Habitat Use by Red and Grey Squirrels: Results of Two Recent Studies and Implications for Management

INTRODUCTION

The scientific name for the red squirrel *Sciurus vulgaris* (Figure 1) means ‘common’ squirrel, and reflects their former widespread distribution. In Britain, the range of the red squirrel was constrained in the 17th and 18th centuries due to habitat fragmentation and loss of woodland. However, a more recent decline has largely been linked to the introduction of the grey squirrel *Sciurus carolinensis* (Figure 2) from North America in the 1870s (Lloyd, 1983).

This decline has led to concern over the conservation status of the species, prompting their listing as one of the priority species in the UK Biodiversity Action Plan (Anon., 1995) and making them subject to legal protection.

Aims of the two studies

This Information Note describes the results and practical implications of two studies designed to improve our understanding of the ecology of red and grey squirrels in planted forests. The studies sought to provide recommendations for the long-term management of habitats for red squirrels – a key objective of the UK Strategy for Red Squirrel Conservation (JNCC, 1996).

It has been suggested that habitat composition is important in determining the rate at which red squirrels are replaced by greys; grey squirrel colonisation being faster in the presence of large-seeded broadleaves. Furthermore, there is evidence that red squirrel populations have persisted in the presence of greys for up to 50 years in several conifer-dominated woods in Scotland and Northern Ireland (Bryce, 2000; Teangana *et al.*, 2000). The studies examined patterns of habitat use by individual red and grey squirrels in two conifer-dominated forests and assessed the extent of competition for resources. Both studies examined habitat use at a number of spatial scales, comparing patterns of use with availability. In particular:

- selection of the habitats forming the home range as compared with those available in the wider forest;
- use of different tree species within the home range.

SUMMARY

This Information Note summarises the results of two PhD studies which examined the patterns of habitat use of red and grey squirrels in planted forests. The studies at Clocaenog Forest in Wales and Craigvinean Forest in Scotland have resulted in a number of scientific papers in addition to university theses. This Note presents the main findings, discusses them in relation to other work and suggests possible management implications; it does not establish new policy or guidance.
The parallel studies were based in Clocaenog Forest in North Wales and Craigvinean Forest in Perthshire, Scotland. Clocaenog Forest is host to the largest remaining red squirrel population in Wales. A small population of grey squirrels has also been resident there since at least the beginning of the 1990s. Craigvinean was selected for study because both species of squirrel were known to have been present in the area for more than 20 years. Both forests are large, mixed conifer plantations dating from the mid-1900s, and both are managed by the Forestry Commission.

Clocaenog Forest (total area 6400 ha) is an upland plantation bounded by pasture and open moorland to the west (Figure 3a). The research focused on two areas: Bod Petrual (75 ha) on the southern edge, planted in 1939, and Bryn-yr-Wyn (97 ha) in the centre of the forest, planted in 1949 and restocked in 1976 and 1989. Grey squirrels have only been present in this second area since 1996.

Craigvinean Forest (total area c. 2000 ha) extends from the banks of the river Tay to heather moorland at 500 m and is contiguous with private planted and native woodlands (Figure 3b). The study focused on the lower slopes, nearest to the rivers Tay and Braan, where there was thought to be the greatest overlap between red and grey squirrels. This area (100 ha) was mostly planted in 1949, but some mixed stands with ash, wych elm, planted oak and beech, date back to the 1850s. The tree species composition of the Clocaenog and Craigvinean study areas are set out in Table 1.

Both studies employed standard trapping and radio-tracking techniques (under licence). Thirty independent radio-locations were used to define a squirrel’s home range: the area in which their activity is focused. Centres of activity within the home range were identified as core areas (Figure 4).

