The Distribution and Habitat Selection of Introduced Eastern Grey Squirrels, *Sciurus carolinensis*, in British Columbia

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Eastern Grey Squirrels were first introduced to Vancouver in the Lower Mainland of British Columbia in 1909. A separate introduction to Metchosin in the Victoria region occurred in 1966. I surveyed the distribution and habitat selection of Eastern Grey Squirrels in both locales. Eastern Grey Squirrels spread throughout both regions over a period of 30 years and were found predominantly in residential land types. Some natural features and habitats, such as mountains, large bodies of water, and coniferous forests, have acted as barriers to expansion for Eastern Grey Squirrels. Given that urbanization is replacing conifer forests throughout southern British Columbia, it is predicted that Eastern Grey Squirrels will continue to spread as habitat barriers are removed.

Key Words: Eastern Grey Squirrels, *Sciurus carolinensis*, distribution, habitat selection, invasive, British Columbia.

The vast majority of introduced species do not successfully establish populations in novel environments (Williamson 1996). Many successful non-native species are human comensals which thrive in human-modified environments (Williamson and Fitter 1996; Sax and Brown 2000). Eastern Grey Squirrels (*Sciurus carolinensis*; hereafter EGS), a charismatic species endemic to eastern and central North America, have been intentionally introduced to Great Britain, Italy, Ireland, South Africa, Australia, and western North America (Robinson and McTaggart-Cowan 1954; Seebeck 1984; Gurnell 1987; Lever 1994). Their gregarious nature has made them a popular addition to city parks and they generally flourish in this land type whether they are native or introduced. The ability of EGS to establish populations in association with humans is likely a key to their success as an invader. This study aims to update what is known about the spread and distribution of introduced EGS in southwestern British Columbia. I also analysed their habitat usage and predicted that EGS would be found predominantly in residential areas, areas that more closely resemble their native environment.

EGS occur naturally in the eastern United States and central Canada. Their distribution coincides with eastern hardwood forests; especially nut producing trees such as oaks (*Quercus* spp.), hickories (*Carya* spp.), and, formerly, American Chestnut (*Castanea dentata*). Their coats are often grey or black and, more rarely, red, blonde, and white. EGS eat nuts, fruits, fungus, and, opportunistically, eggs and nestlings (Orr 1971). EGS are most successful in deciduous forests, mixed deciduous-conifer forests, and residential areas (Barkalow and Shorten 1973; Pasitschniak-Arts and Bendell 1990; Riege 1991). The highest densities of EGS in the wild occur in mature maple-oak forests and the lowest in fir-cedar forests (Riege 1991). Very high densities of EGS have been observed in residential areas such as backyards, parks, and cemeteries (Pasitschniak-Arts and Bendell 1990). EGS co-occur with North American Red Squirrels (*Tamiasciurus hudsonicus*) throughout much of their range where habitat specialization and not competition determines the differences in their distributions (Riege 1991).

EGS have had negative economic and ecological effects in the places where they have been introduced. In Europe, EGS strip the bark from trees, damaging both native and plantation species (Kenward and Parish 1986). EGS may also replace European Red Squirrels (*Sciurus vulgaris*) in Great Britain (e.g., Lloyd 1983; Wauters and Gurnell 1999; Gurnell et al. 2004), although studies demonstrating the mechanism of replacement have been inconclusive. Attempts to eradicate, control, or slow the spread of EGS have been costly failures, in part due to a lack of understanding of the population biology and methods of spread of EGS (Sheail 1999; Gonzales 2000*; Bertolino and Genovesi 2001). Conifer forests and plantations, mountainous terrain, and bodies of water have slowed spread or were barriers to movement, while deciduous forests and poplar plantations have provided suitable habitat for EGS in Europe (Williamson and Brown 1986; Wauters et al. 1997; Ó Teangana et al. 2000a, 2000b). EGS were found in conifer forests in Great Britain, but the maintenance of those populations required immigration from neighbouring habitat types (Kenward and Hodder 1998; Bryce et al. 2002). The role of conifer forests in limiting the spread and establishment of EGS has led to broad scale land management recommendations that involve the maintenance of conifer forests/plantations and the removal of large seed deciduous trees, particularly oaks (Kenward and Hodder 1998; Bryce et al. 2002).

Conifer forests historically dominated British Columbia and habitat conversion from conifer forest to

residential development with deciduous trees may have increased the amount of suitable habitat for EGS. Today, residential areas in the Victoria region and Lower Mainland are well treed with deciduous species. Gardens, bird feeders, garbage and hand-outs provide an abundance of food while trees and human dwellings provide nesting locations.

