

INFORMATION NOTE

BY J. BRYCE, S. CARTMEL AND C.P. QUINE

OCTOBER 2005

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.



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).

Figure 1 Red squirrel *Sciurus vulgaris*.



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

Figure 2 The grey squirrel *Sciurus carolinensis*.



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.

THE STUDIES

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 Petruall (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

Figure 3

(a) Clocaenog Forest and (b) Craigvinean Forest.



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

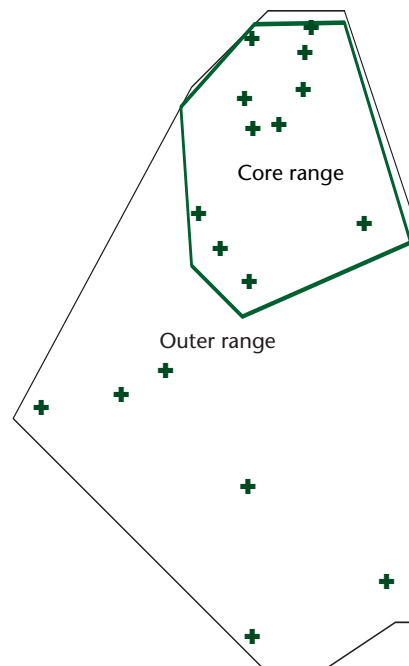
Composition of study forests as % cover of main tree species.

Tree species	Clocaenog		Craigvinean
	Bod Petruall	Bryn yr Wyn	
Sitka spruce (<i>Picea sitchensis</i>)	23.7	47.5	29.3
Norway spruce (<i>Picea abies</i>)	5.3	48.8	16.8
Larch (<i>Larix</i> spp.)	9.5	-	11.6
Stands containing pine (<i>Pinus sylvestris</i> / <i>P. contorta</i>)	50.8	1	32.8
Douglas fir (<i>Pseudotsuga menziesii</i>)	-	-	4.8
Mixed conifers and broadleaves*	9.5	0.6	3.8
Felled	1.3	2.3	-

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

Figure 4

Diagram illustrating the total (outer) and core (inner) home range of an individual red squirrel.



Based on 100% and 70% of the area derived from radio-tracking fixes (+)

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.

