BTO Research Report No. 328

Impacts of Grey Squirrels on Woodland Birds: An Important Predator of Eggs and Young?

Authors

C.M. Hewson & R.J. Fuller

A report by the British Trust for Ornithology

June 2003

British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU
Registered Charity No. 216652

British Trust for Ornithology

Impacts of Grey Squirrels on Woodland Birds: An Important Predator of Eggs and Young?

BTO Research Report No. 328

C.M. Hewson & R.J. Fuller

Published in June 2003 by the British Trust for Ornithology
The Nunnery, Thetford, Norfolk, IP24 2PU, UK

ISBN 1-902576-70-5

LIST OF CONTENTS

Page No.

Summary

(1) The Grey Squirrel (*Sciurus carolinensis*) has become an abundant resident in much woodland in England, Wales and southern Scotland. The native Red Squirrel is smaller and typically occurred at far lower densities than the Grey. This, together with the fact that several woodland bird species have declined in recent decades has given rise to concern that the Grey Squirrel may have become a major predator of the eggs and young of songbirds in British woodland. This report presents a review of published and other evidence of the extent to which Grey Squirrels eat the eggs and young of woodland songbirds. It also considers other ways in which Grey Squirrels may interact with birds in British woodland.

(2) Squirrels, in general, are major nest predators of birds, both in North America and Europe. However, there is a lack of published information on the extent to which the Grey Squirrel in particular is an important predator. We are unaware of any long-term study of an open-nesting woodland bird in Britain that allows an assessment of the relative importance of predation by Grey Squirrels. Nor have we found any published North American study that clearly demonstrates that the Grey Squirrel has had a significant impact on nesting success of a bird within its natural range. This lack of published information should not be taken as evidence that Grey Squirrels do not act as significant predators of birds' nests.

(3) A large body of anecdotal / circumstantial evidence exists that Grey Squirrels frequently predate the nests of woodland birds in Britain. This is based on a survey of contributors to the BTO's Nest Records Scheme and on correspondence with other professional biologists and amateur naturalists. There appears to be considerable spatial variation in rates of predation and the perception of the importance of Grey Squirrel as a predator. It seems that there could, at least, be locally severe impacts on songbird breeding success.

(4) Two principal factors likely to cause this variation in predation rates by Grey Squirrels are differences in squirrel densities and the availability of alternative foods. It is also possible that individual squirrels may specialise on predating the nests of birds.

(5) The species potentially most at risk from Grey Squirrel predation are those that nest in the canopy, specifically Chaffinch (*Fringilla coelebs*) and Hawfinch (*Coccothraustes coccothraustes*). However, no species, even those nesting on the ground or in holes / nest boxes, are completely immune.

(6) In North America, squirrels and other rodents, are involved in complex ecosystem interactions whereby seed masting affects their abundance, with knock-on effects on numbers of their predators (birds of prey) and their prey (nests of songbirds). In addition there may be competitive interactions between mice and squirrels with implications for the relative importance of squirrels as predators. To our knowledge such ecosystem-level interactions have not been studied in British woodland; the fact that numbers of both mice and Grey Squirrels are affected by mast events raises the possibility that predation pressure by Grey Squirrels may vary in time as well as space.

(7) Grey Squirrels potentially compete with woodland birds for nest sites; this is especially true for species using large cavities or nest boxes. In some woods, anecdotal information suggests that rates of occupancy of cavities and nest boxes have been sufficiently high to prevent some species, such as Tawny Owl (*Strix aluco*), from breeding. Competition may also occur for food; Grey Squirrels consume large quantities of seeds and buds that may otherwise form food resources for seed-eating birds.

(8) Grey Squirrels may have the capacity to alter habitat structure and composition in terms of tree species through their effects on seed dispersal, seed predation and bark stripping. The implications for birds are, however, difficult to predict at present.

(9) In conclusion, there is no firm evidence that any of the national declines in woodland birds are caused by Grey Squirrel predation. However, there is a dearth of relevant research on the importance of Grey Squirrels as nest predators. It is possible that predation by Grey Squirrels could be acting in combination with other factors (e.g. deer impacts, reductions in woodland management, reductions in insect numbers) to limit numbers of some songbirds. Four areas of research are identified as especially important: (a) assessment of the importance of predation by Grey Squirrels relative to other predators and causes of nest losses; (b) removal experiments to assess the effects of reduction of Grey Squirrel numbers on breeding success and densities of woodland songbirds; (c) monitoring the density and breeding success of songbirds in relation to the spread of the Grey Squirrel in Italy; (d) further research on the diets, ranging behaviour and landscape structure on Grey Squirrels.

1. INTRODUCTION

Since its introduction from North America around the beginning of the 20th century, the Grey Squirrel (*Sciurus carolinensis*) has spread throughout much of Britain. It now occupies England, Wales, and much of southern Scotland (where its range continues to expand slowly) and it is common throughout much of its British range. Recent estimates have put the pre-breeding population at in excess of 2,500,500 individuals, with 2 million in England, 0.32 million in Wales and 0.2 million in Scotland (Harris *et al*. 1995). Nevertheless, it is predicted that its range will continue to spread and predicted climate changes are thought likely to result in increases in its abundance (Sparks & Gill 2002).

Unfortunately there is no information available on long-term changes in density within woodland but in many areas population densities have probably continued to rise for a considerable period after colonisation. Densities within woodland currently reach up to nine (and are typically greater than two) individuals per hectare but even this pales in comparison to the 14 per hectare that can be attained in urban areas (Macdonald & Barrett 1993, Harris *et al*. 1995). Its presence has not been universally welcomed. In addition to causing relatively minor "nuisance" damage to dwellings and installations, the Grey Squirrel widely causes serious damage to forestry due to its habit of stripping the bark from young trees, which can kill them (Kenward 1982, Gill *et al*. 1995). It is also increasingly vilified for its effects on wildlife, having been strongly implicated in the demise of the Red Squirrel (*Sciurus vulgaris*) in Britain (Usher *et al.* 1992, Gurnell & Pepper 1993, Macdonald & Tattersall 2003) and in Italy (Gurnell & Wauters 1999). Speculation has increased about its importance as a predator of birds' nests. Potentially, the impacts of Grey Squirrels as predators could be higher than those of Red Squirrels due to their larger body size and higher population densities. The body mass of Grey Squirrels is typically in the range 450 – 650 g compared with 250 – 350 g for Red Squirrels (Macdonald & Barrett 1993). The densities of Red Squirrels are typically 0.2 – 1.6 per ha compared with up to 9 per ha for Grey Squirrel after a good mast (Macdonald & Barrett 1993).

As introduced animals have only a short evolutionary history within the environments they invade, they often encounter competitors and prey that have not evolved defences against them. Furthermore, their natural enemies are usually absent, so they may have especially virulent effects on the ecosystems they invade (Pimentel 2002, Clay 2003). In this review, we outline some of the various ways in which the Grey Squirrel may impact upon birds in British woodlands and review the evidence for this.