The first introduction of EGS to British Columbia occurred in 1909 when at least six individuals from the New York Park Department were brought to the peninsula of Stanley Park in Vancouver (Steele 1993). The population increased and had achieved a stable size by the 1920s (Robinson and McTaggart-Cowan 1954). Robinson and McTaggart-Cowan (1954) surveyed the population and natural history characteristics of EGS in Stanley Park in 1950. EGS were found predominantly in deciduous forests, mixed deciduous-conifer forests, and developed areas rather than in the conifer forests that dominate Stanley Park. Their diet was primarily composed of hand-outs from visitors, nuts from horticultural trees, and samaras from native maple trees. Although EGS are known to eat eggs and nestlings, these authors did not find any occurrences of this. The authors speculated that EGS would remain confined to Stanley Park because it was effectively an island, surrounded by the Burrard Inlet and downtown Vancouver. EGS remained on the peninsula until the mid-1970s, when populations began spreading to adjacent areas (Merilees 1986, 1992; Gonzales 1999).

EGS were first introduced to Vancouver Island in 1945 (Ringuette 2004). A small population was introduced to Beacon Hill Park in the city of Victoria. They disappeared, however, and the current population of EGS are believed to be descendants of an introduction that occurred in the autumn of 1966. Three individuals were acquired from southwestern Ontario for a private game farm in Metchosin, within the Greater Victoria area (Guiguet 1975; Fraser 1987). These EGS were released some years after their arrival and had spread to neighbouring municipalities by 1975 (Guiguet 1975).

Study Areas

Both study sites are in southwestern British Columbia, Canada, and are separated from each other by a 40 km ocean strait (Figure 1). Both sites have mild climates and mean annual temperatures of 8°C-10°C. The Lower Mainland, an area of approximately 1500 km^2, is located in the moist Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1991). Prior to development, this region was predominantly conifer forest. Natural areas are still dominated by conifers, particularly Western Hemlock (*Tsuga heterophylla*), Western Red Cedar (*Thuja plicata*), and coastal Douglas-fir (*Pseudotsuga menziesii*). Residential areas have numerous horticultural trees, both in private gardens and along boulevards. For example, the Vancouver Park Board maintains over 124 000 trees comprising over 600 species and cultivars, the majority of which are deciduous (Vancouver Board of Parks and Recreation 2005*).

The Victoria region is an area of approximately 460 km^2 located in the Coastal Douglas-fir biogeoclimatic zone (Nuszdorfer et al. 1991) on the southeastern tip of Vancouver Island. Natural areas are dominated by coastal Douglas-fir, Shore Pine (*Pinus contorta*), and Western Red Cedar. Residential areas have a large variety of horticultural trees. The most common boulevard trees are Japanese flowering cherries (*Prunus* spp.) and Horse Chestnuts (*Aesculus hippocastanum*). Garry Oaks (*Quercus garryana*) are endemic to the region and the acorns may provide a food source for EGS.

Given the negative effects of EGS in Europe, there is speculation that EGS have negative ecological impacts in British Columbia. EGS may eat and damage a sufficient number of Garry Oak acorns to impede their regeneration (Bruemmer et al. 2000*). EGS may also compete for resources with endemic squirrels (Garry Oak Ecosystem Recovery Team 2003). North American Red Squirrels are endemic to the Victoria region and Douglas Squirrels (*Tamiasciurus douglasii*) and Northern Flying Squirrels (*Glaucomys sabrinicus*) are endemic to the Lower Mainland.

Methods

I conducted field surveys and solicited sightings of squirrels from the public, particularly naturalists, from 1996 to 2000, through paper and telephone surveys and a web page. A series of questions determined the presence or absence, location, coat colour and the year that EGS were first sighted at a location. A lack of squirrel sightings from the public surveys could be due to an absence of squirrels or a sampling effect. To ensure representative sampling across all land types, I conducted surveys in areas that were underrepresented by the public surveys. Using Geographic Information Systems (GIS), I overlaid a grid comprised of 5 km × 5 km cells onto each study area. Cells without sightings of squirrels were identified by land type on

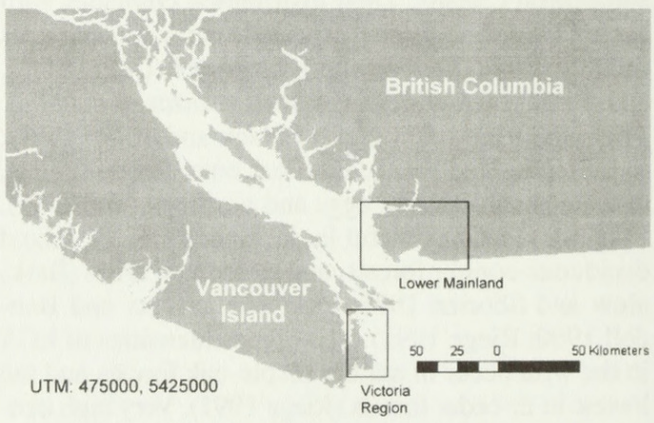

FIGURE 1: Map of southwestern British Columbia showing the Lower Mainland and the Victoria region.

