. niger*. Twelve of the fifteen litters (80 percent) were born during the four-month span between March and June (Figure 17). Single litters were additionally admitted to wildlife centers as nestlings during February, August and September. Due to the low number of gray squirrel litters received by suburban wildlife centers, the number of gray squirrel litters was adjusted in each month to the same total number fox squirrel litters in each month for a more accurate comparison of breeding seasons between the two species (Figure 18).

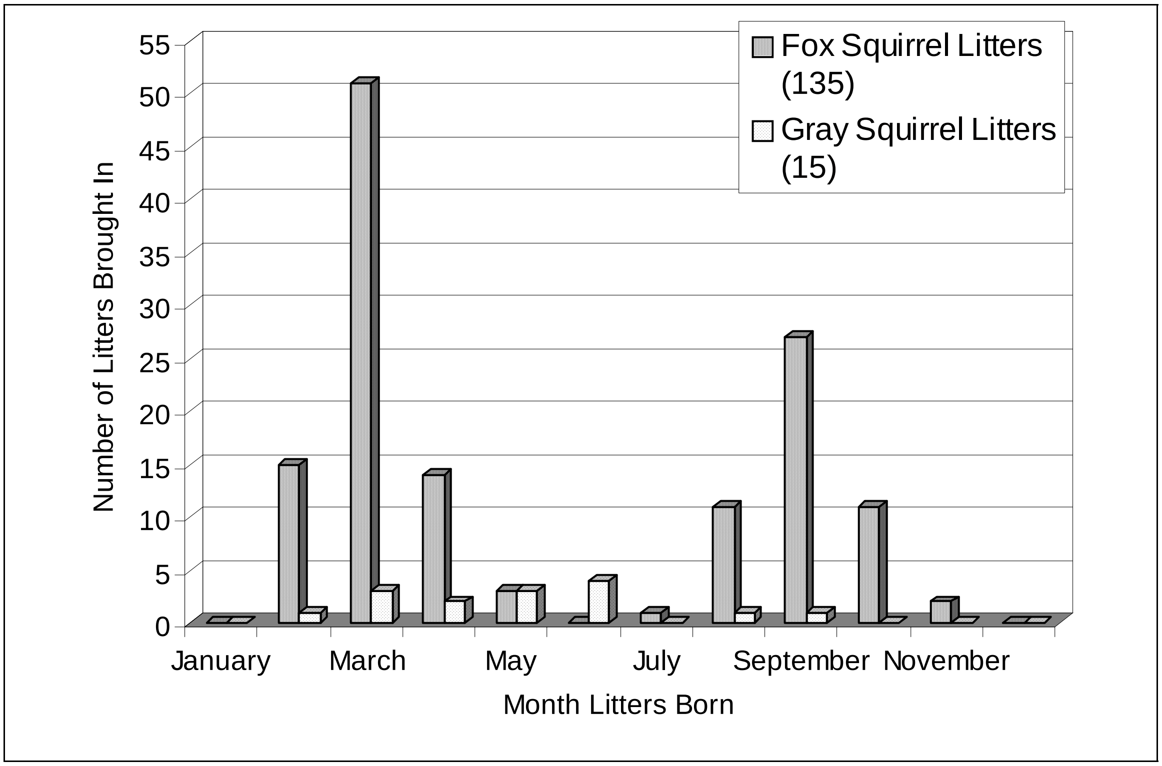

Figure 17. Actual number of fox and gray squirrel litters admitted to 3 wildlife rehabilitation centers in Los Angeles County during 2002-2003.