A number of woodland bird species have shown worrying declines in range or abundance in recent decades (Gibbons *et al*. 1993, Baillie *et al.* 2001). This is reflected in a decline in government's headline indicator for woodland birds and the fact that several woodland species are now red-listed or amber–listed as Birds of Conservation Concern (Gregory *et al*. 2002). Amongst these species are Tree Pipit (*Anthus trivialis*), Spotted Flycatcher (*Muscicapa striata*), Nightingale (*Luscinia megarhynchos*), Song Thrush (*Turdus philomelos*), Willow Warbler (*Phylloscopus trochilus*), Willow Tit (*Parus montanus*), Marsh Tit (*Parus palustris*), Bullfinch (*Pyrrhula pyrrhula*) and Hawfinch (*Coccothraustes coccothraustes*). Nest predation by the Grey Squirrel has been proposed as one of several hypotheses explaining some of these declines (Vanhinsbergh *et al*. 2003).

In this report we review the evidence that Grey Squirrels are important predators of woodland birds, including reporting the results of a survey we carried out of some contributors to the BTO's Nest Record Scheme. In this survey we asked nest recorders to outline their perception of the prevalence and relative importance of nest predation by Grey Squirrels, what evidence they had to back up their view and what factors they thought were important in determining its impact. We examine some of the other ways in which the Grey Squirrel potentially impacts upon the indigenous birds of British woodland habitats, including competing for food and nest sites. We also consider the possibility that Grey Squirrels may be involved in complex ecological interactions between species within British woodland that may have indirect implications for birds. Although we concentrate on the Grey Squirrel, we discuss some other squirrel species, particularly the Red Squirrel, for comparative and background purposes.

2. NEST PREDATION BY SQUIRRELS – A REVIEW OF THE LITERATURE

In this section we summarise knowledge from the published literature about the role of squirrels in general as predators of birds.

For a long time the Grey Squirrel has been known to be at least an occasional predator of birds' eggs and young (Bailey 1923, references in Møller 1983). Birds and their eggs and young are not known to be a major dietary component in North America and are mentioned only in passing as "other food" by Koprowski (1994) (citing only Bailey1923), whilst Corbet and Harris (1991) make no mention of birds' eggs and young as food of Grey Squirrels, and Macdonald and Barrett (1993) list "occasionally insects and birds' eggs". Møller (1983) says "birds' eggs and young are eaten" by Grey Squirrels and also says that the Red Squirrel eats birds' eggs, young and even small adult birds (citing several references). The predation of full-grown birds could be a more likely event for the Red Squirrel on account of its greater agility but Eason (1998) saw a Grey Squirrel capture, kill and consume a fully-flighted female House Finch (*Carpodacus mexicanus*); whilst Montague and Montague (1985) witnessed a Blue Jay (*Cyanocitta cristata*) fledgling fall prey to one. It is clear, therefore, that the Grey Squirrel along with other squirrel species (e.g. Shaffer & Baker 1991), is clearly capable of capturing full grown birds as well as predating nests. Nonetheless, the point needs to be made that birds, and their nests and young, probably form a rather small part of the diet of the Grey Squirrel in most situations. The Grey Squirrel is a generalist feeder, rather than a specialist, and appears to exploit a wide range of food types depending on their relative availability and particular nutritrional requirements; both these factors may vary in time and space. We discuss factors that may influence variation in predation rates on birds below (section 4).

Squirrels in general are major predators of birds' nests in the USA. The American Red Squirrel (*Tamiascurus hudsonicus*) and Gray-necked Chipmunks (*Eutamias cinereicollis*) are primary nest predators according to Martin (1988, 1993, 1998), whilst Holmes (1990) reports that a camera showed most frequent predators in hardwood forest at Hubbard Brook, New Hampshire, were Eastern chipmunk (*Tamias striatus*), American Red Squirrel (*Tamiasciurus hudsonicus*), Flying Squirrel (*Glaucomys volans*), Blue Jay and Raccoon (*Procyon lotor*). The American Red Squirrel is a major predator of forest birds' nests in parts of the USA according to Reitsma *et al*. (1990). In Europe there is also a general recognition that squirrels can be important nest predators. Using plasticine eggs in deciduous forest fragments in Belgium, Nour *et al*. (1993) found that Red Squirrels were responsible for 45% of nest predation perpetrated by mammals. In European coniferous woodland, Shuttleworth (2001) found that Red Squirrels consumed "some Great Tit (*Parus major*) eggs and nestlings". Tomiałojć & Wesołowski (1990) listed the Red Squirrel as one of several important predators of birds in Białowieża Forest, Poland. Indeed, in 1988 in Białowieża Forest, Rob Fuller watched a nearly fully-fledged Chaffinch (*Fringilla coelebs*) being eaten alive by a Red Squirrel. Interestingly, squirrels may also scavenge, as well as predate, birds. Shorten (1954) noted that the Grey Squirrel sometimes eats dead birds, concentrating on the head of young birds and the crops of adults.

Clearly, squirrels in general are major nest predators but most of the evidence in the literature concerns squirrel species other than Greys. There is a dearth of quantitative published evidence as to whether the Grey Squirrel is indeed a serious predator with the potential to affect population levels of woodland birds. We are unaware of a single long-term systematic British study of on open-nesting woodland bird species (as opposed to nestbox populations which may generally be at less risk from squirrel predation) which could give an insight to the relative importance of Grey Squirrels as predators. More surprisingly, we have found no published North American studies that provide convincing evidence that the Grey Squirrel has had severe impacts on the nesting success of any species of bird. Although Tarvin and Garvin (2002) thought nest predation, possibly by Grey Squirrels, was the major cause of nest failure in Blue Jays in central Florida, they found no relationship between nesting success and Grey Squirrel relative abundance at any scale. (This does not exclude the possibility of Grey Squirrel culpability, however, since a few "specialist" individuals may have a disproportionate effect.). We stress that this absence of evidence does not mean that Grey Squirrels are not significant predators of birds, for few studies appear to have addressed this specific question on either side of the Atlantic.

3. NEST PREDATION BY GREY SQUIRRELS – ANECDOTAL AND CIRCUMSTANTIAL EVIDENCE

Circumstantial and anecdotal evidence has led to many naturalists implicating it as a voracious predator of birds' nests and eggs. For example, Monckton (1991), writing on the timing of GS control, says "…they are great egg eaters. If you allow squirrels during late March and you have a large stock of squirrels when you start baiting in April, then you will lose part of a generation of songbirds and most of your early pheasant and partridge nests". In this section we have drawn together a considerable amount of information and observations that broadly support the contention that predation by squirrels could be a significant factor in the productivity of birds at some locations at certain times.

