

Positive relationship between non-native and native squirrels in an urban landscape

E.K. Gonzales, Y.F. Wiersma, A.I. Maher, and T.D. Nudds

Abstract: Paradoxically, non-native species sometimes displace native species that appear to be well adapted to local landscapes. That many landscapes have been altered by humans, creating habitat suitable for non-native species, helps explain this apparent paradox. We asked whether the abundance of native Douglas (*Tamiasciurus douglasii* (Bachman, 1839)) and northern flying (*Glaucomys sabrinus* (Shaw, 1801)) squirrels was best explained by the abundance of non-native eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788), the proportion of urban development, or both using available squirrel abundance data from wildlife shelters and land-use maps. There was no evidence that non-native squirrels replaced native squirrels since their abundances were positively related, whereas native squirrels varied negatively with the amount of development. The best model explaining variation in the abundance of Douglas and northern flying squirrels incorporated both eastern grey squirrels and development, which is consistent with the hypothesis that regional declines in native squirrels are more likely to be predicated by the alteration of native conifer habitats by humans independent of the effects of non-native squirrels.

Résumé : Il arrive paradoxalement que des espèces non indigènes évincent des espèces indigènes qui semblent bien adaptées aux paysages locaux. Le paradoxe apparent s'explique en partie par la modification anthropique de nombreux paysages, ce qui crée des habitats pour les espèces non indigènes. Nous nous demandons si les abondances des écureuils de Douglas (*Tamiasciurus douglasii* (Bachman, 1839)) et du grand polatouche (*Glaucomys sabrinus* (Shaw, 1801)) s'expliquent mieux par l'abondance de l'écureuil gris (*Sciurus carolinensis* Gmelin, 1788) non indigène ou par l'importance du développement urbain, ou encore par les deux phénomènes; nous utilisons les données d'abondance des sciuridés disponibles dans les refuges de faune sauvage, ainsi que des cartes d'utilisation des terres. Il n'y a aucune indication que les écureuils non indigènes évincent les sciuridés indigènes puisqu'il y a une corrélation positive entre leurs abondances respectives; en revanche, l'abondance des écureuils indigènes est en corrélation négative avec l'importance du développement. Le meilleur modèle explicatif de l'abondance des écureuils de Douglas et des grands polatouches tient compte à la fois des écureuils gris et du développement, ce qui s'accorde avec l'hypothèse selon laquelle les déclin régionaux de sciuridés indigènes sont plus vraisemblablement attribuables à la modification des habitats indigènes de conifères par les humains, indépendamment des effets des écureuils non indigènes.

[Traduit par la Rédaction]

Introduction

As species are translocated around the globe, ecosystems become composed of increasing numbers of non-native species (Sax et al. 2002). Some of these have negative effects on the new environment (Wilcove et al. 1998), and are hereinafter called “invaders” to distinguish from non-invasive non-native species (Alpert et al. 2000; Davis and Thompson 2000). However, we currently have little ability to predict what controls the demographic success of non-native species or the demographic response of native species to non-native

species (Levine et al. 2003). The success of non-native species has often been interpreted in the context of biotic interactions such as competitive exclusion (Mitchell et al. 2006), whereby the increasing abundance of a novel species is correlated with the decreasing abundance of native species and this relationship is taken as evidence of causation (Conroy et al. 1989; Gurevitch and Padilla 2004). However, there is little empirical evidence for a relationship between invasion and extinction (Davis 2003); in fact, frequently there are positive relationships between native and non-native species (Lonsdale 1999; Sax and Brown 1999; Sax and Gaines 2003) because the same environmental conditions favour both (Stohlgren et al. 1999).

Alternatively, negative relationships between native and non-native species can be mediated by indirect effects such as habitat alteration (Gurevitch and Padilla 2004). Thus non-native species may be “passengers” of anthropogenic disturbance rather than “drivers” of native species declines (MacDougall and Turkington 2005). Testing alternative hypotheses can clarify the mechanisms driving species declines in situations of apparent competitive exclusion (Didham et al. 2005). Recent theories on the success of non-native species address multifactor mechanisms (Mitchell et al. 2006). Non-native species lose interactions with enemies, mutual-

Received 26 June 2007. Accepted 14 January 2008. Published on the NRC Research Press Web site at cjz.nrc.ca on .

