Annotated Bibliography on the Ecology and Management of Invasive Species: Eastern Grey Squirrel (*Sciurus carolinensis*)

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Applied Vegetation Dynamics. 2000. Fact sheet: TA/M/13. Invasive Alien Terrestrial Animal Species *Sciurus carolinensis* (Gmelin, 1788.) - Grey Squirrel. Website:www.appliedvegetationdynamics.co.uk/IAAPwebsite/FactSheet/Squirrel.doc Accessed: November 20, 2002.

The website is maintained by a research unit based at the University of Liverpool that aims to provide information on the ecology and management of invasive species in the United Kingdom. The site provides species descriptions, life history details, range information as well as discussing the impacts and potential control measures of eastern grey squirrels. Eastern grey squirrels were introduced to Britain in the late 19th century and now cause major damage to ecosystems. They gnaw the bark of trees which kills or slows the growth of the trees. Squirrels remove the bark 30 cm above the ground. Grey squirrels also impact European red squirrels through competition and by possibly acting as a vector for the disease parapoxvirus. Grey squirrels are found primarily in deciduous woodlands but also occurs in coniferous and mixed stands. Although the red squirrel is a different species from the native red squirrel in British Columbia, the potential impacts may be similar although this requires further research. The best control options for grey squirrels include the use of Warfarin (rodenticide) in specialized hoppers (used only where there are no red squirrels) and cage trapping in conjunction with shooting. These techniques may also be useful Garry oak ecosystems. However, new individuals from adjacent populations will rapidly repopulate an area and total eradication is unlikely. Baits can be used to lure squirrels away from sensitive sites. Immuno-contraception methods require more research before they can be implemented.

Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto, Toronto, ON.

This comprehensive field guide provides detailed species description and life history information. The dated range map does not show the introduction of grey squirrels to Vancouver Island. Eastern grey squirrels are described as tree squirrels with a long flat tails. Grey squirrels have lighter undersides, brown faces feet and flanks and white tipped brownish tails. There are also black and red forms of the same species. Grey squirrels are described as "socially tolerant" and individuals may feed or den together. Grey squirrels will give up territory to the more territorial native red squirrels however they can outnumber red squirrels and are not prevented from feeding in the red's territory. Peak activity is between 7 and 8 am and also between 3 and 6 pm. Grey squirrels nest in cavities or loosely woven dreys in conifers or large deciduous trees. Historically, grey squirrels are known to undergo mass emigrations to new areas for unknown reasons that are not related to food shortages. Grey squirrels feed on buds of deciduous trees, flowers, seeds, fruits, insects, birds' eggs and hard nuts that are cached for the winter. Grey squirrels are found in hardwood or mixed forests as well as urban and suburban habitats. Detailed reproductive biology is outlined in this reference including the habit of two breeding seasons, breeding rituals, number of litters (average of 1.4/year), gestation (45 days), number in litter (4-6) and development of the young. The ecology of the grey squirrel gives important background for potential management options in Garry oak ecosystems.

Barthelmess, E. L. 2001. The effects of tannin and protein on food preference in eastern grey squirrels. Ethology Ecology and Evolution 13 (2): 115-132.

Author's abstract: Although some mammalian generalist herbivores avoid foods high in plant secondary compounds, it has not been adequately shown that eastern grey squirrels (*Sciurus carolinensis*), who regularly encounter tannin in acorns, avoid high tannin diets. Dietary tannin can inhibit nitrogen assimilation; hence herbivores that eat tannin should seek high protein diets to compensate. I presented free-ranging grey squirrels with four types of dough balls that differed in tannin and protein content. Squirrels consistently preferred low to high tannin foods but did not distinguish between low and high protein foods. Intensity of preference for low tannin foods was greatest during early to mid autumn, when food is relatively abundant, and declined into the spring and early summer, when food is relatively scarce. Food availability, partitioning foraging effort between eating and scatterhoarding, physiological competence, and nutrient complementarity may explain why squirrels consume tannin in natural diets, in spite of preference for low tannin dough balls demonstrated here.

Bloemacher, S. (Aliens-L listserve) 2002. Translation of German Grey Squirrel Fact Sheet. Website: http://www.biologie.uni-rostock.de/zoologie/neozoa/steckbriefe.html

In Germany, eastern grey squirrels are found only in captivity although there are unconfirmed sightings in the wild. Grey squirrels have caused serious problems in other locations in Europe by competing with European red squirrels (*Sciurus vulgaris*) for food and habitat, damaging gardens, stripping tree bark, competing with birds for food and destroying bird nests. Grey squirrels also try to mate with European red squirrels

although no viable hybrids have been observed. All efforts should be made to prevent the release of grey squirrels to the wild in Germany.

Bowers, M. A. and B. Breland. 1996. Foraging of gray squirrels on an urban-rural gradient: Use of the gud to assess anthropogenic impact. Ecological Applications 6 (4): 1135-1142.

Authors' abstract: Responses of organisms to urbanization may involve adjustments in behavior. To qualify such behavioral plasticity we measured the degree to which gray squirrels (*Sciurus carolinensis*) exploited sunflower seeds in pans distributed over an urban-rural gradient of 78 sites in Virginia. Our objective was to use squirrel GUDs as a functional, relativistic measure of the effects of urbanization. Results showed that a higher proportion of pans were foraged from and that the GUDs were lower (more seeds were removed) in relatively high-density urban and suburban areas than in more rural agricultural areas, or in relatively human-free forest controls. For sites near or within human settlements, GUDs were lower nearer to human-occupied structures than at a greater distance from them, where more squirrels were observed, and where the density of trees was higher; GUDs were higher where there was substantial ground cover and where domestic pets (i.e., cats/dogs) were present nearby. Squirrels living in close proximity to humans appear to be either more limited by food or less sensitive to predatory risk than those living in more natural areas. We argue that the GUD represents a valuable metric with utility for measuring the separate and combined impact of anthropogenic actions at the individual and population levels.

Brenner, F. J. and T. Johnson. 1989. Use of habitat suitability index HSI models to evaluate fox and gray squirrel habitat in western Pennsylvania, USA. Journal of the Pennsylvania Academy of Science 63 (2): 77-80.

Authors' abstract: The Habitat Suitability Index (HSI) model was used to evaluate fox (*Sciurus niger*) and gray squirrel (*S. carolinensis*) habitat on four woodlots in Western Pennsylvania. Two woodlots were inhabited by both species while only gray squirrels were observed on the other two areas. The cover/reproduction component of HSI appears to be more important than winter food in determining the suitability of habitat for fox squirrels. With a decline in fox squirrels, there is a corresponding increase in the number of gray squirrels inhabiting the woodlots. The presence of agricultural land in close proximity to the woodlot appears to be an important factor in determining whether or not the area will be inhabited by fox squirrels, whereas the presence of den trees in an important component of gray squirrel habitat.

Brown, B. W. and G. O. Batzli. 1985. Field manipulations of fox squirrel *Sciurus niger* and gray squirrel *Sciurus carolinensis* populations. How important is interspecific competition? Canadian Journal of Zoology 63 (9): 2134-2140.

Authors' abstract: The role of competition in free-living populations of tree squirrels was evaluated in two field experiments. (i) Numbers of adult female fox squirrels (*Sciurus niger*) were manipulated and the response of gray squirrels (*Sciurus carolinensis*) was

monitored. (ii) Supplemental feeding with native mast was used to determine if food was limiting for squirrel populations in east-central Illinois [USA]. Although sample sizes were small, a trend towards increased survival and reproduction in supplemented woodlots lent support to the idea that food availability limits squirrel densities during some winters. The manipulation of adult female fox squirrels did not indicate that densities of either fox or gray squirrels could be explained simply by competition. Some dispersion patterns on the larger plots were consistent with competition, but other explanations could not be completely ruled out.

Bruemmer, C., P. Lurz, K. Larsen and J. Gurnell, 2000. Impacts and management of the alien eastern gray squirrel in Great Britain and Italy: lessons for British Columbia. Pp. 341-349 in: Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, British Columbia, 15-19 Feb., 1999 (L. Darling, ed). Ministry of Environment, Lands and Parks, Victoria, BC.

Bruemmer *et al*. outline the impacts and history of grey squirrels' introduction to England. The authors use this information to identify possible impacts of the introduction of grey squirrels to similar habitat in Garry oak ecosystems. Grey squirrels were first introduced to Britain in 1876 and there was a long time lag before they began to spread quickly through England, Wales and Scotland. The introduction of grey squirrels to Vancouver Island also exhibited a lag time before the squirrels began to spread throughout southern Vancouver Island from Sooke to Swartz Bay to Nanaimo. In England, grey squirrels cause serious environmental problems throughout their new habitat. European red squirrels (*Sciurus vulgaris*) are now extinct in most of southern England probably due to competition with grey squirrels for food and habitat. Grey squirrels in their native range are closely associated with hardwood forests including oaks and may digest acorns more efficiently than red squirrels. European red squirrels are more closely associated with conifer forests but previously inhabited woodlands before grey squirrels were introduced. Grey squirrels may also infect red squirrels by acting as a vector for parapoxvirus. Red squirrels native to Garry oak ecosystems in British Columbia, are conifer dwelling like European red squirrels. Native red squirrels may also be outnumbered by grey squirrels adapted to deciduous forests and be infected by diseases carried by grey squirrels. Although British Columbia's red squirrels are highly territorial in conifer stands, when the squirrels inhabit deciduous forests, their home ranges overlap and they do not defend their territories. Grey squirrels impact timber production in England by removing bark from either the base of the trunk, stem or crown of the tree and making trees more susceptible to infections. Bruemmer *et al*. suggests grey squirrels may have a similar impact in Garry oak ecosystems although further research is needed to support this. In England, grey squirrels impact the natural regeneration of oaks by biting out the radicles and preventing oak germination. Notched acorns have also been observed in Garry oak ecosystems. Although other authors believe the squirrels are effective dispersers and partially eaten acorns are still viable, the vigour of the seedlings may be less than seedlings grown from unpredated acorns. Grey squirrels also predate birds' eggs and nestlings and may compete with other native acorn-eating species. In England, short-term management to lesson the impact of grey squirrels on red squirrels includes trapping of grey squirrels, reintroduction of red squirrels, use of

rodenticides such as warfarin in areas where there are no red squirrels and additional feeding of red squirrels (by using "red-only" feeders) although the latter has not been proven effective in Europe. Long-term management options include promoting red squirrel habitat by maintaining continuous forest cover with an appropriate food supply. More research is needed in the development of immuno-contraceptives to sterilize squirrels by oral vaccination. Many of these control techniques may also be effective in Garry oak ecosystems.

