for birds
for people
for ever

THE PREDATION OF WILD BIRDS IN THE UK

A review of its conservation impact and management

Starlings David Kjaer (rspb-images.com)

THE PREDATION OF WILD BIRDS IN THE UK

A review of its conservation impact and management

Gibbons DW, Amar A, Anderson GQA, Bolton M, Bradbury RB, Eaton MA, Evans AD, Grant MC, Gregory RD, Hilton GM, Hirons GJM, Hughes J, Johnstone I, Newbery P, Peach WJ, Ratcliffe N, Smith KW, Summers RW, Walton P and Wilson JD (2007). *The predation of wild birds in the UK: a review of its conservation impact and management*. RSPB Research Report no 23. RSPB, Sandy.

ISBN-10: 1-905601-02-6
ISBN-13: 978-1-905601-02-8

Avocet chick David Tipling (rspb-images.com)

CONTENTS

1. Introduction

Despite the trials and tribulations of our daily lives, very few people on this planet are worried about being killed and eaten by another predatory species. However, for practically every other species on earth, predation is a real, daily threat. Animals have evolved a wide range of defences, such as camouflage, vigilance, speed and armoury, to avoid ending up as someone else's dinner. Predators, in turn, have evolved as impressive an array of adaptations to try to win this evolutionary arms race – keen senses, greater speed and greater power. The possibility of death at the hands of another species is, then, a fact of life.

Generally speaking, the numbers of predators and prey remain in some sort of balance. If we were able to travel forwards in time to the UK countryside of 20, 40 or 60 years hence and if, and it's a big if, the countryside were generally similar in nature, we would expect to see roughly the same numbers of predator and prey species as now. Sparrowhawks would still be much rarer than sparrows but both would still be around – as they have been for thousands of years. In most cases, it is human interventions that upset the balance of nature between the eaten and the eaters. Some of the most obvious, and damaging, of these interventions are releases of predators into places where they are not naturally found – such as rats onto islands, or American mink into the countryside. Under these circumstances, a new predator can have a field day and rapidly deplete the numbers of prey that have no experience of these predators or defences to cope. But there are other, more subtle, ways in which we have affected this balance: by removing some native predators such as wolves, wild cats, otters and polecats from all or large parts of the country; by reducing the number and size of patches of wild habitats such as forests and floodplain marshes; by altering the climate with unpredictable impacts on predators and prey; and by providing some predators with extra food, for example from landfill sites and road kills, or by releasing large numbers of non-native pheasants and red-legged partridges.

So, in this highly altered countryside there may well be cases where predators are having a greater influence on the populations of their prey than would be the case in a more natural landscape. These situations are not easy to identify, but this report attempts to do so by reviewing the scientific evidence on the impacts of predators on wild birds in the UK. While the RSPB has contributed considerably to the studies presented in this review, the science in this area is not as complete as one might wish.

The review concludes that generalist ground predators, such as foxes, can sometimes reduce the population levels of their prey, and that this is a growing worry if we are to conserve populations of threatened ground-nesting birds, for example lapwings. This conclusion accords with the RSPB's considerable practical experience as a land manager of over 130,000 hectares in the UK. The review also concludes that the evidence to implicate predators such as sparrowhawks in the declines of songbirds is very weak.

It is one thing to say that predators may sometimes affect population levels of species of conservation concern, and another thing to decide what – if anything – to do about it. The RSPB's strong preference is to concentrate on habitat measures that favour the prey species and make life more difficult for the predator. For example, where lapwing productivity and numbers on our nature reserves are poor, we concentrate first on improving the habitat for lapwings and on creating physical barriers such as electric fences to limit fox access. Sometimes, however, we resort to predator control. More research needs to be done on habitat restoration and management, but also on non-lethal means to reduce predation – this latter aspect seems to be sadly neglected at present. The RSPB is keen to continue to be involved in both areas of research with a wide range of partner organisations.

I hope that you find the review interesting and informative.

Dr Mark Avery
Director, Conservation
RSPB

2. Summary

Predation is a natural phenomenon to which all bird species are subject, and predators have lived alongside most of their current natural bird prey for millennia without eliminating them. However, bird populations can decline or their numbers can be held low where levels of predation on them are high.

Numbers of many predators of birds have increased in the UK in recent decades. Many are recovering from the deleterious impacts of pesticide pollution, human persecution or both. Changing land management practices may have boosted numbers of some, and others are spreading following their introduction into the UK or parts of it to which they are not native. Over a similar time-period, populations of some of the bird prey of these predators have declined, leading to the suggestion that these declines were caused by predation.

However, demonstrating that bird populations have declined, or their numbers have been kept low because of predation, is not so straightforward. Simply documenting high levels of predation is generally insufficient, as predators may be taking similar numbers of birds as would have died for other reasons anyway, and many bird species have evolved to cope with high levels of predation. Instead, studies are needed that compare numbers of bird prey at sites (or times) where predator numbers differ; those performed as experiments are generally most convincing.

Growing evidence from such studies in the UK and elsewhere suggests that breeding populations of some ground-nesting birds, such as wading birds and gamebirds, are more likely to be limited by predation than other groups, perhaps because their nests or young are

Peregrine falcon Mark Hamblin (rspb-images.com)

Grey partridges Bob Glover (rspb-images.com)

more vulnerable to predation. By contrast, the evidence that breeding songbird numbers are limited by predation is weak. Rather, there is compelling evidence – some of it experimental – that changes in farming practices have led to the declines of many farmland songbirds, and emerging evidence that numbers of some woodland songbirds have declined due to long-term changes in woodland structure.

While it is tempting to think that declines of bird populations are due either to predation or to other environmental causes, such as changes to their habitat, these two potential causes are often linked. Thus, while predation may be the apparent cause of a species' decline, habitat change may still be ultimately responsible. For example, grey partridge populations are most likely to be limited by predation after being reduced to low densities by habitat deterioration.