a digital landscape map and the total area of each land type was computed. I calculated the number of public responses by land type to get a measure of "survey effort" by land type. Surveys were conducted in each of the land types so that each land type had an equal level of survey effort proportional to its presence on the landscape. Trained volunteers and I conducted 175 hours of auditory and visual searches for EGS, Douglas and Red squirrels. Surveys occurred from 8 am to 11 am, when squirrels are generally more active. Surveyors stayed at a point location for 10 minutes before moving to the next location approximately 100 m away. In addition to watching for EGS, Douglas, or Red squirrels, surveyors also listened for their calls to confirm their presence.

I also acquired submission records for EGS, Douglas and Northern Flying squirrels from three wildlife shelters located in different municipalities in the Lower Mainland for the years 1983 to 2003. Submission records begin in 1983, before EGS had spread to most municipalities in the Lower Mainland. The shelter records were used to augment the public surveys to plot the spread of EGS by year across the Lower Mainland. The records did not state the specific location where the squirrels were found, and therefore were not used in the habitat selection analysis.

I tested whether EGS use the land types proportional to their availability using a log-likelihood chi-square test with 95% confidence limits and a Bonferroni correction (Neu et al. 1974; Manly et al. 1993). The locations of EGS, given by nearest street intersection, landmark or GPS coordinates, were converted into UTM coordinates and overlaid onto digital maps using ArcView 3.2 (Environmental Systems Research Institute 1998*). Six land type categories, each ground-truthed with field surveys, were categorized on maps and included: (a) *Agriculture* (farmland and treeless fields); (b) *Parks* (municipal, regional, and provincial parks); (c) *Schools* (including fields, treed and undeveloped areas around a building or buildings; (d) *Industrial* (city centres and heavily developed areas); (e) *Residential* (urban and suburban areas); and (f) *Open* (cleared areas). Department of National Defence lands in the Victoria region (fields with some development) were included in the *Open* category. Land types in which squirrels were never sighted, such as lakes and gravel pits, were excluded from the analysis.

Results

In total, 212 responses were received for the Lower Mainland and 383 for the Victoria region. Wildlife shelter records provided an additional 4937 municipal locations of squirrels for the Lower Mainland. Over the 20 years, there were a total of 264 Northern Flying Squirrels, 656 Douglas Squirrels, and 4017 EGS brought to the wildlife shelters (Figure 2). EGS first arrived at the shelters in 1985 and their numbers have increased exponentially until 2000. EGS did not move contiguously through the municipalities in the two study sites. While it is likely that there were gaps in