Chung, M. A. L., A. E. Hagerman and R. L. Kirkpatrick. 1997. Effects of tannins on digestion and detoxification activity in gray squirrels (*Sciurus carolinensis*). Physiological Zoology 70 (3) 270-277.

Authors' abstract: Acorn tannins may affect food preferences and foraging strategies of squirrels through effects on acorn palatability and digestibility and squirrel physiology. Captive eastern gray squirrels (*Sciurus carolinensis*) were fed 100% red oak (*Quercus* and the higher glucuronidation activities observed in squirrels. Although the white oak acorn diet had lower apparent protein digestibilities than the reference diet, it did not suppress dry matter intake for a prolonged period or stimulate glucuronidation. Negative physiological effects of a 100% red oak acorn diet suggest gray squirrels may require other foods to dilute tannin intake and provide additional nutrients. To distinguish the roles of different tannin types in the observed effects of acorn diets on squirrels, squirrels were fed rat chow containing no tannins, 4% or 8% tannic acid (hydrolyzable tannin), or 3% or 6% quebracho (condensed tannin). Apparent protein digestibilities were reduced by tannic acid and quebracho diets. Only the 8% tannic acid diet tended to increase glucuronidation. Specific effects of tannins may largely depend on tannin type, composition, and source and on other nutritional and physiological factors.

Craine, N. G., P. A. Nuttall, A. C. Marriott and S. E. Randolph. 1997. Role of grey squirrels and pheasants in the transmission of *Borrelia burgdorferi sensu lato*, the Lyme disease spirochaete, in the U.K. Folia-Parasitologica Ceske Budejovice 44 (2): 155-160.

Authors' abstract: In Britain, grey squirrels (*Sciurus carolinensis* Gmelin) and pheasants (*Phasianus colchicus* Linnaeus) are important hosts of larvae and nymphs of *Ixodes ricinus* L., the principal European vector of the Lyme disease spirochaete, *Borrelia burgdorferi sensu lato*. To test whether squirrels are competent hosts of *B. burgdorferi s.* l., three females were trapped in the wild and then held in captivity. Following treatment, each animal was exposed to uninfected xenodiagnostic *I. ricinus* ticks. Squirrel A (an adult) which was inoculated experimentally with *B. burgdorferi s.l.*, transmitted the infection to xenodiagnostic ticks. In contrast, as C (an adult) became infected and subsequently transmitted the infection experimentally to an uninfected hamster. The results indicated that squirrel C had a disseminated infection acquired in the wild and which persisted for at least 11 weeks. These data clearly demonstrate that grey squirrels are amplifying and reservoir hosts of *B. burgdorferi s.l.* The strain associated with squirrels was related to the *B. afzelii* genotype. Two observations implicated pheasants in a similar role: (i) a high prevalence of infection in engorged larvae collected from trapped pheasants, and (ii) the detection of *B. burgdorferi s.l.* (*B. garinii* genotype) in the wattle

of 1/10 pheasants using PCR. Xenodiagnostic experiments similar to those undertaken with the squirrels are needed to confirm the role of pheasants in the transmission cycle of Lyme disease spirochaetes.

Drake, J. C. and F. J. Brenner. 1995. Comparison of habitat preferences of gray and fox squirrels in northwestern Pennsylvania. Journal of the Pennsylvania Academy of Science 69 (2): 73-76.

Authors' abstract: Three woodlots in Crawford, Forest and Warren Counties in Northwestern Pennsylvania were monitored for squirrel activity over a four month period to determine if the black and gray morphs of the gray squirrel (*Sciurus carolinensis*) and the fox squirrel (*S. niger rufiventer*) exhibit different habitat preferences. Based on 65 hours of observation, the two color morphs of the gray squirrel exhibited preferences, with the black morph occurring more often in bottomland forests dominated by hemlock (*Tsuga canadensis*) and American beech (*Fagus grandifolia*); whereas, the gray morph and fox squirrels preferred the more open upland forests. The preference of the black morph for the dense bottomland forest would provide a selective advantage against predation while the reverse would be true for the gray morph and fox squirrels in the more open upland habitats.

Eason, P. K. 1998. Predation of a female House Finch, *Carpodacus mexicanus*, by a Gray Squirrel, *Sciurus carolinensis*. Canadian Field Naturalist 112 (4): 713-714.

Author's abstract: I observed a Gray Squirrel (*Sciurus carolinensis*) capture, kill, and consume a fully flighted female House Finch (*Carpodacus mexicanus*). Gray Squirrels rarely prey on vertebrates, and previous reports of their predation on birds record them eating only birds' eggs and nestlings.

Ennis, T. 2002. *Personal communication.* The Nature Conservancy of Canada, Victoria, BC.

Ennis is involved with restoration of the Cowichan Garry Oak Preserve. He states that pellet rifles which meet the 200ft/s legal limit are very effective against both rabbits and squirrels.

Faccio, S. D. 1996. Predation of an Eastern Chipmunk, *Tamias striatus*, by a Gray Squirrel, *Sciurus carolinensis*. Canadian Field Naturalist 110 (3): 538.

Author's abstract: I observed a Gray Squirrel (*Sciurus carolinensis*), attack and kill an Eastern Chipmunk (*Tamias striatus*) in Orange, Massachusetts. Published reports of Gray Squirrel predation upon other vertebrates consist only of bird eggs and nestlings.

Fenske, C. T. J. and G. J. Niemi. 1997. Predation of artificial ground nests at two types of edges in a forest-dominated landscape. Condor 99 (1): 14-24.

Author's abstract: Artificial ground nests were placed in medium-age or older forests

adjoining (a) stands of regenerating forest (vegetation lt 2 in high) where 'hard' edges were created, and (b) stands of young forest (vegetation 2-8 m high) where 'soft' edges were created. Nests were placed at three distances from the forest edge (0 in, 50 m, and 100 m). Two Northern Bobwhite Quail (*Colinus virginianus*) eggs were placed in each nest and monitored after 7 and 14 days of exposure between late May and mid-July, 1994. Overall nest predation was 72% after 7 days and 85% after 14 days of exposure. Predation near soft edges was significantly higher than near hard edges after both 7 and 14 days of exposure. Predation near the edges was significantly higher than away from the edges after both 7 and 14 days of exposure. Two motion-sensitive cameras were used to record the identity of predator species. Cameras documented 28 predation events during 1,728 hours of operation, caused by eight species of mammals. The predators included, in order of decreasing predation: fisher (*Martes pennanti*), Eastern chipmunk (*Tamias striatus*), red-backed vote (*Clethrionomys gapperi*), red squirrel (*Tamiasciurus hudsonicus*), deer mouse (*Peromyscus maniculatus*), black bear (*Ursus americanus*), gray squirrel (*Sciurus carolinensis*), and striped skunk (*Mephitis mephitis*). The relationship between edges, predator assemblages, and nest success is complex; more studies at the landscape level are required to better understand the effects of these factors on avian population dynamics.

Figala, J. and J. R. Tester. 1986. Comparison of seasonal rhythms of activity of gray squirrels *Sciurus carolinensis* Rodentia in captivity and in the wild. Vestnik Ceskoslovenske Spolecnosti Zoologicke 50 (1): 33-48.

Authors' abstract: Seasonal changes in the activity rhythm in captive grey squirrels (*Sciurus carolinensis*) were recorded by a photocell system at the Cedar Creek Natural History Area, Minnesota [USA]. Photocell recordings from grey squirrels near the Arctic Circle at Kuusamo, Finland and at Andechs, West Germany were analyzed and compared with those from Cedar Creek. Activity rhythms of wild squirrels, and also of the captives, were monitored by radio telemetry at Cedar Creek. The duration of activity time (.alpha.) in both captive and wild squirrels did not follow the duration of the photoperiod throughout the year. The very short .alpha. in late winter might be under the control of exogenous factors other than light, especially in wild squirrels. The marked increase in length of activity in September in wild squirrels was probably related to mast harvesting behavior. Seasonal differences in phase angle and duration of activity indicate larger variations in wild than in captive squirrels. Secondly, our data on grey squirrels suggest that day-active mammals exhibit larger variations in phase angle differences and duration of activity than day-active birds.

Fischer, R. A. and N. R. Holler. 1991. Habitat use and relative abundance of gray squirrels in southern Alabama, USA. Journal of Wildlife Management 55 (1): 52-58.

Authors' abstract: We studied habitat use and estimated relative abundance of gray squirrels (*Sciurus carolinensis*) in 3 habitats at the Solon Dixon Forestry Education Center, Covington and Escambia counties in southern Alabama, from January 1987 to September 1988. Three representative stands of even-aged pine, mixed pine-hardwood, and hardwood were selected for study, and a 50-station trapping grid was established in

each. We captured 603 squirrels 1,586 times. Relative abundance was based on the minimum number of squirrels known alive. Squirrel abundance in hardwood and in mixed pine-hardwood habitat did not differ ($P = 0.47$), but abundance in even-aged pine was lower ($P < 0.001$) than that in either of the other 2 habitats. We measured 6 habitat variables in each study area. Moderately open understories with a dense shrub crown (vegetation between 1 and 5 m) component appear to be important to squirrel abundance. To determine habitat preference, we fitted 17 gray squirrels with radio transmitters. Narrow bands of hardwoods along ephemeral streams (i.e., hardwood stringer) were an important component of gray squirrel habitat in even-aged pine and mixed pine-hardwood stands. Forest management should include the retention of hardwood stringers within pine and mixed pine-hardwood stands.

Fisher, J. T. and G. Merriam. 2000. Resource patch array use by two squirrel species in an agricultural landscape. Landscape Ecology 15 (4): 333-338.

Authors' abstract: Eastern grey squirrels (*Sciurus carolinensis*) and North American red squirrels (*Tamiasciurus hudsonicus*) were studied among wooded patches within an agricultural mosaic. Fifteen sites south of Ottawa, Canada, with differing landscape and local features were censused using tracking boards placed in a woods or wooded fencerow. Regression analyses of landscape compositional and physiognomic variables within a 1-km radius isolated the best predictors of grey and red squirrel abundance and activity. Grey squirrels were found in both small woods and fencerows in farm landscapes but were not found in large woods. A polynomial regression of wooded patch size explained 79% of the variance in grey squirrel abundance. Grey squirrel activity was correlated with the percent cover of soybeans in the landscape. Red squirrels were found in fencerows, small and large woods; activity was correlated with the percent cover of both woods and corn crop in the surrounding landscape. These results indicate that distributions of both species are influenced by multiple landscape elements, but that grey squirrels may rely on fragmented agricultural landscapes whereas red squirrels make more use of both native woodland and altered landscapes.

Fitzgibbon, C. D. 1993. The distribution of grey squirrel dreys in farm woodlands: The influence of wood area, isolation and management. Journal of Applied Ecology 30 (4): 736-742.