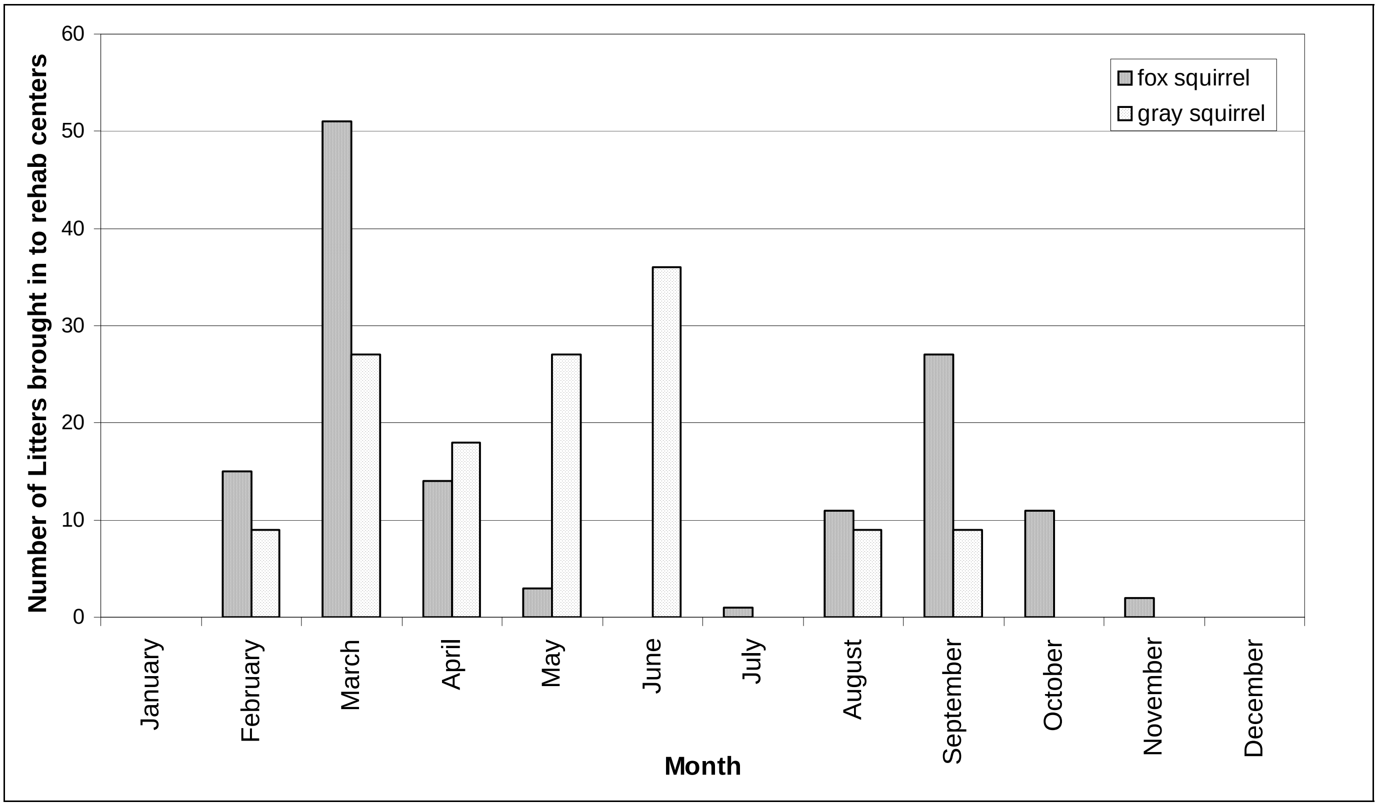

Figure 18. Total litters for the gray squirrel was adjusted to the same total number of litters for the fox squirrel. Each individual bar for the gray squirrel represents a proportion of total adjusted litters.

Graphs displaying the timing of litter production were compared against the mating chases documented during observations made at SDCP. Gestation for both species is approximately 44-45 days (Carraway and Verts 1994; Koprowski 1994), so by adding 45 days to any mating chase documented, birth dates could be compared. Additionally, nestlings first seen crawling along branches outside of their nests at 8-10 weeks of age can be backdated 8-10 weeks, then with the subtraction of 45 days, a mating chase should coincide with the date.

Mating chases taking place between males and females of each species were not included in the aggressive interaction totals. Thirty-three fox squirrel, and 8 gray squirrel mating chases were documented, while no interspecific mating chases between fox and gray squirrels were observed. Fox squirrel mating chases at SDCP occurred primarily during the months of November, December and January (October 31-January 31) which resulted in spring litters, while the second phase of mating chases occurred during June and July (June 4-July 10), resulting in late summer to early fall litters.

Gray squirrels were only observed participating in mating chases during November, December, and January (October 31-January 22), resulting in spring litters.

CHAPTER 4

DISCUSSION

Distribution of the fox squirrel (*S. niger*)

An investigation of the distribution of the fox squirrel (*S. niger*) throughout Los Angeles, Orange, and Ventura Counties was necessary to assess its present range and population status. Determining the extent to which an introduced species has become established may be important in assessing or forecasting impacts on native species such as the western gray squirrel (*S. griseus*). Results indicate that the distribution of the fox squirrel in Southern California has expanded at a rapid rate into urban and suburban areas as well as into foothill areas that were previously only occupied by the western gray squirrel.

The introduction of a non-native agricultural pest species such as the fox squirrel into an urban area may present new challenges to wildlife managers once establishment of a viable population is successful. By determining the periphery of the current fox squirrel distribution and their rate of expansion in the Greater Los Angeles Metropolitan Area, wildlife managers in surrounding communities may be able to anticipate the locations where future range expansions may occur. With this knowledge, they can develop preemptive management strategies for pest control thus avoiding future damage.

With the rapid technological advances that have taken place during the past decade and accessibility to the World Wide Web, wildlife managers now have a plethora of new management tools that collect, process, and analyze data at a fraction of the time and manpower that was needed before. The Internet therefore becomes an extraordinarily effective tool for disseminating information at relatively low cost to thousands, even millions, of people. Over time, the Internet may become a powerful urban and suburban wildlife survey tool as well (Fitzpatrick and Gill 2002).

The use of an Internet website as a survey tool for collecting wildlife data proved to be extremely effective in this study and has similarly been used at educational institutions such as the University of Illinois at Chicago (http://squirrel.bios.uic.edu), Cornell Laboratory of Ornithology (http://www.birdsource.org), the Los Angeles County Museum of Natural History (http://www.nhm.org/spiders) as well as several natural history societies in the United Kingdom (http://www.essexfieldclub.org.uk) in establishing species distribution maps.

The use of the Internet in this survey of Southern California fox squirrel populations greatly enhanced my ability to gather both current and historical fox squirrel distributional data throughout Los Angeles, Orange, and Ventura Counties. This survey tool potentially saved hundreds of hours and dollars worth of personal driving time that would have been necessary in order to collect a comparable sample size. More importantly it offered individual citizens throughout the three target counties an opportunity to play an active role in data collection.

Pest control agencies responsible for the cities of Fresno and Bakersfield in California's Central Valley region may similarly benefit from the establishment of a website that allows area residents to submit information pertaining to the presence or absence of fox squirrels in their area (M. Freeman, personal communication, March 2, 2004). Fox squirrels were introduced into Roeding Park in Fresno in 1900 or 1901 from Missouri (Storer papers; Lidicker 1991) and had remained within the urban and suburban areas such as neighborhoods, greenbelts, parks and college campuses through 1965 (Ingles 1965). The rapid expansion of suburban sprawl into the borders of agricultural land in the subsequent years has resulted in the fox squirrel expanding its distribution from residential areas into the highly profitable almond, walnut and pecan groves. Once established within these groves, the fox squirrel has the potential to cause hundreds of thousands of dollars in yearly damage while becoming near impossible to completely eradicate. Distributional data collected from nut growers and surrounding residents may assist pest control agencies in anticipating future movements by the squirrel (M. Freeman, personal communication, March 2, 2004).