If predation is thought to be limiting bird numbers, wildlife managers may intervene to reduce its impact. Such interventions include removal or exclusion of predators, habitat management, diversionary feeding and conditioned taste aversion.

Reviews of predator removal studies undertaken around the world demonstrate that while removal of predators – generally by killing them – often increases numbers of prey alive at the end of the breeding season, it is less consistent at increasing breeding numbers in subsequent years. Producing a surplus for shooting in the autumn is thus more readily achievable than increasing breeding numbers. Both are objectives of game managers, while only the latter is for conservation managers, which may explain why predator removal is more widely used and promoted by game managers. Nevertheless, there are examples, most commonly involving ground-nesting birds, where predator removal has increased breeding numbers, and this form of intervention can provide an additional useful tool for conservation managers too.

Excluding mammals with electric fencing can reduce levels of predation on nesting colonies. However, in the UK at least, such fencing is usually only employed to protect relatively small areas, can be breached by mammals and is wholly ineffective at reducing predation by birds. Exclosures that protect individual nests can improve hatching success, but can also increase levels of predation on incubating adults.

Habitats can be managed to lessen predation by reducing predator numbers, by making prey less vulnerable and by allowing them to re-nest thus compensating for losses to predation. For example, hedgerows, grassland, field margins and cereal crops could be managed to make nests and chicks less likely to be found by predators. Habitats rich in bird food could be provided to ensure that chicks do not go hungry and their begging calls do not attract predators, and that adult birds aren't forced to forage for longer and in more dangerous places than otherwise. Potential predator breeding sites and perching places could be removed, and food supplies and fragmented habitats that sustain populations of generalist predators could be better managed.

Alternatively, rather than attempting to reduce predation, habitats could be managed to boost productivity or survival of bird prey, thus compensating for losses to predation. While each of these potential solutions seems sensible, disappointingly few have ever been tested. Such testing is needed in order to develop practical and effective solutions.

Diversionary feeding – providing predators with alternative food in the hope that they kill less prey – might provide a practical non-lethal solution but, so far, trials in the UK have been few and have met with only partial success. Further tests are needed to improve upon these techniques. While conditioned taste aversion has been used to reduce predation on birds' eggs in the US, no successful field trials have been conducted in the UK.

In summary, this review shows that:

- Numbers of many predators of birds have increased in the UK in recent decades.
- There is growing evidence that breeding populations of some ground-nesting birds are limited by predation.
- By contrast, there is little evidence that breeding songbird numbers are limited by predation.
- Post-breeding numbers of ground-nesting birds can be successfully increased by killing their predators, although this less consistently increases their breeding numbers in subsequent years.
- Many other, non-lethal solutions to reduce predation and its impacts are available, though their efficacy is poorly known. There is clear scope for more research here.

Crynodeb

Mae ysglyfaethu yn elfen naturiol o fywyd pob rhywogaeth o adar, ac mae ysglyfaethwyr wedi byw ochr yn ochr â'r rhan fwyaf o'u hysglyfaeth adar naturiol ers miloedd o flynyddoedd heb eu dileu. Ond, gall poblogaethau adar leihau neu gael eu cadw'n isel lle mae ysglyfaethu sylweddol arnyn nhw.

Mae niferoedd yr ysglyfaethwyr ar adar wedi cynyddu yn y DU yn y degawdau diwethaf. Mae nifer yn ffynnu o'r newydd ar ôl dioddef effaith niweidiol llygru gan blaladdwyr, erledigaeth gan ddyn neu'r ddau. Efallai fod newidiadau i arferion rheoli tir wedi cynyddu niferoedd rhai ysglyfaethwyr, mae eraill yn cynyddu ar ôl eu cyflwyno i'r DU neu rannau o'r wlad lle nad ydynt yn frodorol. Dros gyfnod tebyg, mae poblogaethau cyfran o ysglyfaeth adar yr ysglyfaethwyr hyn wedi gostwng, sy'n awgrymu bod y gostyngiadau hyn wedi'u hachosi gan ysglyfaethu.

Fodd bynnag, nid yw dangos bod poblogaethau adar wedi gostwng, neu fod eu niferoedd wedi'u cadw'n isel oherwydd ysglyfaethu, ddim mor syml. Nid yw cofnodi lefelau uchel o ysglyfaethu yn gyffredinol yn ddigonol, oherwydd gall ysglyfaethwyr fod yn lladd niferoedd tebyg o adar ag y byddai wedi marw beth bynnag am resymau eraill, ac mae nifer o rywogaethau adar wedi esblygu i ymdopi â lefelau uchel o ysglyfaethu. Yn hytrach, mae angen astudiaethau sy'n cymharu niferoedd ysglyfaeth adar ar safleoedd (neu ar amseroedd) lle mae niferoedd yr ysglyfaethwyr yn amrywio; cynnal arbrofion yw'r dull mwyaf argyhoeddiadol o gyflawni hyn.

Mae tystiolaeth gynyddol yn sgil astudiaethau o'r fath yn y DU ac mewn mannau eraill yn awgrymu fod poblogaethau rhai adar magu sy'n nythu ar y ddaear, fel adar hirgoes ac adar hela yn fwy tebygol o fod yn gyfyngedig yn sgil ysglyfaethu na grwpiau adar eraill, efallai oherwydd fod eu nythod neu eu cywion yn fwy agored i niwed yn sgil ysglyfaethu. Ar y llaw arall, mae'r dystiolaeth fod niferoedd yr adar cân sy'n magu yn cael eu cyfyngu gan ysglyfaethu yn brin. Yn hytrach, mae tystiolaeth gref – rhywfaint ohoni'n arbrofol–yn dangos fod newidiadau mewn arferion ffermio wedi achosi i nifer yr adar cân ar ffermydd ddirywio. Mae tystiolaeth newydd yn dangos fod niferoedd rhai adar cân mewn coetiroedd wedi lleihau yn sgil newidiadau tymor hir yng nghyfansoddiad y coetiroedd.