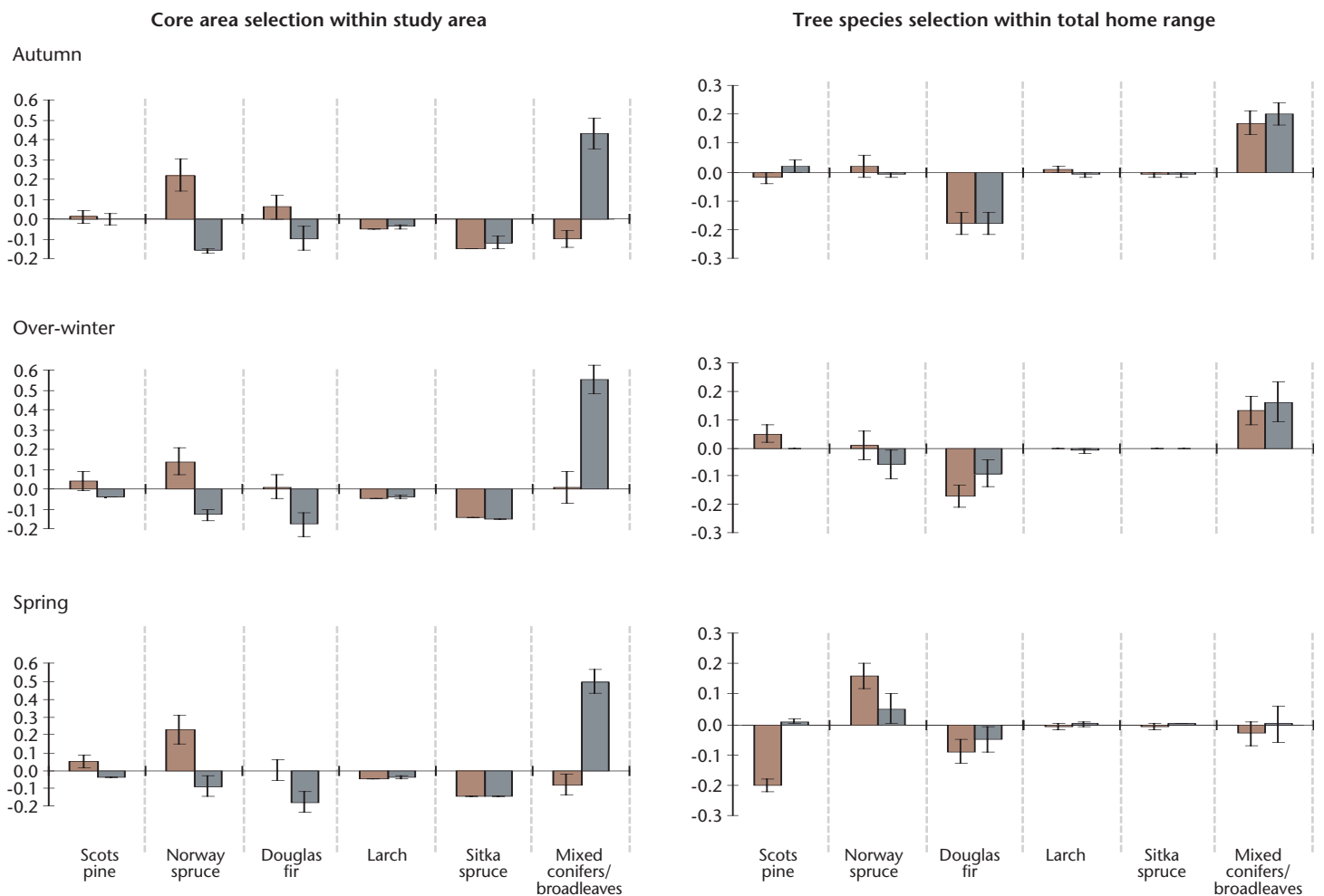


Table 2

Ranked selection of home ranges within Clocaenog study areas.

Rank	Red squirrels		Grey squirrels	
	Bod Petruel	Bryn yr Wyn	Bod Petruel	Bryn yr Wyn
1	Norway spruce/ Scots pine	Norway spruce	Norway spruce/ Scots pine	Norway spruce
2	Japanese larch	Old Sitka spruce	Japanese larch	Old Sitka spruce
3	Sitka spruce/ Norway spruce	Mixed conifers and broadleaves	Mixed conifers and broadleaves	Mixed conifers and broadleaves
4	Mixed conifers and broadleaves	Norway spruce/ Lodgepole pine	Norway spruce	Norway spruce/ Lodgepole pine
5	Scots pine	Young Sitka spruce	Sitka spruce/ Norway spruce	Young Sitka spruce
6	Norway spruce	N/A	Scots pine	N/A
7	Sitka spruce/ Scots pine	N/A	Sitka spruce/ Scots pine	N/A
8	Sitka spruce	N/A	Sitka spruce	N/A

Table 3

Ranked use of tree species within Clocaenog home ranges.

Rank	Red squirrels		Grey squirrels	
	Bod Petruel	Bryn yr Wyn	Bod Petruel	Bryn yr Wyn
1	Scots pine	Norway spruce	Norway spruce/ Scots pine	Norway spruce
2	Norway spruce	Old Sitka spruce	Scots pine	Old Sitka spruce
3	Sitka spruce/ Scots pine	N/A	Norway spruce	N/A
4	Norway spruce/ Scots pine	N/A	Sitka spruce/ Scots pine	N/A
5	Japanese larch	N/A	Sitka spruce/ Norway spruce	N/A
6	Mixed conifers and broadleaves	N/A	Japanese larch	N/A
7	N/A	N/A	Mixed conifers and broadleaves	N/A

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).

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.

Figure 6

The remains of cones eaten by red squirrels.