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ists, and competitors from their native ranges and gain interactions with new species under new environmental conditions (Hiero et al. 2005). Determining the direct and indirect mechanisms that mediate the abundances of native and non-native species has important implications for management decisions about whether and how to control established non-native species (White et al. 2006). However, demographic data for non-native species are not typically available during the time when control efforts are most effective (Simberloff 2003), presenting a challenge for management. We used available data to examine the relationships between the abundance of two native species with a confamilial non-native species and habitat distribution.

Perhaps one of the most well-known and well-studied examples of competitive exclusion is the replacement of Eurasian red squirrels (*Sciurus vulgaris* L., 1758) by eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788), hereinafter grey squirrels, following their introduction to Europe (Gurnell et al. 2004). Three hypotheses, (1) competitive exclusion, (2) habitat modification, and (3) disease transmission, may explain the shift from native to non-native squirrels (Reynolds 1985). Eurasian red and grey squirrels compete for the same resources in deciduous forests (Wauters et al. 2002) and fitness of Eurasian squirrels was shown to be lower in the presence of grey squirrels (Gurnell et al. 2004). However, Eurasian red squirrels persist with grey squirrels in some conifer forests (Bryce et al. 2002), suggesting that habitat influences competitive interactions. Grey squirrels are also asymptomatic carriers of a poxvirus lethal to Eurasian red squirrels (Thomas et al. 2003; Tompkins et al. 2003), although red squirrels also declined in the absence of the disease (Reynolds 1985; Gurnell et al. 2004). Regardless of the mechanism, Eurasian red squirrels generally disappear within 10–20 years of the arrival of grey squirrels in deciduous forests (Usher et al. 1992). Grey squirrels, native to parts of central and eastern North America, were introduced around the world (Gurnell 1987), including western North America (Robinson and [McTaggart-]Cowan 1954). Interactions between native and introduced grey squirrels have rarely been studied outside of Europe and their effects on native species are largely unknown.

Two native arboreal sciurids, Douglas squirrels (*Tamiasciurus douglasii* (Bachman, 1839)) and northern flying squirrels (*Glaucomys sabrinus* (Shaw, 1801)), inhabit mainland North America's Pacific coast. Douglas squirrels are diurnal, conifer-associated squirrels whose range extends west of the Cascade Mountains to the coast ([McTaggart-]Cowan and Guiguet 1965). Northern flying squirrels are nocturnal, widely distributed in North America, and tend to be found in older forests where suitable nest sites are more abundant (Martin and Anthony 1999). Sciurid populations are known to fluctuate with food supply and both native and grey squirrels have catholic dietary preferences that include seeds, fungi, and occasionally bird eggs and nestlings (Robinson and [McTaggart-]Cowan 1954; Sullivan and Sullivan 1982).

There is concern that non-native grey squirrels displace native squirrels in western North America (Bruemmer et al. 2000; Garry Oak Ecosystems Recovery Team 2003). The density and reproductive output of Douglas squirrels in Stanley Park, where grey squirrels were first introduced to

