

CHAPTER 2. SQUIRREL POPULATION TRENDS

The first record of the grey squirrel in Britain was from Denbighshire in 1828 (Harris 1995) and a number of records exist for Montgomeryshire prior to 1830. In 1876 the first grey squirrel was released in Cheshire as an ornamental species. It was introduced from the USA to England from 1876 to 1929 and to Scotland from Canada between 1892 and 1920. In Ireland, the introduction took place in Castle Forbes, County Longford in 1911 when six pairs were released. From then until 1929 there were a number of introductions around Britain and in 1938 it became illegal to import grey squirrels. Despite this ban in Britain, two pairs of this alien species were introduced to Northwest Italy to Piedmont in 1948 from Washington and released at Stupinigi. In 1966 in Genova, five animals were released from Norfolk (Virginia, USA) into the park of Villa Groppallo at Genoa Nervi and as recently as 1994 a further three pairs into the Ticino valley at Trecate in an urban park. The latter two populations have been contained or recaptured, but the Piedmont population has shown a rapid increase. The spread of the grey squirrel in Great Britain, Ireland and Italy has, through competitive exclusion, caused the progressive disappearance of the native red squirrel in each country the mechanisms for which are discussed elsewhere in this review. Secondly, its impact on the forest ecosystem and timber activity through debarking is also a major concern. In just a hundred years the population in Britain has exploded:

Table 2.1. Squirrel Population Estimates for Britain (Harris 1995)

	* Total Woodland (ha)	Grey squirrel Colonised (ha)	Grey squirrel Population	Red squirrel Population
England	1,104,000	431,826	2 million	30,000
Scotland	1,324,000	28,280	200,000	121,000
Wales	288,000	3,790	320,000	10,000
Total British breeding population:			2.5 million (1995) 3.0 million (Red Alert NW 2003)	161,000

**Total woodland areas from Forestry Commission statistics 2002*

The subsequent spread of the grey squirrel in Britain is well catalogued by several commentators with the greatest spread considered to have taken place between 1930 and 1945 when the species became entrenched in the midlands and most of southern England apart from Cornwall. East Anglia remained largely clear until the early 1970s, but animals were found as far north as Cheshire and North Wales in the west and north Yorkshire in the east. In England, by the early 1960s only parts of Cumberland, East Anglia and north Lancashire and Westmoreland remained mostly uncolonised.

The range of the red squirrel extends throughout Eurasia from the Pacific to the Atlantic wherever there are trees. It occurs in Siberia, Korea and northern Japan. In Europe, reds are found from Scandinavia to the Mediterranean but are largely absent from the Iberian peninsular. In Britain the range of the red squirrel has progressively declined during the last century as the grey squirrel has spread. In Ireland, although referred to as native, Irish red squirrels became extremely scarce, if not extinct during the late 17th and early 18th centuries due to extensive tree felling and hunting for fur. Re-introductions occurred from 1815 - 1876. The range of the red squirrel in Ireland is steadily being encroached upon by that of the non-native grey squirrel which is now becoming the dominant species. Reds are now absent from many parts of Ireland and have been completely replaced by greys across large areas of their former range. The worry is that the same will now occur right across Europe and reach Eurasia because both enjoy the same habitat.

ITALY

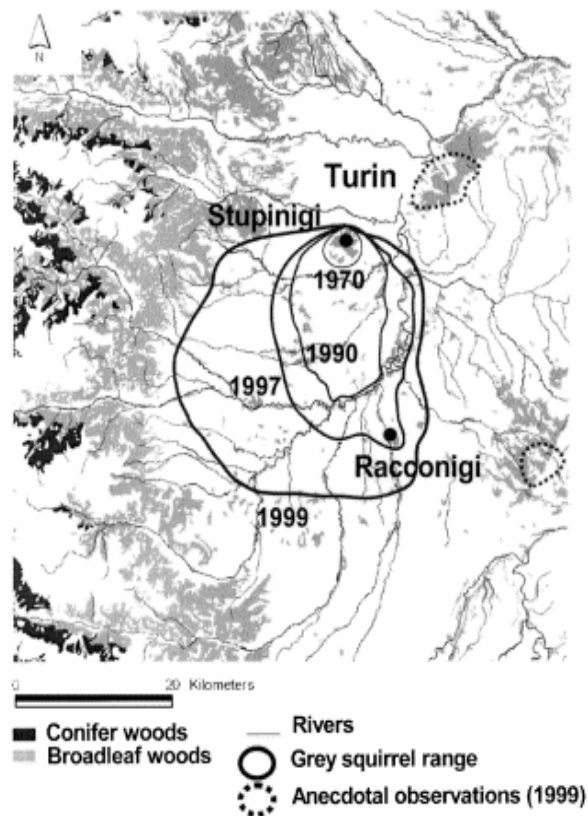


Figure 2.1. Grey squirrel expansion in Northern Italy in the 1970–1999 period. Distribution in 1970, 1990 and 1997 defined from data published in Wauters *et al.* (1997) (modified). Distribution in 1999 defined on the basis of hair-tube data. (Bertolino & Genovesi 2003).

