# CHAPTER 1. SQUIRREL ECOLOGY

## GREY SQUIRREL (*Sciurus carolinensis*) ECOLOGY

The eastern grey squirrel is a small 'game' mammal that occurs naturally in the eastern hardwood forests of North America (Teaford 1986). It can be found from the Gulf of Mexico in the South, west to southern Manitoba, and to southern Quebec and southern Ontario in the north. It is an important North American game species and hunted in every state within its natural range to the extent that the combined annual harvest of grey and fox squirrels totals approximately 40 million animals.

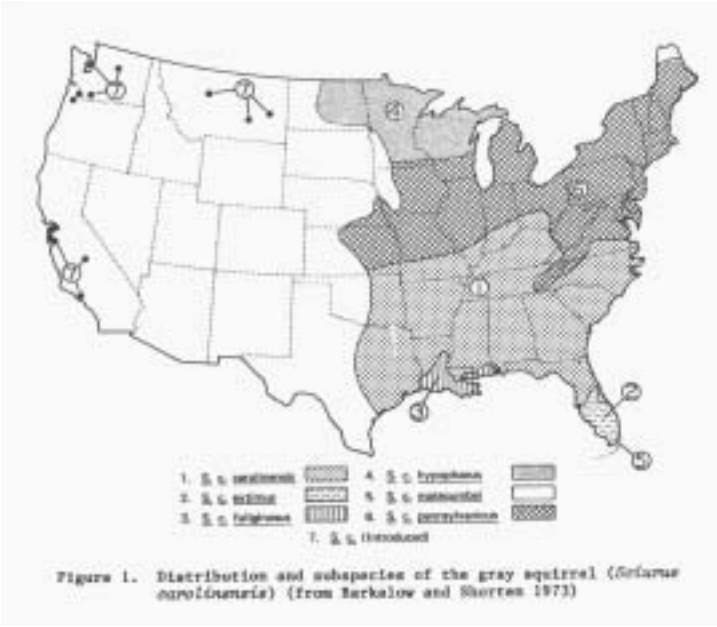


**Figure 1.1. Map taken from Teaford (1986) showing the distribution of the grey squirrel in its native USA.**

Age determination is in four categories: the nestling - birth until weaning; the juvenile from weaning until the eruption of permanent teeth when they are sub-adult. The fourth stage, adulthood is marked by the replacement of the sub-adult pelage with the adult coat. It is at this stage, at 11 - 12 months of age, that the female squirrel normally produces her first litter. Gestation is roughly 44 days.

Young are born and weaned in dreys, which are balls of twigs, leaves and bark strips situated in branches high off the ground and close to the trunk. Hollows in trees and disused nests will also be used. Greys have also been known to den in roof-spaces. Most winter-spring litters are born in tree cavities, while spring-summer litters are born in leaf nests. Adult females generally have larger litters than yearlings and spring-summer litters are generally larger than winter-spring litters. During any year, breeding will be significantly influenced

**Figure 1.2. "Large breeding drey, built in a fork of a tree – frequently oak – is easily seen and destroyed during the winter months" (Forestry Commission 1960).**

**Figure 1.3. Adult grey squirrel. "The body is about 25 cm long, and bushy tail 23 cm" (Forestry Commission 1960)**

by the previous autumn's mast crop and food availability. The grey squirrel's preference for broad-leaved habitat dominated by mature, mast-producing species with closed or nearly closed canopy is extensively chronicled. But although primarily suited to life in broad-leaved forest this squirrel is very adaptable and is also found in conifers (Corbet 1980). They are common in urban parks and suburban gardens wherever there are suitable trees. Equally, they are seldom found far from an open water source. Greys prefer timber stands with canopies dense enough to permit continuous travel through the tree crowns. The density of the under-storey is also important because they spend so much time on the ground. Having a closed canopy above and little ground cover is advantageous for the grey squirrel as it prefers to travel on the ground. They are active during the daytime with most activity occurring in the early hours of the morning and before dusk, with a minor peak at midday. Most eat only 1 or 2 food items during a feeding period. Grey squirrels do not hibernate but reduce their activity in the winter, and sleep in dreys high up in a tree. As an integral part of the overall feeding activity, grey squirrels bury (cache) many nuts and acorns during the autumn when these foods are abundant. Cached foods are then dug up and eaten during the winter through to spring, thus effectively extending the available supply. Grey squirrels have an acute sense of smell, and during cold winter spells can find foods, which they stored previously underground.