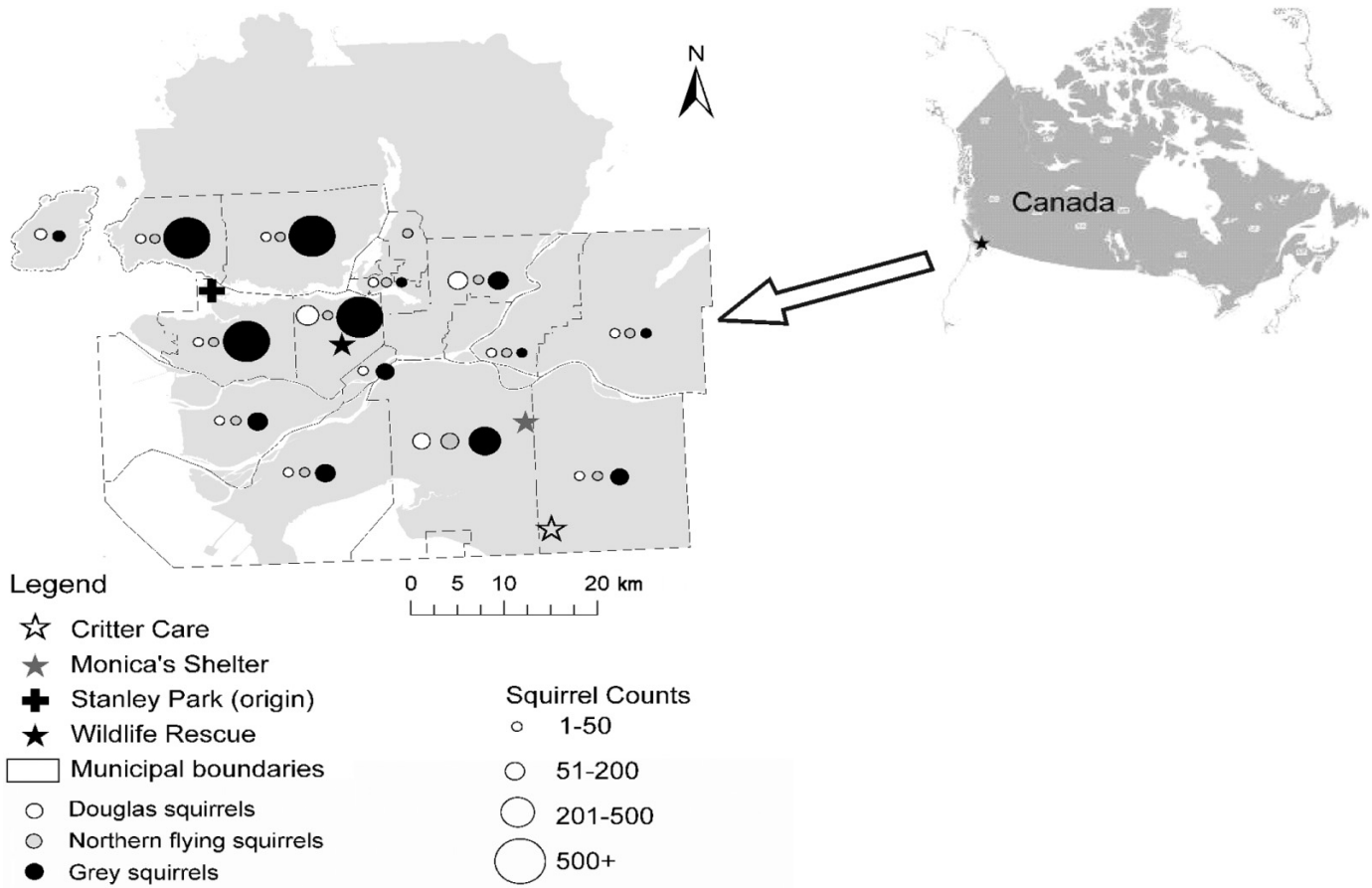
western Canada, were lower than at an ecological reserve 8.5 km south of Stanley Park, where only Douglas squirrels occurred (Hwang and Lariviere 2007). Therefore, grey squirrels may suppress the density and reproductive output of Douglas squirrels. Differences between the two habitats, as well as squirrel habitat preferences, might also explain the variation in abundances. The ecological reserve is a mature conifer forest, whereas Stanley Park consists of a variety of habitat types including conifer forest, deciduous woodlands, and developed areas (Robinson and [McTaggart-]Cowan 1954). Grey squirrels are not present in the reserve but are abundant in the habitats surrounding it, perhaps because they do not generally select coniferous habitats (Robinson and [McTaggart-]Cowan 1954; Gonzales 2005). Non-native species with habitat requirements that differ from native species may establish with relatively little resistance or consequence for native species (Gilbert and Lechowicz 2005). Therefore, habitat segregation can allow coexistence (Bryce et al. 2002), but may create the perception of competitive exclusion if suitable habitat increases for non-native species while simultaneously declining for native species.

We explored whether the distribution and abundance of eastern grey squirrels, the proportion of urban development, or both accounted for the distribution and abundance of Douglas and northern flying squirrels in 15 municipalities in Greater Vancouver, British Columbia, Canada. Submission records from wildlife shelters, facilities that rescue and rehabilitate wild animals, provided squirrel abundances by municipality from 1983 to 2003. Negative relationships between squirrel abundances could imply competitive exclusion, whereas positive relationships suggest common environmental influences such as weather conditions and food availability. Alternatively, squirrel abundances may be independently related to habitat availability. Finally, non-native squirrel abundances and habitat may both contribute to variation in abundances of native squirrels. Tests for poxvirus in 100 grey squirrels from British Columbia were negative (C. Bruemmer, personal communication (2007)), therefore we did not explore disease transmission as a mechanism for potential native squirrel declines.