The results of the survey of BTO nest recorders are summarised in Box 1. These indicate that Grey Squirrel nest predation is very widespread but that rates are variable. It is also clear from the responses that at some sites, other predators are thought to be more important than, or of similar importance to, Grey Squirrels. Great Spotted Woodpeckers (*Dendrocopos major*) and Weasels (*Mustela nivalis*) (and Pine Martens (*Martes martes*) within their range) in particular, followed by Jays (*Garrulus glandarius*), appear to be especially significant predators of woodland birds' nests. Open-nesting birds and ones using poorly constructed or dilapidated nest boxes appear to be at greatest risk from Grey Squirrels and these other predators, though birds using natural cavities are not immune to predation.

We have sought additional information from professional biologists and amateur naturalists who have undertaken studies on breeding woodland birds. This correspondence demonstrates that nest predation by Grey Squirrels can be a severe problem, at least on a local scale. Brian Cannell (*in litt.*) explains how at one farm in Norfolk, an overall nest predation rate of 85% for 134 nests of 38 open-nesting bird species in 1983 was reduced 5-10% in 1984 after Grey Squirrels were culled by shooting. All open-nesting species were affected, ranging from those nesting on the ground to those nesting in the canopies of trees. He also witnessed a similar change in nesting fortunes at another Norfolk estate after Grey Squirrels were culled (although initial nest predation rates were lower, at 80%, here). Apparently other mammalian predators were rare at these sites. Bill Grainger (*in litt.*) attributed a perceived decline in the abundance of open-nesting species such as thrushes and finches in Durham to the invasion of the area by Grey Squirrels, and noted that these species did not decline higher up Weardale where the Grey Squirrel did not invade. Chris du Feu (*in litt.*) noted that Stock Doves (*Columba oenas*) were eradicated from his garden by Grey Squirrels following the loss of his 'squirrel-controlling dog' but that they returned to breed once he instigated Grey Squirrel control.

There is no doubt that Grey Squirrels do eat the contents of avian nests and even birds away from nests on occasion. But how often does this happen, under what circumstances, and what are the impacts of this behaviour on woodland bird populations? It would appear from the limited available information that predation pressure from Grey Squirrels is variable from one location to another and it seems that there may, at least, be severe **local** impacts on certain species. This does not necessarily mean that predation by Grey Squirrels is driving large-scale (or even local scale) changes in population levels of birds because there may be several mechanisms by which bird populations could be buffered against increased predation (Newton 1993). In the next section we discuss the factors that may affect spatial variation in predation rates.

Box 1: Summary of responses from woodland nest recorders concerning predation by Grey Squirrels (GS). All these recorders were regular contributors to the BTO's Nest Record Scheme with each contributing data for a range of woodland species.

Responses: A total of 25 responses were received from nest recorders who have been examining nesting success of birds in woodland for >5 years. In 11 cases, the studies involved only nests in nest boxes. Of the 25 studies, 22 had GS in their study areas.

Perceived incidence of GS predation: Overall, 13 out of 25 studies suspected GS predation had occurred. Of the 12 out of 25 studies which were not based solely on nest boxes, and which had GS in their study areas, nine believed that it occurred and seven of these considered they had proved it.

Evidence: Of the 13 people who suspected predation by GS, four had actually witnessed it taking place, five thought nests pulled out or pulled apart was caused by GS and four provided no supporting evidence or thought it likely based on circumstances.

Relative importance of GS compared with other predators: No-one provided quantitative evidence that GS was a serious nest predator, especially compared to other nest predators. Only one said explicitly that the Grey Squirrel was the most serious nest predator. In three to four cases, it was thought they were a serious menace with a major impact, based largely on circumstantial evidence (one of these says it has biggest impact due to the numbers of GS). Examples of estimated levels of predation by GS in particular woods are as follows:

- 4-7% of occupied nest boxes by Blue Tit (*Parus caeruleus*), Great Tit, Pied Flycatcher (*Ficedula hypoleuca*) and Redstart (*Phoenicurus phoenicurus*) (Stirling)
- 17 & 27% of total nest failures of tits in nest boxes in two different years (Notts)
- 3-6% of open nests, including Chaffinch, Greenfinch (*Carduelis chloris*) and thrushes (Notts)
- 8-10% of Long-tailed Tit (*Aegithalos caudatus*) nests (Yorkshire).
- 0.02% of nesting attempts of Blue Tit in nest boxes (North Wales)

4. FACTORS INFLUENCING VARIATION IN NEST PREDATION RATES BY GREY SQUIRRELS

A range of factors could be responsible for variation in predation rates by Grey Squirrels. These include: (1) the local density and distribution of the squirrels, (2) the behaviour of individual squirrels, (3) the availability of alternative food, (4) the behaviour of the nesting birds themselves. We consider each of these in turn.

First, predators are often patchily distributed. Holmes (1990) noted that at Hubbard Brook, nest predation was often patchy in space, and that artificial eggs may be taken in one place but untouched in another. He attributed this to the patchy distribution of particular predators. It is unlikely that Grey Squirrels will be evenly distributed either between or within woodlands. The highest densities of Grey Squirrels are usually found in habitats containing relatively large quantities of large-seeded trees (Oaks, (*Quercus* spp.) Beech (*Fagus sylvatica*), Sweet Chestnut (*Castanea sativa*), Hazel (*Corylus avellana*)). However, these habitats may be relatively rich in plant food for squirrels which may mean that they resort less frequently to predating birds' nests. This may mean that simple linear relationships between squirrel density and predation rate may not apply.

It is possible that food supplies can influence Grey Squirrel population sizes in different ways. Population sizes may depend on food supplies, either natural food such as mast crops in the previous autumn (Gurnell 1989, McShea 2000, Smith 2001) or supplementary food provided by humans. The Birklands Ringing Group in Nottinghamshire report that rates of songbird nest failure are high around Centre Parks village, where the Grey Squirrel population is very high on account of supplementary feeding by people. Chris du Feu (*in litt.*) says that Grey Squirrel nest predation is very variable between years and thinks this is down to population sizes of the squirrels combined with abundance of alternative prey.

Landscape structure affects the relative abundance of different types of predator (Andrén 1992, 1995). It is unclear, however, to what extent this applies to the Grey Squirrel. There is a considerable body of evidence indicating that predation rates on bird nests are often relatively high at the interface of farmland and forest, though this appears often to be a consequence of avian predators that are primarily associated with the surrounding farmland (Paton 1994, Andrén 1995, Chalfoun *et al*. 2002). Predation rates at edges within forests, for example between clearcuts and mature stands, do not appear to be generally so high (Bayne 1997, Cotterill 1999, Song 1999, Tittler 2000, Ibarzabal 2001, Rodewald 2001). In general there is a need to learn more about how Grey Squirrel abundance is affected by the size and fragmentation of woodland in British landscapes.