Tra'i bod yn demtasiwn tybio bod poblogaethau adar yn disgyn unai oherwydd ysglyfaethu neu ffactorau amgylcheddol eraill, fel newidiadau yn eu cynefinoedd, mae'r achosion posib hyn yn aml yn gysylltiedig. Er y gall ymddangos mai ysglyfaethu sy'n achosi dirywiad mewn rhywogaeth, efallai mai newid mewn cynefin yw'r rheswm yn y pen draw. Er enghraifft, mae poblogaethau'r petris llwyd yn fwy tebygol o fod wedi cael eu gostwng gan ysglyfaethu ar ôl i'w niferoedd ddirywio wrth i'w cynefinoedd gael eu lleihau.

Os credir bod ysglyfaethu yn cyfyngu ar niferoedd adar, gall rheolwyr bywyd gwyllt ymyrryd i leihau ei effaith. Gall ymyriadau o'r fath olygu cael gwared ar ysglyfaethwyr neu eu cau allan, rheoli cynefinoedd, darparu ffynhonnell fwyd amgen a chyflyru i gysylltu bwyd â blas drwg.

Mae adolygiadau o astudiaethau cael gwared ar ysglyfaethwyr ym mhedwar ban byd yn dangos tra bod cael gwared ar ysglyfaethwyr – yn gyffredinol trwy eu lladd – yn aml yn cynyddu cyfran yr ysglyfaeth sy'n fyw ar ddiwedd y tymor magu, mae'n llai cyson o ran cynyddu niferoedd yr adar sy'n magu mewn blynyddoedd dilynol. Mae cynhyrchu adar ychwanegol er mwyn eu saethu yn yr hydref yn fwy llwyddiannus na chynyddu niferoedd sy'n magu. Mae'r ddau beth ymhlith amcanion rheolwyr adar hela, tra mai dim ond yr ail o'r rhain sy'n berthnasol i reolwyr cadwraeth. Efallai fod hyn yn egluro pam fod cael gwared ar ysglyfaethwyr yn fwy cyffredin ac yn cael ei hybu gan reolwyr adar hela. Serch hynny, ceir enghreifftiau sy'n ymwneud ag adar sy'n nythu ar y ddaear yn bennaf lle mae cael gwared ar yr ysglyfaethwyr wedi arwain at gynyddu'r niferoedd sy'n magu. Gall y dull yma o ymyrraeth fod yn arf defnyddiol ychwanegol hefyd i reolwyr cadwraeth.

Gall codi ffens drydan i rwystro mamaliaid ostwng ysglyfaethu ar safleoedd nythu adar. Ond, yn y DU o leiaf, dim ond i amddiffyn llecynnau cymharol fach y defnyddir ffensys. Gall mamaliaid dorri ffens ac mae'n gwbl aneffeithiol o ran lleihau ysglyfaethu gan adar. Gall amddiffynfeydd sy'n gwarchod nythod unigol wella llwyddiant deori, ond gall hefyd gynyddu lefelau ysglyfaethu ar adar sy'n deori.

Gellir rheoli cynefinoedd er mwyn lleihau ysglyfaethu trwy leihau nifer yr ysglyfaethwyr, trwy wneud yr ysglyfaeth yn llai agored i niwed, a thrwy ganiatáu iddynt ail-nythu ac felly adfer y colledion a gafwyd yn sgil ysglyfaethu. Er enghraifft, gellid rheoli gwrychoedd, glaswelltiroedd, ymylon caeau a chnydau grawn fel ei bod yn fwy anodd i ysglyfaethwyr ganfod nythod a chywion. Gellir creu cynefinoedd sy'n gyfoethog o ran bwyd i adar fel na fydd

Curlews Mark Hamblin (rspb-images.com)

cywion yn llwgu, na'u sÕn yn denu ysglyfaethwyr ac na fydd yr oedolion yn cael eu gorfodi i chwilota'n hir am fwyd mewn mannau mwy peryglus. Gellid cael gwared ar safleoedd magu yr ysglyfaethwyr a'u mannau clwydo, a gellid rheoli cyflenwadau bwyd a chynefinoedd gwasgaredig sy'n cynnal poblogaethau ysglyfaethwyr cyffredinol yn well.

Fel arall, yn hytrach na cheisio lleihau ysglyfaethu, gellid rheoli cynefinoedd er mwyn cynhyrchu mwy o ysglyfaeth adar a sicrhau ei fod yn goroesi, gan wneud iawn am y colledion a gafwyd yn sgil ysglyfaethu. Tra bod yr atebion posib yma'n ymddangos yn synhwyrol, mae'n siomedig mai ychydig iawn ohonynt sydd wedi'u profi erioed. Mae angen cynnal profion o'r fath er mwyn cael atebion ymarferol ac effeithiol.

Darparu ffynhonnell fwyd amgen – gall rhoi bwyd gwahanol i ysglyfaethwyr yn y gobaith y byddan nhw'n lladd llai o ysglyfaeth ateb y broblem heb orfod lladd, ond hyd yma, prin fu'r profion yn y DU a llwyddiant rhannol a gafwyd. Mae angen cynnal profion pellach i wella'r technegau yma. Tra bo'r dechneg o gysylltu bwyd â blas drwg wedi'i defnyddio i leihau ysglyfaethu wyau adar yn y UDA, nid oes profion maes llwyddiannus wedi eu cynnal yn y DU.