All data gathered in Britain and Italy confirm that in areas colonised by the grey squirrel, the native red squirrel rapidly becomes extinct. In Piedmont (NW Italy), the grey squirrel had been confined until 1970 within the suburbs of Turin in Stupinigi Park where the red squirrel was also present (Genovesi 2000). The last observation of a red squirrel there was recorded during the winter of 1979-80. In 1990 the grey squirrel's range had largely increased while the red had disappeared from Stupinigi and surrounding woodland fragments in the grey's range. In 1990 the grey's range was 243 km². Between 1991 and 1997, the extinction rate of the red was very rapid with a decrease of reds by 55%. By 1997 the grey squirrel expanded significantly to 380 km² and by 1999 the grey squirrel was present in an area of 880 km² (Bertolino & Genovesi 2003) (See Figure 2.1 and Table 2.2).

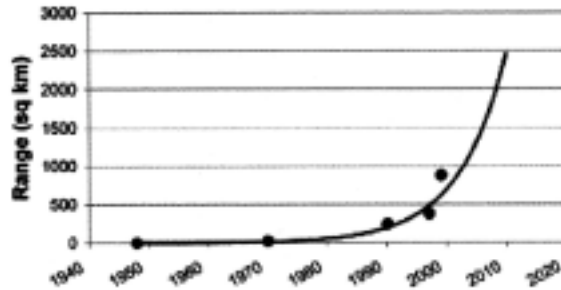
In 1997 the red was still present only in two locations - the Racconigi Park -where a dramatic decrease was observed, and the small Borgo Cornalese park where the grey squirrel arrived only in 1996 (Wauters *et al.* 1997). The observational data until 1997 may have underestimated the grey's range, but since 1999 presence was assessed using hair tubes and this revealed an exponential growth in its distribution. Over the whole 1948-2000 period, the grey squirrel has colonised at a mean rate of 17.2 km²/year (Bertolino & Genovesi 2003) although the colonisation has not been constant. In the first phase (1948-1970), the spread at 1.1 km²/year was hindered by the presence of extended cultivated fields with very reduced and fragmented woods. This increased to 10-20 km²/year once the greys started spreading along rivers and recently 250 km²/year when it reached the continuous broadleaved woods of the hilly areas of eastern Piedmont and the Po River (See Table 2.2).

Table 2.2. Area colonised by the grey squirrel in Piedmont, from its introduction until 1999 (Bertolino & Genovesi 2003).

Period	Number of years	Range by the end of the period (km ²)	Range increase during the period (km ²)	Mean annual colonised area (km ² /year)
1948-1970	22	25	25	1.1
1971-1990	20	243	218	10.9
1991-1997	7	380	137	19.6
1998-1999	2	880	500	250
Total	51	880	880	17.2

Bertolino & Genovesi (2003) cite Elton (1927) when they say that the exponential range increase recorded in Piedmont (See Figure 2.2) is consistent with the pattern predicted by Elton for the establishment of the species. It is described by a sigmoid growth curve, characterised by a first settlement, when the possibility of extinction is high, a phase of rapid increase, and finally a stabilisation phase.

Figure 2.2. An exponential growth model (from introduction until 2010) applied to grey squirrel range data (black dots). (Bertolino & Genovesi 2003)



The potential expansion of the Italian grey squirrel population to the Alps and to a large portion of Eurasia represents a major threat to biodiversity at a continental scale (See Figure 2.3). A colonisation of the entire Alps in the middle term and of a large part of Europe in the long term is predicted, potentially threatening the survival of the red squirrel in the continent.