Introduced fox squirrel colonization is not specific to the Greater Los Angeles Metropolitan Area. According to information compiled by Byrne (1979), fox squirrels were similarly introduced into Golden Gate Park in San Francisco before 1890. They were intentionally introduced into Balboa Park in San Diego from the San Diego Zoo in 1920 (Staff Writer 1929), to the campus of Cal Berkeley circa 1926 (Boulware 1941), and Mt Diablo in 1960 (Pelonio 2004).

Since 1933 when importation of squirrels into California became illegal (CDF&G Code Section 2118), most introductions have involved movements of individuals within the state. Due to the multitude of introductions and transfers of squirrels, and the general lack of academic interest in the phenomenon, details of the introduction and spread of the fox squirrel in Southern California are difficult to reconstruct. The numerous accounts of fox squirrels being intentionally relocated to new areas by citizens submitting data to the Southern California Fox Squirrel Project website was surprising and shed light onto the prevalence of the problem. One resident wrote, “In 2002 I have caught 23 squirrels [fox] and moved them to a park near USC.” Another resident confessed, “I have trapped 5 fox squirrels that were destructive to my garden and released them at golf courses.” This appeared to be common practice among residents fighting a losing battle against fruit and nut robbing squirrels in their neighborhoods.

Many of the introductions to parks and golf courses that have taken place throughout Los Angeles, Orange and Ventura Counties over the last several decades were surely results of frustrated but well-intentioned people. Other anecdotal accounts of fox squirrel introduction into Los Angeles County include that of former CSULA professor Dr. Richard Vogl who believed that fox squirrels had been introduced into Long Beach during WWII by a group of displaced Iowans working for the aerospace industry. Apparently members of the group trapped fox squirrels in Eastern Iowa and brought them out west, releasing them into a few parks in the Long Beach area to help ease their feelings of homesickness (R.Vogl, personal communication, November 4, 2002). The intentional introduction of two-dozen fox squirrels relocated from Fresno by a board member of the Stockdale Country Club into the city of Bakersfield in 1985 even after he was repeatedly warned against it, has subsequently resulted in hundreds of thousands of dollars of damage to homes throughout the city limits (Sheehey 2004).

Members of the community frustrated with house and garden damage often opt for live-trapping, but are then faced with the problem of how to humanely kill the live animal and where to dispose of them. Most individuals do not wish to hurt the offending squirrels, however, it is illegal to abandon any animal (Penal Code Section 597s). Because fox squirrels have the potential to carry diseases and are agricultural pests, they cannot be released into the wild without written permission of the California Department of Fish and Game (CDF&G Code Section 671.6a (2), (3)). Residents who live-trap and release depredating animals in places other than the immediate location therefore, are considered to be performing an illegal activity in California.

Additional community input via the Southern California Fox Squirrel Project website as it pertained to the presence or absence of the fox and gray squirrel over time became incredibly valuable for reconstructing the historic movement of the fox squirrel throughout Los Angeles in the decades following 1940. Details of historical sightings submitted in the comments section of the online data form were compared to collection locations of museum specimens, and filled in many of the historical gaps.

Over three hundred individuals throughout the community provided valuable historical information via the website such as, "I have lived here [Woodland Hills] for the past 50 years and have always seen fox squirrels in my yard.” A West Los Angeles gentlemen wrote, “I have lived here since 1934. When I left for the army in 1946 there were no tree squirrels, but upon my return in 1953, fox squirrels were sighted regularly in our neighborhood.” Other individuals whom had lived at their residences during similar time periods, reported seeing *S. niger* for the first time 5, 10, or 20 years prior to 2003. For example, one submitter wrote, “I have lived at this address [El Segundo] for over 50 years and although we have had opossums for many years, fox squirrels and raccoons are new in the last 4 or 5 years”. A woman living in Whittier commented, “I have lived here nearly 35 years and first saw a fox squirrel on a telephone wire approximately half mile from my home about 5 years ago. Since then, they have proliferated wildly and over the entire neighborhood”. An account indicating a decline in the gray squirrels seen in West Covina read, “I’ve lived in this location for 28 years and often saw the gray squirrels pass by. In the last 3 or so years however, a population explosion of the fox squirrels have taken over the neighborhood”. The first sightings of the fox squirrel at Cal Poly Pomona in October 2003 and their subsequent arrival to the city of Claremont in February 2003 were similarly reported by local biologists via the website.

Suburban wildlife rehabilitation centers throughout Southern California such as the California Wildlife Care Center in Malibu, South Bay Rehab in Palos Verdes, and Wildlife on Wheels in Sunland, admit tens to hundreds of nestling and injured fox squirrels to their individual facilities each year. For example, large facilities with veterinary hospitals such as the Lindsay Wildlife Museum in Walnut Creek admitted 170 fox squirrels during the first six months of 2004 and expected to receive at least that number during the second half of the year, to coincide with the second breeding season (P. Nave, personal communication, June 18, 2004.). By comparison, this facility only received a single western gray squirrel during this same time period while the three other facilities mentioned received zero western gray squirrels. Squirrels admitted to rehabilitation facilities are primarily nestlings that will be hand-raised and eventually released into "the wild."

Prior to 2002 when new laws governing release protocol were instated, rehabilitation centers had liberty regarding where to release their squirrels. Many were released in areas of Los Angeles County not formerly inhabited by fox squirrels under the belief that they would do well there and have an increased chance for survival. Current California Department of Fish and Game code states that rehabilitation centers must release recuperated animals "as close to" and "as far as 5 miles from" the original location of capture, or into "suitable like habitat." Suitable like habitat certainly leaves room for personal interpretation, occasionally resulting in the release of squirrels into non-urbanized areas or similarly developed areas yet void of the fox squirrel. Citizens hoping to save fox squirrel nestlings by taking them to a rehabilitation center are often willing to drive several hours to reach a facility that has agreed to accept the animal, resulting in that animal not being returned to its place of origin and opening up the possibility of disease or parasite transmission into a new area.