Secondly, the behaviour of individual Grey Squirrels may vary and nest predation rates may be very high locally on account of the behaviour of a single or a few Grey Squirrels. Southern (1964) mentions one Grey Squirrel that learnt to stalk and catch full-grown House Sparrows (*Passer domesticus*), for instance! Shelley Hinsley (pers. comm.) says that Grey Squirrel predation rates on nest boxes vary within Monk's Wood and that all the nest boxes within the territory of a single Grey Squirrel may be systematically attacked at times. (This may be related to shortages of alternative foods).

The third factor affecting spatial variation in predation by Grey Squirrels may be the availability of alternative foods. The spectrum of food available to a potential nest predator at any one time will influence nest predation rates (Schmidt 1999). It is widely recognised that the preferred food of the Grey Squirrel is the seeds of trees and that animal matter, including insects and the contents of birds' nests, is taken less frequently. Tree seeds are likely to be least available in spring and summer, once the previous autumn's crop has been exhausted and before trees have set seed for the year. It is possible that in woods where this food shortage is especially acute, birds' eggs and young become an important food of Grey Squirrels. Chris Knights (pers. comm.) says that he has observed Grey Squirrels switch to behaviour he interprets as nest searching in the summer at times of drought. It may be that some alternative foods such as insects become less available in such conditions, leading

to this prey switching. It is unclear, however, to what extent any such food switching in the Grey Squirrel represents an adaptive response to changing demands during the annual cycle, rather than a response to environmental constraints. For instance, it is possible that lactating female Grey Squirrels may experience increased calcium demand that can be satisfied by deliberately switching to eggs and nestlings.

Fourthly, variation between woods in the abundance and habitats and nest sites used by a species will affect predation risk. Schmidt (1999) suggests that nest predation generally will be highest when the density of active nests is highest and when there is a food shortage for birds as the adults may be less vigilant and their young may be more noisy, attracting attention. The characteristics of birds' nests, such as their location within the wood, site within the habitat, their physical appearance and their construction, influence how easily a predator such as the Grey Squirrel can find them and access their contents. For instance, Brian Cannell (*in litt.*) suggests that nests within dense Hawthorn and Blackthorn thickets suffer lower predation rates because Grey Squirrels cannot readily access the interior of these sites to search for nests. So the nature of nesting sites available to birds within a wood could affect Grey Squirrel predation rates. Martin and Roper (1988) and Yahner and Morrel (1991) both suggested that the density and diversity of understorey vegetation could affect the ability of predators to locate nests.

The threat of nest predation can also drive the evolution of nest site characteristics in birds, such as where open nesters choose to place their nests within the vegetation (Martin and Roper 1988) and the characteristics of holes used by hole-nesters (Wesołowski 2002), through affecting the success of nests placed in different locations.

Since the behaviour and other characteristics of potential nest predators differ, it is likely that the predator spectrum found at any one location can have an effect on evolution of nest site characteristics. As the Grey Squirrel is not native to Britain, birds may not have adapted to its particular style of nest predation and may therefore be more vulnerable to predation from it. It is also possible that the Grey Squirrel has already caused a shift in nest characteristics of some species, if predation is a significant selective force.

5. WHICH SPECIES MIGHT BE MOST VULNERABLE TO GREY SQUIRREL PREDATION?

Interactions between the vulnerability of nests and both the foraging behaviour and habitat preferences of nest predators will influence species-specific predation rates. It is likely that the characteristics of the nests of different bird species will lead to differences in their detectability and accessibility to nest predators. Two examples concerning differential effects of North American squirrels on birds are as follows. Rangen (1999) found that squirrels usually raided nests positioned above ground in habitats with relatively few shrubs but high densities of trees. This reflected a situation where high nest exposure was combined with high squirrel abundance. Norment (1993) found that 34% of Harris' Sparrow (*Zonotrichia querula*) nests in Alaska were depredated, mostly by Arctic Ground Squirrels (*Spermophilus undulates*), but no White-crowned Sparrows (*Zonotrichia leucophrys*) were predated, possibly due to the fact that Harris' Sparrows nest in more open locations.

Grey Squirrels spend a large proportion of their time foraging high up in trees, although they also forage in a wide variety of locations all the way down to the woodland floor. Based on his experiences in Białowieża Forest, Ludwik Tomiałojć (*in litt.*) has suggested that Hawfinches and Chaffinches, species that place their nests in forks within the crowns of trees, might suffer particularly high predation of their nests by squirrels. The Chaffinch is generally one of the most abundant breeding woodland birds in Britain but occasionally one finds woods where they are surprisingly rare or absent. One example concerns Sweet Chestnut coppice in Oaken Wood, Kent where Mrs. M. Wilkinson (*in litt.*) suggests that the cause may be nest predation by Grey Squirrels. She has found many Chaffinch nests in the gardens and orchards surrounding the wood and despite being well camouflaged, all had had nestlings taken from them and often the nests had been pulled to pieces during predation, presumed to be by Grey Squirrels. Caution is needed in interpreting such cases, however, for Chaffinch densities in other areas of Sweet Chestnut are low (Fuller & Moreton 1987) and it is possible that the habitat is sub-optimal for the species.

Ludwik Tomiałojć (*in litt.*) says that in Białowieża Forest, Poland, Hawfinches have low breeding success (17-30%, once even 10%) compared to secondary habitats across Europe (30-71%). He attributes this to the presence of high numbers of nest predators. The Jay is the most important predator of the species there, followed by Common Buzzards (*Buteo buteo*) and Red Squirrels. He believes the Grey Squirrel may be responsible for the decline of the Hawfinch in Britain (Langston *et al.* 2002) since its larger size would make it a stronger predator of nest contents than the Red, and that its densities in English woods may be up to 10 times those of the Red in Białowieża, leading to it having a pervasive predatory effect throughout the canopies of British woods. It is possible, therefore, that the Grey Squirrel might have a devastating effect on the Hawfinch populations of mainland Europe when and if it spreads from its toehold in northern Italy. It would be interesting to see what Hawfinch nest predation rates are like in northern Italy now that the Grey Squirrel is established. The view that Grey Squirrel is responsible for the Hawfinch decline in Britain has become widespread although it should be noted that it is also very vulnerable to the Jay (L. Tomiałojć *in litt.*, J. Lewis *in litt.*).

Bill McShea, a forest ecologist from the Smithsonian Institute, considers that much predation from Grey Squirrels in North America is likely to occur high in the canopy rather than on or near the ground where most nest predation studies are conducted (pers. comm.) and suggests that Scarlet Tanagers (*Piranga olivacea*), a canopy-nesting species, will be especially vulnerable. However, Grey Squirrels could also be potentially important predators on species that nest much closer to the ground. Leimgruber *et al*. (1994) recorded Grey Squirrel predation of artificial nests placed on the ground and suggest that as the Grey Squirrels found a large number of the artificial nests that were used, they could well be important predators of passerine birds.

