

CHAPTER 3. FATE OF THE RED SQUIRREL

ECOLOGICAL COMPETITION and REPLACEMENT

Red and grey squirrels occupy a similar ecological niche: they are both small tree-dwelling mammals that rely on similar food sources and are capable of producing similar numbers of young at the same times of the year. It is these comparisons and similarities that inevitably make one or other species vulnerable to the stronger of the two, and so competition for survival commences. While it is clear that the decline in red squirrels in Britain, Ireland and Italy is linked to the spread of the grey squirrel, the precise mechanism for replacement will vary. We can identify that the red squirrel is the weaker competitive species because before the influx of greys took place the red was in reasonable balance with nature. But it is more than that. The grey squirrel, because it is a non-native alien, must by definition be competitive in order to survive in a non-native environment. Added to this, the red squirrel endures a fragile existence at the best of times, particularly in broadleaved woodland. Starvation in the summer months is a real threat to young reds waiting for fruit and nuts to ripen. Competition with greys for limited food supplies simply tilts the balance too far. So we see displacement occurring through competitive exclusion.

Competitive exclusion

Competitive exclusion by grey squirrels is the greatest single threat to the red squirrel (Kenward & Holm 1989). Greys live in deciduous woodland at higher densities (population) than reds. Although the two species can co-exist for up to 20 years (Harris 1995), red squirrels generally decline when grey squirrels colonise an area and are soon reduced to scattered 'island' populations that may persist for only a few years. Kenward and Holm (1993) have shown that red squirrels are unlikely to persist with grey squirrels in woods with more than 14 % oak canopy. They realised that oaks in most British broadleaved woodlands give grey squirrels a food refuge that reds fail or are unable to exploit resulting in the replacement of reds by feeding competition alone. Greys quite simply are better at exploiting the food available. They thrive on acorns which they can digest more easily than reds, and which their strong jaws allow them to break open while still green. This is further exacerbated by the fact that reds only increase their body weight in late autumn by about 10% (greys increase theirs by about 20%).

This makes red squirrels more vulnerable to food shortages during the winter period and is most likely to occur when the two species coexist and are competing for food resources (Gurnell & Pepper 1993). Since maintenance of body weight is important for reproduction, reduced reproductive success rather than reduced survival may explain why red squirrels

have declined in conifer forests that also contain grey squirrels. Gurnell and Wauters (1999) suggest that the main impact that grey squirrels have on red squirrels is on juvenile recruitment – that is young reds find it difficult to establish territories when young greys are also present in an area. The presence of grey squirrels may also suppress the number of red squirrel females that breed. Skelcher (1997) believes that competition between red and grey squirrels is stronger through breeding success than adult survival. He says that this could be the case in predominantly coniferous woodlands where the grey's advantages in exploiting the small proportion of broadleaved seeds are less significant and could explain why red squirrels and grey squirrels have often been observed to coexist in mixed woodlands. Such woodlands contain a high proportion of conifers so it may be many years before the red squirrels start to decline and eventually become extinct. Squirrels of both species in good condition can produce two litters in a year but will normally only rear one litter either in the spring or summer. If a squirrel is in poor condition it will not breed at all conserving energy for individual survival (Gurnell 1987). Consequently in deciduous and mixed woodland, greys may still breed in years when reds produce no offspring. This will obviously affect the population pendulum resulting in a gradual replacement.

Such an advantage in breeding success of grey squirrels will be less pronounced in mixed woods with a high conifer content. This claims Skelcher (1997) would explain why reds and greys have often been observed to coexist in such woods for many years although the red squirrels have slowly declined. In such situations it seems that small blocks or belts of seed-producing broadleaved trees within extensive conifer forests enable initial grey squirrel colonisation. These then act as survival habitats from which grey squirrels can expand into and out of conifer stands according to prevailing conifer seed supplies (Gurnell 1996 in Skelcher 1997).