Materials and methods

In 1909, grey squirrels were introduced to the peninsula of Stanley Park (Robinson and [McTaggart-]Cowan 1954) and began spreading to neighbouring municipalities sometime around the 1970s (Merilees 1986). They presently inhabit ~1500 km² in Greater Vancouver (Gonzales and Gergel 2007) (Fig. 1). We used submission records from Greater Vancouver wildlife shelters as a novel approach to estimate squirrel abundances. Submission records document the age of the squirrel submitted, the municipality of origin, and the reason for admission. There are no formal surveys encompassing the spatial and temporal breadths of the invasion; however, native squirrels were captured using mark-recapture techniques from 1995 to 1999 in forested areas in 1 of the 15 Greater Vancouver municipalities (Coquitlam) by Ransome and Sullivan (2003). We calculated Pearson correlations for the mark-recapture estimates and total wildlife shelter submissions for Douglas and northern flying squirrels to test whether native squirrel abundances followed

Fig. 1. Wildlife shelter locations, point of origin of the non-native eastern grey squirrels (*Sciurus carolinensis*), and total counts of two native (Douglas, *Tamiasciurus douglasii*, and northern flying, *Glaucomys sabrinus*, squirrels) and one non-native sciurid species submitted to wildlife shelters from 15 Greater Vancouver municipalities between 1983 and 2003.



similar trends in those years. Specifically, we used estimates collected from a second-growth forest located in Coquitlam (for methodology see Ransome and Sullivan 2003).

As with more formal sampling techniques, we assumed that the encounter rate for squirrels submitted to wildlife shelters approximated their abundance in the landscape. This assumption would be violated if there were regional differences in submission rate, e.g., if urban dwellers had different attitudes toward squirrels than rural residents or if native squirrel abundances differed between the shelters. First, we surveyed rural and urban attitudes (positive, negative, or no opinion) toward grey squirrels. Posters, a Web page, and publications (newspaper announcements and Gonzales 1999) solicited local residents for information regarding native and non-native squirrels. Differences were tested with a χ^2 analysis. Wildlife Rescue Association and Critter Care are separated by 32 km and the Fraser River, a large water barrier; therefore, their submissions are likely to represent independent observations. We pooled submissions to a third shelter, Monika's Wildlife Shelter, with Critter Care because Critter Care, which opened in 1993, eventually took over care of mammals from Monika's Wildlife Shelter.

Second, we compared abundances of native squirrels between the shelters. Regional differences between the abundances of native squirrels and the shelters would suggest (i) native squirrel abundances differed through time between

shelters, possibly indicating declines in one region, or (ii) undesirable variability between the wildlife shelter submissions. Grey squirrels were actively spreading through the region with time; therefore, grey squirrels were expected to differ between the shelters, whereas native squirrel abundances were expected to be stable. We tested differences with generalized estimation equations using Proc GENMOD (SAS version 9.1; SAS Institute Inc. 2003) with a "repeated" statement and assumed a negative binomial distribution of the response variable, counts of native squirrels, with a log-link function. Generalized estimation equations provide unbiased standard errors of the parameter estimates for longitudinal and other correlated data (Liang and Zeger 1986). We inputted "year" as the repeated subject and hypothesized a first-order autoregressive covariance structure. We used the negative binomial distribution rather than a Poisson distribution because of overdispersion (Lawless 1987).

Our primary question was "are native squirrel abundances best predicted by non-native squirrel abundances, the amount of undeveloped area, or both?" We compared four models (Table 1) using each explanatory variable and both variables together. Digital land-use maps (1 : 250 000) provided by the Greater Vancouver Regional District Policy and Planning Department for 1996 and 2001 were used to calculate the proportion of urban development in each of

Table 1. Generalized linear model selection for native squirrels (*Douglas, Tamiasciurus douglasii*, and northern flying, *Glaucomys sabrinus*), including the number of parameters (K) and the ratio of Pearson χ^2 to degrees of freedom (df), which is the estimate of dispersion for each model where 1 is a good fit.