Males and females are for the main part solitary, associating only to the breed. They maintain an exclusive core area within their home range while the remaining peripheral areas may

overlap extensively with those of neighbouring animals. Family groups consisting of a female and her young may be seen and as many as 10 - 12 individuals may be observed feeding in a single tree. Grey squirrels are promiscuous and typically engage in "mating chases" which have been reported to involve from 3 - 34 squirrels for periods ranging from 1/2 hour to an entire day.

Greys are larger than reds with a head and body length of 23 - 30 cm, a tail length of 14 -24 cm (which is proportionately smaller than for reds) and a body weight of 400 - 800 gms. Signs of feeding activity often indicate the presence of squirrels. Grey squirrels will strip pine cones, hollow out acorns and crack hazel nuts cleanly in half, often leaving the remains scattered on the stumps of trees. Kenward & Holm (1993) have shown that in oak-hazel woods, grey squirrel foraging, density and productivity are related to oak and acorn abundance. They will also gnaw through the tips of horse chestnut shoots and stems, tree bark, flowers and fungi, but greys are primarily seedeaters. The seed and fruit of deciduous trees is the most favoured food type just as the favoured woodland habitat will contain many broad-leaved tree species that can produce large quantities of nutritious seeds such as oak (*Quercus spp*), beech (*Fagus sylvatica*), sweet chestnut (*Castanea sativa*) and hazel (*Corylus avellana*). The presence of weevil larvae in acorns and other nuts does not prevent grey squirrels from eating the nuts. They are also known to eat lichens, mosses, adult insects and larvae and occasionally birds' eggs and nestlings - records as far back as 1954 reveal this. Their diet will vary considerably according to the season, location, individual behaviour and opportunity.

Greys are capable of living for eight or nine years. This is thought to be twice as long as reds. Variation in the amount of the annual seed crop from the trees in which they live will have direct impact on both population size and breeding capabilities. Greys are capable of breeding twice yearly, and even three times a year has been recorded. The availability of seed (mast) supplies right through the breeding season will clearly affect this potential and will also have a knock-on affect on:

- the length of breeding season,
- the number of females producing at least two litters,
- the numbers of adults and yearlings which can breed, and
- the number of young per litter (usually three but can be as many as nine).

A good seed crop will also enhance ability to over-winter, survival rates and resistance to disease. Fluctuations in population densities can generally be correlated with the availability of mast food supplies during the preceding autumn. Autumn to autumn densities have been

observed to double or even quadruple in response to bumper crops of mast, and they have also been observed to plummet to levels only 15% to 25% of the previous autumn density in response to mast crop failures. That numbers peak in autumn and vary between years is quite usual in rodent population dynamics. Estimates of autumn population densities can range from 0.5 to as high as 14 squirrels per hectare (Mosby 1969) although a density of 3.2 squirrels per hectare is considered high for extensive forested habitats (Teaford 1986).

While it is generally accepted that grey squirrel population declines occur primarily as a result of mast crop failures, most of the mortality is concentrated in the nestling, juvenile and sub-adult age classes; 75% of the young born during any year normally die within 12 months. First-year mortality is greater within the summer-born litter. This is most likely to result from shortage of food at that time of year. The spring-born litters benefit from the presence of ample and varied food supply when leaving the nest, the summer-born are probably surplus animals that must disperse to other areas or die. Dispersal movements for sub-adults normally occur as they approach sexual maturity at 8 - 11 months of age. Although not migratory, grey squirrels have been reported to emigrate. These emigrations are one-way movements in which the majority of the squirrel population of an area travels in one general direction. These movements continue until they are finally dissipated by mortality factors (accidents, disease, exhaustion, predation etc). Most reported emigrations are generally associated with above-average population densities and regional mast crop failures or an imbalance between the food supply and population densities.

Apart from the Goshawk, within the British Isles there are no known natural predators of the grey squirrel as there are in the USA, where the bobcat, raccoon, various owls, hawks and snakes can happily enjoy such a snack. In addition no known disease provides regular death-threatening circumstances here as there are across the Atlantic, where there have been reports of virtual elimination from scabies mange (*Sarcoptes spp*). Up to 80 endoparasites and ectoparasites are associated with the grey squirrel in the USA and the botfly, chiggers, fleas and ticks are commonly reported as serious parasites (Teaford 1986).