Intentional introductions of the fox squirrel into new urban areas by well-intentioned citizens do not represent the sole method by which the distribution of this non-native species has expanded in Los Angeles, Orange, and Ventura Counties since 1904. Although adult squirrels are capable of moving >1 km (0.62 miles) on occasion (Sheperd and Swihart 1995) most dispersal involves juveniles and subadults (Koprowski 1996; Nixon et al. 1974, 1986) during April and May or July through October as the young of the year and yearlings set out in search of a new home (Thompson 1978). This bi-yearly movement may greatly contribute to the fox squirrels' range expansion in Southern California. Koprowski (1996) found the distance from natal areas to new home range centers varied from 0.14km to 3.5km (0.09- 2.17 miles) for female and male fox squirrels respectively while the record movement for a fox squirrel is 64.24 km (39.9 miles) (Allen 1943). Individuals have also been known to return home from a distance of 4.5km (2.8 miles) after experimental displacement (Hungerford and Wilder 1941).

Sciurus niger has been extremely successful at using riparian corridors such as those found along the Santa Clara, Los Angeles, and San Gabriel Rivers to facilitate its dispersal into new habitats in Southern California. This is similarly described by Geluso (2004) and Hoover and Yeager (1953) as the mechanism facilitating fox squirrel colonization of northeastern New Mexico and its westward expansion through Colorado.

Fox squirrels living in urban or suburban areas such as Los Angeles, also utilize above ground utility cable as a relatively safe means of traveling throughout their home range and dispersing into new areas. They are able to cross busy streets in rush hour traffic without danger from domestic cats, dogs or automobiles which are the primary sources of fox squirrel mortality in urban areas (Phillips and Lopez 2003; Watkins 1979). As of 1979, Pacific Telephone Company had approximately 2000 miles of aerial cable in the San Fernando Valley alone, presenting squirrels with an extensive aerial highway system (Watkins 1979) For aesthetic reasons, most housing developments in Los Angeles, Orange and Ventura Counties after 1967 have transitioned from pole-mounted electrical, telephone and television cable to underground utilities cable (CPUC Rule 20A; Los Angeles County Code), thus decreasing the ability of the fox squirrel to safely cross busy thoroughfares and quickly disperse into new housing developments in the future.

The distribution of the fox squirrel population in Los Angeles County was found to be expanding at rates ranging from 0.68 km/yr to 6.84 km/yr (0.42-4.25 miles/yr) during varying time periods over the 100 years since their introduction at the Sawtelle Veterans' Home in 1904. This rate is compatible with the previously described yearly natal dispersal distances reported by Koprowski (1996). This rate is also comparable with the 0.22 km/yr to 3.26-km/yr rate of range expansion exhibited by the introduced eastern gray squirrel *S. carolinensis* in Vancouver, British Columbia, Canada (Gonzales 1998) and 7.7 km/yr for *S. carolinensis* introduced into Great Britain (Lloyd 1983). Gonzalez (1998) found variation among years, yet over an 83 year period, found the eastern gray squirrel distribution had expanded at a straight-line distance of 91.3km. This too is comparable to my findings of the fox squirrel moving a straight-line distance of 66.34 km (41.26 miles) from Sawtelle to Claremont in 99 years.

The only potential limits to the natural expansion of the fox squirrel distribution into the surrounding San Bernardino, Riverside, and Kern Counties may include unsuitable habitat i.e. sparse fruit or nut producing trees, a lack of habitat corridors, or the absence of aerial phone lines in which to travel and cross highways. Continued eastward range expansion by the fox squirrel along the southern foothills of the San Gabriel Mountain Range would enable *S. niger* to reach the San Bernardino Mountain Range over time and establish future populations in this county. Natural dispersal of previously introduced populations in Orange County (Irvine) may result in fox squirrel populations becoming established in bordering Riverside County via the Santa Ana River Corridor, Chino Hills State Park, or the Cleveland National Forest.

As the range of the fox squirrel continues to expand in Southern California, it will inevitably come into contact with more populations of western gray squirrels. These zones of overlap may constitute marginal habitat for both species, allowing them to coexist for extended periods of time. At San Dimas Canyon Park for example, fox squirrels and gray squirrels have coexisted for at least 10 years (R. Gregory, personal communication, September 9, 2004). Likewise, Byrne (1979) found fox squirrels and eastern gray squirrels (*S. carolinensis*) introduced in the vicinity of Sunol, California to have co-existed for at least four, and possibly up to 15 years preceding her study. This area too may represent an intermediate between ideal habitat for each species, indicating fundamental niche overlap, in which some niche space is shared and some is exclusive.

According to Byrne (1979) the establishment of introduced fox squirrel populations in Northern California has "proceeded without a major displacement of the western gray squirrel, although in some local areas native squirrels have been supplanted". In areas such as the foothills of the Santa Cruz Mountains of Northern California or the foothills of the San Gabriel Mountains in Southern California, where the ranges of both species overlap, the fox squirrel tends to be associated with human habituation while the western gray squirrel is associated with active woodlands.

Sexton (1990) however documented the replacement of the fox squirrel by the eastern gray squirrel (*S. carolinensis*) in as little as 12 years and 2 months at a new subdivision in suburban St. Louis County, Missouri. Initially, the fox squirrel invaded the cleared areas while the local population of eastern gray squirrels declined. As the forests regenerated in subsequent years, the gray squirrel again increased its population numbers and distribution.

Nests

Brown and Yeager (1945) found summer to be the period of greatest nest-building activity in Illinois for both fox squirrels and eastern gray squirrels (*S. carolinensis*). This was also true of fox squirrels and western gray squirrels inhabiting SDCP. With daily summer temperatures in San Dimas often reaching 90-100 degrees Fahrenheit (37° C), fox and gray squirrels alike constructed open leaf nests high in the trees where afternoon breezes were common. Leaf nests, also called dreys, were primarily constructed of twigs, leaves, grass and vines, were generally greater than 20 feet above the ground, and built on down-sloping branches away from the trunk of the tree. Squirrel nests were distinguished from great horned owl and crow nests in the park by placement and construction: avian nests appeared as open, loose assemblages of sticks and were always well supported in the crotch of a tree.