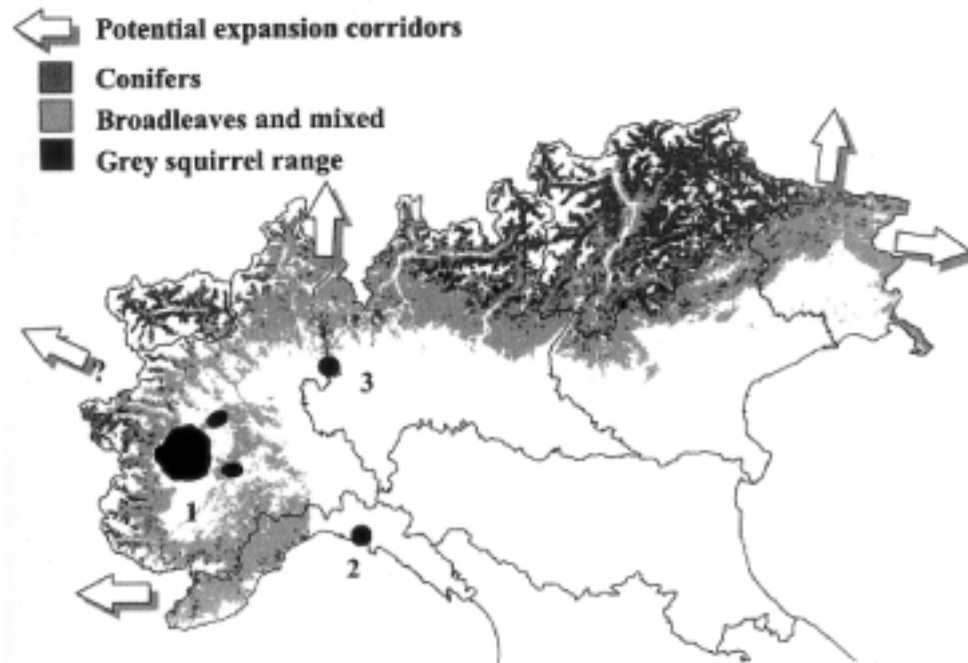


Figure 2.3. Woodland cover in the Italian Alps, grey squirrel colonies and possible expansion corridors to the rest of Europe. 1: main colony (Piedmont); 2: Genoa Nervi; 3: Trecate (province of Novara) (Bertolino & Genovesi 2003).

The grey squirrel is replacing the red squirrel and producing significant damage to forests and commercial tree plantations in Italy. These include sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvatica*) and also local poplar (*Populus sp*) plantations which are widely distributed in the Alps and represent the dominant species in some ecosystems (Bertolino & Genovesi 2003). Lurz *et al.* (2001) developed a model at landscape scale combining GIS (Geographical Information System) and population dynamics – SEPM (Spatially Explicit Population Dynamics Model) in collaboration with biologists at the University of Turin to:

- (i) analyse past grey squirrel spread and
- (ii) illustrate the potential expansion of the introduced grey in the region of Piedmont and beyond.

The model predictions plainly indicate that in the absence of grey squirrel control, it is only a matter of time before the grey expands both dynamically and in density across the rest of northern Italy and beyond (See Figure 2.4). Control of the grey squirrel is not only a conservation issue with regard to the native red squirrel or an economic problem due to damage to tree and agricultural crops. It is also an ethical issue that deserves careful

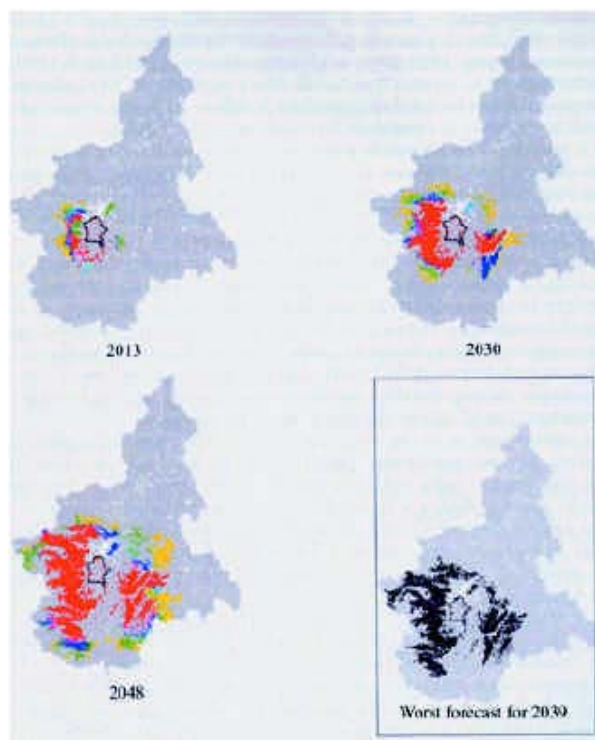


Figure 2.4. Potential expansion of the grey squirrel in Piedmont (Italy) according to a range of probabilities for 2013, 2030, 2039 and 2048 (red 0.9–0.99, violet 0.7–0.89, blue 0.5–0.69, azure 0.3–0.49, green 0.1–0.29, yellow 0.0–0.09). The black outline shows the extent of grey squirrel expansion in 1996. The worst forecast for 2039 is in black (Lurz *et al.* 2001).

consideration (Lurz *et al* 2001). However, the future of the grey squirrel in Piedmont or other introduced species should not just be considered on a regional or national scale, but in the context of expected range expansion. Large areas of Europe contain potentially good habitat for grey squirrels. Grey squirrels do not recognise national boundaries and are likely to disperse where continuous woodland cover connects Piedmont with France. Recent translocations of grey squirrels to the north-east of Piedmont and into Lombardia were not included in the model simulations (S. Bertolino; L. Fornasari personal communication to P. Lurz). These are likely to result in grey squirrels spreading also into Switzerland. Lurz *et al.* (2001) predict that grey squirrels are likely to spread beyond the Alps into neighbouring countries and eventually beyond into Central and Eastern Europe.