I grynhoi, mae'r adolygiad yma'n dangos bod:

- Niferoedd llawer o ysglyfaethwyr adar wedi cynyddu yn y DU dros y degawdau diwethaf.
- Mae tystiolaeth gynyddol yn dangos fod poblogaethau rhai adar sy'n magu ar y ddaear yn cael eu cyfyngu gan ysglyfaethu.
- Ar y llaw arall, ychydig o dystiolaeth sy'n dangos bod ysglyfaethu wedi cyfyngu ar niferoedd adar cân.
- Gellir cynyddu niferoedd adar cân sy'n magu'n llwyddiannus trwy ladd eu hysglyfaethwyr,er nad yw hyn yn cynyddu niferoedd yr adar sy'n magu mewn blynyddoedd dilynol, mor gyson.
- Mae sawl ateb arall heblaw lladd, er mwyn lleihau ysglyfaethu, er na wyddom pa mor effeithiol ydynt. Mae'n amlwg fod angen gwaith ymchwil pellach.

3. A review of the effects of predation on bird populations

3.a. A theoretical background

Birth, death and population regulation

Bird numbers rise or fall depending on the balance between births (eggs laid) and deaths, and whether individuals move into or out of the local population. Birds die for many reasons, but principally because of lack of food, exposure to extreme conditions, parasites, disease and injury, or being killed by other animals. The latter form of mortality, predation, is the subject of this review.

In many bird species, predation is the major cause of egg and chick losses, and an important component of fledgling and adult mortality (Newton 1998). The loss of a single bird to a predator will immediately reduce that species' population by one. Common sense would thus seem to dictate that an increase in predation would inevitably lead to a reduction in population size over time, and vice-versa. However, by the end of the breeding season, populations of many bird species have more than doubled due to the numbers of young fledged. So, for a population to remain stable, more than half the birds alive at the end of the breeding season must die before the beginning of the next, if not from predation then for other reasons. When birds are killed, the resources that they would have used – such as food or nest sites – become available for others that might otherwise have died or been unable to breed. Consequently, these remaining birds are more likely to survive and breed, and thus may compensate for the loss of those birds killed by predators (Newton 1998; see Figure 1).

Compensation like this can buffer populations against high levels of predation. For example, when sparrowhawks were present in Wytham Woods, Oxfordshire, they killed 18–34% of fledgling great tits each year. Despite this, numbers of breeding great tits were similar whether sparrowhawks were present or not (see Figure 2). The sparrowhawks were thus killing a similar number of birds that in their absence would probably have died anyway – most likely starved – before the next breeding season (Perrins and Geer 1980; McCleery and Perrins 1991). The sparrowhawks simply changed the cause of death, from over-winter starvation to predation; they were taking an otherwise doomed surplus.

The important concept of additive mortality

There are, however, limits to which losses of birds to predation can be compensated for in this way. If levels of predation continue to rise, losses may become so great that they add to, rather than replace, others forms of mortality, and the population may decline. Such predation losses are termed 'additive mortality' by ecologists. Only if predation losses are additive can a predator limit its prey. In Wytham Woods, mortality due to predation would have become additive had sparrowhawks killed all the doomed surplus of great tit fledglings, as well as some of those that would otherwise have survived to breed the following year. Had this occurred, the great tit breeding population would have declined, yet it did not. In this instance, mortality was not additive and sparrowhawks did not limit great tit numbers.

Many studies of predation in wild birds have been unable to determine whether predation mortality is additive or not, and this frequently confounds the interpretation of these studies. Except in extreme cases, it is not possible to conclude that predators have driven the decline of a population of their prey simply by measuring high levels of predation.

The magnitude of predation that can occur before the mortality caused becomes additive varies between populations and species, and is influenced by clutch and brood size, and also by the season during which predation occurs. Clutches of eggs, if predated, can be replaced reasonably easily in some bird species thus compensating for the losses, whereas predation of adult birds just prior to the breeding season is more likely to be additive as they cannot be so easily replaced before nesting begins (Newton 1998). In addition, short-lived species that produce a large number of young, such as the Wytham great tits, are better able to compensate for increased mortality from predation than long-lived species that produce few, such as some seabirds.

Specialist and generalist predators and predator 'traps'

If a predator that specialises on a single prey species causes its prey population to decline, more of the predator population will starve and predator numbers will fall. The two populations may thus regulate each other, and even though a specialist predator may reduce prey numbers, it cannot normally drive its prey to extinction.

However, a predator's numbers need not be regulated by its prey. If prey numbers increase, for example due to an abundance of food, predator numbers may increase too, but only up to a point at which the predator then becomes limited not by its prey, but by something else, such as lack of space for breeding territories. Numbers of prey, however, could continue to rise until they too become limited,

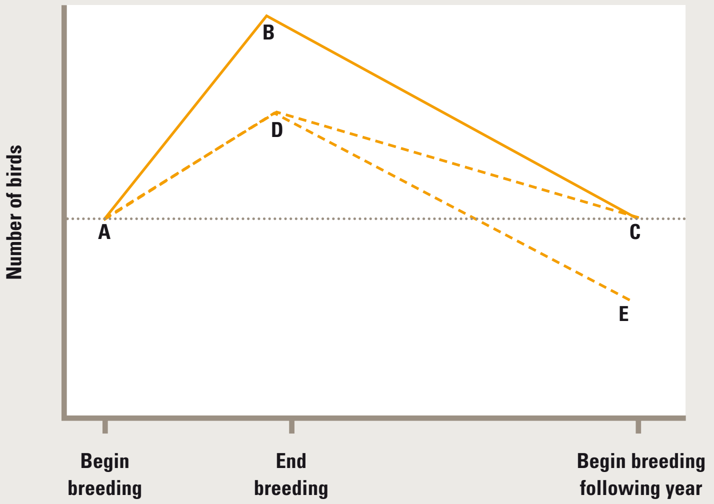


Figure 1 An explanation of how predators might, or might not, limit their prey.