Fox squirrel leaf nests were constructed in a variety of tree species as was demonstrated by their utilization of 5 of 14 tree species within SDCP. Los Angeles County residents submitting data to the Southern California Fox Squirrel Project webpage, also provided accounts of fox squirrels nesting in avocado, orange, cypress, coral, pine, ash, walnut and elm trees within residential areas; demonstrating that fox squirrels show considerable plasticity in their preference for nest-tree species available. Their willingness to nest in residential areas suggests that habitat disturbance and fragmentation due to urbanization may not have detrimental effects on the abundance and persistence of fox squirrels in the Greater Los Angeles Metropolitan Area. This is supported by Salsbury et al. (2004) who found fox squirrel nest density in Central Indiana to be significantly greater at disturbed sites compared to nature preserve sites. On the University of Missouri golf course, the fox squirrels nest and forage in the trees scattered between fairways while the eastern gray squirrels nest and forage in the dense woods surrounding the course (Smith and Follmer 1972). Robb et. al. (1996) proposed that this greater use of edges by fox squirrels than eastern gray squirrels was the result of habitat selection rather than competition.

Gray squirrels within SDCP constructed nests only in oak and eucalyptus tree species, indicating a narrower range of habitat requirements than that of the fox squirrel. The preference of the western gray squirrel to nest in closed canopy, undisturbed forested areas with a dense understory (Ryan and Carey 1995), accompanied with their unwillingness to nest in developed residential areas, is further reinforced by online data submission to the website in which zero of the 91 gray squirrel accounts documented the presence of a gray squirrel nest or nestlings on their suburban property.

A total of ninety leaf nests were documented within 12.8 acres of SDCP between 2002 and 2003, indicating both species of tree squirrel were using multiple nests throughout the year. The mean number of leaf nests per fox squirrel has been estimated to range from 3.2 to 17.3 over variable time periods (Edwards et al. 1989; Hilliard 1979; Kantola and Humphrey 1990; Moore 1957) while Cross (1969) reported western gray squirrels in Oregon using an average of 3.5 nests. The number of nests per individual may be in response to irritating nest-inhabiting parasites such as the squirrel flea (*Orchopeas howardi*). By relocating to a new nest on a regular basis, squirrels may be able to reduce parasite loads in their nesting area. A second factor that favors the abundance of multiple nests per individual includes the additional refuge from man that the nest provides (Moore 1957). Suburban parks such as SDCP often have large numbers of daily community visitors, often accompanied by unleashed dogs, which present a constant threat and need for quick escape by the squirrels.

Winter represented the period in which the fewest leaf nests were observed in SDCP. Most nests were blown down or rendered unusable during October, November and December when seasonal Santa Ana winds blow 40-70 miles per hour below the passes and canyons of the coastal ranges of Southern California and the Los Angeles Basin (National Weather Service 2002). High wind velocity is considered by several writers as one of the most important weather factors influencing fox squirrel activities. Baker (1944), Brown & Yeager (1945), Goodrum (1937), Hicks (1949) and Seton (1929) mention the effect of wind on squirrel movement such as increasing the animal's difficulty in maintaining balance while traversing branches and measuring jumps between trees. Cavity nests therefore may be utilized by both fox and gray squirrels during this time for protective shelter and the raising of young. Only a single cavity nest however was positively linked to a female fox squirrel and her nestlings in SDCP.

Neither fox squirrels nor gray squirrels were radio-collared in this study, hence tracking individuals to determine cavity use was not possible. Numerous cavities having an appropriate entrance size of 7.5 cm to 11.9 cm (Baumgartner 1938) and visible chew marks at the entrance were observed on the trunks of western sycamore, oak, and eucalyptus trees within SDCP. The presence of Northern flickers, Acorn, Downy, and Nuttall's woodpeckers, within the park however, made distinguishing current squirrel use from avian use near impossible without daily vigilance at each tree possessing a cavity.

Reports of cavity use by fox squirrels in other Southern California studies also appear to be low or unaccounted for. Lenchner (1976) found fox squirrels inhabiting the Historical Orange Grove on the campus of California State University, Northridge as having multiple leaf nests within the orange grove as well as in the eucalyptus trees bordering the northern edge of the grove. No cavity nests were discovered. Edwards and Guynn (1995) also found little evidence to support the hypothesis that the absence of cavities represents a limiting factor for fox squirrels.

Cavity use by fox squirrels in the Southeastern United States also appears to be low. Only 7% of the nests used by fox squirrels in Georgia (Hilliard 1979) and Florida (Kantola 1986) were in cavities, and similarly, only 20% of fox squirrel nests in South Carolina were found in cavities (Edwards et al. 1989). Cavities, however, may still be vital to fox squirrels living in the Midwest where subzero winter temperatures result in an increased need to conserve energy (Edwards et al. 1989; Kantola 1986). Havera (1979) showed that fox squirrels in Illinois using nest boxes with nesting material did not have to increase their heat production until ambient temperature dropped to -8°C. Without shelter, increased heat production begins at 20° C (Loeb and Moncrief 1993). Average winter low temperatures throughout the Los Angeles Basin are mild and rarely dip below 48°F (8°C); possibly alleviating fox squirrel dependence on cavities for energy conservation in Southern California. By relying upon leaf nests instead of cavity availability, the fox squirrel has the ability to expand its range and nest in residential areas supporting exotic tree species such as palms, citrus, and macadamia, which do not provide cavities, yet provide a source of nesting material and abundant food.