Lurz *et al.* (2001) also present a 'worst case' scenario in which grey squirrels experience improved reproductive success due to the availability of high quality habitats beyond the Po plain. In any scenario, they believe they could disperse along existing continuous woodland corridors into France between 2039 and 2048. The case of the grey squirrel highlights the problems of implementing conservation conventions and the resulting conflicts between wildlife management, public perception and local political support and the narrow time frame that is available to control alien species effectively before it is too late. If allowed to spread, grey squirrels have the potential to become a European forest pest species and are likely to replace the native red squirrel in large parts of its range.

IRELAND

The distributions of the red and grey squirrels were surveyed in Northern Ireland and the Republic of Ireland between 1994 and 1996 (See Figures 5 and 6) (O'Teangana *et al.* 2000). The combined results indicate that the red squirrel remains widespread and locally abundant and is present in all but two counties. The grey squirrel is now more widespread than ever before and can be found in 22 of the 32 counties. Its expansion rate has varied from 0 km / year to an estimated 13.4 km / year. Wherever it has been introduced, the grey has been regarded as an actual or potential forestry pest and/or competitor of the native squirrel species (O'Teangana *et al.* 2000).

The present population of reds in Ireland is probably derived from re-establishments to about 10 sites between 1815 and 1856 (O'Teangana *et al.* (2000) cites Barrington (1880)) based on animals imported from English stocks and thereby possibly indirectly from the Continent. While some form of competitive replacement is generally accepted in England and Wales as the method of species replacement, in Ireland, due to the absence of relevant studies, the relationship between reds and greys is unknown.



Figure 2.5. Grey squirrel distribution in Ireland, 1997, showing Castle Forbes, Co. Longford, the site of grey squirrel introductions in 1911. (O'Teangana *et al.* 2000)



Figure 2.6. Red squirrel distribution in Ireland, 1997 (O'Teangana *et al.* 2000)

Since its introduction into Ireland, the range of the grey squirrel has increased greatly. By 1923, it was reported 10 miles (16 km) from its site of introduction in 1911 (Watt 1923). By the mid-1940s, the grey squirrel was increasing its range northwards (which is well documented), and southwards and eastwards (but not as well documented). From its introduction the River Shannon has provided an effective barrier to grey squirrel expansion. The grey squirrel is now ubiquitous in the midland counties, and its expansion eastwards to the coast is virtually complete. It has now extended its range to southern Tipperary and Wexford and is also showing signs of crossing the Shannon by expanding north of the river's source westward through Leitrim.

In Northern Ireland the grey is more widespread than the red. In the Republic, the survey done by O'Teangana *et al.* (2000) was compiled using a grid square system (10 x 10 km) assuming that greys were present in a grid square from the year they were first recorded there. The rate of spread was measured by calculating the shortest distance from the centre of previously occupied square to a newly occupied one. This measurement was then divided by the number of years between the respective surveys to determine spread in kilometres per year. The rate was found to be between 0.0 and 2.9 km / year with the mean rate of spread calculated at 1.94 km / year (see Figure 2.7).



Figure 7. Grey squirrel range expansion in Ireland from the 1911 introduction. (O'Teangana *et al.* 2000)

The rarity or absence of the red squirrel in the west of Ireland, claim O'Teangana *et al.* (2000), may be explained by:

- the scarcity of organised releases there in the last century;
- the prevailing mountainous topography hindering disbursement;
- coniferous plantations being the only available habitat giving poor survival.

BRITAIN

In Britain, despite efforts to eradicate the grey, it has spread unremittingly. A succession of national surveys done extending from Middleton (1930) to the Forestry Commission (1992) have documented this spread and the contrasting diminishing distribution of the red squirrel (See Figures 9 and 10). In England and Wales, the red was widely distributed before the grey's arrival and is now restricted to just a few sites (Kenward & Holm 1989). Genetic isolation of the red squirrel and the possibility of inbreeding, if not total extinction, are becoming increasingly realised. Indeed, it may be significant to establish the provenance of the British grey squirrel. Where was the original introduction from in the USA and did all released species come from the same area? If they were introduced to different locations from different sources has there been any interbreeding so that the British grey squirrel is not the original *Sciurus carolinensis*, but a separate sub-species. Since the introduction of the alien American grey squirrel to Britain in the late 19th century there has been much discussion as to whether its spread has been responsible for the decline of the indigenous red squirrel. Earlier popular beliefs that the grey pursued the reds, chasing them out of woodlands, and killing their young were dispelled early on. It quickly became clear from literature such as