**Table 1**
Composition of study forests as % cover of main tree species.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Clocaenog</th>
<th>Craigvinean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sitka spruce (Picea sitchensis)</td>
<td>23.7</td>
<td>47.5</td>
</tr>
<tr>
<td>Norway spruce (Picea abies)</td>
<td>5.3</td>
<td>48.8</td>
</tr>
<tr>
<td>Larch (Larix spp.)</td>
<td>9.5</td>
<td>-</td>
</tr>
<tr>
<td>Stands containing pine (Pinus sylvestris/P. contorta)</td>
<td>50.8</td>
<td>1</td>
</tr>
<tr>
<td>Douglas fir (Pseudosuga menziesii)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mixed conifers and broadleaves*</td>
<td>9.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Felled</td>
<td>1.3</td>
<td>2.3</td>
</tr>
</tbody>
</table>

*Largely beech (Fagus sylvatica) and birch (Betula pendula).

**Figure 3**
(a) Clocaenog Forest and (b) Craigvinean Forest.

**Figure 4**
Diagram illustrating the total (outer) and core (inner) home range of an individual red squirrel.
ECOLOGICAL FINDINGS AND DISCUSSION

Patterns of habitat use

Grey squirrels evolved in the hardwood forests of North America and red squirrels in the boreal forests of Europe and Asia. Therefore we might expect them to show different habitat preferences.

At Craigvinean, red squirrels consistently selected stands of Norway spruce for their core areas in all seasons (Figure 5). Scots pine, Douglas fir and larch were used in proportion to their availability. Mixed conifers and broadleaves were not used in autumn and spring and Sitka spruce was avoided throughout the year. Grey squirrels selected strongly for mixed conifers and broadleaves in all seasons. Scots pine and larch were used in proportion to their availability, while Sitka spruce, Norway spruce and Douglas fir were rarely used. With regard to occupation of different tree species within the home range, red squirrels selected for mixed conifers and broadleaves in autumn and winter, Norway spruce in spring and Scots pine over winter. Grey squirrels selected for mixed conifers and broadleaves in autumn and winter, avoided Douglas fir and used other species in proportion to availability.

In Clocaenog, the ranked preferences in choice of home range for both species (Tables 2 and 3) indicates that Norway spruce and Scots pine were the most preferred and Sitka spruce the least. These preferences were evident in the selection of home ranges and in their use of habitats within the home range.

Analyses of more detailed characteristics of habitat patches that were used by squirrels in Craigvinean, compared with other random locations, indicated that red squirrels selected unthinned stands of Norway spruce, and stands with large Douglas fir and Scots pine but few oak trees. Conifer habitats favoured by grey squirrels were characterised by

Figure 5

Seasonal patterns of habitat selection in Craigvinean (after Bryce et al., 2000, summary of three-years data 1996–1998.) Above the axis indicates selection, below avoidance. Red squirrels are the left column of each pair and grey squirrels the right column.

Core area selection within study area

Tree species selection within total home range
having a mixture of Douglas fir and Norway spruce, and mixed stands had more large Scots pine, Douglas fir and beech than comparative random locations. However, patches that were used by both species tended to be similar to random locations, and so these analyses did not detect strong preferences for woodland structure and all patches probably represented potential squirrel habitat.

Other studies have found that red squirrels use larch more than expected (Halliwell, 1997). Although Sitka spruce was rarely used in either of these forests during the years of study, nor in studies with only red squirrel present (Lurz, 1995; Halliwell, 1997), it was selected by both red and grey squirrels in Hamsterley Forest, Co Durham (Wauters et al., 2000). Habitat preferences are known to be density dependent, with the less suitable habitats only being occupied at higher squirrel densities (Andrén and Lemnell, 1992). The habitat preferences observed in these studies were not density dependent, hence are likely to reflect preferences. In contrast, the use of Sitka spruce by red squirrels in Hamsterley was attributed to avoidance of high grey squirrel densities.

The similarity of resources used by red and grey squirrels was compared at Craigvinean using two different indices. The first compared the proportion of each habitat type within the core areas of individual red and grey squirrels and indicated that overlap in habitats used by both species was 59%. The second index compared the proportion of radio-locations in each tree species between squirrel species and this indicated a greater habitat overlap of 77%. Both values suggest that the potential for dietary overlap is considerable. However, the difference between the two indices suggests that competition may have been ameliorated at this site by red and grey squirrels selecting for different habitats at the scale of their core home range areas (Bryce et al., 2002).