### Energy Requirements

One area of squirrel biology that has not received much attention is their energy usage, even though the energy expenditure of any animal is central to our understanding of many aspects of its ecology. Recent work has shown that the energetic requirements of the species mirrors that of their biomass difference. Teaford (1986) states that grey squirrels require approximately 0.7 kg (1.5 lb) of food per week. In Britain, the decline in the red squirrel distribution has been attributed mainly to the spread of the introduced grey squirrel.

However, Bevan & Lurz (2003) consider that there are habitats such as spruce dominated forest in which the red is able to apparently coexist with or even out compete the grey squirrel. They believe this to be due mainly to the constraints of the higher daily energy expenditure (DEE) of the larger grey squirrel. So they endeavoured to measure the DEE of red and grey squirrels in different habitats, namely:

(i) red squirrels in typical conifer plantation habitat;
(ii) grey squirrels in typical conifer habitat;
(iii) grey squirrels in good quality deciduous habitat.

The study was conducted during the breeding season as this is when the females will be most energetically stressed. Lactating females of both species had a DEE that was between 2 and 2.5 times higher than that of non-reproductive individuals. The DEE of red squirrels was 141 kJ/day while that of the grey was 387kJ/day. Smith & Gurnell (1997) studied the feeding preferences of grey squirrels in coniferous forests in Britain by trapping greys in Cannock Chase and examining their stomach contents. In the main, Scots pine (*Pinus sylvestris*) was the favoured food, followed by Lodgepole pine (*Pinus contorta*) and then larch (*Larix kaempferi*). They found that the metabolic requirements of squirrels in conifers are much higher and that in stands of Corsican pine (*Pinus nigra*), 74 cones per day were required to sustain the grey squirrel. It is possible for grey squirrels to gain their daily requirement in coniferous stands, but they have to work hard for it. Life for red squirrels in coniferous stands is much easier than for greys because they need less food to sustain them (Smith 2003).

Grey squirrels in deciduous woodlands have been reported to increase their body weight much more than red squirrels in the autumn – as much as up to 20%. This would give them a significant advantage for over wintering and breeding capacity the following spring. However, this has not been investigated in relation to patterns of seed availability or habitat composition and there is little published information on whether these increases in body weights occur in conifer woodland in either red or grey squirrels. Lurz & Lloyd (2000) studied seasonal body weight changes in red and grey squirrels in the north of England in spruce dominated conifer forests and found that neither red nor grey squirrels in conifer plantations significantly increased their body weight. The responses of both red and grey squirrels to the different foraging conditions in deciduous and conifer woodlands and the accumulation of seasonal fat stores may have to be seen in the context of habitat type and the pattern and predictability of seed availability. They consider that fat accumulation is less pronounced in conifer habitats where autumn and winter food supplies are more predictable and manoeuvrability to feed on cones in the canopy is important.

## RED SQUIRREL (*Sciurus vulgaris* L.) ECOLOGY

This is the only native, diurnal tree squirrel in Europe and can, for several reasons, especially during summer time, be quite easily confused with the non-native grey squirrel. Despite the difference in weight - reds weigh between 200 and 480 gms - the overall length of both species is not dissimilar. The colour of the red squirrel varies much during the year owing to two moults - a complete moult in October and all except the tail in May. It is a rich reddish brown with white under-parts in summer when the grey squirrel can also show a certain amount of red. Equally in autumn they moult to a duller greyer brown but the main significant difference then is the appearance of prominent ear tufts. The ear tufts are virtually worn away by the following spring and are not replaced until autumn. The tail is the same colour as the back following the autumn moult, but a peculiarity of the British and Irish race of red squirrel is that the tail progressively fades, so that by the following spring and summer it becomes a light creamy brown. In extreme cases it is almost white.

**Figure 1.4. Red Squirrel in Cumbria (Val Corbett 2003)**

### Genetic variation

This is a particularly important factor with regard to the status of the British red squirrel as the continental red squirrel is a much deeper red in colour all over, and is not native to Britain but has been introduced in several areas eg Formby, Lancashire. The only indigenous red squirrel (originally a distinct sub species of *Sciurus vulgaris - S v leucorurus*) to be found in Britain is in Cumbria (Kitchener 2003). Introductions of European stock during the 18th and 19th centuries may mean that the endemic red squirrel in Britain is no longer validly distinct (Harris 1995). A mitochondrial DNA survey showed that the majority of extant populations of British *S.vulgaris* are of continental European ancestry, many with a very recent (last 40

years) Scandinavian ancestry (Hale & Lurz 2003). The Scandinavian haplotype has rapidly become the most dominant haplotype in the northeastern British populations, despite not appearing in the northern English populations until 1966. This suggests that these squirrels may have an adaptive advantage in the non-native spruce dominated conifer plantations of northern England.