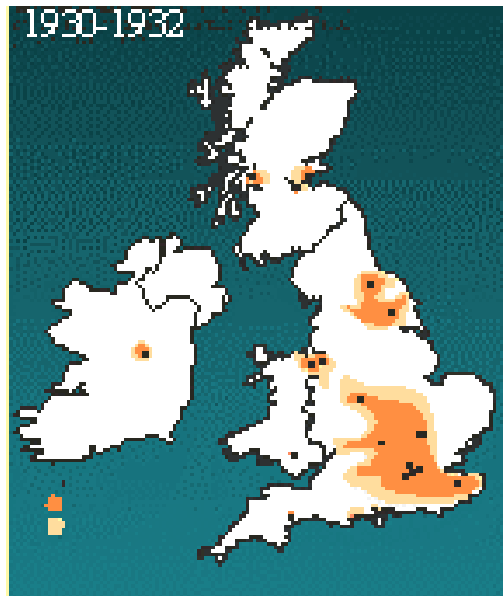


Figure 2.8. The range of the grey squirrel in the British Isles in 1930 and the approximate area colonised from 1930 - 1932 after Middleton (1932). The map shows the principal introduction locations and subsequent colonisation. The distribution by 1st January 1930 is shown in orange and the distribution 2 years later in 1932 is shown in cream. (Reproduced courtesy of Forest Research 2003).

Ritchie (1920), Middleton (1930) and Shorten (1946 - 1957) that red populations had often disappeared long before the arrival of the grey having suffered many fluctuations throughout its recorded history including across Eurasia. Stories of extinction in both Ireland and Scotland during the 18th century and recovery during the 19th century due to re-introduction are well recorded. This decline can largely be attributed to the need for timber in industry, agriculture, and war, and the felling of large areas of woodland. With a new drive to replace the trees that had been lost, new planting in the 19th century boosted red squirrel numbers and by the start of the 20th century there was a thriving population of red squirrels across Britain (Ritchie 1920).

The red squirrels at Formby (Lancashire) were introduced from Europe about 1930 and now occupy 70 ha of mixed coastal forest of which 40 ha are conifers (Gurnell & Pepper 1993). Due to supplementary feeding, densities are very high, up to ten times those found in natural habitats. The largest populations remaining in England are those in Cumbria, north Lancashire and Northumberland. These make up about 85% of the red squirrel population in England. In Scotland, Harris (1995) shows that there are no records to suggest that red squirrels are indigenous south of the Firths of Forth and Clyde but that to the north they were widespread and common. However they became very rare due to widespread forest

destruction during the 18th century persisting only in Inverness-shire and boosted by re-introductions from England, the increase in young woodlands, and possibly the control of predators.

Against this, Anderson (1967) cites many local Scottish records collected by Ritchie (1920) of the red squirrel "abounding" in many parishes, referring to the squirrel invasion being brought about by the "deliberate extermination of the weasel and cat families". He talks of "misguided persons" introducing it, of it "penetrating and multiplying so enormously that they have come to be regarded as one of the prime pests of the forester". Munro (1911) describes two woods in the north, each of several hundred acres "... and there was not a Scotch fir in them that had not been more or less destroyed by squirrels". He put the damage at £15 per acre. "The main damage is done to coniferous trees of pole size, especially Scots pine. In the early spring when the sap is rising they sit on the branch whorls high up on the stem and by removing strips of bark partially girdle the stem – seldom completely. Over these rings no new growth takes place, but the crown is still kept alive through the portion of bark remaining. The unhealed scar presents a weakness on the stem and with the first high wind the top is almost certain to be broken off". Reference is made to 'this disastrous invasion' as far back as 1871. So serious did this pest become that a Highland Squirrel Club was formed in 1903 covering, by 1905, 47,000 acres of woodland, and by 1917, killed over 60,000 red squirrels.

Anderson also talks of the release by 'some lunatic' of a pair of grey American squirrels at Loch Finnart in about 1890 which became an equally grave pest to Scottish forestry. "Records of serious damage by this creature had not yet been made. These were to come".

By the end of the 19th century, red squirrels were abundant in England, Scotland and Wales, increasing in the newly wooded areas but there were more declines in the 1920s with some, but not all populations recovering. All these population changes occurred before the grey squirrels were introduced to these areas.

Following the spread of grey squirrels, the red squirrel has shown a steady decline in England and Wales in both range and numbers. In Scotland red squirrels currently occupy more 10 x 10 km squares than they did 50 years ago due to increased afforestation (Gurnell & Pepper 1993). Harris (1995) cites a survey done by Usher, Crawford & Banwell (1992) showing that there was a dramatic decline in the distribution of the red squirrel in Wales from 1973-1988, but failed to suggest that it would become extinct. In the ensuing 15 years however, it has become clear that the future status of individual populations is questionable.