Finally, the defences that birds have against Grey Squirrel will also influence the rates of predation, although anecdotal evidence of active, aggressive defence by birds suggests it meets with variable success. John Clarke (*in litt.*) says that he has observed a pair of Spotted Flycatchers successfully

defending their nest against attempted Grey Squirrel predation. Chris du Feu (*in litt.*) has found the remains of a Grey Squirrel, which he believes attempted to predate a Tawny Owl (*Strix aluco*) nest, in the owl's nest box! On the other hand, Ludwik Tomiałojć (*in litt.*) recounted a vivid account of an heroic but ultimately unsuccessful attempt by a pair of Hawfinches (*Coccothraustes coccothraustes*) to stave off the predatory advances of a Red Squirrel in Białowieża Forest. He witnessed a Red Squirrel predating a nest with half-grown Hawfinch nestlings, and that… "in spite of a short defence by the Hawfinch female, which hit the squirrel with her body kamikaze-style (but then disappeared), the squirrel returned to the Hawfinch nest and killed the nestlings one-by-one, which it later hung in forks of the spruce branches."

6. COMPLEX ECOSYSTEM INTERACTIONS: INDIRECT EFFECTS

Interactions occurring between components of woodland ecosystems can be complex. Fluctuations in the main food resources of rodents, including both mice and squirrels, can drive nest predation rates indirectly, via their influence on competitive and predator-prey relationships within the system. For example, Schmidt and Ostfeld (2003) found that high rodent densities following mast production of acorns, can result in increased nest predation for Veeries (*Catharus fuscescens*), Red-eyed Vireos (*Vireo olivaceus*) and Wood Thrushes (*Hylocichla mustelina*) in Hudson Valley, New York. However, the rodent densities also increased hawk densities, which subsequently led to higher predation of these birds by hawks during periods of low rodent density. So these songbirds fared best when rodent densities were intermediate, when neither hawk predation nor rodent nest predation was most intense.

Indirect interactions of this kind could be important in determining responses of some birds to Grey Squirrel abundance. One possible relevant interaction involves Goshawks (*Accipiter gentilis*) that predate both squirrels and birds (Petty *et al*. 2003, S. Newson pers. comm.). Grey Squirrel numbers are influenced by masting events and this may affect Goshawk productivity and population sizes in subsequent years. Where Grey Squirrel populations subsequently decline due to a failure of the mast, birds may then experience increased predation by Goshawks. We emphasise that this is pure speculation.

In West Virginia, McShea (2000) showed that numbers of Grey Squirrels (and other small mammals) correlated with acorn mast production. Artificial nest predation rates were related to acorn crop size but not to rodent abundance *per se*, possibly because predation of the model nests was caused by both small mammals and medium-sized carnivores, for which small mammals are alternative prey, and because the methods under-estimated predation by the small mammals. But the index of abundance for two understorey birds across the state (Worm-eating *Helmitheros vermivora* and Hooded *Wilsonia citrina* Warblers) was negatively correlated with mast production with a two-year time lag, suggesting that they may have pulsed productivity in response to mast failure and subsequent release from nest predation pressure. McShea (2000) also suggested that as deer compete with Grey Squirrels and other small mammals for acorns, they may reduce the populations of these (and therefore their nest predation impact) where acorns are scarce and limiting, but not where or when acorns are more abundant.

Schmidt (2001) found that White-footed Mice (*Peromyscus leucopus*) were the strongest nest predator due to their numbers, compared to Eastern Chipmunks, and their removal had the biggest effect on nest predation rates. However, because mice depleted alternative food sources, non-mice nest predators were found where mice densities were lowest and were then responsible for causing nest predation rates that were greater than those found where mice were abundant. Interestingly, Chris du Feu (in litt.) has suggested that Wood Mice (*Apodemus sylvaticus*) were a problem for nesting birds in Tresswell Woods, Nottinghamshire. It is possible that they and Grey Squirrels interact in some British woods such that predation rates by squirrels may be influenced by Wood Mouse abundance via its effect on the availability of other foods, such as tree seeds.

In conclusion, it is possible that levels of predation by Grey Squirrels may not be constant at any one location. Availability of food (mast) may affect numbers not only of squirrels but also of their competitors (mice) and their predators (birds of prey). This could lead to complex temporal patterns of predation by Grey Squirrels on birds in British woodland.

In a rather different vein, Grey Squirrels and some bird species share common predators in some areas. For instance, Goshawks eat squirrels, both Red (Petty *et al*. 2003) and Grey (S. Newson, pers. com.). Some squirrels are known to produce predator-specific alarm calls (Macedonia 1993), which could provide birds with warnings of approaching danger if they learn to recognise them. It is therefore possible that positive interactions may also occur between squirrels and birds, and that some of the interactions that the Grey Squirrel has with the birds it shares its habitat with may be more subtle and complex than is presently known.

7. COMPETITION FOR RESOURCES

Grey Squirrels may compete with birds for various resources, including food and places to nest. It is very common for Grey Squirrels to monopolise food provided for birds in gardens, especially peanuts from feeders - the advent of the squirrel-proof peanut feeder is testimony to their dominance, persistence and ingenuity! Such ready-made caches of nuts clearly prove irresistible to Grey Squirrels, as do caches of seeds which have been created by other birds. The squirrels are able to use their sense of smell to locate acorns hidden by Jays, for instance. Goodwin (2002) tells how Grey Squirrels frequently take acorns which Jays have hidden even well away from Oaks or trees of any kind, and describes an instance of a Jay trying to relocate the acorns it had hidden in a lawn after realising a Grey Squirrel was "on to it". The Grey Squirrel, however, soon chased the Jay away from the scene. In woodland habitats, Grey Squirrels consume large quantities of seeds and buds that may otherwise form important food resources for birds such as Nuthatch (*Sitta europaea*), Bullfinch and Hawfinch.

Our survey of participants to the BTO's Nest Record Scheme illustrates that the Grey Squirrel is also an effective competitor with large birds for places to nest. Ten respondents voiced concerns over Grey Squirrels occupying larger nest boxes, provided primarily for Tawny Owls, but also for Kestrels (*Falco tinnunculus*), Jackdaws (*Corvus monedula*), Stock Doves, Starlings (*Sturnus vulgaris*), Goosanders (*Merganser merganser*) and Mandarins (*Aix galericulata*). Grey Squirrels will apparently even kill the occupants of nest sites to gain possession of them, as well as eating their eggs (Counsell 1998, B. Cannell *in litt.*). In the USA, Grey Squirrels are known to do the same at platforms provided for Cooper's Hawks (*Accipiter cooperii*).

Rates of occupation of potential nest sites by Grey Squirrels are often very high and it is likely that this problem is ubiquitous where the squirrels are common. Apparently all large nest boxes are often occupied by Grey Squirrels and sometimes they commandeer boxes after birds had commenced breeding and too late for the birds to re-nest. Several observers believed that rates of occupation of nest boxes and natural holes by Grey Squirrels were so high that some birds, such as Tawny Owls, have been prevented from breeding. Open-nesters are not immune to such interference. For instance, Brian Cannell (*in litt.*) once saw a Grey Squirrel eat the eggs in a Rook's (*Corvus frugilegus*) nest and build its dray on top of the nest!

