A Test of Interspecific Effects of Introduced Eastern Grey Squirrels, *Sciurus carolinensis,* on Douglas's Squirrels, *Tamiasciurus douglasii,* in Vancouver, British Columbia

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We compared the effects of absence and presence introduced Eastern Grey Squirrels (*Sciurus carolinensis*) on the demography of native Douglas's Squirrels (*Tamiasciurus douglasii*) in two urban parks in Vancouver, British Columbia: Ecological Reserve #74 in Pacific Spirit Regional Park (Douglas's Squirrel only) and Stanley Park (Douglas's and Eastern Grey squirrels). Based on the exploitative competition hypothesis, we predicted that in the presence of introduced Eastern Grey squirrels, Douglas's Squirrels would occur at lower densities, have larger home ranges, lower body mass, and poorer reproduction. Using mark-recapture methods, we found no differences in density, home range, or body mass of Douglas's Squirrel between parks. However, the proportion of breeding Douglas's Squirrels was higher in Ecological Reserve #74 in the absence of Eastern Grey Squirrel, than in Stanley Park. We found no evidence that Eastern Grey Squirrels are displacing Douglas's Squirrels in Stanley Park, but less conspicuous negative effects such as reduced breeding propensity may still reflect the competitive interactions of the two squirrel species.

Key Words: Density, home range, body mass, reproduction, Eastern Grey Squirrel, *Sciurus carolinensis*, Douglas's Squirrel, *Tamiasciurus douglasii*, exploitative competition, British Columbia.

In western Canada, Eastern Grey Squirrels (*Sciurus carolinensis*) were introduced to Stanley Park in the city of Vancouver, British Columbia, shortly before 1914. The three to four pairs of introduced Eastern Grey Squirrels came from eastern Canada (Robinson and Cowan 1954). In the early 1980s, Eastern Grey Squirrels colonized the rest of the city of Vancouver, including many of its urban parks. Since then, Eastern Grey Squirrels have spread to many parts of the Greater Vancouver Regional District (Gonzales 1999, 2000).

On the mainland in southwest British Columbia, the native tree squirrel is the Douglas's Squirrel (*Tamiasciurus douglasii*); it is the ecological counterpart of the Red Squirrel (*T. hudsonicus*) that is widespread in temperate forests of North America (Steele 1998, 1999). The Eastern Grey Squirrel is native in eastern North America (Hall 1981) and its geographical range overlaps broadly with that of the Red Squirrel. Although Red Squirrels are associated with conifer forests and Eastern Grey Squirrels with mast-bearing hardwood forests, the two species often coexist in mixed forests or urban parks (Riege 1991). Forty years after Eastern Grey Squirrels were introduced to southwestern British Columbia, Robinson and Cowan (1954) conducted a live-trapping and observational study on Eastern Grey Squirrels in Stanley Park. They noted that, in deciduous habitat in Stanley Park, Eastern Grey Squirrels lived at high densities together with lower densities of Douglas's Squirrels. They suggested that the Eastern Grey Squirrels outcompete Douglas's Squirrels for food, and thus restrict Douglas's Squirrels to areas of predominately coniferous habitat (Robinson and Cowan 1954). Whether competitive interactions between the two species still exist today (> 80 years since the introduction of Eastern Grey Squirrels) remains unknown.

In Great Britain, Eastern Grey Squirrels were introduced at the end of the 19th century, and have caused the decline of the smaller native European Red Squirrel (*Sciurus vulgaris*) from its former range (Gurnell and Pepper 1993; Wauters and Gurnell 1999; Teangana et al. 2000). The mechanisms of replacement of European Red by Eastern Grey squirrels are not yet fully understood (Skelcher 1997). Juvenile recruitment of European Red Squirrels is typically lower when Eastern Grey Squirrels are present (Wauters et al. 2000, 2001). Also, diseases such as parapoxvirus have been hypothesized to facilitate the replacement of European Red Squirrels by Eastern Grey Squirrels in the United Kingdom (Tompkins et al. 2003).