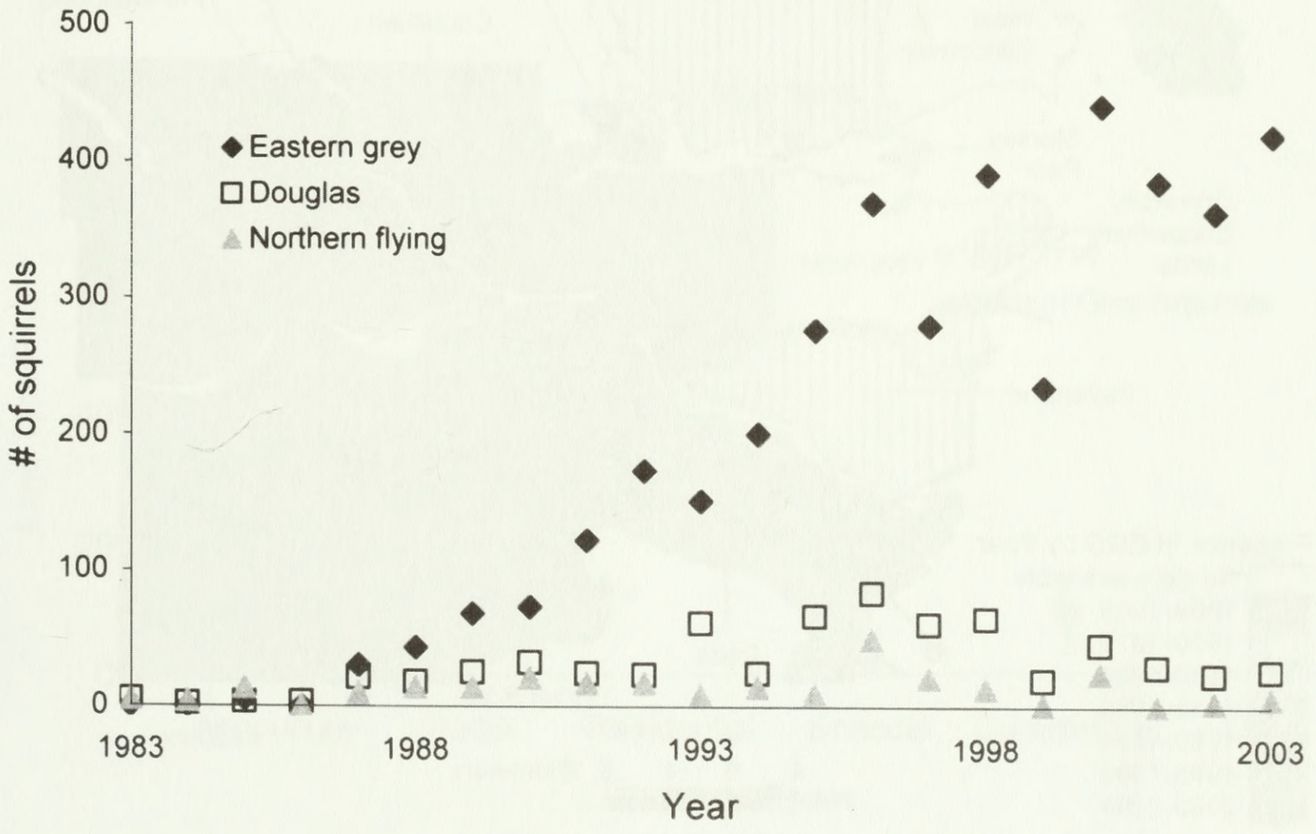

FIGURE 2. Number of Eastern Grey, Douglas and Northern Flying squirrels from wildlife shelters in the Lower Mainland from 1983 to 2003.

the temporal data, the translocation of EGS by humans also explains the discontiguous pattern of expansion. The surveys revealed that residents and pest control companies translocated live EGS, often beyond a "barrier" such as a river or mountain in the hopes that nuisance EGS would not return (Pynn 1999*). By 2004, EGS occurred throughout the Lower Mainland (Figure 3) and the Victoria region (Figure 4).

The habitat selection analysis revealed that EGS did not use the land types in proportion to their prevalence ($\chi^2 << 0.001$, df = 5). EGS were found predominantly in the land type when the proportion of EGS is significantly above the proportion of the land type's availability (Figures 5 and 6). EGS in the Lower Mainland were found predominantly in *Residential* land types and not in *Agricultural* or *Open* land types (Figure 5). EGS in the Victoria region were also found predominately in *Residential* land types and not in *Agricultural*, *Open*, or *Parks* land types (Figure 6).

Discussion

EGS have spread predominantly toward *Residential* areas. In the Lower Mainland, the Pacific Ocean to the west and conifer forest and mountains to the north have acted as barriers to their spread. Suitable habitat, specifically residential development, is available south and east and spread has proceeded further and more quickly in these directions. A similar pattern was seen in the Victoria region where EGS spread throughout the eastern peninsula of Vancouver Island, toward residential areas rather than west and north into areas dominated by conifer forests. The results suggest that EGS may continue to invade British Columbia, but are more likely to do so in residential areas and are unlikely to spread in areas still dominated by conifer forests. The land type categories were very general, however, because of the size of the region. I used the most detailed landscape data available for the breadth of the study areas. Localized studies that defined spe-