The population-level consequences of this will depend on a variety of factors, including how prevalent such instances are under natural circumstances, how often this behaviour curtails the breeding attempts of individual birds and how important breeding success is relative to other factors limiting the fitness of each bird species. Such nest site competition can be very important under some circumstances. For instance, in the USA it was found that removal of Southern Flying Squirrels lifted competition for nesting cavities and allowed recovery of a population of an endangered bird, the Red-cockaded Woodpecker (*Picoides borealis*) (Franzeb 1997), whilst Loeb (1997) found that providing an excess of nest boxes reduced competition for cavities between the squirrels and woodpeckers.

Seed predation by squirrels may have more subtle consequences for birds. Benkman (1995) shows that the co-evolutionary arms-race between bird-dispersed pine trees and their American Red Squirrel seed-predators can constrain the evolution of large kernels and divert the trees' resources to seed defences, thus reducing the resources available to the birds such as the corvids which disperse these seeds. Benkman (1999) has also shown that in North America the squirrels are effective pre-emptive competitors of Red Crossbills (*Loxia curvirostra*) for pine seeds.

8. "HABITAT ENGINEERING"

Squirrels can affect the environment of birds in a variety of other ways. Caching behaviour can promote the dispersal and germination of tree seeds, whilst predation of seeds can limit regeneration. Both of these processes could affect the regeneration and dynamics of the woodlands and the quality of habitats available to birds. Although it is not known to what extent Grey Squirrels affect regeneration over and above the effects of other seed predators and dispersers, it is thought that they have a negative effect and can severely reduce regeneration of Oak, Beech and Sycamore (*Acer pseudoplatanus*) (Gill *et al*. 1995 and references therein). Hulme (1999) said that Grey Squirrels may be among seed predators that remove significant amounts of Ash (*Fraxinus excelsior*), Yew (*Taxus baccata*) and Elm (*Ulmus* spp.) seeds from woods in Durham, affecting patterns of regeneration of the Elms. The Grey Squirrel is unlikely to be a vital seed disperser of native trees due to their lack of co-evolutionary history, although it may have taken on a role played by the Red Squirrel. Seed dispersal by birds is likely to be more critical due to the possibility it creates for long-distance dispersal. Dispersal distance may be an increasingly important factor determining the capacity of plant species to adapt to climate change through occupying new geographical areas with suitable climatic conditions.

Bark stripping can provide an entry point for fungal attack (Gill et al 1995), which could ultimately influence the habitat for woodpeckers and other saproxylic species. The knock-on effects of such damage can be both subtle and complex and could even increase the local diversity of bird species (Daily *et al*. 1993).

In the long-term, it is possible that Grey Squirrels could have consequences for the tree species composition of some British woods. This might come about due to a shift in planting strategy to avoid species especially favoured by squirrels or as a result of effects on the dispersal and survival of trees. Surprisingly little is known about the preferences of individual tree species by birds in European forests (Fuller 1995). This makes it extremely difficult to predict the effects on birds of any long-term changes in tree species composition. It does appear, however, that Sycamore is a preferred feeding tree for insectivorous birds because of the high abundance of aphids associated with it; for this reason, the presence of some Sycamore in a wood may be beneficial to birds (Fuller 1995).

9. CONCLUSIONS AND FURTHER RESEARCH NEEDS

It is clear from the information accumulated for this review, that Grey Squirrels do predate the nests of a wide range of bird species both in North America and Britain. The species most at risk appear to be ones that have open nests positioned in the canopy although birds that use lower nest sites, including the ground, are by no means immune. However, it is not clear how ubiquitous this phenomenon really is; based on the scant evidence available there appears to be considerable variation from one wood to another. There is little hard information giving an insight as to the likely causes of this spatial variation but we suggest that it is likely to relate mainly to (a) to variation in Grey Squirrel abundance and (b) to the availability of alternative foods.

There is no firm evidence to link the national declines that are occurring in several woodland species directly with predation by Grey Squirrels. An exception, however, may be the Hawfinch. Whether Grey Squirrel predation is suppressing or reducing population levels of woodland birds more generally will be an extremely difficult question to answer. Whilst nest predation is often thought to be the most important factor limiting the breeding productivity of birds (Martin 1992, Heske *et al*. 2001) its effects on population levels are extremely difficult to determine (Newton 1993). Bird populations can be buffered, at least up to a point, against increasing predation pressure by several mechanisms including compensatory mortality and the availability of a surplus of non-breeding individuals that can be recruited into the population (Newton 1993). The situation with the Grey Squirrel is perhaps rather different to that with several other predators that have increased in recent years because it is an introduced species that has several different characteristics to our native Red Squirrel. We feel that there is a need to understand more clearly the impacts of the entire suite of potential predators on breeding woodland songbirds.

Some argue that Grey Squirrels are unlikely to be important predators of woodland birds. For example, J. Gurnell (quoted by Counsell 1998) says that "squirrels are opportunistic feeders and will take eggs and nestlings occasionally, but these are not significant items in their diet, nor do they constitute an important mortality factor for bird populations….. I remain to be convinced that they are significant predators of wild bird populations." This view is perhaps too sanguine. Even if Grey Squirrels in isolation are not a generally significant factor in driving widespread declines, they could be one of several factors acting in combination to place some woodland birds under serious pressure. In a review of the declines in woodland birds, Vanhinsbergh *et al*. (2003) have identified several strong candidate factors. These include (a) habitat deterioration as a consequence of intensified browsing by deer, (b) reduction in habitat quality at woodland edges, (c) reduction in woodland management, (d) changes in the availability of insect food. It is possible that these factors, together with increasing predation pressure from Grey Squirrels, could be acting in various combinations on population levels of some woodland birds.

There is a general dearth of quantitative information on the role of Grey Squirrels as nest predators, both in Britain and in North America. This needs to be rectified through three types of field research as follows.

(1) Autecological work on selected bird species is needed to assess the relative importance of predation by Grey Squirrels, compared with other predators and causes of nest losses. This work ideally needs to take place across a range of Grey Squirrel densities and in a variety of woodland types to establish more fully the spatial variation in predation rates. Appropriate target species include Blackbird (*Turdus merula*), Song Thrush and Chaffinch. Finding nests of Chaffinch, especially high in the canopy, is of doubtful practicability. Therefore we suggest that extensive use should also be made of artificial nests. It is suggested that the study should examine whether predation rates differ with distance from external and internal woodland edges, and (if resources allow) whether they differ with age of woodland stand. As part of this study there is a need to develop methods of detecting signs of Grey Squirrel predation with greater certainty (several observers have commented that the field signs left by Grey Squirrels are not clearly documented).