The Eastern Grey Squirrel averages 400–700 g in body mass (Koprowski 1984), and is larger than Douglas's Squirrel, which averages 250-300 g (Steele 1999). Douglas's Squirrels feed primarily on coniferous seeds, new shoots of conifers, green vegetation, acorns, nuts, mushrooms, fruits, and berries. Also, Douglas's Squirrels actively defend food middens within their territory

(Steele 1999). In its native range, the Eastern Grey Squirrel feeds heavily on hickory nuts, beechnuts, acorns, and walnuts (Koprowski 1984); however, introduced Eastern Grey Squirrels in British Columbia feed extensively on maple, oak, hazelnut, mushrooms, berries and pine cones (Robinson and Cowan 1954). Both species prefer seeds, and other plant foods predominate in the diet only when seed crops are small (Moller 1983). Also, in Stanley Park, a few Eastern Grey Squirrels depend almost entirely on "hand-outs" from park visitors as an artificial food source. Eastern Grey Squirrels living in close proximity to humans often venture out of the forests and feed on artificial food sources.

Eastern Grey Squirrels have a dominance hierarchy and are not territorial (Flyger 1955; Thompson 1977) whereas Douglas's Squirrels are territorial year round (Steele 1999). Territorial behaviour exhibited by Douglas's Squirrels is mainly used against conspecifics similar to Red Squirrels (Smith 1981). Intruding Eastern Grey Squirrels are generally free to enter their territory (Robinson and Cowan 1954).

The interspecific effects of the introduced Eastern Grey Squirrels on the native Douglas's Squirrels are unknown in southwestern British Columbia. We tested the hypothesis that Eastern Grey Squirrels negatively impact native Douglas's Squirrels through exploitative competition for resources. With the introduction of Eastern Grey Squirrels, resources such as food and nest sites in areas where both squirrels occur would decrease, causing an increase in home range size of Douglas's Squirrels because larger ranges are needed to collect more food (Schoener 1971). Larger home ranges would decrease the density of Douglas's Squirrels in the given area. Also, with increased home ranges, Douglas's Squirrels would expend more energy foraging and defending the area and would have less energy for reproduction and maintenance. Therefore, we predicted that in areas with Eastern Grey Squirrels, Douglas's Squirrels would occur at lower densities, have larger home ranges and lower body mass, and that they would reproduce less well.

Materials and Methods

We worked at two study sites. The species co-occur in Stanley Park, which was the original site of Eastern Grey Squirrel introduction to western Canada, and of Robinson and Cowan's (1954) study. The control study site was Ecological Reserve #74 (Pacific Spirit Regional Park) where only Douglas's Squirrels occur. Although Eastern Grey Squirrels do not occur in Ecological Reserve #74, they do occur in residential areas nearby and are abundant on the University of British Columbia campus only 1-2 km distant.

Both study areas are in the Coastal Western Hemlock biogeoclimatic zone. The dominant coniferous species in Stanley Park were Western Hemlock (*Tsuga heterophylla*), Western Redcedar (*Thuja plicata*), and Douglas Fir (*Pseudotsuga menziesii*). Stanley Park is a mosaic of second- (> 50 years old) and old-growth (> 120 years old) conifer stands. Ecological Reserve #74 represented a mature conifer stand (> 90 years old) with Western Hemlock, Western Redcedar, Douglas Fir, and Sitka Spruce (*Picea sitchensis)* with scattered Red Alder (*Alnus rubus*) and Big Leaf Maple (*Acer macrophyllum*). Understory and ground cover in both study areas consisted mainly of Vine Maple (*Acer circinatum*), Salmonberry (*Rubus spectabilis*), Red Huckleberry (*Vaccinium parvifolium*), Salal (*Gaultheria shallon*), leaf litter, ferns and mosses.

In each study area, we established a 9-ha live-trapping grid consisting of 96 (6 by 16) stations located at 30 m intervals. We set Tomahawk live-traps (model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) at alternate trap stations, resulting in 48 traps per live-trapping grid. We live-trapped squirrels for 2 days every 2 weeks from May to August 1997 (9 trap sessions) in both study areas.

We baited the traps with sunflower seeds and set them in early morning and checked traps 4-6 hours later. Captured squirrels were ear-tagged with numbered metal tags (Monel #1, National Band and Tag Co., NewPort, Kentucky), sexed and weighed (± 5 g using a Pesola® spring balance). We noted breeding condition by palpation of male testes and female mammaries (Sullivan and Moses 1986).