Kitchener (2003) has examined more than 300 squirrels for geographical variation and has found distinct differences between populations of red squirrels in size, shape, colour, skull and mandibles. Four main populations were compared with presumed differing origins: Jersey (introduction from France), Formby (possible introduction from Europe), Cumbria (indigenous) and the Highlands of Scotland (re-introduced from England, possible Swedish introductions). The results of this study contradict genetic studies done so far. But it does provide some answers to the question of the sub-specific distinctiveness of British red squirrels, while raising a question about the reasons for conserving the red squirrel in some parts of the British Isles today where a non-native red squirrel is resident.

Another (partial) mitochondrial DNA survey in red squirrels compared haplotypes of red squirrels from England (UK) with those from Korea (East Asia) by Koh *et al.* (2003). This showed that all haplotypes from both locations were in fact strongly intermingled suggesting that such dispersal will probably have occurred rapidly in the late Pleistocene after the last glaciation.

Efforts to conserve the red squirrel therefore must be conducted at international levels rather than on a national scale.

Red squirrels are found in both coniferous and deciduous woodland (particularly beech) reaching 2000 metres in the Alps and Pyrenees. They were once very common in all wooded parts of England, particularly in conifer woods. From the days of the Wildwood right through to the introduction of the grey squirrel, the red squirrel was common in deciduous woodlands and is renowned for its association with the hazelnut. However the grey squirrel's gastric efficiency at digesting large nuts such as acorns and hazelnuts has given them a significant competitive advantage over reds in broad-leaved woodland. This, in turn has resulted in reduced breeding success for red squirrels and the swift disappearance of our native species from deciduous woodland. Greys appear to be less partial to certain coniferous cones giving the reds the opportunity of hanging on to their existence in larger coniferous forests. Indeed, among Scots pine, red squirrels can have densities and breeding success as high as grey squirrels in deciduous woodland. The grey however has proved to

be so adaptable that many believe it will not be long before their density and demography dictates that all conifer seeds as well as the fruits of broadleaved species will become a part of their diet. This will obviously have significant consequences for the red – a species that is already on its way to extinction outside self-contained islands if the grey is not removed.

**Behaviour**

Reds are very similar in behaviour to greys but spend much more time (70%) off the ground foraging in the trees than greys. They too are active throughout the day, especially just after dawn and before sunset. In their European range, reds are predominantly associated with coniferous forests where food remains in the tree canopy for most of the year. They do forage on the ground, carrying food up a tree before eating it. They can climb and leap with great agility and usually come down a tree trunk, head first. They feed predominantly upon tree seeds, especially those of conifers, but beech mast is also important. Red squirrels thrive and reach their highest densities in mature coniferous forest but will also inhabit deciduous woodland. Compared to the grey squirrel, the red will forage more widely for food. Conifer seeds, when available, are the most important component of red squirrel diet. Research shows that between 50 - 85% of stomach contents comprise spruce and pine seed. Cones will even be eaten while still green and unripened. Rooney & Hayden 2002 consider that reds prefer spruce to pine cones since they are easier to open and strip. However they do not prosper in monocultures of Sitka spruce due to what is thought to be its low food value and require other species such as Scots pine and Norway spruce.

Sitka spruce seeds well on average, every 3-5 years, but Norway spruce rarely seeds heavily and no interval is given for the number of years between good seed years in the Forestry Practice (B Mayle Forest Research pers comm). However, Lurz *et al*. (2003) quote 3 – 11 years as the interval between good seed crops for Norway spruce, and Hart (1991) cites Aldhous, stating that full seeding is from 2 – 11 years. Research is on going on numbers of cones per tree, seeds per cone and energy contents, and numbers will always depend on size, age of tree, and how much competition it experiences from its neighbours (Peter Savill pers comm 2003). For example an isolated tree produces more seed than a closely grown one. He supports Forestry Practice and says that seed is rarely produced in any quantities in Britain, largely because it does not mature properly. The earliest age at which the tree bears seeds is 30 – 35 years, but the best crops are usually between 50 and 60 years (Savill 1991).