Even the security of the Isle of Wight population is believed to be at risk should greys become established on the island, because the population is scattered (Kenward & Holm (1989) and Gurnell & Pepper (1993)). Harris shows in 1995 that red squirrels appear vulnerable to extinction south of a line from Morecambe Bay to the Tees Estuary and that greys are already expanding into northern England. In 1991 a survey in Wales showed that all but four reports of red squirrels were from state forests and all but two 10 x 10 km squares with red squirrels also contained grey squirrels.

Attempts to provide sanctuaries in Cannock Chase and Thetford have failed and funds to continue work have dried up. A three year study on controlling grey squirrels for red squirrel conservation was carried out in Thetford Forest between 1998 and 2001 using multi-capture, ground-placed cage traps to remove grey squirrels within the 4.5 thousand hectare study area. (Thetford Forest comprises 20,000 hectares of the largest lowland pine forest in the UK). The results showed that the control effort was too low at all stages to reduce grey squirrel numbers significantly, or indeed maintain them at low numbers. However the Regional Defence Strategy accepts the non-elimination of the grey squirrel because control is expensive, needs to be high, targeted and may not be effective. Sadly the cheapest way of applying control through the use of warfarin is not permitted, despite the existence of tested and proven modified hoppers that exclude red squirrels (Pepper 1997) as it is deemed illegal wherever "reds are likely to be present" (Forestry Commission 2001).

Densities

Densities for the grey squirrel averaged over several years are usually greater than 2.0 /ha and are often much greater. For reds, population densities of 0.5 – 1.5 animals / ha are the average across most habitat types (Gurnell 1987). However in extremely rich habitat, numbers may reach peak levels of 7.5 / ha in eg Scots pine forest. In Ireland, reds were noted as living at densities of 1.2 / ha in coniferous forest with an average home range of 6.15 ha (Rooney & Hayden 2002). Harris cites Gurnell (1983) as showing a mean of 7.4 greys / ha in oak woodland in southern England with a range of 5.2-9.8/ha, and Kenward *et al.* (1998) adds support to this quoting densities as high as seven or more greys per hectare in a good habitat, eg oak and hazel woodland. However densities of 1.5 – 4 / ha during summer is considered the norm (Harris *et al.* 1995). Suburban and urban areas such parks and gardens can often support higher densities of greys due to their scavenging behaviour and through feeding by the public. In Ireland, greys have recorded at densities of 2.5 per ha in deciduous woodland and 1.64 per ha in coniferous habitats where their average home range size was 3.65 per ha.

Long term densities of greys in pure coniferous woodland are not known. In Wareham Forest, Dorset, densities of between 2 and 3.6 / ha were recorded in good Scots pines and 1.1/ha pre-breeding to 1.6/ha for summer in mature Corsican pine (Harris 1995). However both these plantations were good conifer habitats and most plantations will have fewer grey squirrels. Being sited in southern England where fertility and climate are extremely favourable for tree growth and in turn, good seeding, this will inevitably lead to higher squirrel densities. In 8 upland conifer sites in the Upper Derwent valley in the Peak District, pre-breeding density was 0.5/ha and post breeding 0.7/ha. So we can identify several difficulties in trying to estimate true population densities: ecologically annual population cycles will always show peaks in autumn before dispersal and trough in the spring before recruitment. Food availability will also have a significant impact on population numbers and this will be controlled by habitat suitability:

- ❖ the tree species, density and age that are present in a given habitat;
- ❖ urban habitats enable bird table feeding, litter bin scavenging and direct feeding in parks;
- ❖ climatic variation at both micro and macro scales;
- ❖ site size fertility and ground cover present.

Spread of the grey squirrel

The spread of the grey squirrel continues. Harris (1995) quotes Reynold (1985) in estimating a mean rate of spread at 7.7 km / year. He considers that distribution in England and Wales is nearly stable but that there has been a steady increase in north-west England and Scotland. This “stability” of course does not account for the increase in densities where spread is no longer possible and the red squirrel disappeared decades ago, but just geographical spread. It also does not refer to the other consequences that the increase in population brings.

Grey squirrels have been known to “leap-frog” through unsuitable habitats so it is not clear what natural barriers will limit their spread. They are now more abundant than red squirrels in north Lancashire and are well established in the Lake District as far north as Windermere and Ambleside. One of the last bastions against this spread is the valley of Thirlmere, which has been protected on two sides by high mountains and to the south by Dunmail Raise. It was also protected to a limited extent by the very size of the forest – 2,000 acres – for that is something not appreciated by greys. But that appears to have failed now as well. According to Wren (2003), Thirlmere was named in 2000 as the first refuge site in Cumbria for the red squirrel but the official launch was delayed for 2 successive summers, first by the fuel embargo and then in 2001 by Foot and Mouth disease. In that time the first grey appeared in

the valley and since then nine have been shot. It would appear that the grey has made its way into the valley from the Keswick direction – i.e. from the north. Because the Keswick area as a whole has been free from grey squirrels until the past few years, the Lake District National Park Authority has taken a keen interest in this invasion and adopted the policy of shooting all grey squirrels in an attempt to protect the reds. The alarming fact is that while in the whole of 2001 only 6 were seen and shot in the Keswick area, in just 9 months of 2002, 60 had to be culled writes Wren. The invasion is clearly gathering serious momentum.