We estimated population size, proportion of reproductive squirrels, body mass, and home range size. Population size and trappability were estimated for each trap session using the Jolly-Seber mark-recapture model (Jolly 1965; Seber 1965). We were not able to use radio-telemetry to estimate the territory size of Douglas's Squirrels in this study; therefore we estimated home range size by using trapping location for animals that were captured ≥ 2 times using the exclusive boundary strip method (Hayne 1949, 1950; Stickel 1954). Also, we only considered home ranges of females because in late spring and early summer, males roam extensively while searching for potential mates.

We used chi-square test to examine the trappability of squirrel populations between both sites. We used one-tailed t-test to compare densities of Douglas's Squirrels between sites. Due to unequal variances for Eastern Grey Squirrel densities in Stanley Park, we used Mann-Whitney U test to compare differences in densities between both species in the two study areas. We used two-way Analysis of Variance (ANOVA) to examine the difference in body mass and home ranges of Douglas's Squirrels between Ecological Reserve #74 and Stanley Park. The *Z*-test was used to test for significant differences in the proportion of squirrels in breeding condition (Sokal and Rohlf 1995). Since sample sizes of breeding individuals were small, the statistical power of the Z tests is very low in detecting

Table 1. Summary of demographic parameters for Douglas's Squirrels (DS) and Eastern Grey Squirrels (EGS) in Ecological Reserve #74 and Stanley Park, Vancouver, British Columbia, Canada from May to August 1997. Values shown are mean≠± SE.

	Ecological Reserve #74	Stanley Park	
	DS	DS	EGS
Density (individuals/ha)	3.5 ± 0.4	2.9 ± 0.1	2.5 ± 0.4
Home range (ha)	0.37 ± 0.096	0.44 ± 0.11	–
Trappability (%)			
Male	74.7	60.3	30.0
Female	80.9	74.0	30.0
Body mass (g)			
Male	181.8 ± 2.69	184.5 ± 3.81	608.6 ± 11.91
Female	177.4 ± 4.62	181.1 ± 4.40	603.7 ± 15.59
Proportion of breeding females (%)	20	5	77

a significant effect; however, the *Z*-statistic was used as an index of differences between study areas. All values are reported as mean ± SE.

Results

Density and home range

From May to August 1997, we captured 30 male and 24 female Douglas's Squirrels in Pacific Spirit Park. In Stanley Park, we caught 19 male and 25 female Douglas's Squirrels. Eastern Grey Squirrels were only found in Stanley Park, and we caught 22 males and 17 females. See Table 1 for a summary of demographic parameters.

Trappability of Douglas's Squirrels in Pacific Spirit Park was similar between males and females, at 74.7% and 80.9%, respectively. Male and female Douglas's Squirrels in Stanley Park also have relatively high trappability values, both ranging from 60.3% to 74.0%. On the other hand, Eastern Grey Squirrels had very low trappability, with males and females both having 30%. Trappability of Eastern Grey Squirrels was significantly lower in Stanley Park ($\chi^2 = 14.54$, df = 1, $P < 0.001$) than for Douglas's Squirrels.

Densities of Douglas's Squirrels did not differ ($t = 1.65$, df = 12, $P = 0.12$) between Ecological Reserve #74 (3.5 individuals/ha ± 0.4) and Stanley Park (2.9 individuals/ha ± 0.1). In Stanley Park, density also did not differ (Mann-Whitney T = 56, $P = 0.71$) between Eastern Grey Squirrel (2.5 individuals/ha ± 0.4) and Douglas's Squirrels (2.9 individuals/ha ± 0.1).

No effect of sex ($F_{1,64} = 0.18$, $P = 0.67$) or study area ($F_{1,64} = 1.24$, $P = 0.27$) on the home range of Douglas's Squirrels, nor were significant interactions detected ($F_{1,64} = 0.44$, $P = 0.51$). Home ranges averaged 0.31 ± 0.05 ha ($n = 96$).

Body mass and reproduction

No effect of study area ($F_{1,93} = 0.075$, $P = 0.78$) on body mass of Douglas's Squirrels was found, but there was a gender effect ($F_{1,93} = 5.41$, $P = 0.022$), with males (185.3 ± 4.1 g, $n = 48$) being heavier than females (177.2 ± 5.3 g, $n = 49$) in both parks.