ID	Model	K	χ^2/df	AIC_c	Δ_i	w_i
1a	Douglas = grey	2	1.5	1161.2	49.23	0.00
B	Douglas = development	2	1.26	1149.2	37.23	0.00
C	Douglas = grey + development	3	1.17	1111.97	0	1.00
2a	Northern flying = grey	2	1.07	728.81	45.01	0.00
B	Northern flying = development	2	1.32	715.43	31.63	0.00
C	Northern flying = grey + development	3	0.92	683.8	0	1.00

Note: Non-native squirrels and the proportion of urban development were input as fixed effects. The best approximating models (in boldface type) were selected among a to d for each native squirrel based on the lowest Akaike’s information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i), which represent the relative likelihood of a particular model, given the set of candidate models.

the municipalities. We merged land-use categories into two broad classes, urban development and undeveloped, and excluded bodies of water from the analyses. The urban development class consisted of industrial, residential, commercial, institutional, and transportation land-use types. The undeveloped class consisted of agricultural, research, harvesting (selective logging), parks and protected natural areas, rural, and other undeveloped lands. We estimated the proportion of development for each municipal group through time by calculating the percent change in urban development between 1996 and 2001, and then estimated an annual rate of development that we back and forward cast for 1983–2003. Although municipalities were unlikely to have a stable rate of development through time, our goal was to approximate a dynamic development variable and to increase the realism of the representation of the landscape relative to a static estimate. Spatial operations were performed using ArcView version 3.3 (Environmental Systems Research Institute, Inc. 2002) and maps were prepared in ArcGIS version 9.2 (Environmental Systems Research Institute, Inc. 2007).

Mixed-effects models enable the modeling of the correlations that often exist with spatially and temporally grouped data. The explanatory variables, counts of grey squirrels and the proportion of urban development in each municipality from 1983 to 2003, were put into the model as fixed effects. Fixed effects are associated with the entire population, whereas random effects are used to model the behaviour of individual experimental units, which are drawn at random from the population and govern the variance–covariance structure of the response variable (Buckley et al. 2003). Treating variables as random effects also has the advantage of using up fewer degrees of freedom than treating variables as fixed effects with multiple levels.

We first fit the four candidate models for each native squirrel using Proc GLIMMIX (SAS version 9.1; SAS Institute Inc. 2003) with negative binomial distributions and log-link functions, inputting the fixed but not the random effect variables because selection techniques for models with random effects are still in development. There was a good fit to the models (Pearson $\chi^2/\text{df} \approx 1$; Table 1). We used Akaike’s information criterion corrected for small sample sizes (AIC_c) and subtracted the minimum AIC_c value from each candidate set of models for each model in its associated set to make inferences about the best model

(Burnham and Anderson 2002). We also used Akaike weights (w_i), which represent the relative likelihood of a particular model given a set of candidate models to assess the likelihood of the model being supported (Burnham and Anderson 2002). Akaike weights were calculated as $w_i = \exp(-1/2\Delta_i) / \sum_{g=1}^g \exp(-1/2\Delta_g)$, where g is the number of models in each set.

We then input random effects for the selected models to incorporate the spatial clustering and temporal autocorrelations inherent in this data set (Schabenberger and Pierce 2002). As before, temporal relationships were assumed to have a first-order autoregressive error variance–covariance structure and the class variable “year” was inputted as a random effect. Given that municipal groups were likely to also contain non-independent variance, we categorized the class variable “municipality” as a random subject to separate the variance of the spatial clustering from the fixed effects.

Results

The shelters recorded 238 northern flying, 590 Douglas, and 3786 grey squirrels in the 15 municipalities over the 20-year period (Fig. 2). Most squirrels were described as orphaned young (northern flying = 24%, grey = 30%, Douglas = 27%), although staff clarified that many orphaned young were from disturbed nests or nuisance squirrels rather than abandoned. Predators and pets accounted for the next most common injuries (northern flying = 15%, grey = 12%, Douglas = 23%). Adult squirrels were also submitted without injuries when their nesting locations were disturbed or as nuisance squirrels (northern flying = 2%, grey = 10%, Douglas = 4%). Other reasons for submission included vehicular collisions, unspecified injuries, parasites, and intra-specific aggression between grey squirrels. No inter- or intra-specific squirrel conflict was reported for native squirrels.

Flying squirrel estimates from mark–recapture techniques were correlated with wildlife shelter submissions ($P = 0.77$), but Douglas squirrels were not ($P = 0.24$). The poor relationship was related to a year shift between the years of greatest abundances. The peak in Douglas squirrel shelter abundances occurred in 1996, whereas the mark–recapture

Fig. 2. Mean (1 SD) number of northern flying (*Glaucomys sabrinus*), eastern grey (*Sciurus carolinensis*), and Douglas (*Tamiasciurus douglasii*) squirrels submitted to three local wildlife shelters from Greater Vancouver municipalities ($n = 15$) from 1983 to 2003.