(2) A removal experiment is highly desirable in which the breeding performance of birds is compared in woodland areas in which Grey Squirrels are eradicated with areas where they are not controlled. After a period of time the treatments would be switched. Predator control experiments involving effects on Grey Partridge (*Perdix perdix*) breeding success would form a useful model (Tapper *et al*. 1996). It should be acknowledged, however, that there are several difficulties that would need to be surmounted in order to undertake a valid experiment. Firstly, it would be necessary to match experimental and control sites very closely by habitat and the suite of predators. This could be difficult as study plots will need to be at least 10 ha in order to obtain a reasonable sample of nests (though artificial nests could be used as well as real nests). Second, a series of replicates is vital. This is essential given the apparent spatial variation in Grey Squirrel predation identified in the present review. It may be possible to combine a removal experiment with the type of work suggested under (1) above. However, we suggest that undertaking an initial study of type (1), effectively as a pilot for say two years, would provide information that would assist greatly in designing the most effective type of removal experiment.

(3) The Grey Squirrel was introduced into northern Italy in 1948 (Macdonald & Barrett 1993). This creates an opportunity to assess whether predation rates and densities of songbirds change as woodland becomes colonised by the species.

(4) There is a need for more research on the ecology of Grey Squirrels themselves. This would involve (a) examining diets in different habitats, (b) seeking to understand the ranging behaviour of Grey Squirrels at different scales, (c) documenting the effects of landscape structure on Grey Squirrel abundance, in particular the effects of woodland size and dispersion.

Acknowledgements

We thank a number of private woodland owners and Woodland Heritage for funding this project.

Greg Conway provided valuable assistance with the preparation of references.

We are very grateful to the contributors to the BTO's Nest Record Scheme who provided valuable information by responding to our questionnaire: John Clarke, James Cobb, Bob Danson, N. and P. Fenwick, Chris du Feu, Dave Francis, Bill Grainger, Peter Johnson, Jerry Lewis, John Lloyd, Andrew Lowe and Birklands Ringing Group, R.N. Macklin, Merseyside Ringing Group (Steve Binney, Pete Coffey, Dave Norman, Neville Powell and Ed Samuels), A.B. Old, Henry Robb, Mike Rogers, Ian Spence, Bob Swann, David Warden and John Walshe.

We also thank the following for valuable information used in this report: Brian Cannell, Andy Gosler, Shelley Hinsley, Ian Kinley, Chris Knights, Bill McShea, Stuart Newson, Ludwik Tomiałojć and Mrs. M. Wilkinson.

References

Andrén, H. (1992) Corvid density and nest predation in relation to forest fragmentation. A landscape perspective. *Ecology*, **73**, 794-804.

Andrén, H. (1995) Effects of landscape composition on predation rates at habitat edges. Pp. 225-255. In *Mosaic Landscapes and Ecological Processes* (eds L. Hansson, L. Fahrig, & H.G. Merriam). Chapman & Hall, London, UK.

Bailey, B. (1923) Meat-eating propensities of some rodents of Minnesota. *Journal of Mammalogy*, **4,** 129.

Baillie, S.R., Crick, H.Q.P., Balmer, D.E., Bashford, R.I., Beaven, L.P., Freeman, S.N., Marchant, J.H., Noble, D.G., Raven, M.J., Wernham, C.V. & Thewlis, R. (2001) *Breeding Birds in the Wider Countryside: their Conservation Status 2000*. BTO Research Report No. 252. British Trust for Ornithology, Thetford. See http://www.bto.org/birdtrends.

Bayne, E.M. (1997) Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology*, **11,** 1418-1429.

Benkman, C.W. (1995) The impact of tree squirrels (Tamiasciurus) on limber pine seed dispersal adaptations. *Evolution*, **49,** 585-592.

Benkman, C.W. (1999) The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *American Naturalist*, **153,** S75-S91.

Chalfoun, A.D., Thompson, F.R. & Ratnaswamy, M.J. (2002) Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology*, **16**, 306-318.

Clay, K. (2003) Parasites lost. *Nature*, **421,** 585-586.

Corbet, G.B. & Harris, S. (1991) *The Handbook of British Mammals.* Blackwell Scientific Publications.

Cotterill, S.E. (1999) No evidence of short-term effects of clear-cutting on artificial nest predation in boreal mixedwood forests. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere*, **29,** 1900-1910.

Counsell, D. (1998) Predation of nesting Stock Doves by Grey Squirrels. *Nest Record News*, **14**, 17.

Daily, G.C., Ehrlich, P.R. & Haddad, N.M. (1993) Double keystone bird in a keystone species complex. *Proc. Natl. Acad. Sci. USA*, **90**, 592 – 594.

Eason, P.K. (1998) Predation of a female House Finch, *Carpodacus mexicanus*, by a Grey Squirrel, *Sciurus carolinensis*. *Canadian Field-Naturalist*, **112,** 713-714.

Franzreb, K.E. (1997) Success of intensive management of a critically imperiled population of Red-cockaded Woodpeckers in South Carolina. *Journal of Field Ornithology*, **68,** 458-470.

Fuller, R.J. (1995) *Bird Life of Woodland and Forest.* Cambridge University Press, Cambridge.

Fuller, R.J. & Moreton, B.D. (1987) Breeding bird populations of Kentish sweet chestnut (*Castanea sativa*) coppice in relation to age and structure of the coppice. *Journal of Applied Ecology*, **24**, 13-27.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991*. Poyser, London, UK.

Gill, R.M.A., Gurnell, J. & Trout, R.C. (1995) Do Woodland Mammals Threaten the Development of New Woods? In *The Ecology of Woodland Creation*, (ed. R. Ferris-Khan). Wiley and Sons Ltd.

Goodwin, D. (2002) Interactions between Eurasian Jays and Grey Squirrels. *British Birds*, **95,** 531-532.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Proctor, D.A., Gibbons, D.W & Galbraith, C.A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. *British Birds*, **95**, 410-450.

Gurnell, J. (1989) Demographic implications for the control of grey squirrels. In *Mammals as Pests.* (ed. R.J. Putman) pp 186 – 190. Chapman and Hall, London.

Gurnell, J & Pepper, H. (1993) A critical look at conserving the British red squirrel (*Sciurus vulgaris*). *Mammal Review*, **23**, 127-137.

Gurnell, J. & Pepper, H. (1998) Grey Squirrel damage to broadleaf woodland in the New Forest: A study on the effects of control. *Quarterly Journal of Forestry*, **92**, 117-124.

Gurnell, J. & Wauters, L. (1999) *Sciurus carolinensis.* In *The Atlas of European Mammals*. (eds A.J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Krystufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Voralik and J. Zime). Poyser Natural History, London.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A Review of British Mammals: population estimates and conservation status of British mammals other than cetaceans*. JNCC, Peterborough**.**

Heske, E.J., Robinson, S.K. & Brawn, J.D. (2001) Nest predation and neotropical migrant songbirds: piecing together the fragments. *Wildlife Society Bulletin*, **29,** 52 – 61.

Holmes, R.T. (1990) The structure of a deciduous forest bird community. In *Biogeography and Ecology of Forest Bird Communities* (ed. A. Keast).