Author's abstract: 1. Sixty-eight deciduous woodlands, ranging in size from 0.2 to 12.5 ha, were surveyed in East Anglia, UK, and the density of grey squirrels *Sciurus carolinensis* estimated from drey counts. 2. Squirrel dreys were more likely to occur in woods that (i) were larger, (ii) were closer to another wood of at least 5 ha in size, (iii) contained oak *Quercus* spp., beech *Fagus sylvatica* or hazel *Corylus avellana*, and (iv) were surrounded by a greater density of hedgerows. 3. The overall density of woodland in the vicinity, the distance to a wood of at least 0.5 ha in size, and the presence/absence of five other tree species did not influence squirrel drey distribution between the woods. 4. In woods that contained squirrel dreys density was higher in woods with a greater density of large trees (diameter in excess of 50 cm) and in woods which were closer to another wood of at least 0.5 ha in size. 5. Since reducing the probability of squirrels inhabiting a

plantation will reduce the risk of young trees being bark-stripped, the results of this study have implications for the design of new farm woodlands.

Fox, J. F. 1982. Adaptation of gray squirrel behaviour to autumn germination by white oak acorns. Evolution. 36(4): 800-809.

Author's summary: Acorns of some species of white oaks are nondormant, germinating in autumn soon after falling to the ground. When burying acorns of at least three such white oak species, gray squirrels often kill the growing point of the seed. This prevents the loss (to the squirrel) of up to 50% of the food material, which would otherwise be transferred into the seedling before the squirrel recovered the seed in winter. Nondormant acorns that are buried undamaged produce a seedling taproot engorged with food reserves; because of this, if a squirrel subsequently removes the acorn in winter, the seedling is still capable of growth the following spring. Squirrels do not kill the growing point of acorns of red oaks, which are dormant-seeded, before caching them. The squirrels' behavior is interpreted as a countertactic evolved to deal with autumn-germinating acorns. Autumn germination may be a tactic evolved as an 'escape' from post-dispersal predation by squirrels. Escape is not completely eliminated by the squirrels' countertactic; because of exceptions to the behavior, especially among juvenile squirrels, some 48% of white oak acorns are cached unharmed and capable of 'escape'.

Genovesi, P. 2000. Box 3: Eradication of the grey squirrel in Italy: failure of the programme and future scenarios. In: Convention on the conservation of European wildlife and natural habitats standing committee: Guidelines for eradication of terrestrial vertebrates - a European contribution to the invasive alien species issue. Website: http://www.nature.coe.int/CP20/tpvs65e.doc Accessed: November 16, 2002.

At the time of publication, Italy was the only continental location in Europe where eastern grey squirrels were found in the wild. Genovesi outlines the impact of eastern grey squirrels including stripping bark from trees, competing with European red squirrels, and acting as a vector of parapoxvirus. After the introduction of grey squirrels, there was a lag time before the population spread. In order to prevent the spread to other countries and other regions within Italy, the Italian government recommended the eradication of grey squirrels from the country. A plan for experimental removal of grey squirrels was developed using live traps and humane euthanasia with halothane anaesthesia administered under veterinary supervision. Demonstrations by animal rights activists and subsequent legal action by the activists brought the project to a standstill. In the absence of any control, the range of the grey squirrel continues to expand. This project provides valuable lessons on the need for public education and involvement with any form of small mammal control in Garry oak ecosystems.

Gonzales, E K. 1999. Eastern grey squirrels in British Columbia: an introduction to an introduction. Discovery 28: 22-25.

Author's abstract: The eastern grey squirrel (*Sciurus carolinensis*) was introduced to British Columbia sometime prior to 1914. The population remained isolated in Stanley

Park until sometime in the 1970's, when viable populations were reported in several municipalities. Naturally adept at adaptation and dispersal, the squirrels have since expanded their density and distribution throughout Greater Vancouver. A human commensal species, they have probably had anthropogenic aid in their dispersal to other cities on mainland British Columbia and Vancouver Island.

Gonzales, E. K. 2000. Distinguishing between modes of dispersal by introduced eastern grey squirrels (*Sciurus carolinensis*). M.Sc. Thesis, University of Guelph, Guelph, ON.

Although the spread of grey squirrels in Europe has been well documented, the mechanism for dispersal has not been carefully analyzed. The stochastic spread of the species in Europe has been associated with variations in the habitat but no models have been created to describe the spread. Gonzales used records of grey squirrels populations in British Columbia to determine whether humans have assisted the dispersal of this species. Grey squirrels were introduced to Vancouver in 1909 and Victoria in 1966. There was a time lag before the populations spread due in part to small population effects. Gonzales analyzed the dispersal of both populations by using weighted surface analysis. This approach takes into account habitat preferences, rate of spread and landscape barriers to dispersal. She concludes that humans have translocated grey squirrels and helped spread this species.

Gonzales, E.K. 2002. *Personal communication*. Ph.D. student, Centre for Applied Conservation Research, University of British Columbia, Vancouver, BC. November 14, 2002

Gonzales has researched the habitat preferences and spread of eastern grey squirrels (*Sciurus carolinensis*) in Victoria and Vancouver, British Columbia. She concludes that the spread of the squirrels is facilitated by direct translocation by people and by increasing urbanisation that creates their preferred habitat. Grey squirrels do not survive well in coniferous forest and the denser forest seems to slow their spread. Gonzales notes that because grey squirrels do better in modified environments with horticultural species than they do in natural British Columbian environments and Garry oak ecosystems are highly urbanized, it is difficult to determine the effect on Garry oak ecosystems. Gonzales has not found any conclusive literature that confirms that eastern grey squirrels damage acorns of Garry oaks. Instead, the literature she has read indicates the squirrels are effective dispersers, that white oaks (including Garry oak) are not a preferred food source and that even partially eaten acorns are still viable. Both introduced grey squirrels and the native red squirrels eat bulbs and may be a predator on camas in Garry oak ecosystems. Both native and grey squirrels eat birds eggs and nestlings. However, because grey squirrels are in urban areas, cats may be a more serious predator. Gonzales has also found no evidence (other than anecdotal) that grey squirrels displace native red squirrels. She has observed both squirrels coexisting in areas where the grey squirrels have been introduced (e.g. Stanley Park) and the two species prefer different habitat (red squirrels prefer conifer forest, grey squirrels prefer residential areas) although the squirrels may interact at marginal habitats (e.g., Beaver Lake Park, Victoria, British Columbia). During one on one interactions, red squirrels are typically dominant because

of their territorial nature but it is possible that grey squirrels could reach higher densities and "swamp" the red squirrels. Although red squirrels were previously more widespread in Victoria, Gonzales thinks the decrease is probably due to loss of habitat. Other authors have used the decline of European red squirrels (*Sciurus vulgaris*) after the introduction of eastern greys to infer an impact on our native red squirrels in British Columbia. However, Gonzales notes European red squirrels are very different from our red squirrels and European reds have not been displaced in conifer habitats (e. g., in Scotland). Management opinions: Eradication of grey squirrels is very expensive and may be impossible once the species is established because they are efficient dispersers and will quickly reinvade an area. In Britain during the 1950's, millions of dollars were spent to try to eradicate grey squirrels with no real results. The best chance to eradicate grey squirrels is before they establish. However, Gonzales believes that the grey squirrel is already established in most of the Capital Regional District. Gonzales says that before management of grey squirrels is attempted, it is important to determine whether or not they impact Garry Oak ecosystems and whether the increased spread of grey squirrels is due to habitat alteration. In order to prevent further spread of grey squirrels, people should be educated to not translocate grey squirrels and to not to feed them either directly or indirectly. It will be very challenging to avoid feeding grey squirrels because they are attracted to tulip bulbs, open compost, garbage, nut trees, fruit trees, and bird feeders.

Gorman, O. T. and R. R. Roth. 1989. Consequences of a temporally and spatially variable food supply for an unexploited gray squirrel *Sciurus carolinensis* population. American Midland Naturalist 121 (1): 41-60.

Authors' abstract: The demography and spatial distribution of a gray squirrel (*Sciurus carolinensis*) population was studied with respect to differences in habitat quality and food production in a heterogeneous Delaware woodlot from 1972-1973. In 1971 a large mast crop was produced, followed by a poor 1972 crop and a partial recovery in 1973. The squirrel population declined from 116 individuals in summer 1972 to 82 in fall 1973. Major components of the decline were losses of 1972 juveniles and 2-5-year-old females, and curtailed breeding in 1973. Squirrels were segregated among five study plots that represented areas of differing habitat quality and food production within the woodlot. The distribution of the sexes among the plots was significantly heterogeneous in summer and fall 1972 and summer 1973 ($P < 0.10$, G-test); plots with poorer mast production had a preponderance of females (.hivin.x percent of individuals = 62%) while males predominated in plots with the best mast resources (.hivin.x = 64%). In particular, adult males and yearlings (both sexes) were skewed towards high-mast plots while adult females were more abundant in low-mast plots. Juveniles showed no discernable pattern of distribution among plots. Losses were greater than expected from low-mast plots and less than expected from high-mast plots, especially for juveniles, yearlings, and females. The pattern of spatial variation of food abundance, sex (and possibly age) ratios and disappearance rates suggests a model of population regulation in which subordinates are relegated to suboptimal sites and bear major stress and losses when population density is high and food resources dwindle.

Gurnell, J. 1996. The effects of food availability and winter weather on the dynamics

of a grey squirrel population in southern England. Journal of Applied Ecology 33 (2): 325-338.