Imagine a population of birds whose numbers vary throughout an annual cycle, from the beginning of one breeding season to the beginning of the next.

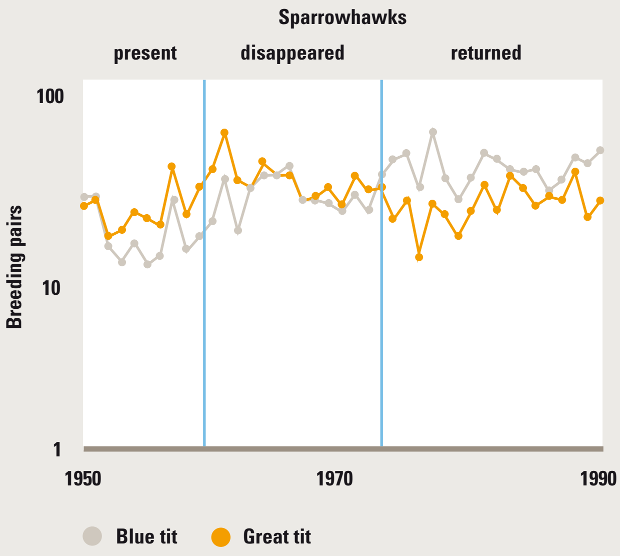
Imagine, in the first instance, that this population has no predators (solid lines). The number of birds in the population will increase between the beginning of the breeding season (point A) and its end (B) as birds reproduce. For the population to remain stable between years, a large number of birds must die (the 'doomed surplus') between the end of one breeding season and the beginning of the next (C). If there are no predators, then the most likely cause of death will be starvation.

Now imagine that there are predators, and that they kill birds during the breeding season (dashed lines). The population at the end of the breeding season will thus be smaller (D) than if predators were absent (B). What happens to the population between the end of one breeding season and the beginning of the next is crucial to understanding the impact of predation.

It is entirely possible that just as many birds will die from starvation as when predators were absent, and the losses from predation will simply add to those from starvation. The mortality due to predation is thus 'additive'. If this happens, the population at the beginning of the next breeding season (E) will be lower than at the beginning of the first (A), and the population has declined. In this case, predators are limiting the population of their prey, and the prey population is lower than it would have been had there been no predators.

An alternative possibility, however, is that since predators have killed birds during the breeding season, there will be more food to be shared by those remaining over winter, and so fewer will starve. This increased survival of the remaining birds allows the population to compensate for the losses to predation earlier in the year, so that by the next breeding season the prey population is the same (C) as at the beginning of the first and as if predators had been absent. Thus, even though predators kill birds, a prey population need not be limited by its predators and can remain stable over time because of compensation.

This is a very simplistic interpretation of a complex set of processes. Clearly, predation, starvation and other causes of death can occur throughout the year, compensation can take other forms (for example re-nesting following predation of an earlier nest, rather than improved survival) and prey populations need not end up only at points C or E. However, it does show the general principles of how predators might, or might not, limit their prey.




Sue Tranter (rspb-images.com)

Great tit

Figure 2 Tit populations at Wytham Woods, Oxfordshire.

The population of blue and great tits in Wytham Woods, Oxfordshire, has been studied since the 1950s. Sparrowhawks were present in the woods until 1960, then disappeared during the organochlorine pesticide era, and returned in the early 1970s. When sparrowhawks were present they killed 18–34% and 18–27% of fledgling great and blue tits, respectively, each year. If mortality due to sparrowhawks had been additive and had they been limiting tit populations, then we would have expected tit populations to rise when sparrowhawks disappeared and fall when they returned. However, there was no evidence of this, thus sparrowhawks did not limit tit populations at Wytham (McCleery and Perrins 1991; redrawn from Newton 1998; Perrins and Geer 1980;).

perhaps by their food. Thus, prey populations can have two ‘equilibrium’ levels; a lower one at which they are regulated by predation, and a higher one where they have ‘escaped’ predator regulation and are now limited by, for example, their food. This may sound highly theoretical, but has important practical consequences as it is possible to see how prey whose numbers have declined can become regulated by their predators when at low densities. Conversely, short-term interventions, such as improving food supplies or controlling predators, may take a prey population beyond the point at which it is ‘trapped’ by predator regulation, and allow it to increase to a higher level.

Most predators of birds in the UK are generalists, preying on a variety of vertebrate species, and sometimes on other foods, such as invertebrates, plant material and refuse. This is important because populations of generalist predators are less influenced by the abundance of any one prey species. Thus, for example, should one species of bird prey become rare, predators may simply switch to alternative food sources allowing the prey population to recover (Newton 1998). Alternatively, and more worryingly for the conservation status of particularly rare prey, if that prey is preferred for any reason – for example, because it is easy to catch – a predator whose numbers are being sustained by alternative, more common, prey could force numbers of the rare prey down, possibly even to extinction.

Habitat modification and predation

Levels of predation can change even if predator numbers remain constant, particularly if habitats are modified in ways that make prey more vulnerable to predation. For example, skylarks are obliged by luxuriant crop growth in autumn-sown cereal crops to nest in the sparser vegetation adjacent to tractor tramlines, and consequently suffer high predation rates (Donald 2004), probably because predators such as foxes hunt along the tramlines. In addition, habitat modification can increase predator numbers. Where forests become fragmented by farmland, numbers of generalist predators, such as foxes and crows, can increase, leading to higher levels of predation on species living in forests and along their edges (Andrén 1992; Chalfoun *et al.* 2002; Paton 1994; Thompson *et al.* 2002).