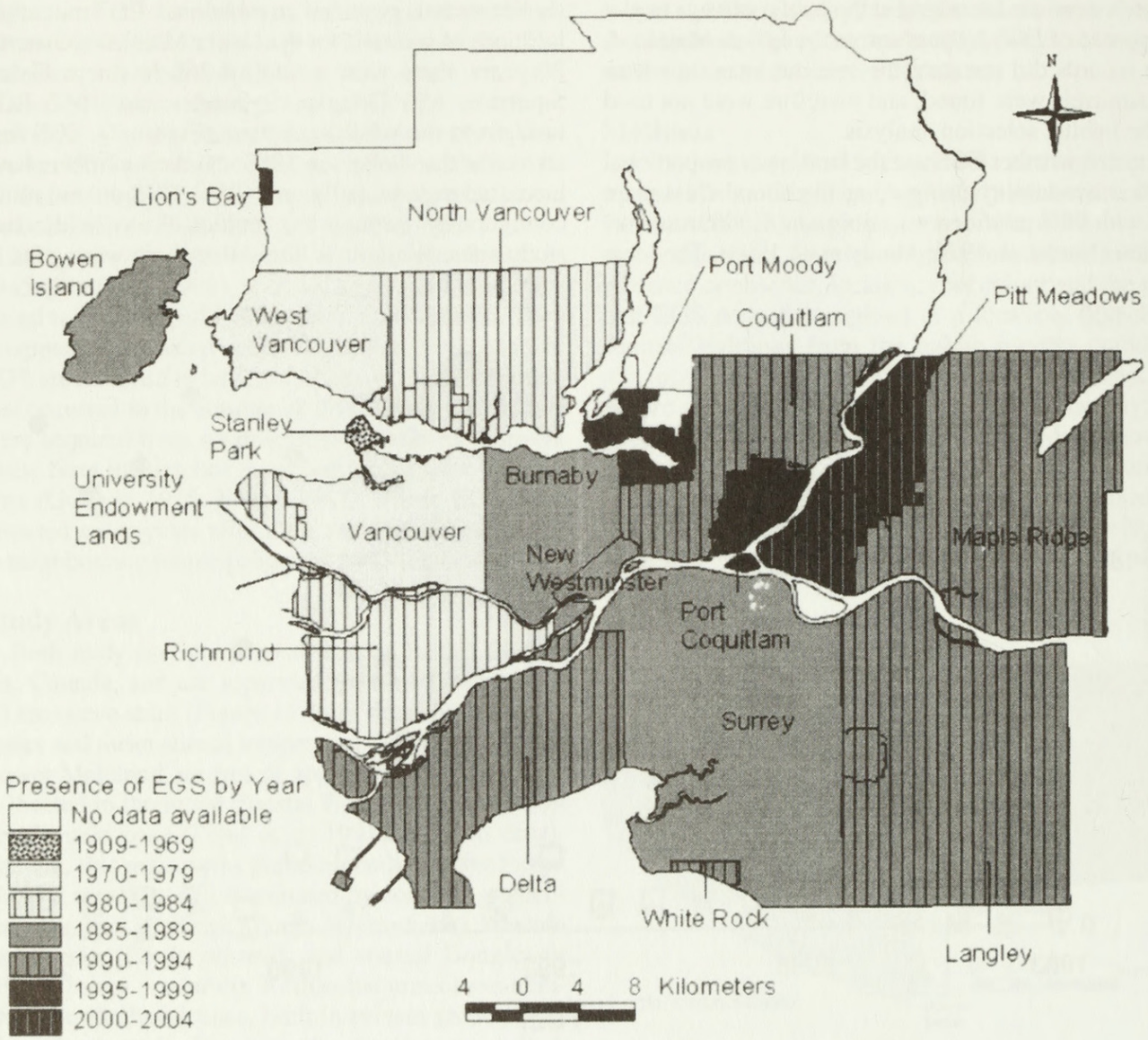

FIGURE 3. The spread of Eastern Grey Squirrels in the Lower Mainland from 1909 to 2004.