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These values for resource overlap are similar to those found for red and grey squirrels in mixed conifer plantations in northern England (75%, Wauters et al., 2000) and in mixed woodland in northern Italy (70%, Wauters et al., 2002a). Wauters et al. (2002a) conclude that, due to the similarity of their requirements, ‘at moderate grey squirrel densities, red squirrels are unable to avoid competition with grey squirrels and that competition for food and/or space will occur when resources become limiting’.

Food availability

Both studies carried out counts of cones in the canopy and counts of squirrel-eaten cones along transects (Figure 6) to assess annual variation in food availability and utilisation.
The Clocaenog study (Cartmel, 2000) produced seven years of data (1993–1999) on the periodicity of coning (Figure 7). Norway spruce and Japanese larch produced a substantial crop in only one of seven years (both 1996), while Scots pine and Sitka spruce produced some cones every year. In three years of data collection in Craigvinean (1996–1999) all conifer species produced at least some cones each year. Norway spruce, Sitka spruce and Douglas fir produced good cone crops in two out of three years. Beech produced mast in two out of three years in Craigvinean and in only one year in seven in Clocaenog. Oak was rare in Clocaenog and acorn crops were poor in every year of study in Craigvinean. Hence, although both sites experienced spatial and temporal variation in the availability of seeds, food appears to have been more predictable in Craigvinean, and may have contributed to the higher squirrel numbers (Figure 8).

A separate analysis of habitat use comparing the three years of study in Bod Petrual, Clocaenog, indicated that the ranking of tree species preferences varied in response to the availability of cones. For example, red squirrels used larch significantly more than mixed stands of Sitka spruce and Scots pine in 1996 when there was a good larch cone crop, but not in 1997 or 1998 when larch cone crops were poor and pine continued to provide some cones.

These results are consistent with findings from Kielder Forest, where red squirrel ranging patterns and habitat preferences were also found to follow the spatial and temporal variations in conifer seed supply (Lurz and Garson, 1995). In Kielder, there was a 50-fold difference in seed availability between the 1991 and 1992 Norway spruce cone crops. In contrast, a continental study found only a 2.5-fold variation in food availability between years in pine forest (Lurz et al., 1997).
The very large ranges of male grey squirrels in Craigvinean are thought partly to be an artifact of linear ranges along riparian corridors of mixed habitat, but may also relate to the low grey squirrel densities. Some individual grey squirrels were observed to travel distances of up to 2 km between patches of broadleaves. Red squirrel daily movements in summer 1998 ranged between 0.2 and 1.8 km.

Core areas of female squirrels are thought to be more indicative of habitat quality than total home ranges. In these studies the core areas of females were very similar between species and sites. There is a tendency for female core areas to be smaller in Craigvinean. However, in contrast to data on food availability and squirrel densities, the observed ranging behaviours do not strongly suggest the squirrels differed in their perception of habitat quality between study sites. Similarly no significant differences were found between the core areas of female red and grey squirrels in Hamsterley, nor between female red squirrels in the presence of grey squirrels and those in Kielder Forest where only red squirrels are present (Wauters et al., 2000).

The energetic requirements of red and grey squirrels have been found to be proportionate to body mass (Bryce et al., 2001). Hence, the similarity of core range sizes suggests that grey squirrels (c. 570 g) at almost double the body weight of reds (c. 300 g), have been more efficient at utilising these habitats.

Many of the home ranges overlapped within others of either species. Analysis of the interactions indicated that red and grey squirrels were neither attracting nor avoiding one another. The location of ranges appears to be more related to interactions with individuals of the same species.