Author's abstract: 1. The population ecology of grey squirrels *Sciurus carolinensis* living in a 9-ha oak *Quercus robur* wood in southern England was studied between 1976 and 1987 using live-trapping techniques. Trapping was carried out in winter, spring and summer. The availability of tree seeds during the autumn of each year, and the severity of cold weather over each winter were also measured to examine their effects on squirrel population dynamics. 2. Capture probabilities of squirrels in winter, and to a lesser extent in spring, were inversely related to food availability and data from these two seasons were not considered dependable. The analyses concentrated on the summer populations. 3. The long-term average summer density of squirrels was high at 8.8 ha-1 (SE 3.41 ha-1) demonstrating that the oak wood was high quality habitat for grey squirrels. Over 10 of the 12 years, summer densities were remarkably similar, ranging between 7 ha-1 and 10 ha-1 (mean 8.5 ha-1, SE 0.95 ha-1).However, numbers were driven upwards in 1977 to a density approaching 18 ha-1 and downwards in 1982 to a density of about 3 ha-1: a 6-fold difference. 4. In good seed years, breeding starts in December, in poor seed years the start of breeding is deferred until the spring. There was no or very little spring breeding in 5 years when food supplies were poor. Female reproductive success was positively associated with food availability. Partial correlation analysis showed that the level of association was not improved when the effects of winter weather were taken into account. The number of new adult females in the summer population was positively associated with food availability but there was no association between new males and food. This suggests that food availability is more important to breeding females than breeding males. 5. Persistence from summer to winter was positively associated with food availability, but persistence from summer to spring and to the following summer were not. Partial correlation analyses showed that the severity of winter weather tended to mask the effects of food availability on persistence and the partial correlation coefficients were higher when the effects of weather were held constant. Adult females had the highest persistence between summers (52%, n = 11, SE 6%), followed by juvenile females (38%, n = 7, SE 8%), adult males (36%, n = 11, SE 4%), and juvenile males (21%, n = 7, SE 7%). The persistence of adult males but not females was inversely related to the initial number of males present. 6. In males, there was no significant difference in winter body mass between years and winter body mass was not associated with food availability, although there were very few data for winters when the food supply was good. In 7 years when the food supply was poor to moderate, there was an increase in mean body mass between summer and winter in 4 years, and a decrease in 3 years. 7. The data were explored using ordination techniques; first a standardized principal component analysis and then the canonical form of principal component analysis or redundancy analysis. The analysis was carried out on years derived from MNA of males and females and various combinations of the environmental variables: food availability (FOOD) and the severity of winter weather (TEMP). The ordination biplots clearly showed the high correlation between MNA males and MNA females and that FOOD was the most important environmental variable. TEMP on its own had no effect but FOOD times TEMP was important. 8. Following on the exploratory data analysis and for predictive purposes, a general linear model between the numbers of

squirrels in the summer populations and sex, FOOD and FOOD times TEMP as explanatory variables accounted for 77% the variance in squirrel numbers among years. 9. This study shows that tree seed availability is the most important factor limiting grey squirrel densities, but this factor both positively and negatively interacts with the severity of winter weather to affect grey squirrel population dynamics.

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 (9): 1533-1543.

Author's abstract: Eastern grey squirrels, *Sciurus carolinensis*, introduced to Britain and northern Italy are replacing the native Eurasian red squirrel, *Sciurus vulgaris*. We studied the pattern of colonization of a high-quality broadleaf woodland by grey squirrels by means of livetrapping and radio-tracking. The studies started in July 1996, when six grey squirrels (four males, two females) first colonized the woodland, and lasted until November 1998, when densities exceeded those of the local red squirrel population. Grey squirrel colonization was rapid, with a high proportion of adult and yearling females breeding. Juvenile recruitment was also higher than in stable populations in Britain. Adult survival was better in 1997 (83%) than in 1998 (47%), with predation accounting for 67% of losses in 1998. This indicates the effects of local predator communities on the colonization process. Densities of grey squirrels were moderate in 1998, with a maximum of 1.9 squirrels/ha and we expect density to increase further. Adult home range sizes were three to four times larger than those of subadults, and male ranges were larger than those of females. Body mass was positively correlated with both total home range size and core-area size. Core-area size for adults was inversely correlated with food availability. Juvenile female grey squirrels were philopatric, forming female kin groups, while most juvenile males settled outside the mother's home range.

Hadj, C. L. Z., M. A. Steele and P. D. Smallwood. 1996. Caching decisions by grey squirrels: A test of the handling time and perishability hypotheses. Animal Behaviour 52 (5): 941-948.

Author's abstract: This study was designed to investigate the relative effects of seed perishability and handling time on the caching preferences of grey squirrels, *Sciurus carolinensis*, and to test the predictions for caching behaviour that follow from these two hypotheses. Free-ranging squirrels were presented with acorns from two oak subgenera, *Erythrobalanus* and *Leucobalanus*, that vary in perishability (due to germination schedules) and handling time (due to acorn size). In six separate caching experiments, individual squirrels were sequentially presented with two acorn types, so that each paired treatment varied in handling time and/or perishability. Caching responses were recorded for each acorn, along with eating and caching times. Squirrels consistently consumed acorns of high perishability and cached acorns of low perishability, without regard to handling time. This result suggests that the perishability of seeds exerts a greater influence than handling time on the grey squirrel's decision to cache acorns.

Huggins, J. G. and K. L. Gee. 1995. Efficiency and selectivity of cage trap sets for

gray and fox squirrels. Wildlife Society Bulletin 23 (2): 204-207.

Author's abstract: We studied 4 cage trap sets for gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) in the Cross Timbers region of southcentral Oklahoma. During 4,308 trap-days in October-December 1991, traps set on platforms caught the highest percent of gray and fox squirrels, but large variation among trap sites prevented statistical differentiation of trap sets. Orientation of traps at sets did not influence mechanical performance of traps. Although more involved to construct, platform-mounted traps were more convenient to monitor than traps mounted on the trunk, a limb, or the ground.

Ivan, J. S. and R. K. Swihart. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. Journal of Mammalogy 81 (2): 549-562.

Authors' abstract: We used cafeteria-style feeding trials with 8 types of mast in various combinations to examine differences in resource selection among 5 syntopic species of granivorous forest rodents in west-central Indiana. Patterns of resource selection corresponded to differences in phylogeny and body size of granivores, with greatest similarities among closely related species of similar body size. Breadth of resource use varied inversely with body size in our trials. Resource selection by *Sciurus carolinensis, S. niger*, and *Tamiasciurus hudsonicus* was correlated positively with caloric and lipid content of mast and its size, whereas selection by *Glaucomys volans* was correlated negatively with the percentage of protective tissue associated with seeds. Laboratory trials indicated that *T. hudsonicus* and *G. volans* discriminate among mast of comparable physical and chemical composition on the basis of size, with a preference for larger seeds. Contrary to our expectations, *T. hudsonicus*, a recent immigrant from the boreal forest, did not exhibit a preference for seeds of red pine (*Pinus resinosa*) relative to mast of hardwood species. *G. volans* and *Peromyscus leucopus* tended to consume perishable white oak acorns immediately and to cache a substantial portion of less perishable seeds of nonpreferred species. Our results demonstrate the potential for considerable overlap in resource use among members of this guild. Guild members also seem to be affected differentially by physical and chemical properties of mast, and patterns of resource selection reflect contrasting foraging constraints under which these animals operate.

Jacobs, L. F. and E. R. Liman. 1991. Gray squirrels remember the locations of buried nuts. Animal Behaviour 41 (1): 103-110.

Authors' abstract: It has previously been assumed that grey squirrels, *Sciurus carolinensis*, cannot remember the locations of nuts they buried, and hence must relocate nuts by their odour. This assumption was tested by measuring the accuracy of cache retrieval of captive squirrels. Each squirrel was released alone into an outdoor arena, where it cached 10 hazelnuts. After a delay of 2, 4 or 12 days, each squirrel was returned to the arena and tested for its ability to retrieve nuts from its own cache sites and from 10 cache sites used by other squirrels. Although each squirrel's own caches were close to the caches of other squirrels, the squirrels retrieved significantly more nuts from their own sites than from sites used by other squirrels, after all delays. The retrieval accuracy of the

squirrels under these conditions indicates that while grey squirrels can locate buried nuts by their odour, they can also remember the individual locations of nuts they have buried.

Kenward, R. E. and K. H. Hodder. 1998. Red squirrels (*Sciurus vulgaris*) released in conifer woodland: The effects of source habitat, predation and interactions with grey squirrels (*Sciurus carolinensis*). Journal of Zoology 244 (1): 23-32.

Authors' abstract: Fourteen radio-tagged red squirrels were released in pine woodland containing grey squirrels. Movements of the squirrels were related to the tree species of the donor site. Survival after release was lower than for the grey squirrels: of 11 red squirrels that survived at least a week, only three survived more than three months and none for four months. More than half were eaten or cached by predators, mainly foxes; an experiment with grey squirrel carcasses indicated that they had been killed, not scavenged after death. Hypertrophied adrenals, disease and loss of weight indicated stress as another factor in the deaths. Data on overlap of core ranges, and reluctance of red squirrels to enter traps used by grey squirrels in the mixed population, indicated interference competition between the two species, with grey squirrels possibly dominant. We recommend: (i) that care should be taken to release translocated animals in similar habitat to their origin; (ii) that grey squirrels should be excluded from future release areas until red squirrels have settled and, before biodiversity is reduced by landscape management for red squirrels; (iii) more research to determine whether interactions with grey squirrels or differential predation will ultimately displace red squirrels in conifers.

Kenward, R. E., K. H. Hodder, R. J. Rose, C. A. Walls, T. Parish, J. L. Holm, P. A. Morris, S. S. Walls and F. I. Doyle. 1998. Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. Journal of Zoology 244 (1): 7-21.

Authors' abstract: The demography of red and grey squirrels was studied by live-trapping and radio-tagging at 14 deciduous and conifer sites in southern Britain and at eight conifer sites for one year in northern England. Densities and productivity correlated with tree seed crops for both squirrel species in deciduous and conifer habitats. Productivity was reduced by high density of full-grown squirrels relative to seed abundance. In oak-hazel woods, demography of grey squirrels correlated with abundance of acorns but not of hazel-nuts, whereas density and productivity of red squirrels correlated with hazel-nut abundance. Correlations of female density and productivity with pine-cone crops did not differ between red and grey squirrels. Predators ate many radio-tagged grey squirrels in conifers, and annual survival was only 50% compared with 80-82% for both species in other habitats. Grey squirrel populations in southern conifer sites were sustained by immigration, and at northern sites female density correlated with oak abundance within 500 m. Failure to exploit acorn crops puts red squirrels at a competitive disadvantage in deciduous woodland. Red squirrels had higher survival than grey squirrels in conifers, which may give them an advantage in that habitat, but could also have been explained by a lack of predators on their island study site.

Koprowski, J. L. 1991. Response of fox squirrels and gray squirrels to a late spring

early summer food shortage. Journal of Mammalogy 72 (2): 367-372.

Author's abstract: The response of adult and juvenile fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) to a shortage in their two major May-June foods was monitored and compared to a year of typical food abundance. Squirrels foraged more frequently, but less efficiently, during the year of fruit failure than during the typical year. Juvenile survival of both species was reduced during the year of fruit failure, but adult survival remained high. Juvenile losses occurred during late June when weights of adults and juveniles were lower than in the year of typical fruit abundance. By influencing juvenile survival and body condition of adults, late spring-early summer can be a critical period for populations of tree squirrels.

Lawniczak, M. K. 2000. S*ciurus carolinesis:* Eastern Grey Squirrel. Website maintained by University of Michigan. Website: http://animaldiversity.ummz.umich.edu/accounts/sciurus/s._carolinensis.html. Accessed: November 19, 2002.