For comparison purposes, Eastern Grey Squirrels in Stanley Park averaged 606.4 ± 19.1 g with no gender difference (t = 0.25, df = 37, $P = 0.80$). On average, male Eastern Grey Squirrels weighed 608.5 **±** 11.9 g, and females weighed 603.8 **±** 15.6 g.

From 20 May to 28 August 1997, proportions of female Douglas's Squirrels in breeding condition differed significantly between sites (Z = 2.56, $P < 0.001$), with a higher proportion of breeding females in Ecological Reserve #74 compared to that in Stanley Park: 20% (15 breeding out of 77 individuals) and 5% (3/62), respectively. In Stanley Park, the proportion of female Eastern Grey Squirrels in breeding condition (77%: 17/22) was higher than for Douglas's Squirrels (5%: 3/62). However, the proportion of breeding male Douglas's Squirrels at the two sites was similar and averaged 98.3% (59/60).

Discussion

We did not detect strong effects of exploitative competition between Eastern Grey Squirrels and Douglas's Squirrels. There was no evidence of reduced density, large ranges, and lower mass in Douglas's Squirrels where the two species co-occurred. However, the proportion of breeding Douglas's Squirrels was significantly lower in Stanley Park compared to that in Ecological Reserve #74, suggesting possible negative effects of Eastern Grey Squirrels on the breeding propensity of Douglas's Squirrels.

Densities of Douglas's Squirrels are limited by food availability (Sullivan and Sullivan 1982; Ransome and Sullivan 1997), and old-growth forests provide higher-quality habitat for Douglas's Squirrels than younger forests due to greater and more reliable quantities of conifer seed (Buchanan et al. 1990). In our study, the densities of Douglas's Squirrels were similar at both sites, suggesting that habitat suitability was similar, and further suggesting that reduced breeding propensity was caused by the presence of Eastern Grey Squirrels, and not simply an artifact of difference in food availability among study areas.

A possible explanation for weak effects of exploitative competition between the two species of squirrels could be due to the fact that Eastern Grey Squirrels often can exploit broadleaved and deciduous woodland to increase breeding success by feeding on high-energy food (Skelcher 1997; Gurnell et al. 2001), but since both study areas consist of mixed woods with high conifer content, advantages in breeding success of Eastern Grey Squirrels were perhaps less pronounced (Teangana et al. 2000). Thus, Douglas's and Eastern Grey Squirrels could coexist for many years although perhaps Douglas's Squirrel would slowly decline due to lower reproductive outputs (Reynolds 1985; Gurnell 1996).

Our density estimates for Eastern Grey Squirrels (2.5 individuals/ha) also were slightly higher than those reported >45 years earlier (1.7 individuals/ha; Robinson and Cowan 1954), suggesting that the population of Eastern Grey Squirrels in Stanley Park is relatively stable, even if their range elsewhere has expanded (Gonzales 1999, 2000). If the combined presence of both Douglas's and Eastern Grey squirrels in Stanley Park accelerates the depletion of the autumn seed crop, this might force a greater dependence on alternative plant foods in the spring and summer, which Eastern Grey Squirrels are better able to use because of their larger body size (Ackerman and Weigl 1970; Steele and Weigl 1993). An investigation into the feeding behavior and space use of both species would provide a better understanding of how Douglas's and Eastern Grey squirrels coexists in anthropogenic environments such as urban parks. This study highlights the need for more long-term population monitoring of the interaction of the two squirrel species in areas where Eastern Grey Squirrels were introduced.

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Literature Cited

Ackerman, R., and **P. D. Weigl.** 1970. Dominance relations of red and grey squirrels. Ecology 51: 332-335.

Buchanan, J. B., R. W. Lundquist, and **K. B. Aubry.** 1990. Winter populations of Douglas's squirrels in different-aged Douglas-fir forests. Journal of Wildlife Management 54: 577-581.

Flyger, V. F. 1955. Implications of social behavior in grey squirrel management. Transactions of the North American Wildlife and Natural Resources Conference 20: 381-389.

Gonzales, E. K. 1999. Eastern gray squirrels in BC: an introduction to an introduction. Discovery 28: 22-25.

Gonzales, E. K. 2000. Distinguishing between modes of dispersal by introduced western grey squirrels (*Sciurus carolinensis*). M.Sc. thesis, University of Guelph, Guelph, Ontario. 98 pages.