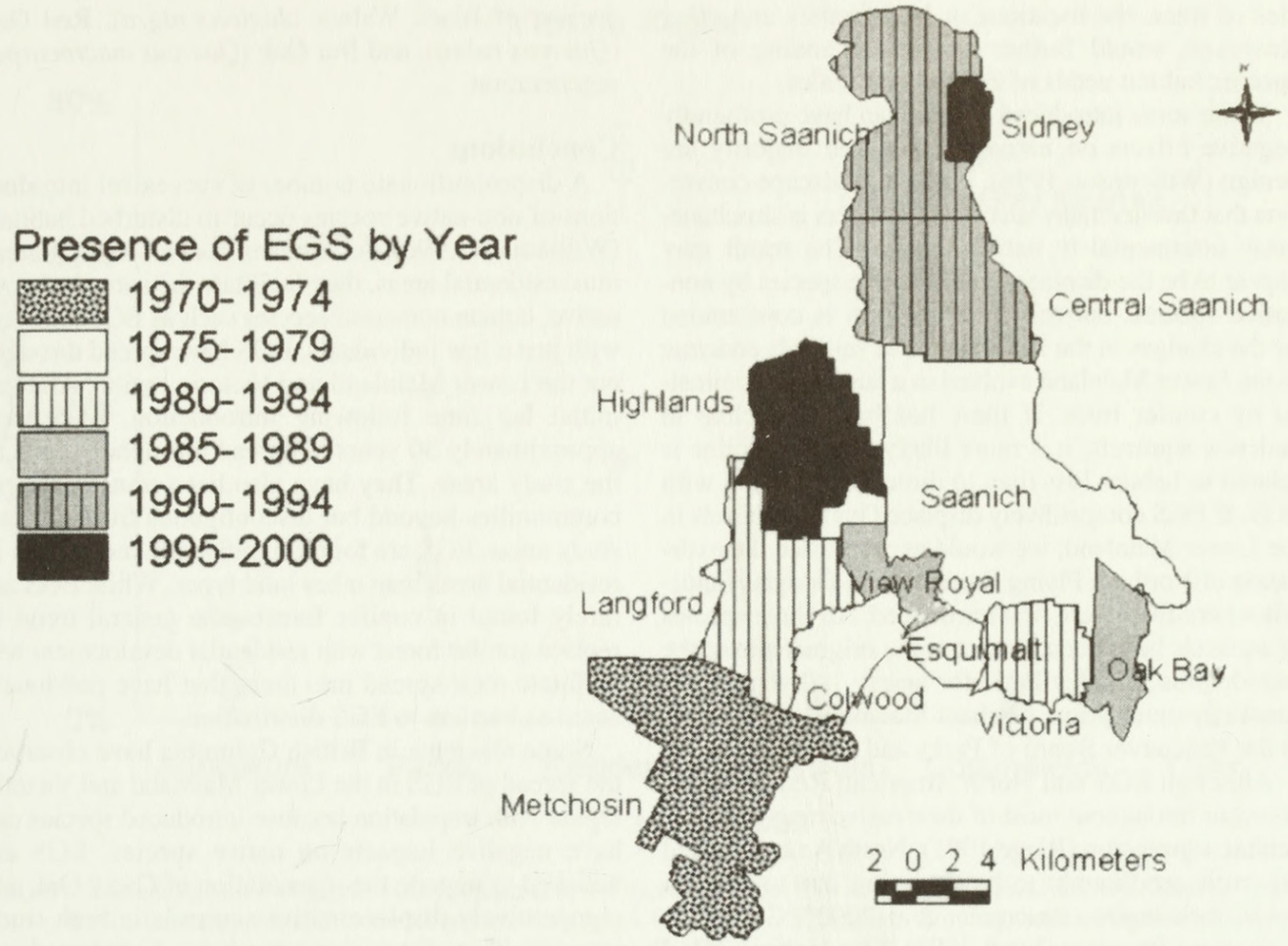

FIGURE 4. The spread of Eastern Grey Squirrels in the Victoria Region from 1970 to 2000.