Furthermore, if habitat deterioration reduces food supplies for birds, they may be forced to forage in more dangerous places, making them vulnerable to predation (Martin 1992). For example, loss of seed food due to changes in agricultural practices may have contributed both directly, through starvation, and indirectly, through predation, to the decline of the bullfinch in the UK (Newton 2004). Predators can even influence the survival of their prey without killing them, as prey may avoid foraging in habitats where they are vulnerable to predation and may thus be more likely to starve (e.g. Hilton *et al.* 1999).

These complex interactions between predation and habitat are considered in detail later in the report.

3.b. Predators and their populations

Native mammalian predators of birds and their eggs in the UK include foxes, mustelids (such as stoats, weasels and badgers), hedgehogs and rodents. Added to this are several introduced species, principally domestic and feral cats, American mink, brown rats and grey squirrels. Furthermore, some mammals are native to some parts of the UK but have been introduced to others, for example hedgehogs on the Outer Hebrides. Mammals take eggs and chicks, although predation of incubating female birds on the ground can also be significant. The main avian predators, all native, are raptors, corvids (particularly crows, magpies and jays), large gulls and great skuas. Corvids take mainly eggs or small chicks, raptors prey mainly on chicks, juveniles or adults, and gulls and skuas will eat eggs and birds at all stages.

It has been suggested that recent increases in predator populations are largely responsible for the declines of many bird species. In this section, we consider the first part of this argument and investigate trends in populations of predatory birds and mammals in the UK.

Predatory birds

Population trends in the majority of bird species in the UK are well known from long-running bird monitoring schemes. Populations of buzzards, sparrowhawks, magpies and carrion crows have increased strongly over the last 35 years – buzzards dramatically so (over five-fold; Eaton *et al.* 2007a; see Table 1 and Figures 3 and 4). Not all of these increases have been sustained, and while magpie and sparrowhawk populations increased rapidly until 1985 and 1990, respectively, their populations have since levelled off. Over the same 35-year period, the kestrel population declined.

Looking over the medium-term, using data from the Breeding Bird Survey for 1994–2006 (see Table 1), a similar picture emerges. Over the UK as a whole, buzzard and carrion crow populations have continued to increase;

Table 1 Trends in populations of widespread predatory birds.

Long- and medium-term trends in populations of widespread predatory birds (Eaton *et al.* 2007a; Raven *et al.* 2007; BTO/JNCC/RSPB). Figures for increasing and declining species are given in black and blue, respectively.

Species	UK 1970–2005	UK 1994–2006	England 1994–2006	Scotland 1994–2006	Wales 1994–2006	N. Ireland 1994–2006
Buzzard	+515%	+49%	+111%	+20%	–5%	–
Kestrel	–28%	–25%	–9%	–65%	–	–
Sparrowhawk	+108%	–1%	–8%	–	–	–
Magpie	+97%	–1%	–4%	+40%	–8%	+24%
Jay	–9%	+1%	–10%	–	+33%	–
Carrion crow	+80%	+21%	+29%	–5%	+30%	–
Hooded crow	–	–28%	–	–48%	–	+70%
Raven	–	+57%	+175%	+49%	+13%	–

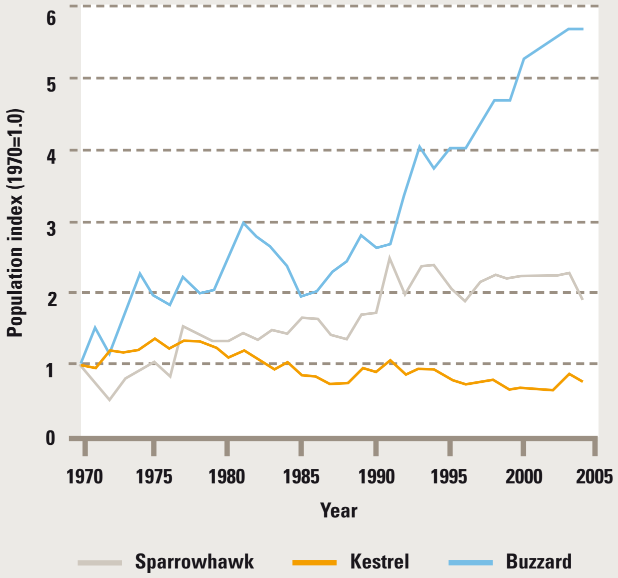


Figure 3 Population trends of sparrowhawks, kestrels and buzzards in the UK, 1970–2004 (data from BTO).

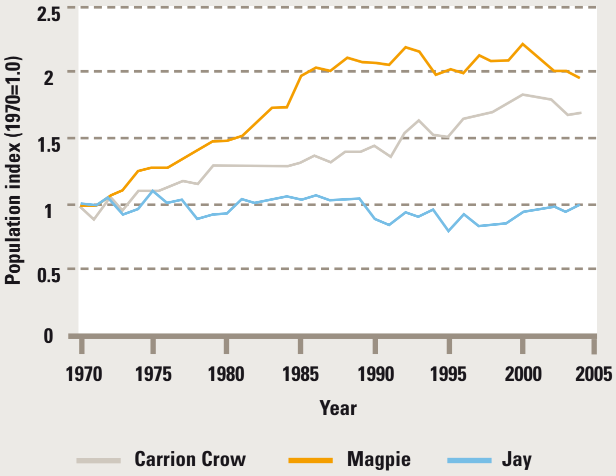


Figure 4 Population trends of carrion crows, magpies and jays in the UK, 1970–2004 (data from BTO).

Table 2 Sizes of breeding populations of birds of prey in the UK, and the percentage of their potential range occupied.

Sources:
[1]Baker *et al.* 2006; [2]RSPB unpublished data; [3]Eaton *et al.* 2006; [4]Sim *et al.* 2007; [5]Holling *et al.* 2007; [6]Eaton *et al.* 2007b; [7]Eaton *et al.* 2004; [8]UK Raptor Working Group (2000), itself taken from Newton 1994.