In stands of Scots pine, red squirrels can have densities and breeding success as high as grey squirrels in deciduous woodland (up to 7.5/ha). Cones are stripped in the same way as greys do. They are held in the paws and the scales gnawed off to expose the edible seeds.

Kenward & Holm (1993) have shown that red squirrels foraged where hazels were abundant, and their relatively low density and breeding success were related to the low abundance of hazelnuts. Buds, nuts, berries, shoots, tubers, flowers, bark, lichen and fungi are also important items of their diet. They cannot fully exploit acorn crops, and apparently have a digestive efficiency for acorns of only 59% because they are much less able to neutralise acorn polyphenols than grey squirrels. Greys can exploit this food source more effectively than reds, in particular feeding on the crop before it is ripe enough for the red squirrel to digest.

**RIGHT**

**Figure 1.5. Norway spruce cones damaged by grey squirrels which have removed scales from the base up, to find and eat the seed. (Forestry Commission 1960).**

**BELOW**

**Figure 1.6. Scots pine cones remains following squirrel feeding activity (Forestry Commission 2003).**

Surplus food is stored rather haphazardly and often forgotten providing an easy opportunity for grey squirrels to obtain extra food supplies. As with the grey squirrel, reds do not hibernate, but similarly build nests (dreys) in a fork close to the main trunk and have long periods of sleep in winter. The autumn and winter seed harvest is extremely important both for the survival through the winter months and to ensure breeding success the following spring.

Wauters *et al.* (2000) studied the effects that grey squirrels had on the use of space and population dynamics of red squirrels in conifer plantations in northern England. They found that grey squirrels colonised all habitat types including Sitka spruce and that red squirrels did not use a pine plantation that contained relatively high numbers of greys. They also found that the key factor for red squirrel decline in these conifer plantations was decreased juvenile

recruitment. In another study, Lurz *et al.* (2000) looked at temporal and spatial variations in food supply and found that adult female red squirrels increased their home range and core-area patches where food was less abundant. Home range was significantly related to habitat quality and the extent of overlap by other females. In addition a considerable proportion of adult males and females were found to shift their home area while a large number of ranges were multi-nuclear, particularly from January onwards when supplies of seeds became depleted. Squirrels were found to track available conifer seeds and regularly used non-adjacent sources.

Like greys, reds are mainly solitary animals, associating mostly during the breeding season. Their social organisation is also similar. Both males and females maintain an exclusive core area within their home range while the remaining peripheries may overlap extensively with those of neighbouring animals. Young are born mostly in spring and summer with one or two litters of 2 - 4 young per year.
Population dynamics and reproductive biology of reds is largely similar to that of greys in that

- numbers peak in autumn but may vary between year;
- females are capable of breeding twice a year;

Equally the size of the annual seed crop and availability of seed supplies will have direct effects on:

- red squirrel densities;
- the length of the breeding season;
- number of females producing two litters;
- the number of adult and yearlings which can breed;
- the number of young per litter (usually 3 but sometimes as many as 7);
- the ability to over-winter, survival rates and resistance to disease.

Young are born and weaned in dreys, tree hollows or disused birds' nests. The average life span of a red squirrel is between 4 and 5 years - purported to be much less than that of a grey.

### Forest Design Plans

Red squirrel conservation in England is now being concentrated on large conifer forests by adopting forest management plans that are considered to render them less attractive to grey squirrels. Researchers consider that the future of red squirrels is likely to depend on the design and management of large, isolated areas of conifer forest (ie > 200 ha) of suitable species and age structure that provide havens for the species. The management of such woodland for red squirrels will often conflict with other objectives for the forest that may

include economic, amenity, landscape or even bio-diversity factors. All these factors would normally influence the mix of tree species present and hence the woodland's attractiveness as a food resource for red and grey squirrels. Conservationists now consider that reds survive better in "their optimum habitat, namely mature expansive coniferous forest where they have an advantage over grey squirrels" (Kenward *et al.* 1998).