In Craigvinean, more grey squirrels were found to have completely shifted their home ranges between seasons. Eighty percent of red squirrels retained some overlap of their core ranges between seasons compared with only 53% of grey squirrels. Other studies have found red squirrels

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**Table 4**  Mean home range sizes from both study sites (ha).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Total home range areas</th>
<th>Core home range areas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bod Petrual</td>
<td>Bryn yr Wyn</td>
</tr>
<tr>
<td>Male red squirrels</td>
<td>8.6</td>
<td>9.1</td>
</tr>
<tr>
<td>Female red squirrels</td>
<td>6.3</td>
<td>5.1</td>
</tr>
<tr>
<td>Male grey squirrels</td>
<td>6.1</td>
<td>7.5</td>
</tr>
<tr>
<td>Female grey squirrels</td>
<td>3.8</td>
<td>-</td>
</tr>
</tbody>
</table>
occupy stable home ranges in high quality (pine) forests, whereas they are more likely to shift their ranges where food availability is less predictable (Lurz et al., 1997). Lurz et al. (1997) found that individuals dispersing from stable habitats tend to be juveniles and sub-adults, but that adults also regularly disperse from less predictable habitats. Hence, it seems likely that the difference between the residency of the two species in Craigvinean reflects the predictability of foods in the habitats they occupied. Reds tended to occupy stable ranges in the coniferous habitats which produced regular cone crops, whilst grey squirrels made greater seasonal movements between the smaller patches of mixed habitats where seed was only seasonally available. The grey squirrels in Clocaenog also appeared to be more transitory, moving to occupy stands of pure Norway spruce during times of high seed availability.

**Population dynamics**

The densities of red squirrels recorded in the coniferous habitats in Craigvinean were high (mean 1.6 ha\(^{-1}\)) compared with those recorded in other mixed conifer forests (range 0.17–1.41 ha\(^{-1}\), Lurz et al., 1995). Red and grey squirrels occupied the mixed habitats at similar densities (c. 0.9 ha\(^{-1}\)) and no grey squirrel had its range exclusively in conifers. Whilst grey squirrels travelled distances of up to 2 km to patches of oak and hazel, they were rarely sighted or caught in the coniferous stands.

Both red and grey squirrel densities were lower in Clocaenog than Craigvinean (means all c. 0.3 ha\(^{-1}\)). These densities are more akin to those of red squirrels in spruce-dominated forests (reviewed in Lurz et al., 1995). In the initial two years of study, grey squirrel numbers were higher in Bod Petruial, which has some Scots pine and beech in addition to Norway spruce. However, both areas experienced a decline in grey squirrel numbers in the third year when the Norway spruce crop of 1996 was exhausted.

The relatively short timescales of the studies did not enable long-term population trends to be established, and it is not possible to comment on the stability of the populations. However, the Clocaenog study suggests that grey squirrels can persist at low densities with very few broadleaves. It is not known whether the populations are maintained in the long term through recruitment or are dependent on continued immigration. Grey squirrels were not resident in the conifer stands at Craigvinean, remaining largely in the riparian corridors of mixed woodland. However, should their numbers increase, grey squirrels might be expected to make more use of the conifer stands as they have done elsewhere. The stability of the apparent co-existence at both sites, seems dependent on the rate of grey squirrel recruitment and immigration.

Recent studies propose that the effects of grey squirrel competition on red squirrels are more likely to be expressed through reduced recruitment of juveniles than through suppressed breeding rates or lower survival of adult squirrels (Wauters et al., 2000; Gurnell et al., 2004). However, competition is only likely to be observed when food supplies are limiting. Hence, the effects of competition with grey squirrels are more likely to have been expressed in Clocaenog where food availability was less predictable. These studies collected limited data on juvenile recruitment rates, but there was a suggestion that red squirrel recruitment in Clocaenog was lower in years with high grey squirrel densities than in years with fewer grey squirrels.

**MANAGEMENT IMPLICATIONS**

These studies, although short-term, have relevance for the conservation management of red squirrel populations. The following are suggested as the main implications for management.

**Choice of tree species**

**Norway spruce**

Norway spruce was found to be strongly selected by red squirrels, a finding consistent with studies where only red squirrels were present. Norway spruce was also found to be important for grey squirrels. However, the degree of red squirrel preference for Norway spruce suggests that providing a continuity of stands of cone-bearing age is likely to be important for maintaining red squirrel populations.