** includes the Isle of Man.*

Species	Population (year)	% of potential range occupied[8]
Honey buzzard	33–69 pairs (2000)[1]	probably <5%
Red kite	>1,000 pairs (2006)[2]	5%
White-tailed eagle	36 pairs (2006)[2]	<5%
Marsh harrier	360 breeding females (2005)[3]	10%
Hen harrier	806 territorial pairs* (2004)[4]	60%
Montagu's harrier	12 pairs (2002)[5]	probably <5%
Goshawk	410 pairs (2000)[1]	15%
Sparrowhawk	40,100 pairs (2000)[1]	100%
Buzzard	31,000–44,000 territorial pairs (2000)[1]	70%
Golden eagle	442 pairs (2003)[6]	60%
Osprey	*c.*200 pairs (2005)[3]	20%
Kestrel	36,800 pairs (2000)[1]	100%
Merlin	1,300 pairs (1994)[1]	90%
Hobby	2,200 pairs (2000)[1]	probably 70%
Peregrine	1,400 pairs* (2002)[7]	95%

sparrowhawk, magpie and jay have remained more or less stable; while hooded crow and kestrel populations have declined. Over the same period, raven numbers increased strongly (Raven *et al.* 2007).

Populations of the UK's rarer predatory birds have mostly increased in recent years. These increases are largely part of a continued recovery from the deleterious impacts of pesticides in the 1960s and 1970s (Newton and Wyllie 1992) and human persecution that led to the loss of five raptor species from the UK just after the turn of the 20th century (Newton 1979; Thompson *et al.* 2003). While peregrine numbers increased by 10% from 1991 to 2002, and from much lower numbers prior to 1991 (Eaton *et al.* 2004), and hen harriers increased by nearly 40% between 1988 and 2004 (Sim *et al.* 2007), golden eagle numbers remained fairly stable between 1992 and 2003 (Eaton *et al.* 2007b), limited by persecution (Whitfield *et al.* 2004). Marsh harrier numbers more than doubled between 1995 and 2005 (Eaton *et al.* 2006), and over the last 25 years goshawk numbers have increased nearly ten-fold (Ogilvie *et al.* 2004). Despite these recent increases, populations of many of the UK's birds of prey still remain well below the level that the habitat could sustain, with some species still absent from large areas of the UK (UK Raptor Working Group 2000; see Table 2).

Predatory mammals

In contrast to birds, monitoring of mammal populations in the UK is generally less well developed, and trends much more poorly known.

The National Gamebag Census, a collation of gamekeepers' and farmers' bag records, has shown a fivefold increase in the numbers of red foxes killed per unit area since 1961 (GCT 2004), albeit with a levelling off, or even a decline, since 1990. Although changes in killing effort and effectiveness, for example by using spotlights, can affect bag sizes, the scale of the change in bags along with evidence of range expansion (e.g. Reynolds and Tapper 1993) does suggest a real increase in fox densities and numbers over the last forty years. This increase may be partly due to large-scale rear and release of gamebirds improving the foxes' food supply (GCT 2004). In addition, reductions in gamekeeper numbers since the end of the 19th century, and abandonment of game management in many areas, may have allowed a recovery of fox (and other predator) numbers.

By contrast, estimates of the UK red fox population from 1981 (252,000 adults: Macdonald *et al.* 1981), 1995 (244,000: Harris *et al.* 1995) and 1999/2000 (258,000: Webbon *et al.* 2004), although each produced with a different method, suggest relative stability over the last couple of decades. However, mammal data collected by the Breeding Bird survey indicated a sharp decline in fox numbers of 34% between 2000 and 2005 (Davis *et al.* 2007). Despite these differing conclusions, and evidence of a recent downturn, it does seem likely that fox numbers increased over the 20th century.

Few data are available on trends in mustelid populations. Game bag records show that following an increase from 1961 to the mid 1970s, stoat bags subsequently declined, most likely due to a reduction in trapping effort associated with a greater emphasis on reared rather than wild gamebirds (GCT 2004; McDonald and Harris 1999). The dramatic decline in weasel bag numbers, down to a quarter of 1960 levels, more likely reflects a genuine trend (GCT 2004) and may be associated with reductions in the extent of rough grassland, an important habitat for voles, a favoured weasel prey. However, reductions in trapping effort cannot be ruled out (McDonald and Harris 1999). Numbers of bag records of the introduced American mink rose dramatically following its first breeding in the UK in 1956, but have stabilised since the early 1980s, with a hint of a recent decline. Pine marten (Balharry *et al.* 1996) and polecat (Birks and Kitchener 1999) populations have increased and extended their range, although there is debate over the status of pine marten in England and Wales (MacDonald and Baker 2005), and both species remain relatively scarce and localised. Badger numbers increased by an estimated 77% between the mid 1980s and the late 1990s, though with large regional variations (G Wilson *et al.* 1997).

Game bag records suggest that grey squirrel numbers rose across most of the UK during 1975–2000 (Whitlock *et al.* 2003), although recent trends are more stable with some range expansion at the northern edge (Battersby *et al.* 2005).

In summary, while populations of most of the UK's avian predators have increased over the last few decades, recovering from the deleterious impacts of pesticide pollution and human persecution, those of a few widespread predators have more recently stabilised (magpie and sparrowhawk). Among the predatory mammals, foxes, badgers, polecats, pine martens, and non-native American mink and grey squirrels have increased, while weasel numbers may have declined.

The trend in stoat numbers is less clear. Changes in land-management practices, such as pig farming, pheasant rearing and sheep husbandry, may have boosted populations of generalist predators, such as foxes and crows.