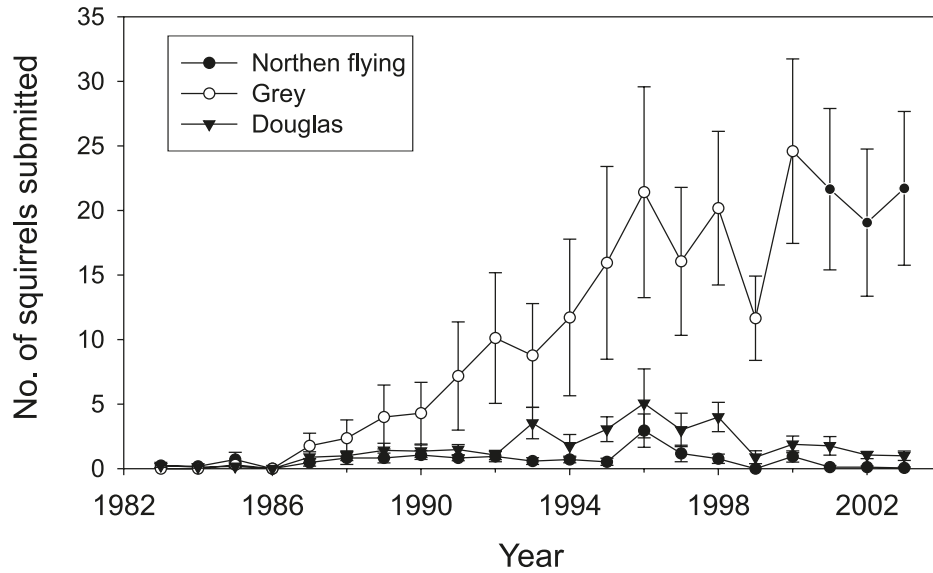
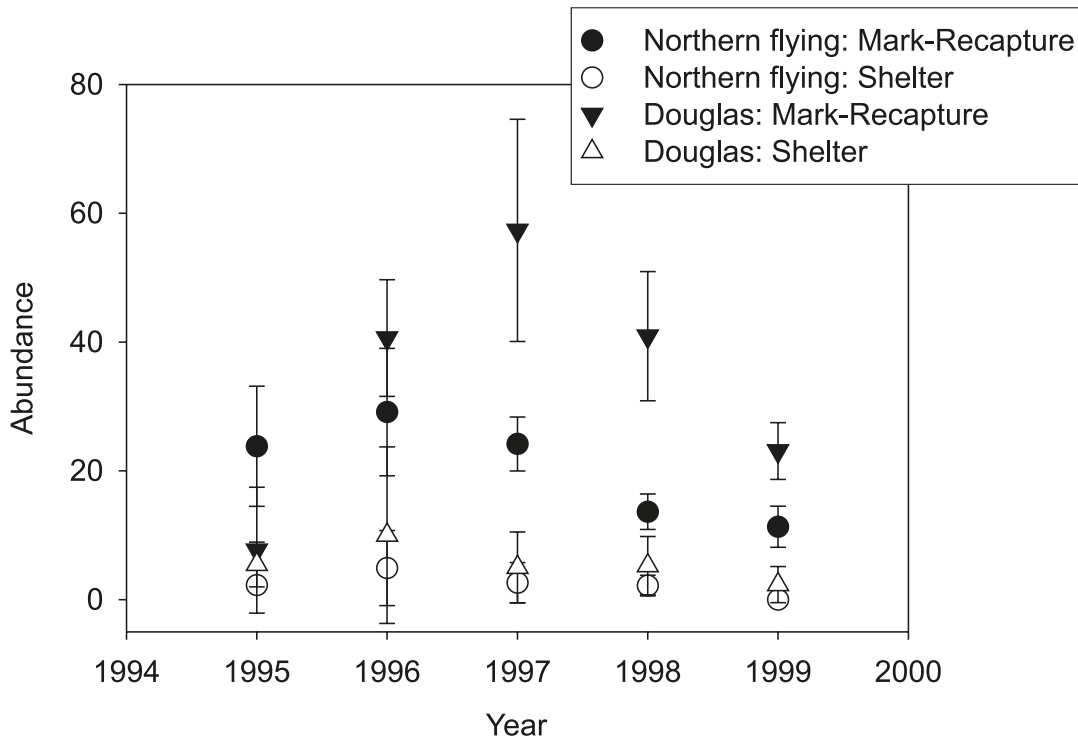