Lawniczak describes the geographic range of the eastern grey squirrel and gives a complete description of the species including body measurements and dental formulas. The diet of grey squirrels is listed as nuts, flowers and buds of hardwood trees supplemented by fruit, seeds, bulbs and flowers of a range of plants, agricultural crops, insects and rarely frogs and birds' eggs and nestlings. Reproductive biology is thoroughly described from mating through weaning. There are two breeding periods and gestation is reported as 44 days. Females usually mate at 1.25 years, will mate with several males and can breed for 8 years producing litters of 2-4 young. Grey squirrels are most active before sunrise and before sunset and have varying home ranges depending on the season and population density. Squirrels nest in cavities and dreys in the crotch of trees. Grey squirrels are reported to prefer continuous forests of greater than 40 hectares that produce foods that can be cached for winter. The website uses only three mammal guides as references and does not refer to any peer reviewed papers.

Linzey, D. and C. Brecht. 2002. Eastern Gray Squirrel. Website maintained by Wytheville Community College, Wytheville, Virginia. Website: www.discoverlife.org/nh/tx/Vertebrata/Mammalia/Sciuridae/Sciurus/carolinensis/#Top Accessed: November 19, 2002.

The website gives a complete species description of the eastern grey squirrel (including body measurements and skull diagrams), phylogeny, and native distribution in North America. In Great Smoky Mountains National Park, Colorado, grey squirrels are native and are most common in oak and beech woodlands and mixed conifer forests. The site also provides reproductive information from the park. There are two mating seasons (September to February and June to July) and young are born 40 days later. The 1-6 young are raised by the mother and are weaned at 8-9 weeks. Grey squirrels can live 20 years in captivity and up to 10 years in the wild. Grey squirrels are most active in early morning and late afternoon and are primarily arboreal. Grey squirrels eat the flowers, fruit, twigs and buds of deciduous shrubs and trees as well as mushrooms and insects.

Grey squirrels have been killed by rattlesnakes, bobcats and automobiles in Great Smoky Mountains National Park.

Lurz, P. W. W., P. J. Garson and S. P. Rushton. 1995. The ecology of squirrels in spruce dominated plantations: Implications for forest management. Forest Ecology and Management 79 (1-2): 79-90.

Authors' abstract: Red *Sciurus vulgaris* and grey *Sciurus carolinensis* squirrel ecology in conifer forests in Europe is reviewed with reference to squirrels in similar habitats in North America. Red squirrels appear to perform best in conifer forests that contain a large proportion of pine *Pinus* spp., with or without Norway spruce *Picea abies*. Grey squirrels, in contrast, perform best in conifer plantations that have oak *Quercus* spp. and acorns available nearby. A generalized linear model to predict red squirrel density based on forest size, composition and the presence or absence of a Norway spruce cone crop is explained and forest management recommendations for a red squirrel conservation area in Kielder Forest are made.

Lurz, P. W. W., S. P. Rushton, L. A. Wauters, S. Bertolino, I. Currado, P. Mazzoglio and M. D. F. Shirley. 2001. Predicting grey squirrel expansion in North Italy: A spatially explicit modelling approach. Landscape Ecology 16 (5): 407-420.

Authors' abstract: There is growing concern about the spread of the North American grey squirrel (*Sciurus carolinensis*) in northern Italy which were introduced into Piedmont in 1948. They have since spread across the Po-plain covering an area of approximately 450 km2 and continue to expand their range. In parallel to what has been observed in Britain and Ireland, grey squirrels replace the native red squirrel (*S. vulgaris*) and damage poplar (*Populus*) plantations through bark-stripping. Spatially explicit population dynamics models have been successfully used to predict the spread of grey squirrels in East Anglia, England. We extended a previous approach employing a sensitivity analysis where life history and other demographic inputs are generated using Latin Hypercube Sampling from the known ranges of each input parameter, and applied it to Italy using field data collected in Piedmont. The analysis indicated that reproductive output was the most important factor determining total population size present in Piedmont. The structure and composition of woodland habitats around the introduction site suggested that initial grey squirrel expansion would have been slow and subject to emigration rates from the available habitat blocks. A comparison of the 1996 survey results with model predictions indicated that a mean litter size of three young gave the best fit with the observed distribution and we use this to predict future grey squirrel spread. We also present a 'worst case' scenario in which grey squirrels experience improved reproductive success due to the availability of high quality habitats beyond the Po plain. In both cases they could disperse along existing continuous woodland corridors into France between 2039-2048. The case of the grey squirrel highlights the problems of implementing conservation conventions and the resulting conflicts between wildlife management, public perception and local political support and the narrow time frame that is available to control alien species effectively before it is too late. If allowed to spread, grey squirrels have the potential of becoming a European forest pest species and are likely to replace the native

red squirrel in large parts of its range.

MacDonald, A. 2002. *Personal communication.* Birder, Victoria, BC.

MacDonald has observed native raptors feeding on eastern grey squirrels. Maintaining habitat for hawks and owls, installing raptor perches and maintaining standing, dead trees, also known as wildlife trees, will also encourage the presence of birds of prey and help control squirrel populations. The introduction of small mammals to Garry oak ecosystems may have caused increases in populations of some native raptors and aided the range extension of barred owls into these areas.

McCarthy, B. C. 1994. Experimental studies of hickory recruitment in a wooded hedgerow and forest. Bulletin of the Torrey Botanical Club 121 (3): 240-250.

Author's abstract: An examination of the vegetation in and around an old-growth oak-hickory forest in Central New Jersey suggested that hickories (*Carya* spp., Juglandaceae) were not regenerating in the forest at the same rate as in adjacent wooded hedgerows (5-7 m wide corridors dominated by trees and shrubs). The goal of this study was to experimentally examine how factors affecting seed and seedling survival might account for these differential recruitment patterns in contrasting landscape elements. To determine seed discovery efficiency by small vertebrates, I planted seeds of mockernut hickory (*C. tomentosa* (Poir.) Nutt.) with and without their aromatic husk in both forest and hedgerow. Regardless of diaspore type or habitat, seed discovery by herbivores was found to be 85-100% after only 5 days. Gray squirrels (*Sciurus carolinensis*), the principal predator-disperser, were determined to be equally abundant in both landscape elements. To assess the effects of diffuse competition and predation on seedling establishment and survival, I constructed split-plot shade/exclosure cages into which 576 seedlings were explanted and subsequently monitored (survival and mortality agent) for three years. Browsing by deer and rabbits resulted in considerable mortality after one year, particularly in the forest (64% mortality) compared to the hedgerow (21% mortality). During the second year, the major source of mortality switched to physiological stress resulting from drought. Mortality due to drought stress was more noticeable in the hedgerow. By the end of the third year few seedlings remained alive (ca. 196 in forest, 10% in hedgerow). Over the 3-yr period, a small percentage of seedlings were lost due to other factors such as root grubbing, whole plant removal, and litterfall. Shading (50%), to emulate diffuse competition by overstory, was not found to affect survival to any significant extent in either habitat. Phytophagous insects did not result in any observable mortality but did remove 1-10% of the leaf area of the majority of seedlings in both habitats in each field season. I conclude that certain stages of recruitment may be significantly influenced by the presiding landscape element.

McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81 (1): 228-238.

Author's abstract: I recorded mast production by oaks (*Quercus* sp.) at 12 forested sites in western Virginia for 6-12 yr and measured its impact on the abundance of small

mammals, understory vegetation, and artificial-nest predation. White-tailed deer (*Odocoileus virginianus*) were excluded from half the 4-ha sites after at least one season of data collection. My hypothesis was that annual variation in acorn crops affected multiple species and that the strength of those interactions is mediated by white-tailed deer. The acorn crop was variable across sites and year, with some of the between-site variability explained by differences in elevation. All sites experienced at least one mast failure, and mast failure years were generally consistent across sites. White-footed mouse (*Peromyscus leucopus*), eastern chipmunk (*Tamias striatus*), and gray squirrel (*Sciurus carolinensis*) populations were significantly correlated with annual fluctuations in the acorn crop. The exclusion of deer had a significant impact on *P. leucopus* and *T. striatus* populations by increasing the number of animals captured following low acorn mast years. Annual fluctuations in the acorn crop, but not in rodent densities, were significantly correlated with the rates of predation on artificial nests the next summer. There was no significant interaction between predation rates and the exclusion of deer. An index from the Breeding Bird Survey (BBS) for Virginia was used to measure regional numbers for 11 common species captured at the sites. The index for two understory species was significantly negatively correlated with the mean acorn crop measured 2 yr previously. The effect of white-tailed deer on the forest community was not consistent across all conditions, as sites with large acorn crops were not strongly influenced by deer. These data are consistent with the hypothesis that mast crops from oaks serve as important determinants of community function within Appalachian forests.

McShea, W J. and G. Schwede. 1993. Variable acorn crops: Responses of white-tailed deer and other mast consumers. Journal of Mammalogy 74 (4): 999-1006.

Authors' abstract: We examined movements and behavior of female white-tailed deer (*Odocoileus virginianus*) relative to the acorn mast-fall from 1986 through 1989 in a mature deciduous forest in Front Royal, Virginia. Ten white-tailed deer with radiotransmitters increased their home range to incorporate acorn-producing areas during mast-fall. Consumption of acorns by deer constituted ca. 50% of foraging time during peak mast-fall; average consumption rate was 0.75 acorns/min searching. Although the number of acorns eaten by deer was correlated with mast-fall, a prolonged time was spent searching for acorns after mast-fall. Deer consumed 70% of marked acorns placed out during mast-fall, while medium-sized animals (e.g., *Tamias striatus, Sciurus niger, Sciurus carolinensis*) consumed 61% of acorns placed out later in autumn. We hypothesize that high densities of deer may limit populations of more mast-dependent species, particularly at low acorn-crop densities.

Moore, H. D. M., N. M. Jenkins and C. Wong. 1997. Immunocontraception in rodents: A review of the development of a sperm-based immunocontraceptive vaccine for the grey squirrel (*Sciurus carolinensis*). Reproduction Fertility and Development 9 (1): 125-129.

Authors' abstract: The strategy for developing contraceptive vaccines for wild rodents will depend on the species. In rats and mice, high all-year birth rates, high levels of dispersal and promiscuous mating systems suggest that, if immunocontraception was

used alone, gt 90% of the population would have to sterilized to achieve the desired control. In Britain, the grey squirrel (*Sciurus carolinensis*) may be a better candidate to investigate the feasibility of a contraceptive vaccine in rodents. This introduced species is a seasonal breeder with a much lower population turnover than rats or mice. As well as causing damage to woodland, it has ousted the native red squirrel (*S. vulgaris*) from most of the UK. A humane and selective method for the control of grey squirrels is therefore highly desirable. Numerous sperm-specific antigens have been identified on rodent spermatozoa. Monoclonal antibodies to particular components block sperm-egg interactions in laboratory animals and cross-react with grey squirrel spermatozoa. In vitro fertilization assays indicate that squirrel sperm-egg binding may be inhibited also. Currently, a cDNA library obtained from grey squirrel testis is being screened to identify genes encoding specific sperm antigens involved in fertilization. Methods of enhancing immunogenicity after oral immunization using microparticle carriers and immune-stimulating complexes are currently under investigation.