Hulme, P.E. (1999) Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology*, **145,** 149-156.

Ibarzabal, J. (2001) Lack of relationship between forest edge proximity and nest predator activity in an eastern Canadian boreal forest. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere*, **31**, 117-122.

Kenward, R.E. (1982) Bark-stripping by Grey Squirrels - some recent research. *Quarterly Journal of Forestry*, **76** (2), 108-121.

Koprowski, J.L. (1994) *Sciurus carolinensis*. In: *Mammalian Species*. American Society of Mammalogists.

Langston, R., Gregory, R. & Adams, R. (2002) The status of the Hawfinch in the UK 1975-1999. *British Birds*, **95**, 166-173.

Leimgruber, P., McShea, W.J. & Rappole, J.H. (1994) Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* **58,** 254 – 260.

Loeb,S.C. (1997) An experimental test of interspecific competition for red- cockaded woodpecker cavities. *Journal of Wildlife Management*, **61**, 1268-1280.

MacDonald, D. & Barret, P. (1993) *Collins Field Guide. Mammals of Britain and Europe*. Harper Collins Publishers.

MacDonald, D. & Tattersall, F. (2002) *The State of Britain's Mammals 2003*. People's Trust for Endangered Species.

Macedonia, J.M. (1993) Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93,** 177-197.

Martin, T.E. (1988) On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the Royal Academy of Sciences (USA)*, **85**, 2196-2199.

Martin, T.E. (1992) Breeding productivity considerations: What are the appropriate features for management? In *Ecology and Conservation of Neotrpoical Migrant Landbirds*, (eds J.M. Hagan and D.W. Johnston) pp 455–473.

Martin, T.E. (1993) Nest predation and nest sites: new perspectives on old patterns. *BioScience*, **43**, 523-532.

Martin, T.E. (1998) Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, **79**, 656-670.

Martin, T.E. and Roper, J.J. (1988) Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor*, **90,** 51–57.

McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, **81,** 228–238.

Moller, H. (1983) Foods and foraging behaviour of Red (*Sciurus vulgaris*) and Grey (*Sciurus carolinensis*) squirrels. *Mammal Review*, **13**, 81-98.

Monckton, A.S. (1991) Grey Squirrel control. *Quarterly Journal of Forestry*, **85**, 268-269.

Montague, C.L. & Montague, W.H. (1985) Grey squirrel kills and eats Blue Jay fledgling. *Florida Field Naturalist*, **2**, 46-47.

Newton, I. (1993) Predation and limitation of bird numbers. *Current Ornithology*, **11**, 143-198.

Norment, C.J. (1993) Nest-site characteristics and nest predation in Harris Sparrows and White-Crowned Sparrows in the northwest-territories, Canada. *Auk*, **110**, 769-777.

Nour, N., Matthysen, E. & Dhondt, A.A. (1993) Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography*, **16**, 111-116.

Paton, P.W.C. (1994) The effects of edge on avian nest success: how strong is the evidence? *Conservation Biology*, **8**, 17-26.

Petty, S.J., Lurz, P.W.W. & Rushton, S.P. (2003) Predation of red squirrels by northern goshawks in a conifer forest in northern England: can this limit squirrel numbers and create a conservation dilemma? *Biological Conservation*, **111,** 105-114.

Pimentel D. (ed.) (1991) *Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal and Microbe Species.* CRC Press, Boca Raton.

Rangen, S.A. (1999) Influence of nest-site vegetation and predator community on the success of artificial songbird nests. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **77**, 1676-1681.

Reitsma, L.R., Holmes, R.T. & Sherry, T.W. (1990) Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos*, **57**, 375-380.

Rodewald, A.D. (2001) Avian nesting success in forested landscapes: Influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk*, **118**, 1018-1028.

Schmidt, K.A. (1999) Foraging theory as a conceptual framework for studying nest predation. *Oikos*, **85**, 151-160.

Schmidt, K.A. (2001) Experimental removal of strong and weak predators: Mice and chipmunks preying on songbird nests. *Ecology*, **82**, 2927-2936.

Schmidt, K.A. & Ostfeld, R.S. (2003) Songbird populations in fluctuating environments: predator responses to pulsed resources. *Ecology*, **84,** 406–415.

Shaffer, B.S. & Baker, B.W. (1991) Observations of predation on a juvenile Blue Jay by a fox squirrel. *Texas Journal of Science*, **43**, 105-106.

Shuttleworth, C.M. (2001) Interactions between the red squirrel (*Sciurus vulgaris*), great tit (*Parus major*) and jackdaw (*Corvus monedula*) whilst using nest boxes. *Journal of Zoology*, **255**, 269-272.

Shorten, M. (1954) *Squirrels.* Collins, London.

Smith, A.V. (2001) Production of tree seed and the abundance of Grey squirrels *Sciurus carolinensis* in the woodland of the Linb Valley, Sheffield. *Sorby Record*, **37,** 18–24.

Song, S.J. (1999) Predation in heterogeneous forests: A comparison at natural and anthropogenic edges. *Ecoscience*, **6**, 521-530.

Southern, H.N. (1964) *Handbook of British Mammals.* Blackwell Scientific Publishers, Oxford.

Sparks, T. & Gill, R. (2002) Climate change and the seasonality of woodland flora and fauna. In *Climate Change: Impacts on UK Forests* (ed. M. Broadmeadow). Forestry Commission.

Tapper, S.C., Potts, G.R & Brockless, M.H. (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *Journal of Applied Ecology*, **33**, 965-978.

Tarvin, K.A. & Garvin, M.C. (2002) Habitat and nesting success of Blue Jays (*Cyanocitta cristata*): importance of scale. *The Auk*, **119,** 971-983.

Tittler, R. (2000) Nest predation in and adjacent to cutblocks with variable tree retention. *Forest Ecology and Management*, **136**, 147-157.

Tomiałojć, L. & Wesołowski, T. (1990) Bird communities of primeval temperate forest of Białowieża, Poland. In *Biogeography and Ecology of Forest Bird Communities* (ed. A. Keast.) pp 141-165. SPB Academic Publishing, The Hague.

Vanhinsbergh, D., Fuller, R.J. & Noble, D. (2003) A review of possible causes of recent changes in populations of woodland birds in Britain. *BTO Research Report No. 245*. British Trust for Ornithology, Thetford.

Usher, M.B., Crawford, T.J. & Banwell, J.L. (1992) An American invasion of Great Britain: the case of the native and alien squirrel (*Sciurus*) species. *Conservation Biology*, **6**, 108-115.

Wesolowski, T. (2002) Anti-predator adaptations in nesting Marsh Tits *Parus palustris*: the role of nest-site security. *Ibis*, **144,** 593–601.

Yahner, R.H. & Morrell, T.E. (1991) Depredation of artificial avian nests in irrigated forest. *Wilson Bulletin*, **103**, 113–117.