Fig. 3. Comparison of mark–recapture data for northern flying (*Glaucomys sabrinus*; $P = 0.77$) and Douglas (*Tamiasciurus douglasii*; $P = 0.24$) squirrels (Ransome and Sullivan 2003) and wildlife shelter submissions.



data recorded a peak in the 1997 (Fig. 3). Ransome and Sullivan (2003) describe a large cone mast in the winter of 1996–1997 to explain the peak in Douglas squirrel abundances, so it is possible that the peaks do coincide.

We also compared submissions of native squirrels between shelters and rural and urban attitudes toward grey squirrels to test for bias. Native squirrel abundances did not differ between shelters (Douglas: $\chi^2 = 1.37$, $p = 0.24$; northern flying: $\chi^2 = 0.13$, $p = 0.72$). Given that grey squirrels were spreading from west to east, however, regional differ-

ences in shelter submissions differed as expected ($\chi^2 = 9.32$, $p = 0.002$). There were no differences between rural ($n = 22$) and urban ($n = 34$) attitudes toward grey squirrels ($\chi^2 = 0.04$, $p = 0.98$).

Both species showed initial increases in abundance, perhaps as an artifact of the public’s increasing awareness of the wildlife shelters for the first few years after they opened. The species richness and abundances of all wildlife brought to the shelters increased during the first 5 years and then stabilized (Roy Teo, shelter staff, personal communication

Table 2. Generalized linear mixed models with non-native eastern grey squirrels (*Sciurus carolinensis*) and the proportion of urban development input as fixed effects and year of submission and municipality input as random factors.

Response variable	Fixed effects	χ^2/df	Parameter estimates	SE	df	F	p
Douglas squirrel (<i>Tamiasciurus douglasii</i>)	Grey squirrel	1.03	0.02	0.006	1, 338	14.6	0.0002
	Development		-0.02	0.007	1, 338	15.49	0.0001
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	Grey squirrel	1	0.02	0.008	1, 337	3.7	0.06
	Development		-0.04	0.009	1, 337	23.79	<0.0001

Note: Parameter estimates, ratio of Pearson χ^2 to degrees of freedom (df), standard errors (SE), and type III tests of the fixed effects including the df values, F test statistic (F), and probability of the F test statistic (p) for the best models are given as assessed in Table 1.

(2003)). The abundance of grey squirrels, however, continued to increase and peaked in 2000 at 426 grey squirrels. Grey squirrels also expanded their range. In 1985 they were found in only two municipalities and by 1999 had spread to all municipalities in the region. Douglas squirrels were present in all Greater Vancouver municipalities throughout the study period, including Stanley Park, where they have coexisted with grey squirrels for nearly 100 years. Both of the predictor variables, grey squirrels and urban development, were retained in the best models predicting native squirrel abundances (Tables 1, 2). Grey squirrels were positively related to Douglas and northern flying squirrel abundances, whereas urban development was negatively related (Table 2).

The abundances of native squirrels were, however, uneven and low and were less likely to represent accurate population trends relative to grey squirrels. This is due, in part, to a bias toward urban wildlife being submitted to wildlife shelters relative to species that prefer natural habitats. In this study, bias toward under-representation of native squirrels increases the chance of a type I error (i.e., grey squirrels are concluded to be competitively dominant when they are not) and therefore does not affect our conclusions.

Discussion

The abundance and spatial distribution of grey squirrels increased from 1983 to 2003, whereas the abundance of Douglas squirrels remained fairly constant regionally (Fig. 2). Northern flying squirrels were frequently absent from most municipalities in any given year; therefore, the interpretations are less robust than for Douglas squirrels. The relationships between sciurid species, however, were positive, which could suggest that common environmental factors influenced squirrel abundances. The relationships between squirrel abundances and urban development were negative, particularly for northern flying squirrels, suggesting that native squirrel abundances at a municipal scale were related to habitat preferences rather than to antagonistic interactions with non-native squirrels.