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 Petruel, 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).

Figure 7

Seasonal pattern of cone consumption by squirrels in Clocaenog: the total number of intact and stripped cones found on cone transect lines (50 m long by 1 m wide) for each season. Autumn = September to November; Winter = December to February; Spring = March to May; and Summer = June to August. Note variation in scale of y-axis.

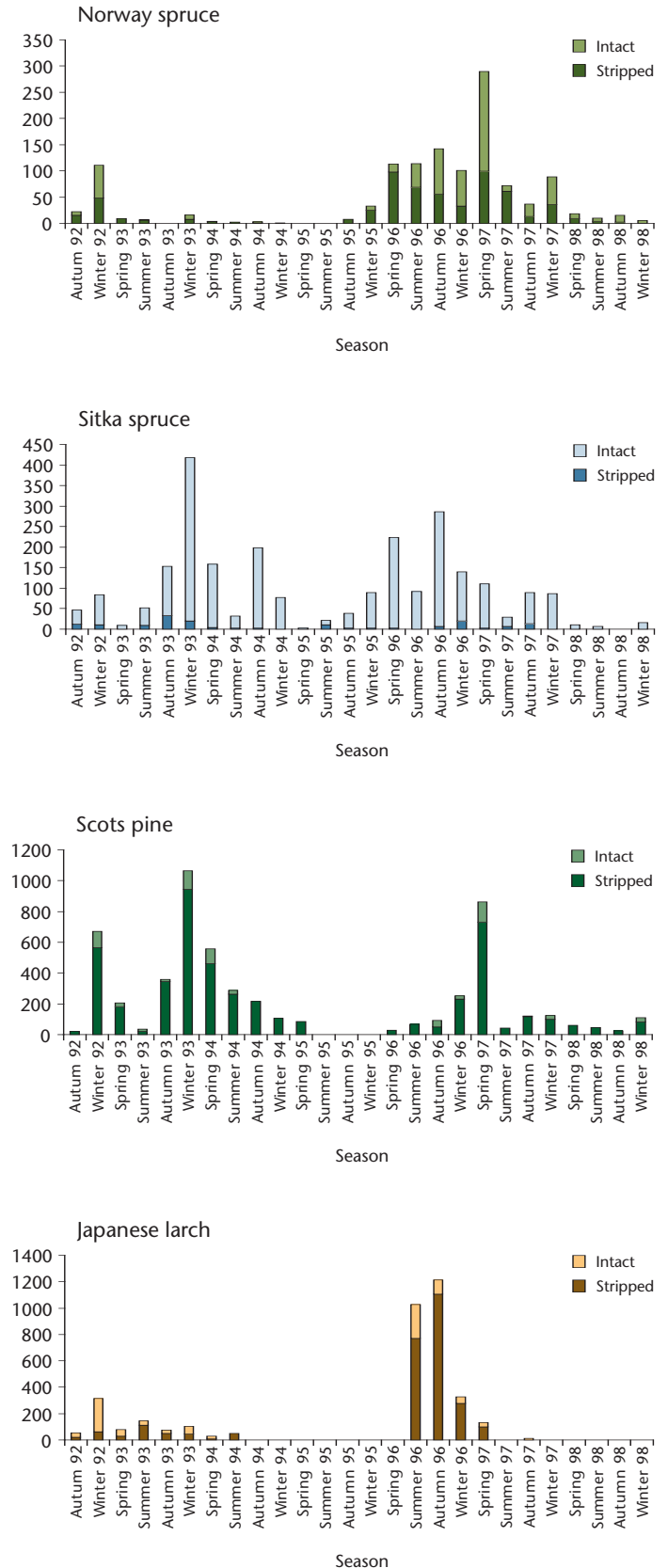
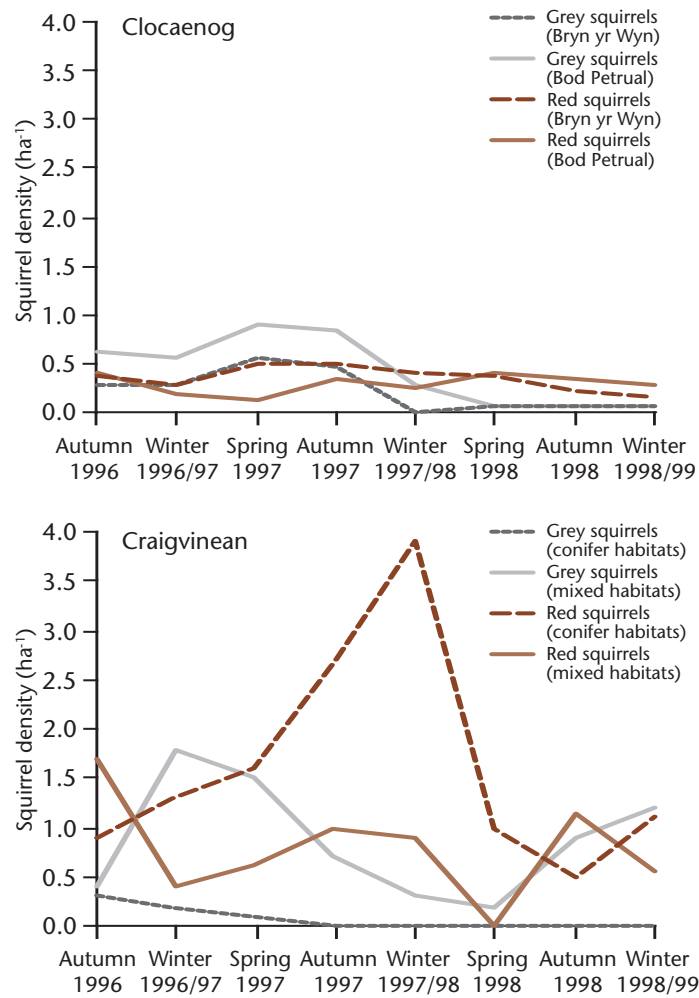