Gurnell, J. 1996. Conserving the red squirrel in Thetford Forest Park: the ecology of a pine forest. *Edited by* P. Ratcliffe and J. Calridge. Forestry Commission, Edinburgh.

Gurnell, J., L. A. Wauters, D. Preatoni, and **G. Tosi.** 2001. Spacing behaviour, kinship, and population dynamics of grey squirrels in a newly colonized broadleaf woodland in Italy. Canadian Journal of Zoology 79: 1533-1543.

Gurnell, J., and **H. Pepper.** 1993. A critical look at conserving the British Red Squirrel *Sciurus vulgaris*. Mammal Review 23: 127-137.

Hall, E. R. 1981. The mammals of North America. Second edition. John Wiley & Sons, New York, New York.

Hayne, D. W. 1949. Calculation of size of home range. Journal of Mammalogy 30: 1-17.

Hayne, D. W. 1950. Apparent home range of *Microtus* in relation to distance between traps. Journal of Mammalogy 31: 26-39.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247.

Koprowski, J. L. 1984. *Sciurus carolinensis*. Mammalian Species 480: 1-9.

Moller, H. 1983. Foods and foraging behaviour of red (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*). Mammal Review 13: 81-99.

Ransome, D. B., and **T. P. Sullivan.** 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy 78: 538-549.

Reynolds, J. C. 1985. Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*) in eastern England. Journal of Animal Ecology 54: 149-162.

Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and grey squirrels. Journal of Mammalogy 72: 152-162.

Robinson, D. J., and **I. McT. Cowan.** 1954. An introduced population of the grey squirrel (*Sciurus carolinenesis* Gmelin) in British Columbia. Canadian Journal of Zoology 32: 261-282.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.

Skelcher, G. 1997. The ecological replacement of red by grey squirrels. Pages 67-78 *in* The conservation of red squirrels, *Sciurus vulgaris* L. *Edited by* J. Gurnell, and P. Lurz. People's Trust for Endangered Species, London.

Smith, C. C. 1981. The indivisible niche of *Tamiasciurus*: An example of nonpartitioning of resources. Ecological Monographs 51: 343-363.

Sokal, R. R., and **F. J. Rohlf.** 1995. Biometry: The principles and practice of statistics in biological research. 3rd edition. W. H. Freeman & Company, New York, New York.

Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species 586: 1-9.

Steele, M. A. 1999. *Tamiasciurus douglasii*. Mammalian Species 630: 1-8.

Steele, M. A., and **P. D. Weigl.** 1993. The ecological significance of body size in fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*). Pages 57-69 *in* Proceedings of the Second Symposium on Southeastern Fox Squirrels, *Sciurus niger*. *Edited by* N. D. Moncrief, J. W. Edwards, and P. A. Tappe. Virginia Museum of Natural History Special Publication Number 1.

Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. Journal of Mammalogy 35: 1-15.

Sullivan, T. P., and **R. A. Moses.** 1986. Red squirrel populations in natural and managed stands of lodgepole pine. Journal of Wildlife Management 50: 595-601.

Sullivan, T. P., and **D. S. Sullivan.** 1982. Population dynamics and regulation of the Douglas's squirrel (*Tamiasciurus douglasii*) with supplemental food. Oecologia 53: 264-270.

Teangana, D. Ó., S. Reilly, W. I. Montgomery, and **J. Rochford.** 2000. Distribution and status of the red squirrel (*Sciurus vulgaris)* and grey squirrel (*Sciurus carolinensis*) in Ireland. Mammal Review 30: 45-56.

Tompkins, D. M., A. R. White, and **M. Boots.** 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. Ecology Letters 6: 189.

Thompson, D. C. 1977. Social system of grey squirrel. Behaviour 64: 305-328.

Wauters, L. A., and **J. Gurnell**. 1999. The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. Ethology 105: 1053-1071.

Wauters, L. A., J. Gurnell, A. Martinoli, and **G. Tosi.** 2001. Does interspecific competition with grey squirrels affect the foraging behavior and food choice of red squirrels? Animal Behavior 61: 1079-1091.

Wauters, L. A., P. W. W. Lurz, and **J. Gurnell.** 2000. Interspecific effects of grey squirrels (*Sciurus carolinensis*) on the space use and population demography of red squirrels (*Sciurus vulgaris*) in conifer plantation. Ecological Research 15: 271-284.

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