Biotic invasions are responsible for global environmental changes and are considered a major threat to biodiversity (IUCN 2000). Furthermore, the biotic homogenisation caused by the introduction of alien species is expected to increase rapidly in the near future, as a consequence of the increasing level of transport, trade and tourism related to economic globalisation (Genovesi (2003) cites Mooney & Hobbs 2000). To prevent this, priority should be given to the prevention of unauthorised introductions. However even with the most stringent regulations in place, prevention against accidental or intentional introductions is not feasible so the best option is the rapid and complete eradication of an invasive alien species. This is the only measure that will prevent future impact on biodiversity and human activities. Eradication is a better alternative than permanent control because the latter strategy cannot definitively resolve the problem, is generally more expensive and in the long term requires the killing of large numbers of animals.

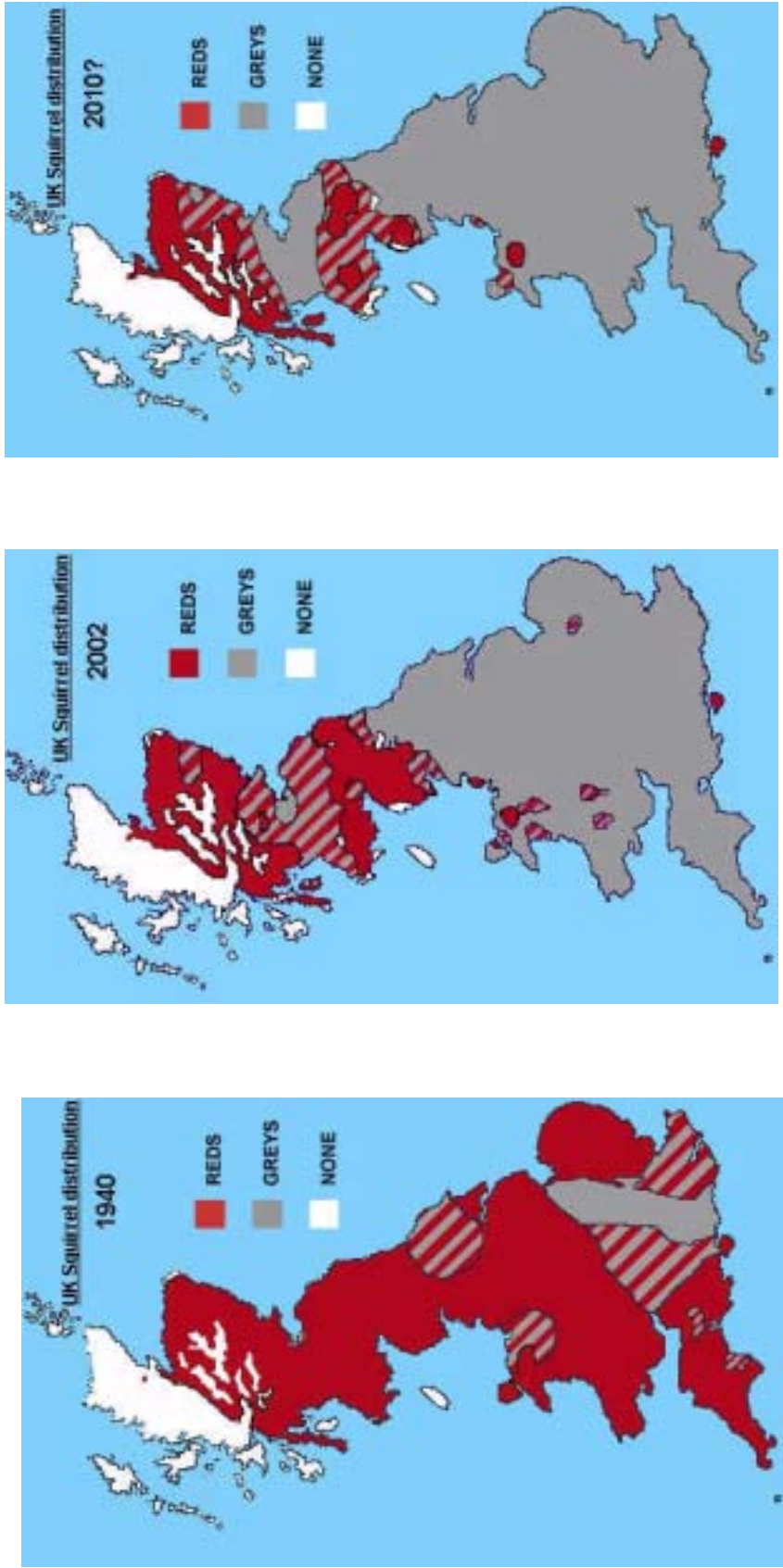


Figure 9. Red and Grey Squirrel Distribution Maps for UK for 1940 and 2002, and projected distribution for 2010
 (Reproduced courtesy of Red Alert 2003)