Woodland Fragmentation

Add this to the loss of red squirrel habitat through continuing fragmentation of woodland habitats and changing forestry practices including the abandonment of hazel coppicing and it becomes clear why the pressure on red squirrels has intensified in post war years. Sadly the resurgence in coppicing of hazel in the south of England has come too late to help all but the red squirrels on the Isle of Wight. The minimum size of woodland necessary to support a viable population of red squirrels is >3.5 ha (Verbeylen *et al.* 2003). The smaller the wood, the fewer squirrels can be supported. If a wood is not linked to others by a tree line or hedgerow, there will be lower dispersal rates and declining populations unlikely to be bolstered by immigrants. Because greys usually live in appreciably greater densities than red squirrels in broadleaved and mixed woodlands (Gurnell 1991), it would seem probable that greys are

capable of living in small woods and marginal habitats that would be unable to support red squirrel populations.

Woodland fragmentation could also result in loss of genetic diversity. Genetic variation is thought to be positively related to population viability and is considered essential to continuing adaptation on the evolutionary level. Loss of genetic variation, possibly caused by inbreeding, can lead to a decline in reproductive traits (Wauters 1997). Genetic isolation and the possibility of inbreeding, if not total extinction, are becoming increasingly realised (O'Teangana *et al.* 2000). Woodland fragmentation and isolation decreases dispersal rates and thus gene flow, local density and genetic diversity. Red squirrels need continuous tree canopy, do not disperse over open landscapes and populations are strongly affected by isolation. Wauters sees that the improvement of habitat quality, connectivity and landscape management is increasingly important and practices that alter the degree of habitat fragmentation can significantly impact upon the genetic structure of animal populations. Hale and Lurz (2003) used a microsatellite DNA survey show that defragmentation of the landscape has resulted in substantial genetic mixing of Scottish and Cumbrian genes in squirrel populations. They say that planting of a large conifer forest has connected groups of forest fragments in the north of England with those in southern Scotland ranging up to 100 km from the site of the new forest.

Co-habitation?

So we have seen that competition from grey squirrels continues to pose a threat to red populations even in predominantly coniferous habitats. Introduced species are, worldwide, one of the most serious threats to biodiversity and native congeners. The rate of competitive replacement of the red squirrel by the grey may be influenced by habitat composition with some red populations persisting for prolonged periods in predominantly coniferous forest in the presence of grey squirrels. Furthermore, appropriate habitat management, claim Bryce & Macdonald (2000) can prolong the length of their coexistence. By adopting the Forestry Commission's Forest Design Plans (FDP) they have produced a 'hit list' of objectives for Craigvinean Forest (Perthshire) managed by Forest Enterprise for the next 25 years and which would apparently enhance the chances of red squirrel survival and tolerance of the grey squirrel (see Table 3.1). Habitat types within the FDP were hailed as 'poor', 'good' or 'very suitable' for red squirrels based on the results of an earlier analysis they had done previously.

To the forester, this list looks like good habitat for grey squirrels as well as reds particularly as contention exists over the suitability of Norway spruce. Grey squirrels are known to strip Norway spruce cones with heaps of cone pieces to be found, not randomly scattered but

collected, especially on tree stumps, in areas where there are no red squirrels. Equally the disfavour for European larch and Douglas fir is disputed. Previously, red squirrels prevailed in broadleaved habitats living predominantly on hazelnuts. It is increasingly clear that both species of squirrel are versatile, adapting to their surroundings as necessary.