**Scots pine**

Scots pine ranked highly in the preferences of both red and grey squirrels in Clocaenog and was selected within red squirrel ranges in Craigvinean. Grey squirrels have largely replaced reds in pine-dominated habitats elsewhere (e.g. Cannock and Thetford), suggesting that Scots pine may not confer any advantage to red squirrels (although there may have been other contributory factors such as transmission of squirrelpox virus). Nevertheless, the presence of Scots pine, which produces cones more regularly than Norway spruce (Gordon, 1992), is likely to be important for ensuring the continuity of seed supply for red squirrel populations.
**Sitka spruce**

Sitka spruce was the lowest ranked species in the preferences of red and grey squirrels in Clocaenog and was little used by either species in Craigvinean. However, other studies have found that both species can occupy stands of Sitka spruce, albeit at low densities. Hence although Sitka spruce appears to represent a habitat of low preference, these stands may hold populations that could be important in terms of conservation (see related discussion under ‘possible refuges’).

**Large-seeded broadleaves**

The proportion of oak in an area is thought to be critical to the balance between red and grey squirrels. Grey squirrel numbers have even been found to be correlated with the abundance of acorns within 500 m of coniferous sites (Kenward et al., 1998). The paucity of acorn crops in these two study sites is likely to have benefited the red squirrel populations.

The presence of beech and hazel are not unequivocally negative for red squirrels. Both species fed heavily on hazel and beech mast in Craigvinean when abundant during autumn. However, the importance of grey squirrels’ pilfering of red squirrel food caches has recently been highlighted (Wauters et al., 2002b) hence competition for these resources may occur in winter and spring.

Grey squirrels exhibited strong selection for mixed habitats where available. Therefore, the findings presented here do support the recommendations of Pepper and Patterson (1998), i.e. the proportion of large-seeded broadleaves should be minimised in areas being managed for red squirrels. A threshold of 10% large-seeded broadleaves was proposed (Pepper and Patterson, 1998), above which grey squirrels are likely to be favoured. The proportion of broadleaves in the whole of Craigvinean and Clocaenog was approximately 7% in both cases. However, regional variation in the size of mast crops and in the availability of alternative seed sources will influence the significance of the composition.

**Species mixtures**

The provision of a diversity of coning tree species has been suggested as beneficial to red squirrels (Pepper and Patterson, 1998). The high levels of red squirrel persistence and stable home ranges in the conifer stands of Craigvinean suggests that red squirrels were able to endure poor seed years by foraging in neighbouring stands and using cached foods from the main tree species. Hence, a mixture of tree species in close proximity is beneficial in providing a continuous supply of seed. Recent work in Clocaenog suggests that the presence of Norway spruce or pine, even at low densities, may make stands of predominantly Sitka spruce more suitable for red squirrels (Cartmel, personal observation).

**Possible refuges**

Red and grey squirrels demonstrated considerable overlap in their use of different tree species. Grey squirrels utilised and occasionally selected for both Scots pine and Norway spruce. Consequently neither of these species appears to provide a refuge for red squirrels. The tree species that were rarely used by grey squirrels (larch and Sitka spruce) were also little used by red squirrels, but may be those habitats most likely to maintain low density populations of red squirrels in the face of higher grey squirrel numbers. However, pure stands of Sitka spruce may not be able to support stable red squirrel populations in the absence of better quality habitats in close proximity.

**Landscape Ecology**

The minimum size of woodland required to maintain viable red squirrel populations cannot be gauged from these studies in large forests. Nevertheless, Craigvinean provides some evidence that where preferred habitats of the two species are spatially separated, large conifer forests may provide opportunities for red squirrels to avoid severe competition with greys. Pepper and Patterson (1998) proposed that a 1–3 km zone is necessary to buffer red squirrel populations from large-seeded broadleaves. The observed ranging behaviours (daily movements of up to 2 km) indicate that even in extensive conifer forest with few broadleaves, most areas were potentially accessible to grey squirrels. Patterns of grey squirrel colonisation in conifer forests have been strongly influenced by the distribution of large-seeded broadleaves (Gurnell, 1996; Gurnell et al., 1997), and a cluster of large-seeded broadleaves may prove to be less detrimental than a scattering throughout the forest.