Mountford, E. P. 1997. A decade of grey squirrel bark-stripping damage to beech in Lady Park Wood, UK. Forestry 70 (1): 17-29.

Author's abstract: The scale and distribution of American grey squirrel (*Sciurus carolinensis*) bark-stripping damage to beech (*Fagus sylvatica*) stems was monitored in a mixed broadleaved woodland retained as a Research Natural Area through the use of permanent transects. During an initial outbreak of debarking damage in 1993 almost one-third of beech individuals gtoreq 4 cm d.b.h. in stands of 40 years' growth were badly damaged and by 1993 this level of damage had risen dramatically to over 50 per cent. One-third of badly damaged individuals in 1983, including a number of potential canopy dominants, died during the decade, but some that survived grew very vigorously. Throughout squirrels preferentially debarked intermediate sized (10-25 cm d.b.h.) stems in particular parts of the stands aged 40-50 years, apparently tending to select stems that were growing rapidly. Other species and stand areas of gt 100 years' growth remained largely unscathed. Within the 10-year period squirrels had critically affected the successional development of the wood.

Nagorsen, D. W. 2002. An identification manual to the small mammals of British Columbia. Ministry of Sustainable Resource Management, Ministry of Water, Land and Air Protection, Royal British Columbia Museum, Victoria, BC.

The field guide is designed for lay identification of mammals and provides detailed measurements, dental formulas and skull illustrations. The eastern grey squirrel (*Sciurus carolinensis*) is described as a “large tree squirrel” with three colour forms (grey intermediate and black); the grey form is most common on Vancouver Island. A range map shows two introduced populations in British Columbia in the Fraser Valley (introduced to Stanley Park in the 1920’s) and Victoria (introduced in the 1960’s). Unfortunately, there are no habitat descriptions in this guide.

Nicolas, K. 2002. *Personal communication*. Professional Ecological Services, Victoria, BC.

Most of the squirrel complaints Nicolas receives are related to squirrel denning in buildings. She recommends excluding grey squirrels from buildings and if no young are present, one way doors allow the squirrels to leave but not return. Bird feeders attract grey squirrels and feeders should be removed if squirrels are a problem. Grey squirrels are "Schedule C" animals which means that under the Wildlife Act, they can be captured or killed anywhere in the province and at any time. Rodenticides such as Warfarin are not recommended for dealing with problem squirrels in buildings. The squirrels either eat a sublethal dose and will never eat the poison again or they eat a lethal dose and then die and decompose on site. If Warfarin is used outside, it must be used in a locked, tamper-proof bait station that is anchored to the ground.

Nixon, C. M., M. W. McClain, and R. W. Donohoe. 1975. Effects of hunting and mast crops on a squirrel population. Journal of Wildlife Management 39(1):1-25.

Nixon *et al.* studied the population densities of grey squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) over 10 years to determine the impact of hunting and hickory mast crops. Hunting kills were related to the density of the squirrel populations prior to the hunt and the amount of "total gun-hours". Squirrel populations increased in years with larger mast crops the previous fall. In years when populations declined, squirrels repopulated the area from adjacent forests.

Okubo, A., P. K. Maini, M. H. Williamson and J. D. Murray. 1989. On the spatial spread of the gray squirrel in Britain, UK. Proceedings of the Royal Society of London Series B Biological Sciences 238 (1291): 113-126.

Authors' abstract: We present a diffusion-competition model to describe the interaction between the externally introduced grey squirrel and the indigenous red squirrel in Britain. We estimate the model parameters from field data. Solution of the model predicts waves of grey squirrel invasion with speed of invasion typical of that observed in the field. Numerical solution of the model on a two-dimensional domain gives population distributions qualitatively similar to those observed. We suggest that competition alone could account for the observed displacement of the red squirrel by the grey in large regions of Britain. The solutions are qualitatively similar to those for a single species spreading in the absence of competition. The quantitative difference is because competition slows down the speed of advance of the invading species.

Oregon Department of Fish and Wildlife. 2001. Backgrounder: Nonnative wildlife in Oregon. Website: www.dfw.state.or.us/ODFWhtml/Nonnative_1.pdf Accessed: November 11, 2002

This public education brochure provides information on the impacts and control options available to prevent the spread and minimize the impact of invasive species. The information can be readily applied to Garry oak ecosystems. The native range of eastern grey squirrels is described as "eastern North America from southern Canada to Florida and east to the Great Plains". The brochure provides details on the squirrels current global

distribution. Grey squirrels were first introduced to Oregon in 1919 and have been repeatedly released to the state since that time. Eastern grey squirrels have displaced native western grey squirrels and in Washington, eastern grey squirrels are suspected of causing a decline in native Douglas squirrels. Western grey squirrels are not native to British Columbia and Douglas squirrels are found in the Fraser Valley, Cascade and Coast Mountains but not within the main range of Garry oak ecosystems. The brochure outlines how to ecologically and humanely dispose of trapped invasive mammals. Humane euthanasia options listed are carbon dioxide, cervical dislocation, decapitation, gunshot to the head and barbiturates administered by veterinarians.

Penner, R., G. E. E. Moodie and R. J. Staniforth. 1999. The dispersal of fruits and seeds of Poison-ivy, *Toxicodendron radicans*, by Ruffed Grouse, *Bonasa umbellus*, and squirrels, *Tamiasciurus hudsonicus* and *Sciurus carolinensis*. Canadian Field Naturalist 113 (4): 616-620.

Authors' abstract: A study was conducted to determine the dispersal potential of seeds and fruits of Poison-ivy (*Toxicodendron radicans* (L.) Rydb.) by mammals and birds in a study plot near Stonewall, Manitoba, Canada. Ruffed Grouse (*Bonasa umbellus*) and Red Squirrels (*Tamiasciurus hudsonicus*) and Grey Squirrels (*Sciurus carolinensis*) were the most common visitors to feeders containing fruits and to fruit-bearing plants. Squirrels acted as seed predators by removing the exocarps and mesocarps from fruits and eating the seeds. However, they often dropped individual fruits or entire infructescences that they had been carrying to dining or caching sites and because of this they were effective dispersal agents for the seeds. Ruffed Grouse behaved as frugivores by eating the fruits and excreting intact seeds. Germination in seeds extracted from grouse faeces was not significantly different from seeds from fruits taken directly from the plants. Germination of seeds from within intact fruit was higher but, not significantly, than that from seeds from which the exocarps and mesocarps had been removed. These results show that the fruit and seeds of Poison-ivy are food resources for Ruffed Grouse and squirrels, respectively. Both kinds of animals are effective seed dispersal agents for seeds of this species.

Pigott, C. D., A. C. Newton, and S. Zammit. 1991. Predation of acorns and oak seedlings by grey squirrel. Quarterly Journal of Forestry 85(3):173-178.

Authors' abstract: Grey squirrels (*Sciurus carolinensis* Gmel.) feed on acorns while they are still on the tree, after they have fallen, and after they have germinated and the shoot is beginning to grow. A single squirrel removes large numbers of acorns from the ground at a rate of 60-80 acorns h^{-1}. Some are consumed immediately, but most are buried in caches. Adult grey squirrels bite a small hole in the pericarp and excise the radicle of the embryo of every acorn they bury. This prevents germination, so that the acorn is effectively destroyed. Young squirrels initially bury acorns undamaged but learn to excise the radicle, probably during their first winter. The removal of acorns and their subsequent destruction, and the destruction of seedlings, are shown effectively to prevent regeneration of oak, at least in limited areas below gaps in the canopy.

Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. Journal of Mammalogy 72 (1): 152-162.

Author's abstract: The spatial distribution, habitat specialization, use of food supply, and interspecific behavior within coexisting populations of red squirrels (*Tamiasciurus hudsonicus*) and gray squirrels (*Sciurus carolinensis)* and the social organization of red squirrels were examined in a 10.2-ha mixed forest in northern Wisconsin [USA] during June 1974-March 1976. Habitat specialization, not interspecific aggression, determined differences in distribution of red and gray squirrels. Distribution and abundance of each species were related to production of principal seed foods. Population densities of red squirrels were highest in fir (*Abies*)-cedar (*Thuja*) cover and in pine (*Pinus*) cover in months following high production of cones. Sighting densities of gray squirrels were highest in mature cover of maple (*Acer*)-oak (*Quercus*) throughout the year and were correlated with the tree size of red oak (*Quercus rubra*). Both species consumed seeds of maple, oak, and hazel (*Corylus*); red squirrels also fed on conifer seeds. Interspecific aggression between red and gray squirrels was rare. Adult red squirrels usually established territories defended solely against conspecifics. Territories were less stable than those found in western conifer forests.

Romanach, S. S. and D. J. Levey. 2000. An experimental test of the predator satiation hypothesis: At what level might it apply?. Florida Scientist 63 (1): 1-7.

Authors' abstract: The Predator Satiation Hypothesis posits that synchronous masting of fruits or nuts will maximize the probability of satiating local seed predators, allowing some seeds to escape predation and germinate. Although the hypothesis is usually applied at the population level to explain synchronous reproduction of many individuals, it also might apply at the individual level. In fact, if individual trees were able to satiate local predators, it would reduce selection for synchronous reproduction at the population level. We tested whether individual laurel oaks, *Quercus hemisphaerica,* could satiate their acorn predators. We simulated mast conditions by adding many acorns under the canopies of some tress, while adding few to other, non-mast trees. We then monitored the rate of acorn removal from both mast and non-mast trees. We predicted that non-mast trees would have a higher rate of acorn removal because they would not be able to satiate the major seed predator at our study site, the gray squirrel, *Sciurus carolinensis.* The results did not support our prediction; we found no difference in the removal rate of acorns from mast and non-mast trees. This may be attributable to two characteristics of our study site: the unusually high density of gray squirrels during the year of our study, and the size of *Q. hemisphaerica* trees at the site, which may have been too small to produce enough acorns to satiate such a large number of seed predators. We conclude that the Predator Satiation Hypothesis is most likely to find support at the level of a population, not at the level of individual trees. Predator satiation appears to be a population level phenomenon, with benefits to individual trees.

Rosell, F. 2001. Effectiveness of predator odors as gray squirrel repellents. Canadian Journal of Zoology 79 (9): 1719-1723.