Figure 8

Squirrel population densities from 1996–1999 at the study sites.



Ranging behaviour

The size of a squirrel’s home range is related to habitat quality, hence the patterns of home range occupancy were examined to assess the perception of habitat quality by the two species.

Male squirrels tend to have larger home ranges than females linked to their respective breeding behaviours (Table 4).

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 home 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

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

Rank	Total home range areas			Core home range areas		
	Bod Petrual	Bryn yr Wyn	Craigvinean	Bod Petrual	Bryn yr Wyn	Craigvinean
Male red squirrels	8.6	9.1	7.1	3.6	3.0	3.2
Female red squirrels	6.3	5.1	4.2	3.0	1.5	1.7
Male grey squirrels	6.1	7.5	19.7	1.5	2.2	3.4
Female grey squirrels	3.8	-	4.1	1.7	-	1.2

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 Petruel, 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 (*Crateagus 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

- ANDRÉN, H. and LEMNELL, P.A. (1992). Population fluctuations and habitat selection in the Eurasian red squirrel (*Sciurus vulgaris*). *Ecography* **15**, 303–307.
- ANON (1995). *Biodiversity: the UK Steering Group report*. London, HMSO.
- BRYCE, J. (2000). *Habitat use by sympatric populations of red and grey squirrels: the implications for conservation management*. Unpublished D.Phil. Thesis, Oxford University.
- BRYCE, J., JOHNSON, P.J. and MacDONALD, D.W. (2002). Can niche use in red and grey squirrels offer clues for their apparent coexistence? *Journal of Applied Ecology* **39**, 875–887.
- BRYCE, J., SPEAKMAN, J.R., JOHNSON, P.J. and MacDONALD, D.W. (2001). Competition between Eurasian red and introduced Eastern grey squirrels: the energetic significance of body mass differences. *Proceedings of the Royal Society* **268**, 1731–1736.
- CARTMEL, S. (2000). *Squirrel ecology in a conifer forest in North Wales*. Unpublished PhD Thesis. Queen Mary and Westfield College, University of London.
- GORDON, A.G. (1992). *Seed manual for forest trees*. Forestry Commission Bulletin 83. HMSO, London.
- GURNELL, J. (1996). Conserving the red squirrel. In: *Thetford Forest Park: the ecology of a pine forest*. Eds. P. Ratcliffe and J. Claridge. Forestry Commission Technical Paper, pp 132–140. Forestry Commission, Edinburgh.
- GURNELL, J., SAINSBURY, A. and VENNING, T. (1997). *Conserving the red squirrel (Sciurus vulgaris) in Thetford Forest*. English Nature Research Report 262. English Nature, Peterborough.
- GURNELL, J., WAUTERS, L.A., LURZ, P.W.W. and TOSI, G. (2004). Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology* **73**(1), 26–35.
- HALLIWELL, E.C. (1997). *The ecology of red squirrels in Scotland in relation to pine marten predation*. Unpublished PhD Thesis, University of Aberdeen.
- JNCC (1996). *UK Strategy for Red Squirrel Conservation*. JNCC, Peterborough.
- KENWARD, R.E., HODDER, K.H., ROSE, R.J., WALLS, C.A., PARISH, T., HOLM, J., MORRIS, P.A., WALLS, S.S. and DOYLE, F.I. (1998). Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *Journal of Zoology* **244**, 7–21.
- LLOYD, H.G. (1983). Past and present distribution of red and grey squirrels. *Mammal Review* **10** (2/3/4), 69–80.
- LURZ, P.W.W (1995). *Ecology and conservation of the red squirrel in upland conifer plantations in the north of England*. Unpublished PhD Thesis, University of Newcastle Upon Tyne.
- LURZ, P.W.W. and GARSON, P.J. (1995). Seasonal changes in ranging behaviour and habitat choice by red squirrels (*Sciurus vulgaris*) in conifer plantations in Northern England. In: *Ecology and Evolutionary Biology of Tree squirrels*. Special Publication, Virginia Museum of Natural History 6. Eds. M.A. Steele, J. Merritt and D. Zegers. Virginia Museum of Natural History, Martinsville, Virginia.
- LURZ, P. W., GARSON, P. J. and RUSHTON, S. P. (1995). The ecology of squirrels in spruce dominated plantations: implications for forest management. *Forest Ecology and Management* **79**, 79–90.
- LURZ, P.W.W., GARSON, P.J. and WAUTERS, L.A. (1997). Effects of temporal and spatial variation in habitat quality on red squirrel dispersal behaviour. *Animal Behaviour* **54**, 427–435.
- MARQUISS, M. and RAE, R. (1994). Seasonal trends in abundance, diet and breeding of the common crossbill (*Loxia curvirostra*) in an area of mixed species conifer plantation following the 1990 crossbill ‘irruption’. *Forestry* **67**, 31–47.
- NIXON, C.J. and WORRELL, R. (1999) *The potential for the natural regeneration of conifers in Britain*. Forestry Commission Bulletin 120, HMSO, London.
- PEPPER, H. and PATTERSON, G. (1998). *Red squirrel conservation*. Forestry Commission Practice Note 5. Forestry Commission, Edinburgh.

POULSOM, L. GRIFFITHS, M. BROOME, A. and MAYLE, B. (2005).

Identification of priority woodlands for red squirrel conservation in north and central Scotland: a preliminary analysis.

Scottish Natural Heritage Commissioned Report No. 089 (ROAME No. FO2AC334). Scottish Natural Heritage, Edinburgh.

SCOTTISH SQUIRREL GROUP (2004).

Scottish strategy for red squirrel conservation.

Scottish Natural Heritage, Edinburgh.

TEANGANA, D.Ó., REILLY, S., MONTGOMERY W.I. and ROCHFORD, J. (2000).

Distribution and status of the red squirrel (*Sciurus vulgaris*) and grey squirrel (*Sciurus carolinensis*) in Ireland.

Mammal Review 30(1), 45–56.