**Forest management**

**Restructuring**

The area of planted forest in Britain has increased over the past 70 years, so that there is currently more conifer seed produced in a greater variety than ever before (Marquiss and Rae, 1994). Some of the current management trends...
towards greater species and structural diversity are likely to benefit red squirrels. As food availability is the main driver for squirrel populations, habitat management should aim to provide a continuous supply of seed both temporally and spatially. Thinning, management for long-term retentions and continuous cover are likely to result in increased crown development and cone productivity.

**Felling and thinning operations**

It has been suggested that red squirrels are better able to tolerate felling of small coupes in mosaics linked by corridors of cone-bearing trees, than they are clearfells (Pepper and Patterson, 1998). The Clocaenog study provided some insight into the effects of forest operations on red squirrels. Squirrels with home ranges in areas that were thinned, moved away whilst operations were taking place, but remained within 200 m and returned when operations ceased. This evidence, combined with ranging behaviour in response to seasonal and annual variations in food availability, indicates that squirrels can adjust their home range areas. However, their continued occupation in an area relies on there being other suitable undisturbed habitats nearby.

Both studies explored the potential impacts on the red squirrel populations of operations detailed in the respective forest design plans. These analyses highlighted the importance of maintaining links between suitable habitats in terms of the maturity of the trees, the size, distribution and timing of felling coupes.

The increase in squirrel numbers in the year following good Norway spruce cone crops (Figure 8) indicates that it would be beneficial to avoid felling operations in good seed years. Early assessments of cone production can be made in spring (Nixon and Worrell, 1999). Delaying felling and thinning until the seed has dropped would also benefit the establishment of natural regeneration under continuous cover.

**Context of single species approach**

While red squirrels are a Biodiversity Action Plan (BAP) species, the BAP process also aims to encourage the restoration and expansion of native woodlands. Hence it may not always be appropriate to manage and extend habitats purely for red squirrels.

Grey squirrels are likely to be able to cross all but the most extreme habitats (as demonstrated by a sighting at c. 900 m on Crib Goch, Snowdon) hence expansion of native woodland habitat networks should not be constrained in an attempt to limit grey squirrel colonisation. Planting of small-seeded broadleaves such as birch (*Betula* sp.), alder (*Alnus glutinosa*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix caprea*) and hawthorn (*Crataegus monogyna*) may provide an alternative to large-seeded broadleaves in buffer zones around red squirrel strongholds.

The existing composition of woodlands in an area will make some areas more susceptible to grey squirrel colonisation than others. This has led Gurnell *et al.* (2004) to conclude that ‘red squirrels will almost inevitably be excluded from deciduous woods’. The statutory agencies and other groups with an interest in squirrels have therefore sought to agree priority areas for red squirrel conservation (Poulsom *et al*., 2005), recognising that in some areas, other interests will take precedence (e.g. the Scottish Squirrel Group, 2004).

**FURTHER RESEARCH**

Further research to examine the efficacy of use of different conifer habitats by red and grey squirrels would assist the development of management recommendations. Given the greater energetic requirements of grey squirrels, it would be particularly useful to have a better understanding of the abilities of both species to exploit Sitka spruce. Such work should examine the maintenance of breeding populations (between good seed years) and the extent to which their persistence is dependent upon continued immigration from high quality habitats. There should be further work to examine the pattern and scale of habitats in the landscape which are required to benefit red squirrel populations. In particular, it would be beneficial to gain an understanding of the consequences of varying proportions of Scots pine on red squirrel populations, given that much of the range that has yet to be colonised by grey squirrels (i.e. central and eastern Highlands) is pine-dominated.
REFERENCES


**FURTHER READING**


**CONTACTS**

Forestry Commission
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Provides funds under the forest/woodland grant schemes to encourage management for red squirrels and manages selected areas for red squirrel conservation.

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Responsible for general advice and information, supporting local projects and issuing licences for conservation, education and survey.

NB: From 2006, English Nature, the environment activities of the Rural Development Service and the Countryside Agency’s Landscape, Access and Recreation division will be united in a single body. The new agency will be called ‘Natural England’.
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