Table 3.1. 'Hit List' of Habitat types as defined by Bryce & Macdonald (2000)

Species	Type	Reason
Norway spruce	Very suitable	Clearly preferred by red squirrels
Scots pine	Good	Not selected for establishing home range, but seed size, nutritional content and availability is good.
Larch	Good	Not preferred by greys so considered good for reds as part of a mix
Douglas fir	Good	Avoided by greys so considered good for reds
Sitka spruce	Poor	Avoided by both reds and greys
Mixed conifers and broadleaves	Poor	No disadvantage to reds but crucial to greys.
Felling coups & other land use	Unsuitable	Tree species only suitable when of coning age.
Mixed conifer stands including restocking	Good	Will contain a mix of spruce /larch/ pine

In the current phase of the FDP for Craigvinean, "there is a high proportion of prime red squirrel habitats with good connectivity between all areas" say Bryce and Macdonald (2000), however this would continue to supply suitable habitat for both red and grey squirrels alike. So in the presence of greys, the future of reds will not be secure long term. Equally the cover of "suitable habitats" is predicted to become more fragmented but will not be separated by more than 500 metres and will be linked by corridors of cone bearing trees. Again this furthers the cause for the grey squirrel and demise of the red. Furthermore there are plans to restock previously broadleaved areas with a mix of conifers and broadleaved species the latter which will include small seeded species such as birch, alder, rowan, aspen and willow because they are considered less detrimental to red squirrels than large seeded species, and are much cheaper. Grey squirrels however will eat whatever seeds they can find. So, Bryce and Macdonald concede, even in large conifer dominated plantations, only upland conifer stands which are sufficiently isolated from suitable grey habitat can provide a refuge for red squirrels. They consider that red squirrel populations are only likely to be sustained in the

presence of greys in a forest with less than 10% broadleaved species – at Craigvinean it is approximately 7% in total. However, the isolated upland area comprises predominantly Sitka spruce – a species we have already seen to be unsuitable for either squirrel.

Craigvinean has experienced apparent coexistence for up to 30 years. In 2002 Bryce *et al.* studied several theories of explanation including spatial overlap of home ranges, dynamic association and niche or food type requirements. They found that while red squirrels occupied areas of Norway spruce, greys preferred corridors of mixed woodland in river valleys creating a partitioning of habitats. This, it could be argued is because the reds are pushed out of remaining broadleaved areas by the expanding density of greys who will eventually push them out of the coniferous areas too. If broadleaved areas are removed, the greys will move into the coniferous areas, quite possibly at lower densities (Kenward 1998) but at the cost of the red squirrels. However, it has yet to be determined if grey squirrels can also out-compete red squirrels in all coniferous habitats (Bryce *et al.* 2002). In England and Wales, red squirrels have persisted longer in areas of large conifer plantation such as Thetford and Clocaenog, but Lurz *et al.* (1998) have suggested that the virtual absence of broadleaved species may not prevent greys from colonising conifer forests.

The replacement of red by grey squirrels has not been as widespread in Scotland as in England despite a similar period of colonisation. It has been postulated that the different rates of replacement may be related to the predominance of conifer plantations and relative scarcity of broadleaved woodland in part of Scotland (Kenward & Holm 1989). With large fluctuations in the size of annual seed crops most commentators agree that food specialisation is predicted to be less significant than habitat specialisation in seed-eating mammals. Indeed, they are more likely to be driven by habitat than one tree species. Both squirrels forage on much the same food and need a varied diet. On Jersey where much work has been done to improve the tenacity of the red squirrel, supplementary feeding with peanuts has been found to be inadequate in isolation from a balanced diet (Magris 2003).

Mean red squirrel density at Craigvinean was found by Bryce *et al.* (2002) to be 1.63 / ha in the coniferous areas where there were fewer greys and 0.92 / ha in mixed conifers and broadleaved habitat, where there were more grey squirrels. Meantime grey squirrel density was found to be 0.88 / ha in mixed habitats and 0.08 / ha in conifer stands. It would be interesting to know whether density of greys in the mixed habitats is increasing and whether this is resulting in greater disbursement into coniferous areas. It is suggested that grey squirrels will become more efficient at utilising smaller or less nutritious conifer seeds in future should availability for their obvious preference of mixed habitats become severely