WAUTERS, L.A., GURNELL, J., MARTINOLI, A. and TOSI, G. (2002a).

Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur?

Behavioral Ecology and Sociobiology 52(4), 332–34.

WAUTERS, L.A., LURZ, P.W.W. and GURNELL, J. (2000).

Interspecific effects of grey squirrels (*Sciurus carolinensis*) on the use and population demography of red squirrels (*Sciurus vulgaris*) in conifer plantations. *Ecological Research* 15(3): 271–284.

WAUTERS, L.A., TOSI, G. and GURNELL, J. (2002b).

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.

FURTHER READING

GURNELL, J. and PEPPER, H. (1994).

Red squirrel conservation field study methods.

Forestry Commission Research Information Note 191.

Forestry Commission, Edinburgh.

GURNELL, J., LURZ, P. and PEPPER, H. (2001).

Practical techniques for surveying and monitoring squirrels.

Forestry Commission Practice Note 11.

Forestry Commission, Edinburgh.

LURZ, P. GURNELL, J. and RUSHTON, S. (2004).

Managing forests for red squirrels.

In: *Managing woodlands and their mammals* eds C.P. Quine, R.F. Shore and R.C. Trout, pp 25–30.

Forestry Commission, Edinburgh.

CONTACTS

Forestry Commission
231 Corstorphine Road
Edinburgh
EH12 7AT

T: 0131 334 0303

www.forestry.gov.uk

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

Forest Research
Alice Holt Lodge
Wrecclesham
Farnham GU10 4LH

T: 01420 22255

www.forestresearch.gov.uk/saps

Responsible for research and technical advice.

UK Red Squirrel Group
www.ukredsquirrels.org

Responsible for co-ordination and delivery of red squirrel Species Action Plan.

Joint Nature Conservation Committee (JNCC)
Monkstone House
City Road
Peterborough PE1 1JY
T: 01733 562626
www.jncc.gov.uk

Responsible for the UK red squirrel strategy and secretariat for the UK Red Squirrel Group.

English Nature
Northminster House
Peterborough
PE1 1UA
T: 01733 455000
www.english-nature.org.uk

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'.

Red Alert North England
Northumberland Wildlife Trust
Garden House
Saint Nicholas Park
Gosforth
Newcastle upon Tyne NE3 3XT
T: 0191 284 6884
www.nwt.org.uk

Countryside Council for Wales
Plas Penrhos
Penrhos Road
Bangor
Gwynedd LL57 2LQ
T: 08451 306 229
www.ccw.gov.uk

Responsible for general advice and information, issuing licences for conservation, education and survey, provision of grants for conservation works and undertaking research.

Scottish Natural Heritage
2 Anderson Place
Edinburgh
EH6 5NP
T: 0131 447 4784
www.snh.gov.uk

Responsible for the national and regional red squirrel strategy, grants and advice under the species recovery programme, and issuing licences for conservation, education and survey.

Red Squirrel Conservation Officers,
Red Squirrels South Scotland
Studio 2
Lindean Mill
Galashiels
Selkirkshire TD1 3PE
T: 01750 23446 Borders
T: 01750 725157 Dumfries and Galloway
www.red-squirrel.org.uk

Department of Agriculture and Rural Development Northern Ireland
Dundonald House
Upper Newtownards Road
Belfast BT4 3SB
T: 01232 520100
www.dardni.gov.uk

Responsible for woodland grants and woodland management and advice in Northern Ireland.

Department of the Environment Northern Ireland
Environment and Heritage Service
Commonwealth House
35 Castle Street
Belfast BT1 1GU
www.ehsni.gov.uk

Wildlife Trusts: for addresses and phone numbers see local directories or via English Nature, Countryside Council for Wales and Scottish Natural Heritage.

Enquiries relating to this publication should be addressed to:

Brenda Mayle
Forest Research
Alice Holt Lodge
Farnham
Surrey
GU10 4LH

T: 01420 22255
E: brenda.mayle@forestry.gsi.gov.uk

www.forestresearch.gov.uk