Direct field evidence for competitive interactions between fox squirrels and gray squirrels over nest sites is limited. Steele (1988) observed (via radiotelemetry) two separate occasions in which a fox squirrel displaced an eastern gray squirrel (*S. carolinensis*) from a nest cavity. Other field observations of aggressive interactions among Midwestern squirrels, however, have failed to demonstrate any clear dominance relation between the two species (Armitage and Harris 1982; Bakken 1952; Fogl 1982). Similarly in SDCP, multiple leaf nests were often constructed on branches of the same tree, yet no observations were made of both *S. niger* and *S. griseus* utilizing nests built in the same tree.

Food Items Eaten

Jodice and Humphrey (1992) found populations of fox squirrels persisting at high densities on golf courses in Southwest Florida; demonstrating a sharp contrast to the densities found in native habitats due to native and exotic plant and tree species offering an unusually diverse and stable year-round food supply. Several studies involving Southern California fox squirrel populations documented food items such as the fruits and/or seeds of eucalyptus (Boulware 1941; Wolf & Roest 1971), walnut, avocado, allepo pine, ash, apple, western sycamore, Russian olive, and the flowers of the silk oak being consumed (Watkins 1979). While stomach analysis was not conducted as part of this study, community responses submitted to our website confirm the aforementioned food items as well as document the fruits and nuts of numerous other exotic species such as guava, macadamia, persimmon, mango and carob.

Birdfeeders and daily hand-feeding of peanuts and walnuts to fox squirrels in residential areas has no doubt assisted the fox squirrel by providing a year-round, protein-rich diet. Water too is often readily available in urban and suburban areas as a result of sprinkler run-off, bird baths, and water bowls left outside for pets. With a more diverse and less variable food supply as well as accessible water, the human commensal fox squirrel in Southern California is probably less affected by seasonal variations in mast or effects of drought as the western gray squirrel (Korschgen 1981; Nixon and McClain 1969; Weigl et. al. 1989).

A number of studies of the food habits of fox and western gray squirrels in their native range have been made (Brown and Yeager 1945; Cahalane 1942; Nixon et al.1968; Stienecker and Browning 1970). Stienecker and Browning (1970) found the principal food by volume of 310 western gray squirrels from Central and Northern California to be hypogeous fungi, pine nuts, acorns, and bay fruit respectively. The role of hypogeous fungi in the diet of the gray squirrel is not well understood, yet it seems that the common subterranean fungi, *Melanogaster sp*, *Richoniella sp*., *Rhizopogon sp*., *Alpova sp*., *Tuber rufum*, and *Leucogaster sp*. play an important part in gray squirrel ecology, often comprising more than half of its diet, while several kinds of epigeous fungi: *Lycoperdales* and gill mushrooms are also known to be utilized (Byrne 1979; Stienecker 1977). The stomach contents of 207 gray squirrels from bordering Kern County revealed hypogeous fungi to be the most important food item eaten throughout most of the year, with a yearly average volume of 48 percent, with the highest volumes found during July (82 percent) while lows occurred in September (15 percent). Acorns were found to be the second most important food item consumed which was also eaten in every month of the year (Stienecker 1977). Drought conditions in Southern California during the 1970s are thought to have caused much of the hypogeous fungi to dry up, thus causing the gray squirrel to be food stressed for an extended period of time and consequently more susceptible to mange which reached epidemic proportions in many Southern California gray squirrel populations during this time. Currently, Southern California, considered a "regional hot bed" of mange, is in its fifth year of drought. The possibility of another mange epidemic within the gray squirrel population therefore may be possible if observations from SDCP are indicative of things to come. Four gray squirrels inhabiting SDCP during the summer of 2003 were observed to be suffering from mange. Although the occurrences took place during separate months, each individual had very little fur, numerous scabs and showed life-threatening lethargy. No fox squirrels however were observed to have mange during this study.

Hypogeous fungi may similarly be utilized by introduced fox squirrels in California as is evidenced from Byrne (1979) in which the stomach contents of three fox squirrels analyzed from the East Bay area contained three species of hypogeous fungi.

Weigl, et. al. (1989) also found hypogeous fungi, especially during the summer during times of low food supply to be important to fox squirrels inhabiting eastern North Carolina. To what extent fungi play a role in the diet of fox squirrels residing in Southern California is unknown as this time.

Eucalyptus trees were abundant in SDCP, yet during 38 hours of observation throughout the year, *S. griseus* was never observed consuming eucalyptus seeds or flowers as was commonly exhibited by *S. niger*. The gray squirrel's unwillingness to utilize eucalyptus may account for their increased time spent traveling and decreased time spent foraging during the summer months as compared to the fox squirrel during this same time period. This indicates that they are spending more time traveling through the trees and on the ground in search of edible food items during this season of sparse resources. Contrary to my observations, Little (1934) described seeing several resident western gray squirrel inhabitants of his yard in Pasadena, California feeding consistently on eucalyptus pods during February and March 1934; believing the eucalyptus provided a substantial portion of the gray squirrels' diet. This has not been documented elsewhere in the literature.

High densities of fox squirrels now inhabiting suburban Southern California areas may represent a significant nest predator to neotropical migratory bird species nesting in areas such as the Palos Verdes Peninsula where prior to 1998 there were no tree squirrels. Other authors have similarly documented the presence of birds and bird eggs in the diet of the fox squirrel (Packard 1956; Shaffer and Baker 1991; Steele and Koprowski 2001).

Accounts of fox squirrels raiding the nests of various bird species (i.e. warbler, nuthatch, and starling) were submitted to my website by several Audubon birding trip leaders as well as school teachers using nest boxes to accompany their biology curriculum. Similar reports of chick predation were submitted as Letters to the Editor of the Los Angeles Times Newspaper (Byhower and Lokitz 2000) in response to the article Tree Squirrels: Good, Bad and Unpredictable which touted the antics and joys of feeding local fox squirrels (Smaus 2000).