restricted. Bryce *et al.* (2002) found in their studies of niche use in red and grey squirrels that while “there was considerable potential for habitat overlap... there was a degree of spatial separation of habitat use suggesting selection of habitats was operating at a landscape scale”. Also the use of the term coexistence could be questioned in that the scale of habitat partitioning observed was relatively crude. The title of Bryce *et al.* (2002) paper implies coexistence between the species when in fact they are known to be separated spatially, yet the extent to which there was overlap at this site is well illustrated in the paper. This is supported by O’Teangana *et al.* (2000) whose study of both red and grey squirrel populations in Ireland shows that in Fermanagh, in Northern Ireland, the habitat associations of the two species are known to differ, and yet the red and grey squirrel have persisted together for over 50 years. Several authors consider there is no evidence that red and grey squirrels can co-exist within the same forest stand, but they see that the two species may be able to co-exist at the landscape scale by habitat separation (Gurnell 1983, 1987, Pepper *et al.* 2001).

DISEASE

While competition might explain the replacement of red by grey squirrels, there is evidence that red squirrel populations in Britain have declined in the past in the absence of any grey squirrels. Greys stand accused of spreading the parapoxvirus, a form of pustular dermatitis which doesn’t affect greys, yet can kill a red squirrel within four or five days. Red squirrels certainly appear to be more vulnerable to disease than greys although pox viruses have been reported in greys in North America but not in Britain until 1994 and then very rarely. While the origin of red squirrel parapox is unknown, it was thought unlikely that it came from grey squirrels because a disease clinically indistinguishable from parapox virus infection was recorded in Norfolk long before the grey squirrels reached anywhere near the county (Skelcher 1997). The role of the grey as a vector in the spread of the disease is becoming increasingly documented (Rushton *et al.* 2000, Tompkins *et al.* 2003), but much more research is essential to establish:

- ❖ Do grey squirrels get parapoxvirus?
- ❖ Are they the reservoir host, a carrier and/or can they infect other species?
- ❖ What densities, proportions and localities of grey squirrels carry the disease?
- ❖ Is the decline of the red squirrel attributable to parapoxvirus carried by the grey squirrel?
- ❖ Is there a third carrier or vector which transposes or passes the disease?
- ❖ A full understanding of the structure, epidemiology and mode of transmission of the disease.



Figure 3.1. Red squirrel suffering the first stages of Parapoxvirus (Corrie Bruemmer 2003)

Both species frequently carry parasites in the intestinal tracts although other protozoan, fungal and bacterial infections appear to be uncommon. Epidemic diseases, independent of grey squirrel presence, have caused mortality in reds in many places throughout Britain between 1900 and 1920. The discovery of dead or dying diseased red squirrels has historically frequently preceded local declines and extinction (Skelcher 1997). During the 1960s reds were found dying of a disease which coincided with the arrival of grey squirrels although the greys were not believed to be connected with the disease. Disease outbreaks can kill high proportions of reds particularly when a shortage of food prevails. This has led to extinction in some places. As most die in the nest it is difficult to estimate the importance of disease as a mortality factor. Greys will take advantage of local red extinction by moving into the vacant woods. But reds almost never re-colonise.

Rushton *et al.* (2000) devised a model that simulated the spread of parapoxvirus between squirrels in fragmented populations based on the dispersal of infected animals, the probability of encounters between individuals and exposure to the virus. The results suggested that parapoxvirus infection could be a mechanism by which red squirrels may be driven towards extinction in areas where grey squirrels act as reservoir hosts. The key factors that determined whether or not red squirrels became extinct in the model were the expansion rate of the grey squirrel, the infection and encounter rates.

Although historical evidence shows that reds have suffered local epidemics of disease in the absence of the grey squirrel, these outbreaks have not caused widespread extinction and probably burnt out rapidly in local populations, killing animals before the disease could spread to other populations. Given the apparent severity of the disease it is likely that parapoxvirus disease would have a similar effect on red squirrels while remaining benign in greys. The results of Rushton *et al*'s study suggest that with very low levels of infection, parapox rapidly spread to all members of the colonizing population i.e. grey squirrels. Thus low severity of the infection in grey squirrels allows it to spread rapidly through the grey squirrel population – the exact opposite of that seen with the red squirrel – enabling it to become a “widespread reservoir host for the disease” Rushton *et al.* (2000).