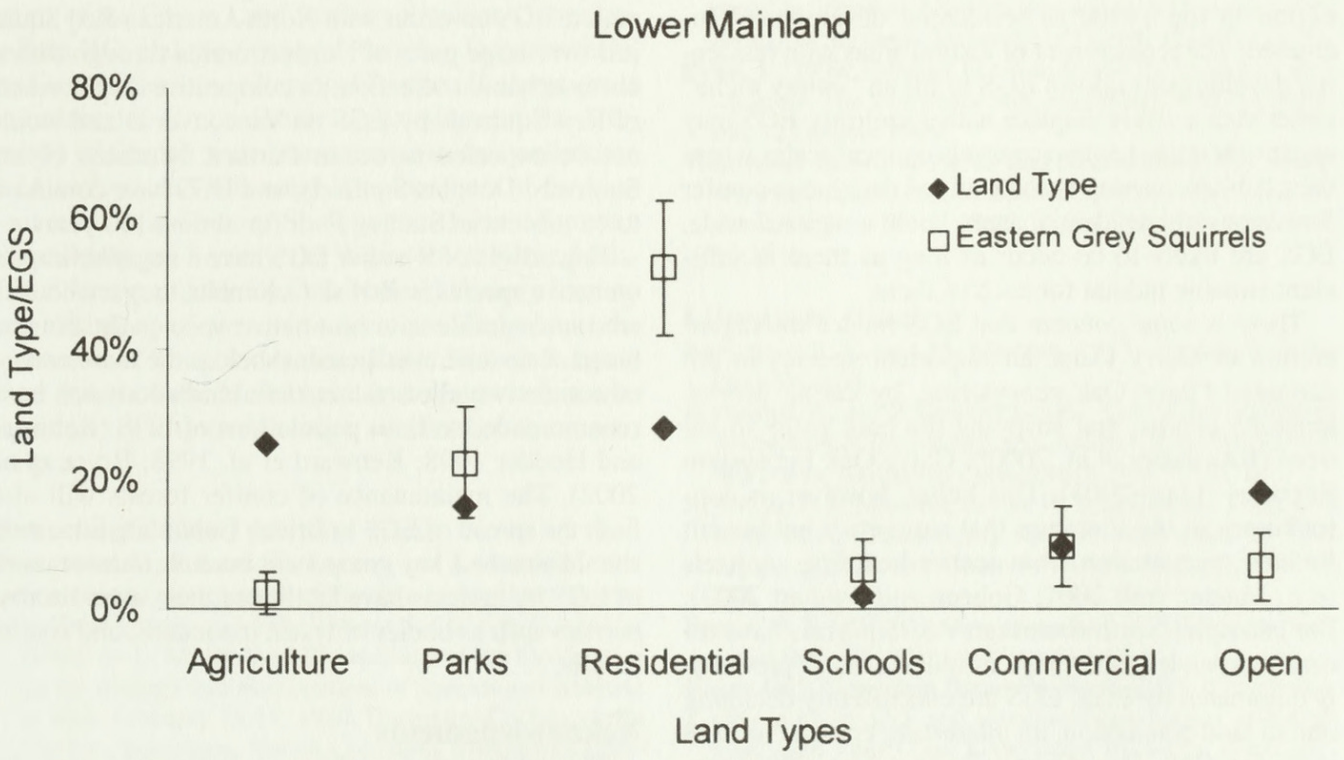

FIGURE 5. Habitat selection of Eastern Grey Squirrels in the Lower Mainland. The proportion of Eastern Grey Squirrels found in each land type with 95% confidence intervals ($\chi^2 << 0.001$, d.f. = 5). Eastern Grey Squirrels were found predominantly in *Residential* land types and not in *Agricultural* or *Open* land types.

cies of trees, the locations of bird feeders and other resources, would further our understanding of the specific habitat needs of EGS at fine scales.

While some introduced species can have profoundly negative effects on native species, the majority are benign (Williamson 1996). Further, landscape conversion that favours many successful invaders is simultaneously detrimental to native species. The result may appear to be the displacement of native species by non-native species, but this interpretation is confounded by the changes in the landscape. The squirrels endemic to the Lower Mainland evolved in a landscape dominated by conifer trees. If there has been a decline in endemic squirrels, it is more likely that the decline is related to habitat loss than to direct competition with EGS. If EGS competitively displaced native squirrels in the Lower Mainland, we would expect to see the extirpation of Northern Flying Squirrels and Douglas Squirrels where EGS were first introduced. All three species of squirrels have been present at the original site of the introduction, Stanley Park, for nearly 100 years (personal communication, Michael Macintosh, Supervisor at the Vancouver Board of Parks and Recreation).

Although EGS and North American Red Squirrels co-occur throughout most of their native range through habitat segregation (Riege 1991), North American Red Squirrels are thought to be declining due to EGS in the Victoria region (Bruemmer et al. 2000*; Garry Oak Ecosystem Recovery Team 2003). The decline of Red Squirrels, however, may be coincident with or exacerbated by habitat loss. For example, a survey respondent reported that North American Red Squirrels disappeared from southeastern municipalities in the Victoria region in the 1940s as residential development increased. The replacement of natural areas with residential development allows EGS to fill an "empty niche" rather than actively displace native squirrels. EGS may negatively impact native squirrels on local scales where their habitats overlap such as mixed deciduous-conifer forests or rural residential areas, but at a regional scale, EGS are likely to co-occur as long as there is sufficient suitable habitat for each of them.

There is some concern that EGS reduce the regeneration of Garry Oaks, an important species in endangered Garry Oak ecosystems, by eating acorns, notching acorns, and stripping the bark from young trees (Bruemmer et al. 2000*; Garry Oak Ecosystem Recovery Team 2003). This belief, however, is contradictory to the literature that supports a net benefit for tree regeneration from scatter hoarding squirrels (e.g., Vander Wall 2001; Goheen and Swihart 2003). For example, North American Red Squirrels have recently expanded their range in Indiana, areas previously dominated by EGS. EGS are concurrently declining due to land conversion, an interesting contrast to EGS in British Columbia. Goheen and Swihart (2003) predict that the replacement of scatter hoarding EGS with larder hoarding Red Squirrels will result in the decline of Black Walnut (*Juglans nigra*), Red Oak (*Quercus rubra*), and Bur Oak (*Quercus macrocarpa*) regeneration.

Conclusions

A disproportionate number of successful introductions of non-native species occur in disturbed habitats (Williamson 1996). As humans convert natural areas into residential areas, they facilitate the spread of non-native, human comensal species such as EGS. Starting with just a few individuals, EGS have spread throughout the Lower Mainland and Victoria region. After an initial lag time following introduction, EGS took approximately 30 years to spread throughout each of the study areas. They have also been translocated to communities beyond but discontiguous from the two study areas. EGS are found significantly more often in residential areas than other land types. While EGS are rarely found in conifer forests, the general trend to replace conifer forest with residential development will facilitate their spread into areas that have previously acted as barriers to EGS distribution.

Some residents in British Columbia have observed the spread of EGS in the Lower Mainland and Victoria region with trepidation because introduced species can have negative impacts on native species. EGS are believed to impede the regeneration of Garry Oak and competitively displace native squirrels in both study areas. Neither of these hypotheses has been tested and it is possible that EGS have negative ecological impacts in British Columbia. There are reasons, however, to be optimistic. EGS are beneficial to hardwood tree regeneration, particularly oaks, in regions where EGS are native. EGS co-occur with North American Red Squirrels over large parts of North America through differences in habitat selection, so competitive displacement of Red Squirrels by EGS on Vancouver Island would not be expected to occur. Further, Northern Flying Squirrels, Douglas Squirrels, and EGS have continued to be present in Stanley Park for almost 100 years.