Aggressive Interactions

Mutual avoidance probably best described the behavior exhibited by fox squirrels (Hansen and Nixon 1985) and gray squirrels observed at SDCP. Observations, similar to those made by McClosky (1975), revealed that both the fox squirrel and gray squirrel "displayed a tolerance of conspecifics nearby feeding as long as their personal sphere was not violated." Conspecifics approaching too closely were often met with threats and, if necessary, aggressive chases in order to protect their immediate area. Neither the fox squirrel or western gray squirrel are considered territorial; however, males and females of both species exhibit agonistic behavior in the presence of conspecifics, establishing a linear dominance hierarchy, wherein adults are dominant over subadults, and males over females (Lenchner 1976; McCloskey 1975; Nixon et al 1984; Pack et. al. 1967).

While both fox squirrels and western gray squirrels seem to be solitary much of the time, Allen (1943) and Thompson (1978) found aggressive interactions to be the most common interactions between individuals. Aggression most often consists of threat “displays” used to “signal an aggressor’s intentions” (McCloskey 1975) and the establishment of a “dominant-subordinate relationship among two individuals” (Steele and Koprowski 2001). Such displays include staring at another animal, an upright stance with tail over the back, rapid fore-and-aft tail waving and teeth chattering (McCloskey 1975; Steele and Koprowski 2001). These displays commonly escalate to short chases over a five-to-ten meter distance, while aggression resulting in physical combat is rare (Koprowski 1996; McCloskey 1975; Pack et. al 1967). For example, Koprowski (1996) found four percent of 776 aggressive encounters involving fox squirrels and eastern gray squirrels escalated to physical combat. Similar to these findings, fighting among either species observed at SDCP was rare. Only two of 157 total interspecific and intraspecific chases escalated to physical attacks. Each occurrence involved two adult western gray squirrels wrestling, screaming in distress and biting one another. Both vicious attacks resulted in physical injury to the participating animals.

Observations of *S. griseus* initiating and “winning” 43 of 57 (75 percent) of aggressive chases involving *S. niger* at SDCP was not anticipated and was contrary to the initial prediction of *S. niger* being the more antagonistic species, capable of physically ousting *S. griseus* from its preferred feeding and nesting sites. Instead, *S. griseus* appeared to have a wider radius of personal space than *S. niger* and was quick to initiate a chase if a conspecific approached closer than approximately five meters. Brown (1975) similarly suggested that the spatial patterning for *S. carolinensis* and *S. niger* is based on “individual space” and that there is probably an “individual distance at which another individual provokes aggression or avoidance.”

Avoidance behavior was commonly displayed when submissive squirrels were observed in close proximity to dominant squirrels. Even if the submissive individual was not chased, it remained noticeably cautious and anxious in the presence of the dominant individual. This was especially evident in juvenile fox squirrels. Juveniles clearly avoided adult gray squirrels and would not descend trees if a gray squirrel was foraging on the ground below.

Juveniles of both species found themselves to be the recipients of intraspecific aggression by resident adult squirrels as the juveniles attempted to expand their home ranges and establish themselves in the population during the spring and fall. Thompson (1978) suggested that this type of “intraspecific aggression appears to prevent the establishment of immigrant squirrels in, and trigger the dispersal of at least some young squirrels from, the local population.”

Gorman and Roth (1989) and Nixon et al. (1986) have shown that intraspecific interactions regulate population size and structure of eastern gray squirrels and fox squirrels respectively in the Midwest. Opinions differ however, on the effect of interspecific competition on the local distribution of the two species and what factors may contribute to the fact that usually only one species, either the fox squirrel or eastern gray squirrel, persist in urban areas. This also appears to be true of the presence of fox squirrels and/or western gray squirrels.

Armitage and Harris (1982), Brown and Batzli (1985), and Brown and Yeager (1945), found little evidence of interspecific competition in sympatric populations of fox squirrels and eastern gray squirrels in the Midwest. Instead, they proposed that the occurrence of one or both species at a given area appeared to be due to habitat features such as amount of understory, density of overstory and availability of nesting cavities, rather than interspecific competition. Additional authors (Bakken 1952; Flyger and Smith 1980; Steele 1988) suggest that fox squirrels and eastern gray squirrels may be active at different times of day to alleviate interspecific competition; however, my observations of fox squirrels and western gray squirrels in SDCP did not indicate considerable differences in the onset and cessation of daily activity by the two species.

Yearly Litter Production

The breeding seasons of the fox squirrel in the eastern United States are well documented and are often assessed by the dates of mating chases, by "juvenile emergence, by male reproductive readiness and by female reproductive cycles" (Byrne 1979). The dates representing the onset and cessation of the breeding seasons are generally influenced by latitude, climatic conditions and food supply.

Some of the first observations of fox squirrel breeding behavior from the eastern United States were made by Audubon and Bachman (1849) who documented copulation occurring from December through February with young generally born at the beginning of March and into April. Allen (1943) later reported the main breeding period of Michigan fox squirrels to last from the beginning of January to the first week in March, with sexual activity greatest in late January. He documented a second peak in breeding during late June and early July. These two breeding seasons of the fox squirrel are typically synchronous with the "phenology of deciduous trees in the eastern United States" with most litters born when buds and flowers become abundant and the second litter produced when mast crops ripen (Brown and Yeager 1945).

In the Bay Area of northern California, Byrne (1979) determined fox squirrel births occurred from February through August, while no animals in breeding condition were taken in October, November, or December. Observations made at SDCP show fox squirrel mating chases beginning in November and lasting through mid January. Young were later reported being admitted to local rehabilitation centers during February through April. The next pulse of mating chases occurred during June and July with facilities receiving nestlings during the months of August, September and October. These dates are slightly earlier for the winter and later for the summer than those reported from Midwest and eastern populations found at higher latitudes.