Figure 3.2. Dead red squirrel, killed by parapoxvirus (Corrie Bruemmer 2003)

Observations of interactions between red and grey squirrels suggest that direct physical contact is rare. It is possible that intraspecific transmission will occur at a higher rate than interspecific transmission because the probability of within-species physical contact is higher. The virus may be encountered passively from virus particles deposited in the habitat or nests, or via an arthropod vector. Both species use olfactory communication and leave scent marks throughout their home ranges for other individual to encounter. Red and grey squirrels both have scent glands on the side of the mouth and upper and lower lips. Scent marks are left by

face-wiping behaviour on the underside of large branches or exposed branches and roots. Anal dragging may also be used to leave scent. Small abrasions of the skin may facilitate virus uptake in these situations. It is interesting to note that red squirrels showing signs of disease have skin lesions on the toes, medial skin of the legs, genital area, underside of the body and facial area. Arthropod vectors, such as fleas, may be left in nests and could be involved. This requires further investigation. It is also possible that infection has unwittingly been transmitted by human intervention through the use of feeders, traps, hair tubes and hoppers in red squirrel conservation and both species observation programmes.

Whether the decline of the red squirrel is attributable to parapoxvirus infection carried by the grey squirrel rather than interspecific competition is relatively academic, because the common factor in both mechanisms is the grey squirrel (Rushton *et al.* 2000). The results for both suggest similar patterns of decline in red squirrel populations. Clearly there are insufficient data available at present to state with certainty that grey squirrels are the definitive reservoir host for parapoxvirus and that the virus could contribute to the extinction of the red squirrel in Britain. If further work is not done quickly to answer the questions raised above, it may be too late to have an influence on the future conservation of red squirrels in Britain.

Tompkins *et al.* (2003) consider that parapoxvirus has not been considered a major cause of red squirrel decline because infected individuals are rarely observed. They developed a generic (mathematical) model to show that parapoxvirus is likely to have played a crucial role in the red squirrel decline even though the prevalence of infection is low (as seen in Rushton's work above). Unless clinical symptoms are widely documented, parasites and pathogens are still often disregarded as a major cause of mortality. Tompkins *et al.* state that this is a fallacy – low visibility of disease need not indicate low importance and pathogens do not need to be highly prevalent to have regulatory effects on their host populations. Simulated models have indicated that competition alone cannot account for the rate and pattern of red squirrel decline and experimental infections have shown that the virus causes a deleterious disease in reds while having no detectable effect on the health of the grey squirrel.

Tompkins *et al.* (2003) show that parapoxvirus has potentially played a crucial role in the British red squirrel decline. Using a model they investigated the time taken to transform the disease-free red squirrel population equilibrium to either the disease-free grey squirrel population equilibrium (when considering competition-mediated replacement) or the grey squirrel population equilibrium with endemic infection (when considering competition and

/or infection-mediated replacement). The model was applied using the statistics available for the well-documented expansion of greys and decline of reds that occurred in Norfolk (UK)