Regardless of whether EGS have a negative impact on native species in British Columbia, they are considered undesirable as a non-native species. In Europe, broad scale land management such as the maintenance of conifer woodlots rather than hardwoods has been recommended to limit populations of EGS (Kenward and Hodder 1998; Kenward et al. 1998; Bryce et al. 2002). The maintenance of conifer forests will also limit the spread of EGS in British Columbia. Education should also be a key component because translocations of EGS by humans have facilitated their spread across barriers such as bodies of water, mountains, and conifer forests.

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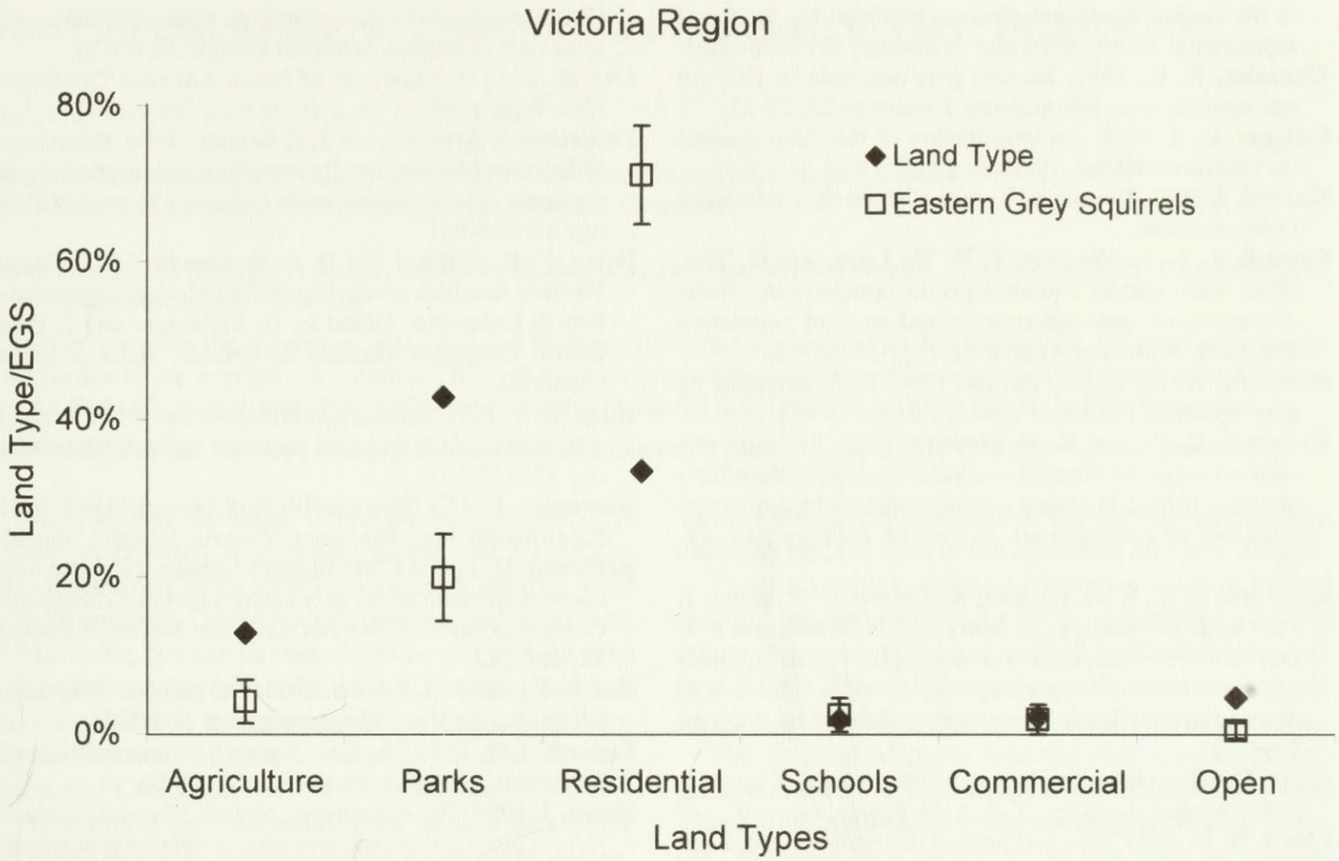

FIGURE 6. Habitat selection of Eastern Grey Squirrels in the Victoria region. The proportion of Eastern Grey Squirrels found in each land type with 95% confidence intervals ($\chi^2 << 0.001$, d.f. = 5). Eastern Grey Squirrels in the Victoria region were found predominately in *Residential* land types and not in *Agricultural*, *Open*, or *Parks* land types.

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