Several authors (Allen 1943; Audubon and Bachman 1849; Byrne 1979; Moore 1957) have documented individual female fox squirrels bearing two litters during the same year. For example, Allen (1943) made note of a female bearing one litter soon after March 1, only to be found lactating again on August 6. In another account he describes an old female lactating on September 1, 1938 and pregnant again on March 5, 1939. Byrne (1979) similarly found four females in northern California harvested in June and July after having produced second litters. Animals displaying poor health or suffering from ailments such as mange, however, may forgo breeding until body conditions have improved (Allen 1943).

Female fox squirrels generally become sexually mature at 10 or 11 months of age and breed only once their first year. Summer-born fox squirrels therefore are able to breed the following summer, while winter/spring-born animals breed as yearlings, skipping the summer breeding season following their birth and entering into estrus the following spring at 10-14 months of age (Allen 1943; Brown and Yeager 1945; Byrne 1979).

After their first year, mature healthy female fox squirrels are capable of producing two litters annually during good food years. As a result, fox squirrel populations are able to “withstand the removal of up to 40 percent of their resident populations through compensatory reproduction (Nixon et al. 1974; Nixon et al. 1975)”. This reproductive output allows the fox squirrel to rapidly populate new areas into which it has been introduced, while quickly repopulating locales from which it had been actively removed via management practices.

Data on the breeding seasons of the western gray squirrel are less extensive than those of the fox squirrel. It is generally believed that the western gray squirrel has a single breeding season per year, with yearlings mating during the winter season after their birth (Asserson 1974). Ingles (1947) documented a single season, lasting from January through May in California, with a peak in parturition in February. Likewise, Byrne (1979) found females in northern California in breeding condition during that time, while all females taken from July through November were reproductively inactive. Eighty percent of gray squirrel litters received by three Los Angeles County wildlife rehabilitation centers were admitted during the months of March through June, with single litters being received in February, August and September. The low numbers of gray squirrel litters admitted to suburban rehabilitation centers is most likely the result of the gray squirrel's resistance to nesting in suburban neighborhoods where local residents may find fallen or injured nestlings and subsequently deliver them to a rehabilitation facility.

No evidence has been published indicating that a single female western gray squirrel has reared two litters in a single year, a commonly described behavior of adult female fox squirrels. Gray squirrels are also not capable of increasing litter production to make up for lean times (e.g. two litters), thus limiting their ability to rebound from catastrophic population declines caused by mange epidemics, extended periods of drought or habitat loss. The fox squirrels greater fecundity therefore allows for a faster population growth in foothill areas where the two species overlap allowing fox squirrels to dominate by sheer numbers provided they have similar survival rates.

Hybridization between the fox squirrel and the eastern gray squirrel (*S. carolinensis*) which are closely related and sympatric throughout much of their native range has not been documented (Gurnell 1987). Only Moore (1968) has reported a fox squirrel involved in an eastern gray squirrel mating chase, ending without a copulation attempt, while Koprowski (1991) documented two male fox squirrels participating in three eastern gray squirrel mating chases. He did not observe an eastern gray squirrel however participating in a fox squirrel mating chase. During my year of observations at SDCP, I did not witness a fox squirrel or western gray squirrel participating in the mating chases of the other species.

Future Studies Planned

Two future studies stemming from this research are currently in the planning stages. The first is to take place at Frank G. Bonelli Regional Park in San Dimas, California. Currently, only the western gray squirrel inhabits this suburban park. Bonelli Park however is rapidly being approached on three sides by the fox squirrel as it continues its eastward range expansion. Dr. Alan Muchlinski will investigate the habitat use, current nesting locations, litter sizes, survivorship and dispersal distances of gray squirrels residing within the park prior to fox squirrel establishment. Once the fox squirrel invades the park and establishes a viable resident population, the gray squirrel parameters will be reinvestigated and compared to pre-fox squirrel findings.

The second study will involve remapping the periphery of the current distribution of the fox squirrel in Los Angeles, Orange and Ventura Counties after a ten-year period. This will allow for a more accurate yearly expansion rate of the fox squirrel to be calculated. It will also provide an opportunity to reassess areas that had supported both fox squirrels and gray squirrels in 2002 and determine if only one species or both species had maintained viable populations at these specific locations.

CONCLUSIONS

The fox squirrel (*S. niger*) has flourished throughout the Greater Los Angeles Metropolitan Area since its first introduction in 1904, and continues to expand its current distribution through natal dispersal, intentional relocation by people residing in the area and wildlife rehabilitation center releases. The fox squirrel and native western gray squirrel (*S. griseus*) overlap on activity levels, food items eaten, nesting sites and breeding times in foothill habitats where the distributions of both species often overlap. The differences in habitat preference and tolerance of human disturbance may allow them to co-exist for extended periods of time in suburban foothill habitats which may represent marginal habitats for both species.

The fox squirrel is a typical generalist species, with broad habitat tolerances, a higher reproductive output and juvenile dispersal distance than the native species, a broad diet which includes many exotic plant species and is human commensal, allowing it to thrive in the highly developed urban and suburban areas where it has been introduced. Currently, the fox squirrel has been unable to invade the drier, undeveloped oak/conifer forests of the San Gabriel, Los Angeles, Los Padres or Cleveland National Forests that support sizeable gray squirrel populations.

As areas supporting stands of mature oaks are lost each year to residential development, the gray squirrel will continue to be pushed back farther into the foothills while the fox squirrel follows the suburban sprawl, gaining access to areas previously occupied only by gray squirrels and putting it into contact with this native species.

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APPENDIX A

Appendix A is not included in this online version of the manuscript

Addresses representing the presence of fox squirrels.

LAID, OCID, and VID identify the unique number associated with the addresses reported from Los Angeles, Orange or Ventura Counties. YAFS refers to Years Ago- First Sighting of the species at that address. YFS implies the year that the resident first saw the species at the reported location.

APPENDIX B

Appendix B is not included in the online version of the manuscript.

Addresses representing the presence of western gray squirrels.

LAID, OCID, and VID identify the unique number associated with the addresses reported from Los Angeles, Orange or Ventura Counties.