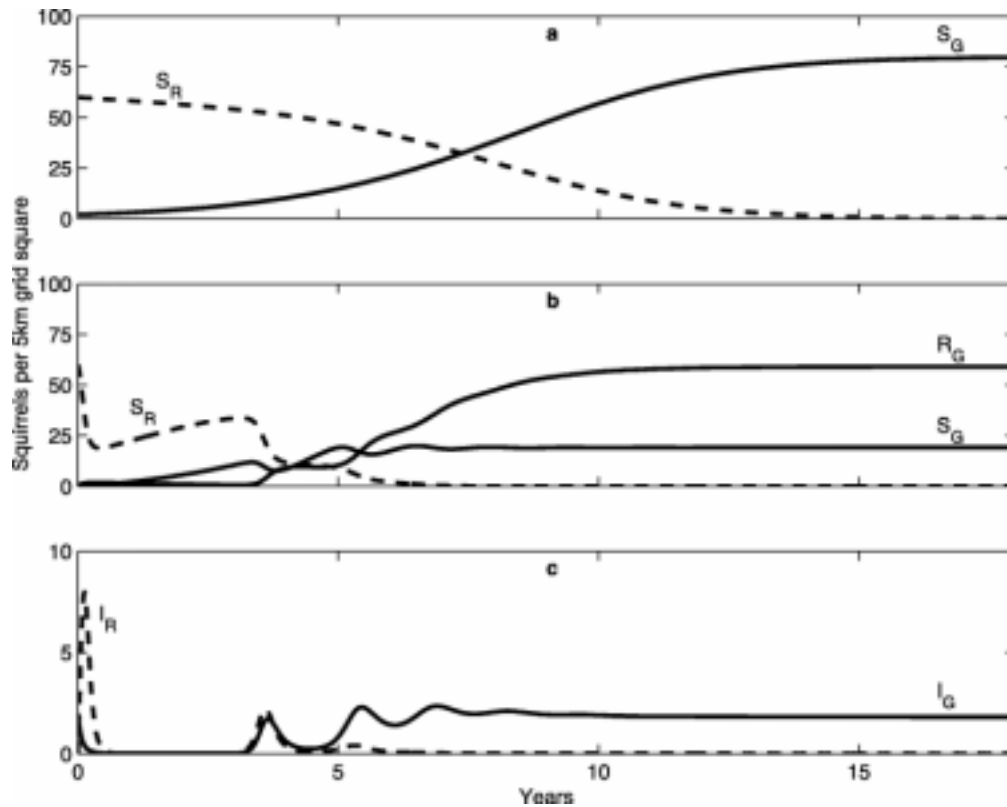


Figure 3.3. Results of a temporal (non-spatial) model of ecological replacement of red squirrels (dashed lines) by grey squirrels (solid lines). (a) shows competition scenario only; (b) and (c) show competition and infection scenarios. (Tompkins *et al.* 2003)

with a woodland cover of half-and-half coniferous and broadleaved trees.

In the competition only (non-spatial) model (Figure 3.3a), the rate of red squirrel decline is relatively slow with complete replacement by the greys occurring after 15 years (S_R = susceptible red; S_G = susceptible grey). In the competition and infection models (R_G = recovering grey) (Figures 3.3b & c), complete replacement of the red squirrel by the grey occurs within 6 years. Note 3b and c are from the same model output but the density scale in c has been expanded so the infected density classes (I_R = infected red; I_G = infected grey) can be observed clearly. The importance of the disease in causing a more rapid replacement of the red squirrel population is clear. Tompkins *et al.* (2003) postulate that without the virus, natural rates of competition alone cannot explain the red squirrel decline. They verify this by stating that the rate of ecological replacement generated by the spatial model (Figure 3.4),

which incorporates both interspecific competition and parapoxvirus, is very close to that seen in the actual Norfolk data.

Figure 3.4 shows the results from the spatial model compared with the actual red squirrel decline (dashed line), and grey squirrel expansion (solid line), observed in Norfolk (UK) from 1960 - 1982 (Reynolds 1985). The actual number of 5-km grid squares occupied by red and grey squirrel over this period is shown in (a). The output of the competition and infection model (b) closely fits the actual ecological (Tompkins *et al.* 2003) replacement observed.