The wildlife shelter data provided a novel estimate of squirrel abundances in each municipality through time and offered a rare opportunity insofar as pre-invasion data were available for a non-native species and the native species it was hypothesized to affect. Whether wildlife shelter data is an accurate representation of squirrel population trends in urban areas, however, is unknown. We compared wildlife shelter abundances to native squirrel estimates from more traditional mark-recapture methods and found the data to be well correlated for northern flying squirrels, but Douglas

squirrels appeared to be correlated with a 1-year lag. Our comparisons, however, were not based on the same habitat types because the mark-recapture data were collected in a conifer forest, whereas the wildlife shelter data were likely biased toward urban habitat types. Future work comparing wildlife shelter data with more traditional measures of species abundances may reveal a useful historical data set that is suitable for studies at coarse spatial scales similar to the use of museum records to document declining populations (Shaffer et al. 1998).

Whereas the correlative nature of the data reduces our ability to comment on potential competitive or facilitative interactions between squirrels, the results are inconsistent with a competitive exclusion hypothesis. Using similarly comparative approaches in Europe, native squirrels were replaced within 15 years following the arrival of grey squirrels (Reynolds 1985; Usher et al. 1992; Gurnell et al. 2004). If the competitive effect of grey squirrels on native squirrels are as strong as they are in Europe, we should have detected negative relationships between native and non-native squirrels or at least a decline in native squirrels in municipalities nearest the original point of introduction.

The increasing abundances of grey squirrels, however, may have created the public perception that grey squirrels were “taking over”. Grey squirrels are charismatic and occupy residential areas, which increases the likelihood that they will be apparent to casual observers. Similar attributes are characteristic of another non-native species such as the purple loosestrife (*Lythrum salicaria* L.). The non-native loosestrife has showy purple flowers, which may influence estimates of abundance (Hager and McCoy 1998), and is more commonly found along roadways and disturbed sites where more people see it than in remote, undisturbed wetlands (Sandlos 1997). The perception of competitive exclusion led to extensive, expensive control measures for purple loosestrife (Hager and McCoy 1998) and for grey squirrels in Europe (Sheail 1999). One of our goals was to establish whether management of grey squirrels or the protection of undeveloped areas would best preserve abundances of native squirrels.

Given that we found no support for declines of native squirrels owing to non-native squirrels, it is possible that protection and connectivity of suitable undeveloped conifer habitat in an urban landscape will help maintain native squirrel abundances. We suggest that habitat segregation permits regional co-occurrence of grey and Douglas squirrels as long as sufficient habitat is available for both species. This conclusion is supported by observations elsewhere. Grey squirrels co-occur with a congener of Douglas squir-

rels, North American red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), throughout much of central North America where competitive interactions are reduced by habitat differentiation (Riege 1991; Nupp and Swihart 2000, 2001). In Indiana, North American red squirrels have expanded their range into native eastern grey squirrel habitat as a result of land conversion (Goheen et al. 2003). Grey squirrels are declining because of increasing fragmentation of deciduous forests, and the loss of these scatter hoarders is expected to have negative consequences for the recruitment of nut-bearing trees (Goheen and Swihart 2003).

Concern regarding the potential negative effects of grey squirrels on native species in British Columbia prompted provincial managers to contract a management plan for grey squirrels; however, little was known about factors influencing abundances of squirrels in southwestern British Columbia. Future investigations with more detailed data into the relationship among squirrel distributions and landscape parameters, such as patch size, quality, and isolation (Verbeylen et al. 2003), will address outstanding questions. For example, are grey squirrels spreading into residential niches where native squirrels are absent? Does forest quality alter competitive relationships between native and non-native squirrels? Do native squirrel populations decline as a function of patch size and (or) isolation? Given that our analyses were comparative, interpretations of underlying mechanisms must be interpreted with caution. Nevertheless, our analyses address a knowledge gap and can be used to direct more formal research in the future.

Acknowledgements

Financial support was provided to E.K.G. by Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarship, Environmental Systems Research Institute Pacific Region, the University of Guelph, Mountain Equipment Co-Op, and NSERC support to T.D.N. Thank you to the Wildlife Rescue Association, Monika's Wildlife Shelter, and Critter Care for providing squirrel submission data and to the Greater Vancouver Regional District for providing digital maps. We are also grateful for the help from numerous volunteers, particularly R. Teo. V. Gonzales and V. LeMay provided excellent statistical instruction to E.K.G.. Thank you to J. Reid, P. Arcese, R. Norris, J. Goheen, I. McEachern, and the anonymous reviewers for their helpful comments on earlier versions of the manuscript.

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