Author's abstract: The ability of gray squirrels (*Sciurus carolinensis*) to discriminate between different predator odors and the use of predator odors to deter gray squirrels from foraging on plants have not been previously investigated. To test the hypothesis that predator scent decreases foraging, I investigated the effect of such scent on consumption of butternuts (*Juglans cinerea*) in the field. Results showed that (i) red fox (*Vulpes vulpes*) scent was significantly more effective than either a control or human scent; (ii) raccoon (*Procyon lotor*) scent was significantly more effective than white-tailed deer (*Odocoileus virginianus*) scent (but only after 7-9 h); (iii) red fox scent was not significantly more effective than raccoon scent; and (iv) human scent was not significantly more effective than the control. The utility of predator odors in controlling damage by gray squirrels should be explored.

Sheail, J. 1999. The grey squirrel (*Sciurus carolinensis*)-A UK historical perspective on a vertebrate pest species. Journal of Environmental Management 55 (3): 145-156.

Author's abstract: The paper reviews from archival sources the experience gained by the UK Agriculture Departments in combating the damage caused by an alien species, the grey squirrel. Insights are provided into the circumstances and significance of the Grey Squirrels Order, 1937, wartime regulations, the free cartridges and tail-bonus schemes and grey squirrels (warfarin) Order of 1973. At times pro-active, policy was more usually driven by the need of Ministers to be seen responding to pressure from farming and forestry, as communicated through such powerful political figures as the Prime Minister himself, Harold Macmillan. Such instances of debate as to the optimal level of pest regulation afforded opportunity not only for scientific study, but for scientists themselves to participate in discussion as to the weight to be given in policy-making to the knowledge, understanding and powers of prediction thereby gained.

Short, M. J. and J. C. Reynolds. 2001. Physical exclusion of non-target species in tunnel-trapping of mammalian pests. Biological Conservation 98 (2): 139-147.

Authors' abstract: We developed and tested physical excluders to prevent non-target animals from entering tunnels containing spring traps intended to kill a range of small (<2 kg) mammalian pest species. In field trials over 82,954 trap-nights, excluders did not significantly decrease stoat (*Mustela erminea*) or weasel (*Mustela nivalis*) capture rates, but did substantially reduce the capture rate of larger target species, notably grey squirrels (*Sciurus carolinensis*) and rats (*Rattus norvegicus*). Excluders virtually eliminated capture of hedgehogs (*Erinaceus europaeus*) - a legally protected species. By inference, larger protected species (polecat *Mustela putorius*, pine marten *Martes Martes*, otter *Lutra lutra* and wild cat *Felis sylvestris*) would be excluded, as would mink (*Mustela vison*), a legitimate target species. These excluders should be advocated where there is a real risk of catching protected species. However, because excluders compromise utility, we recommend that their use should remain discretional unless clearly preferable alternative methods to manage target pest species are developed.

Sieving, K. E and Wilson, M. F. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology. 79(7):2391-2402.

Sieving and Wilson studied the impact of nest predation by constructing open-cup nests and placing them in deciduous and coniferous forests in southeast Alaska and western Canada. One of the main nest predators was the red squirrel (*Tamiasciurus hudsonicus*) especially in coniferous forests. The authors suggest that nest predation may play a role in habitat selection by birds and species diversity.

Steele, M. A., C. L. Z. Hadj and J. Hazeltine. 1996. Caching and feeding decisions by *Sciurus carolinensis*: Responses to weevil-infested acorns. Journal of Mammalogy 77 (2): 305-314.

Authors' abstract: We tested the caching and feeding responses of gray squirrels (*Sciurus carolinensis*) to acorns of three species of oaks (*Quercus alba, Q. palustris,* and *Q. rubra*) infested with weevil larvae (Curculio). Experiments were designed to test the primary hypothesis that squirrels selectively cache sound acorns and the secondary hypothesis that such response may be due to increased perishability resulting from infestation. In an open, suburban oak (*Quercus*) forest in northeastern Pennsylvania, we presented free-ranging animals with whole, infested acorns, whole, noninfested acorns, and noninfested acorns from which the pericarp (shell) was removed to increase perishability. Squirrels cached significantly (2035%) more of whole, intact acorns of red oak, dispersed these acorns significantly greater distances before caching them, and consumed shelled and infested acorns. Squirrels showed a similar response to acorns of pin oak, but ate significantly more of both infested and noninfested acorns of white oak. Squirrels also were observed to consume weevil larvae in gt 76% of all trials with infested acorns. These results indicate that squirrels can distinguish between infested and noninfested acorns, that they often selectively cache sound acorns, and that weevils represent a significant dietary supplement for squirrels. We also suggest that gray squirrels may exert a strong influence on the dispersal of oaks by selecting viable seeds for storage.

Steele, M. A., T. Knowles, K. Bridle and E. L. Simms. 1993. Tannins and partial consumption of acorns: Implications for dispersal of oaks by seed predators. American-Midland-Naturalist 130 (2): 229-238.

Authors' abstract: A common assumption in studies of seed predation is that seeds survive attack and are dispersed only when animals fail to find seeds, drop undamaged seeds or fail to recover seeds after they are cached. This study, however, suggests that many acorn consumers consistently eat only a portion of the cotyledon of several species of acorns and thereby permit embryo survival. Several vertebrates (gray squirrels (*Sciurus carolinensis*), common grackles (*Quiscalus quiscula*) and blue jays (*Cyanocita cristata*)) were observed to consume only 30-60% of the cotyledon from the basal portion (cap end) of willow oak (*Quercus phellos*) acorns. Gray squirrels exhibited a similar preference for the basal end of acorns of several other species of red oaks (*Q. rubra, Q. laevis, Q. nigra, Q. palustris* and *Q. coccinea*) from a wide geographic region. In addition, acorn weevil larvae (Curculio sp.) were observed significantly (gt 35%) more often in the basal portion than in the apical end of Q. alba acorns. Chemical analyses of acorns from two tree species revealed that the concentration of protein-precipitable

phenolics (primarily tannins) was 12.5% (*Q. phellos*) and 84.2% (*Q. laevis*) higher in the apical portion of the seeds where the embryo is located. Moreover, germination experiments revealed equal or greater germination frequencies for partially consumed acorns than for intact acorns. We suggest that the higher tannin levels may render the apical portion less palatable, and thereby increase the probability of embryo survival after attack by seed consumers.

Steele, M. A., P. D. Smallwood, A. Spunar and E. Nelsen. 2001. The proximate basis of the oak dispersal syndrome: Detection of seed dormancy by rodents. American-Zoologist 41 (4): 852-864.

Authors' abstract: Previously we have shown how a range of physical and chemical characteristics of acorns influences the behavioral decisions of food-hoarding rodents which in turn affects the dispersal, establishment and spatial arrangement of oaks. One such behavior involves the selective caching of acorns of red oaks (subgenus: *Erythrobalanus*) over those of white oaks (*Quercus*) because of reduced perishability that results from delayed germination of acorns in the red oak group. In this study, we sought to identify the specific proximate cues (visual and olfactory) that eastern gray squirrels (*Sciurus carolinensis*) use when making these decisions. In two series of field experiments, we presented individual, free-ranging animals with pairs of experimentally altered acorns (that differed with respect to a single chemical or visual characteristic) and recorded their feeding and caching responses. Squirrels cached artificial acorns with pericarps (shells) of red oak acorns and ate those with shells of white oak regardless of the internal chemical composition of either type of acorn. Only when the shells of artificial acorns were first soaked in acetone (to remove potential chemical odors) did animals eat artificial acorns made with the shells of red oak acorns. Squirrels also ate one-year old red oak acorns that had broken dormancy, even when they exhibited no signs of germination. We argue that a chemical cue in the shell of acorns is important in the detection of seed dormancy and the decision to cache acorns, and that such a cue might ultimately contribute to the differential dispersal of red and white oaks by rodents.

Stiles, E. W. and E. T. Dobi. 1987. Scatterhoarding of horse chestnuts by eastern gray squirrels. Bulletin New Jersey Academy of Science 32 (1): 1-4.

Authors' abstract: The scatterhoarding behavior shown by eastern gray squirrels (*Sciurus carolinensis*) is well known (Brown ad Yeager, 1945; Schorger, 1949), but few quantitative studies of the movements of seeds from predispersal sites under the parent tree to scatterhoard locations are available (Cahalane, 1942; Sork and Boucher, 1977; Stapanian and Smith, 1978, 1984). Eastern gray squirrels are a primary dispersal agent for many large seeded, canopy trees in the eastern deciduous forest (Smith and Follmer, 1972). The objective of this study was to examine scatterhoarding behavior by squirrels and measure distances seeds were carried from the parent tree. We also suggest a pattern of seed selection by squirrels.

Stirling, D. 2002. *Personal communication*. Birder, Victoria, BC. November 13, 2002.

Stirling has noticed a connection between the introduction of small mammals and the increase in populations of owls and hawks. Before house mice, rats, grey squirrels and rabbits were introduced in the early 1960s, there were very few small mammals on Vancouver Island (only Townsend's vole, deer mouse and red squirrel). Before the mammals were introduced, there were also very few great horned and barred owls. Now, great horned and barred owls are very common and the introduced mammals make good prey.

Stone, W. B., J. C. Okoniewski and J. R. Stedelin. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. Journal of Wildlife Diseases 35 (2): 187-193.

Authors' abstract: From 1971 through 1997, we documented 51 cases (55 individual animals) of poisoning of non-target wildlife in New York (plus two cases in adjoining states) (USA) with anticoagulant rodenticides-all but two of these cases occurred in the last 8 yrs. Brodifacoum was implicated in 80% of the incidents. Diphacinone was identified in four cases, bromadiolone in three cases (once in combination with brodifacoum), and chlorophacinone and coumatetralyl were detected once each in the company of brodifacoum. Warfarin accounted for the three cases documented prior to 1989, and one case involving a bald eagle (*Haliaeetus leucocephalus*) in 1995. Secondary intoxication of raptors, principally great horned owls (*Bubo virginianus*) and red-tailed hawks (*Buteo jamaicensis*), comprised one-half of the cases. Gray squirrels (*Sciurus carolinensis*), raccoons (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) were the most frequently poisoned mammals. All of the deer originated from a rather unique situation on a barrier island off southern Long Island (New York). Restrictions on the use of brodifacoum appear warranted.

Teangana, D. O., 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 (1): 45-56.