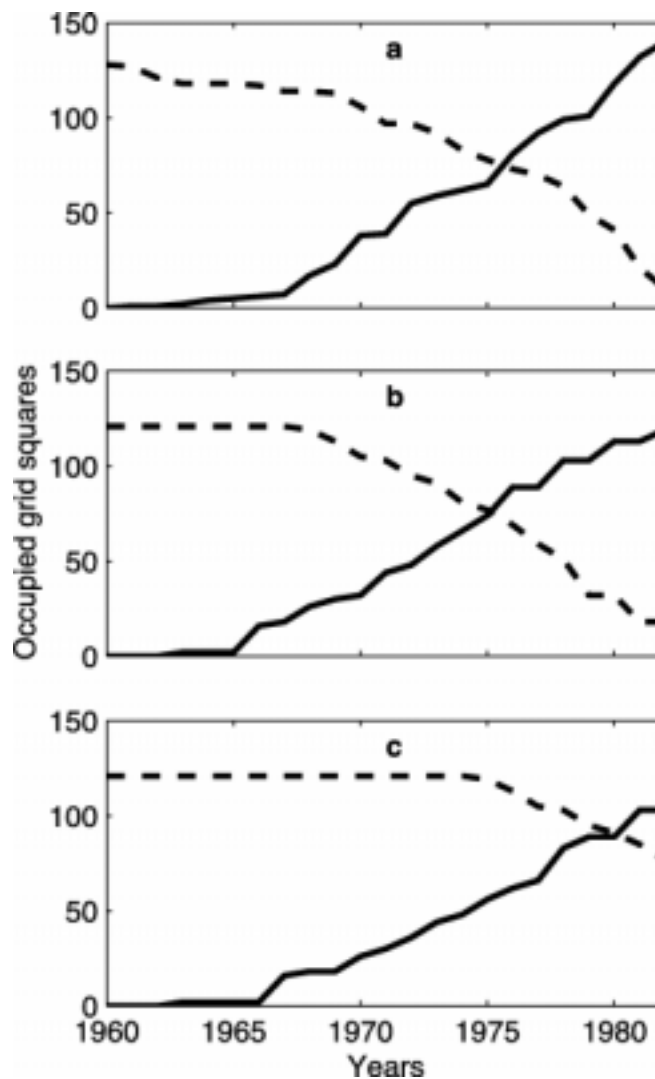


Figure 3.4. Results of a spatial model of ecological replacement of red squirrels (dashed line) by grey squirrels (solid line) in Norfolk, England. (a) is the actual replacement of reds by greys; (b) is the competition and infection model; (c) is competition only (Tompkins *et al.* 2003).

The output from the competition-only model (c) shows a slower decrease in the number of grid squares occupied by red squirrels. Tompkins *et al.* consider therefore that ecological replacement of reds by greys in the UK can only be understood in the light of an interaction between competition and disease (parapoxvirus). In addition, the prevalence of infection in their model is low (Figure 3.1c) although the role of disease is critical in determining the dynamics observed. This highlights how observational studies may incorrectly disregard the role of disease and would support Rushton *et al.*'s (2000) arguments seen above.

There may be additional competitive interactions that have occurred such as in years of good acorn crops it is possible for grey squirrels to reach very high densities that can destroy entire hazel crops (an important food resource for red squirrels) and therefore reduce squirrel survival. This unlikely to have occurred in Norfolk because the habitat is predominantly coniferous. However even if the competitive effect of grey on red squirrels is greater, parapoxvirus will still greatly accelerate the process of replacement and will have wide-ranging implications for the conservation of the remaining UK red squirrel population. For example the planting of large tracts of coniferous forest to connect groups of forest fragments in the north of England with those in southern Scotland to de-fragment habitat is generally considered beneficial for the red squirrel. It has also resulted in a substantial genetic mixing of Scottish and English red squirrel populations (Hale *et al.* 2001).

But parapoxvirus has yet to be recorded in Scotland and increased habitat connectivity can also increase the risk of pathogen transmission leading to the conclusion, say Tompkins *et al.* (2003), that de-fragmentation may ultimately do more harm than good. The conservation implications of this landscape management practice clearly need to be re-assessed. Invasions of exotic species and the subsequent impact on native flora and fauna are key issues in conservation biology. We have seen here that pathogens may play a greater role than is visually appreciated and should not be ignored. Recent occurrences of disease in UK agriculture are just one example. The effect of disease on wildlife would be even more costly to wildlife conservation because the facility of replacement once wildlife species are lost does not exist.