Rooney and Hayden (2002) state that forest design and management can aid the conservation of reds and measures that encourage them should be an integral part of any forest management plan adding that "Supplementary feeding using grey-proof hoppers may help in giving reds an advantage". However, the development of non-native forestry even in selected or targeted areas may have unforeseen consequences for the temperate ecosystem. The more logical approach would be to remove the relevant problem – the grey squirrel. The scheme of forest plans for red squirrel conservation involves the removal of primary native tree species such as oak and beech. This will have a considerable impact on British ecology and landscape, more specifically broadleaved high forest. Where the red squirrel is not being protected, the grey squirrel will continue its destruction on woodlands of all kinds reducing valuable timber to scrub.

The minimum area of conifer woodland that will support a viable population of reds has been estimated at between 2,000 and 5,000 ha (Pepper & Patterson 1998). Such forest design plans indicate that red squirrels do not prosper in monocultures of Sitka spruce (neither do greys) and suggest that other species such as Scots pine and Norway spruce (both attractive to greys) should be included. So to say that with a suitable mix of conifers in areas dominated by Sitka spruce, it is possible to provide refuge for reds because greys avoid these areas is rather confusing. As the grey continues to proliferate both in area and density, the natural versatility of the grey ensures that it can forage on all tree species that support the red, resulting in the exclusion of the red in any habitat. The reason the red squirrel continues to thrive in these refuges may be because the grey has not yet completed its spread across the north of Britain. The spread will necessarily be slower in the north because soil and climate conditions dictate poorer fruiting and cropping than is usual in the south of Britain. This, in less suitable habitats, can result in the grey squirrel failing to acquire sufficient energy requirements to maintain its frame and body weight, and this has an affect on its ability to breed. As the red squirrel does not need so much food to maintain its frame and body weight as the grey, it can continue to breed in these conditions.

Rooney & Hayden (2002) go on to suggest that the alternative forest plan is to create a terrestrial island of 200 - 300 ha. This would be surrounded by a substantial buffer zone of 1 –

3 km wide of "grey-free" habitat such as monoculture coniferous forest or small-seeded broadleaved species, marginal land, moorland or arable land lacking substantial hedgerows or other corridors. A survey done at Clocaenog Forest in north Wales suggested that red squirrels could potentially survive in conifer plantations provided that the right tree species and age classes were present, and that there were sufficient links throughout the forest to enable the squirrels to travel between blocks of suitable habitat. Similarly a study between 1994 and 1998 on Jersey (the Channel Islands) showed that hedgerow planting between an already fragmented habitat for red squirrels on the island, was proving invaluable for survival of the species (Magris *et al*. 1997). Island ecology is not good for the stability of red squirrel populations because it restricts:

- disbursement (after weaning) which can range from 400m to 3 km;
- range for feeding when wider foraging for food is required;
- gene flow and genetic diversity;
- recruitment of sub-adults and young squirrels;
- local density.

The co-habitation argument is unproven because where it has been studied the grey has usually been identified as:

a) occupying spatially different areas and
b) occupying areas containing broadleaved species.
c) taking red food supplies thus depriving them of resources.

There is one area of deciduous woodland at Fazakerley Hospital, Liverpool where red squirrels are thought to be living alongside greys, but it is as yet unstudied and no funds have been forthcoming because this red squirrel is deemed to be of continental European origin and is not indigenous.

The basic problem of the forest design plan is that even if timber quality is ignored, the issues of provenance, indigenous authentic landscape quality and the management of semi-natural woodlands as defined by the National Vegetation Classification are undermined. The loss of traditional high forest species as identified by the Forestry Commission to predominantly non-native plantation forests will have a significant impact on our heritage, and the diversity of native plants and animals. Many woodland species depend entirely on the continued existence of these habitats for their survival. These traditional and authentic landscape features include Upland Mixed Ash woods (FPG4), Upland Oak woods (FPG5), Upland Birch woods and Native Pinewoods (FPG7) and apply to the whole of northern England and much

of Scotland – the areas which have been specifically identified for the application forest design plans.

"Pinewoods occur on strongly leached, podsolic soils in the cooler part of the Highlands. Scots pine is the main tree but the canopy is often open, more especially in the west. Rowan may be locally common. Juniper is sporadic as an under-storey and marginal shrub. Small clumps of other broadleaved trees and shrubs including alder, sallows, aspen, sessile oak, hazel, bird cherry and holly occur on pockets of richer soils." (FC Native Pinewoods FPG7). Such idyllic Highland woodlands are under grave threat from the advance of the grey squirrel.

It will be interesting to see how successful the Forest Design Plan is in conserving the red squirrel and controlling the grey squirrel.