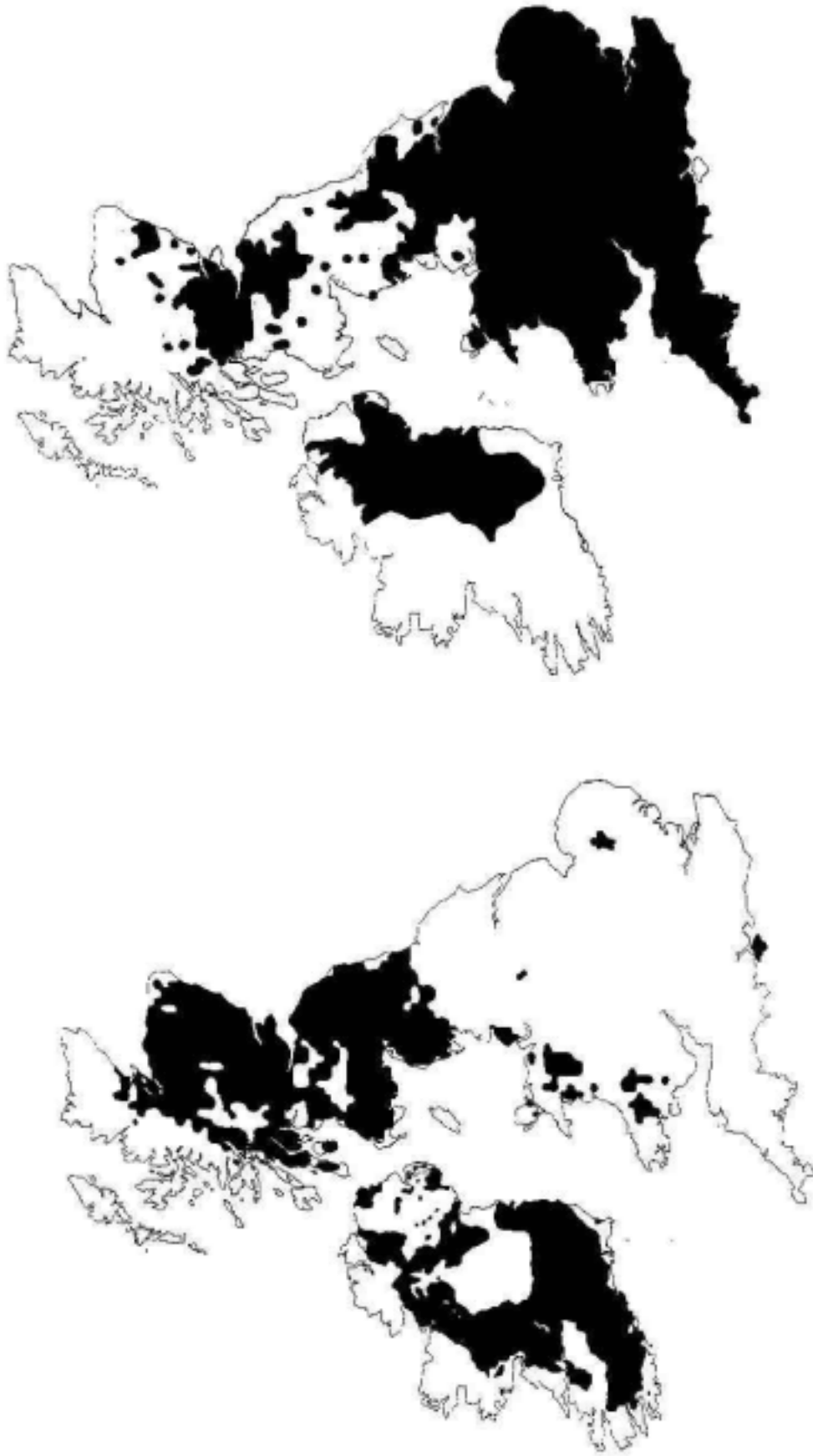


Figure 10. 1998 Distributions of (left) red and (right) grey squirrels in Britain and Ireland. Maps reproduced courtesy of the Forestry Commission