Authors' abstract: The distributions of the Red and Grey Squirrel were surveyed in Northern Ireland and the Republic of Ireland between 1994 and 1996. Survey methods differed between the two studies. In the former, all suitable habitat, of at least 15 ha, was inspected for species presence or absence. In the Republic, data were gathered through questionnaires to governmental and independent wildlife bodies. The combined results indicate that the Red Squirrel remains widespread and locally abundant, and is present in all but two counties. The Grey Squirrel is now more widespread than ever before, and can be found in 22 of the 32 counties. Its range expansion has varied from 0 km/yr to an estimated 13.4 km/yr, as various geographical features, principally rivers, have hindered its progress in certain directions.

Vandruff, L. W. and R. N. Rowse. 1986. Habitat association of mammals in Syracuse, New York, USA. Urban Ecology 9 (3-4): 413-434.

Authors' abstract: A 2-year study of the mammals in Syracuse, NY revealed the presence of 17 non-domestic species. Of the 13 species trapped in 20 greenspaces (Parks,

greenbelts, private woodlots, etc.), white-footed mice (*Peromyscus* spp.), meadow voles (*Microtus pennsylvanicus*) and gray squirrels (*Sciurus carolinensis*) comprised 65% of the 1040 captures from 13344 functional trapnights of effort. Species richness ranged from 3 to 9 species captured in the greenspaces that varied in size from 2 to 22 ha. Three interspecific associations were identified, but several species were associated with similar habitat features. Using Spearman's rank correlation (univariate) and canonical correlation (multivariate), capture success of each species and various combinations were correlated with one or more of 31 physical, biotic or cultural variables obtained from on-site measurements, aerial photographs, and Bureau of Census reports. Generally, variables measured from aerial photographs accounted for more of the variability in mammal abundance among areas than did detailed measurements of on-site physical or biotic conditions. Area of water, area of grass or field, area of pavement or gravel, and total greenspace often were significant, whereas specific characteristics of a vegetative type such as size-class of trees, diversity of herb layer, or percentage of canopy closure in the understory had little effect on the mammalian community. Mammals that can exist in urbanized areas apparently respond to the mosaic of habitats and land uses in the general area rather than those conditions found within specific greenspaces.

Wauters, L. A., J. Gurnell, I. Currado and P. J. Mazzoglio. 1997. Grey squirrel *Sciurus carolinensis* management in Italy-squirrel distribution in a highly fragmented landscape. Wildlife Biology 3 (2): 117-124.

Authors' abstract: American grey squirrels *Sciurus carolinensis* introduced to northern Italy in 1948 have caused damage to commercial poplar plantations and have replaced the native red squirrel *Sciurus vulgaris* from most of the 350 km-2 of the Piedmont Po-plain they currently occupy. In order to plan a control programme aiming to stop grey squirrels from further spreading and to decrease their numbers the current distribution and population size in the highly fragmented landscape of the Po-plain were studied. The probability of finding grey squirrels in woodland fragments increased with habitat quality (diversity of trees producing large, consumable seeds), woodlot size and the proportion of poplar. Adding isolation variables did not improve the fit of the logistic regression model that predicted squirrel presence. The density of squirrel dreys, an index of population density, in the large Stupinigi forest also increased with tree species diversity. An estimate of the minimum population size for all woodlots assessed for squirrel presence was 1,260 animals in the summer of 1996. This extrapolates to a total of ca 2,500 grey squirrels in Piedmont. Grey squirrels continue to increase their range and are getting close to the continuous mixed forests of the pre-Alps and to large hazel plantations. Control measures to stop the spread of grey squirrels, and eventually to eradicate them, should be implemented immediately.

Wauters, L. A., J. Gurnell, A. Martinoli and G. Tosi. 2001. Does interspecific competition with introduced grey squirrels affect foraging and food choice of Eurasian red squirrels? Animal Behaviour 61 (6): 1079-1091.

Authors' abstract: Grey squirrels, *Sciurus carolinensis*, introduced from North America, have replaced red squirrels, *S. vulgaris*, over much of Britain and parts of north Italy, but

the reasons why are unclear. Spatial and temporal changes in the quantity and quality of their primary foods, namely tree seeds, may provide the focus for interspecific resource competition and hence go some way to explain the replacement process. To investigate whether grey squirrels have a competitive advantage over red squirrels, we used radiotelemetry and direct behavioural observations to examine the activity budget, foods, feeding behaviour and body condition of adult red squirrels in two mature, mixed-woodland sites in northern Italy, one site where there were only red squirrels, and one where both red and grey squirrels were present. The studies were carried out between July 1996 and October 1998. We found few differences in the activity and foraging patterns and food choice of red squirrels with and without grey squirrels present, although we could not eliminate possible interspecific competition effects on food choice by red squirrels in summer (June-August) and autumn-winter (September-February). Foraging time and rate of energy intake of red squirrels in the mixed-species site were lower than in the red-only site in winter (December-February). This may have resulted from interspecific competition, but a more plausible explanation is that these site differences resulted from the distribution of preferred tree seeds and home range size. Overall, our results provide little support for the food competition hypothesis. Differences in body size between sites suggest that interspecific competition occurs during the growth phase of red squirrels, when juveniles and subadults disperse and look for a place to settle.

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 plantations. Ecological Research 15 (3): 271-284.

Authors' abstract: Interspecific competition between red squirrels and grey squirrels was investigated by comparing the population demography, spacing behavior and habitat use of red squirrels in two large conifer plantations in northern England: one site had only red squirrels (the 'red-only' site), in the other both red and grey squirrels occurred (the 'red-grey' site). Despite more abundant food at the red-grey site, red squirrel densities (0.26 ha-1 at the red-grey site, 0.29 ha-1 at the red-only site), adult survival rates and the breeding rates of females were similar at both study sites. Grey squirrels at the red-grey site occurred at higher densities (0.92-1.1 ha-1) than did the reds and tended to have higher breeding rates. In the presence of grey squirrels, the recruitment pattern of red squirrels changed and there was little recruitment of subadults. The juvenile recruitment rate in the red-grey site (13%) was much lower than in the red-only site (50%). Grey squirrels, in contrast, had higher juvenile recruitment rates at the red-grey site (41%). The core areas of the home ranges of red squirrels in the red-grey site were more strongly overlapped by grey squirrels than by conspecifics. Red squirrels did not select the habitat with the best tree seed crop (Scots pine) but preferred dense Sitka spruce plantations; they appeared to avoid the Scots pine area with its high grey squirrel density. Data on foot length and body condition indicated decreased body growth in young red squirrels when grey squirrels were present. Our data suggest that adult red squirrels suffered little from interspecific competition with grey squirrels and that the key factor is decreased juvenile recruitment in red squirrels.

Wauters, L. A., G. Tosi and J. Gurnell. 2002. Interspecific competition in tree

squirrels: Do introduced grey squirrels (*Sciurus carolinensis*) deplete tree seeds hoarded by red squirrels (*S. vulgaris*)? Behavioral Ecology and Sociobiology 51 (4): 360-367.

Authors' abstract: Red squirrels (*Sciurus vulgaris*) and introduced eastern grey squirrels (*S. carolinensis*) scatterhoard seeds of broadleaf trees. Scatterhoarded seeds are an essential resource in spring and their consumption increases red-squirrel fitness. We examined whether grey squirrels partly deplete the high-energy food resources cached by red squirrels, reducing their consumption, in two ways: (1) at the population level, comparing energy intake of feeding on cached seeds between a study site with red and grey squirrels and one with only red squirrels present; and (2) at the individual level, in the study site where species co-exist, relating hoard recovery of red squirrels to the amount of core-area overlap with grey squirrels. There were no significant site differences in the mean daily energy intake of red squirrels feeding on seeds recovered from caches. However, in the red-grey site, during spring, red squirrels that had a high percentage of their home-range core area overlapped by grey squirrels had a lower daily energy intake than low-overlap red squirrels. Body mass of red squirrels in spring was negatively correlated with the percentage of interspecific core-area overlap, but not with core-area overlap with other red squirrels. Our data suggest that interspecific competition for scatterhoarded seeds, with grey squirrels pilfering red squirrels' food caches, caused a reduced energy intake in red squirrels with a high degree of interspecific core-area overlap, and reduced body mass in spring. Therefore, cache pilfering is likely to reduce reproductive output in red squirrels, and thus play a role in the replacement of red by grey squirrels.

Weckerly, F. W., K. E. Nicholson and R. D. Semlitsch. 1989. Experimental test of discrimination by squirrels for insect infested and noninfested acorns. American Midland Naturalist 122 (2): 412-415.

Authors' abstract: Vertebrates that consume and disperse seeds are thought to consume and cache only noninfested undamaged seeds. We experimentally tested the preference of free-ranging gray squirrels (*Sciurus carolinensis*) for infested (contain curculionid larvae) and noninfested (fully developed and undamaged) *Quercus nigra* acorns. Equal numbers of infested and noninfested acorns were presented to squirrels in 10 feeding trials. For both foraging behaviors (consumption and dispersal), squirrels showed no preference for either category of acorn, indicating that squirrels cannot discriminate quality of unopened acorns.

Zegers, D. A., S. May and L. J. Goodrich. 2000. Identification of nest predators at farm/forest edge and forest interior sites. Journal of Field Ornithology 71 (2): 207-216.

Authors' abstract: Using cameras at artificial ground nests we found no major quantitative differences in species richness or the relative abundance of nest predators photographed in farm/forest edge and forest-interior sites at five locations in eastern Pennsylvania. Raccoons (*Procyon lotor*) were the most commonly photographed visitors to nests at both farm/forest edge and forest interior sites, followed by female Baltimore Orioles (*Icterus galbula*), southern flying squirrels (*Glaucomys volans*), gray squirrels

(*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), and Gray Catbirds (*Dumetella carolinensis*). Rate of egg loss was higher at the edges than in the forest interior. Although the total number of photographs of predators averaged 11 among the five edge sites and 7.4 among interior sites, this was not significantly different.

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15 (6): 523-533.

Author's abstract: Perceptual range is the maximum distance from which an animal can perceive the presence of remote landscape elements such as patches of habitat. Such perceptual abilities are of interest because they influence the probability that an animal will successfully disperse to a new patch in a landscape. Furthermore, understanding how perceptual range differs between species may help to explain differential species sensitivity to patch isolation. The objective of this research was to assess the perceptual range of eastern chipmunks (*Tamias striatus*), gray squirrels (*Sciurus carolinensis*), and fox squirrels (*Sciurus niger*) in fragmented agricultural landscapes. Animals were captured in remote woodlots and translocated to unfamiliar agricultural fields. There they were released at different distances from a woodlot and their movements towards or away from the woodlot were used to assess their ability to perceive forested habitat. Observed perceptual ranges of approximately 120 m for chipmunks, 300 m for gray squirrels, and 400 m for fox squirrels, suggest that differences in landscape-level perceptual abilities may influence the occurrence of these species in isolated habitat patches.