3.c. Evidence of impacts of predators on bird populations

In this section, we consider the evidence from a range of detailed observational or experimental field studies on the impacts of predators on wild bird populations. Each of these studies has been published, in one form or other, in the scientific literature; here we review this published evidence. We focus on UK studies, so that the evidence used is directly relevant to UK conservation, although in a few instances we draw insight from studies elsewhere. These field studies cover, in turn, those on breeding wading birds, gamebirds, songbirds and seabirds.

When reading this evidence, it is worth bearing in mind the manner in which it was collected, as some scientific approaches provide more compelling evidence than others. For example, as outlined earlier, simply documenting high levels of predation does not on its own provide convincing evidence that predators are limiting their prey, unless combined with further analyses showing that the level of predation is sufficiently high to have caused a reduction in prey numbers. More convincing, however, are studies that compare numbers of prey at sites (or times) where predator numbers differ; those performed as experiments are generally the most convincing.

Breeding wading birds

Curlew

While numbers of breeding curlews in the UK have declined over the last few decades (Gibbons *et al.* 1993; Sim *et al.* 2005), particularly in Wales and Scotland where their populations halved between 1994 and 2005 (Raven and Noble 2006), their numbers in Northern Ireland have fallen even more dramatically, by 58% between 1987 and 1999. These declines occurred on wet grasslands, bogs and moorland, as well as intensively managed grassland (Stanbury *et al.* 2000; Henderson *et al.* 2002).

An RSPB study of curlew breeding success in Northern Ireland found that 82–95% of breeding attempts failed at the nesting stage, with predation accounting for about 90% of nest failures (Grant *et al.* 1999). Foxes appeared to be the most important nest predators at one study area (Antrim), with hooded crows and lesser black-backed gulls most important at another where foxes were largely absent (Lough Erne Islands). Annual breeding success averaged 0.19 young per breeding pair in Antrim and 0.38 young per breeding pair on Lough Erne, with calculations indicating that the breeding success at Antrim was sufficiently low to account for the rate of population decline seen across Northern Ireland as a whole (Grant *et al.* 1999).

In 2003, the Northern Ireland Environment and Heritage Service initiated a management trial in Antrim to determine the effectiveness of killing hooded crows and foxes to promote a recovery in curlew breeding success and numbers. Although the trial is still at an early stage, crow numbers have declined, while the impact on fox abundance is less clear. Despite curlew numbers continuing to decline on all monitored sites – from 72 to 49 pairs between 2002 and 2006 – hatching success seems improved (RSPB, unpublished data), but it is too soon to expect an increase in numbers of breeding pairs.

Golden plover

Evidence that predation may cause declines in breeding numbers has been found for other wading bird species, too. While the UK breeding population of golden plovers has shown mixed trends over the last few decades, with evidence of declines in some regions (Gibbons *et al.* 1993; Sim *et al.* 2005; Raven and Noble 2006), those breeding on a moor in north-east Scotland declined rapidly to extinction during the 1980s. This decline coincided with the cessation of predator control and the planting of conifers close to the breeding area (Harding *et al.* 1994; Parr 1992).

Before these changes in management, numbers of golden plovers varied between 14 and 23 pairs over a ten-year period. During the subsequent decline, nest predation increased and annual breeding success declined, from 0.37 down to 0.02 young per breeding adult. Numbers of common gulls and carrion crows increased rapidly and were the main predators of nests in the first few years after the management changed, with foxes becoming increasingly important (Parr 1993). While the decline could have been explained by increased losses of adult golden plovers over winter, the evidence suggested that the decline was most likely a consequence of high levels of nest predation (Harding *et al.* 1994).

Lapwing

Breeding lapwings have undergone widespread and marked declines in the UK over the last few decades (Baillie *et al.* 2005; Fuller *et al.* 1995; Gibbons *et al.* 1993; Henderson *et al.* 2002; O'Brien 2004; Wilson *et al.* 2001). Changes in farming practices, such as land drainage and the switch from spring-sown to autumn-sown cropping, are almost certainly the main causes of these declines (Chamberlain *et al.* 2000; Sheldon *et al.* 2005; Shrubb 1990; Taylor and Grant 2004; Wilson *et al.* 2001).

Due to population and range contraction, lapwings in some areas may now be more vulnerable to predation than previously. For example, eggs or chicks of lapwings breeding as isolated pairs or at low densities are more likely to suffer predation than those breeding at high densities or in large colonies (Berg *et al.* 1992; Seymour *et al.* 2003; Stillman *et al.* 2006), probably because large concentrations of lapwings can effectively defend their nests against predators. In addition, the loss of gamekeeping from some upland areas may have led to increased predation independent of habitat change.

Very low breeding success, rather than a simple lack of suitable breeding habitat (such as spring tillage and adjacent grassland), may have been responsible for the extinction of lapwing colonies in Hampshire recently, where predation probably accounted for almost 60% of nest failures (Milsom 2005). Similarly, records collated by the British Trust for Ornithology (BTO) show that nest losses to predation were higher during the 1990s than in earlier years, even though for most nests the cause of failure was unknown (Chamberlain and Crick 2003). In a four-year study in northern England, adult and young lapwings were more likely to return to breed in an area with good numbers of gamekeepers – Teesdale, County Durham – than an area with fewer keepers – Eden Valley, Cumbria (Thompson *et al.* 1994). The Teesdale population remained stable over the study period, whereas the Eden Valley population halved.

In 1996, the RSPB began an eight-year experiment to investigate the impact of fox and crow control on lapwings breeding on its lowland wet grassland nature reserves. On each of 11 sites, fox and crow control was undertaken for four consecutive years, and its impact compared with four years without predator control. Adult fox and territorial crow numbers were reduced by 40% and 56%, respectively, during years of predator control, but there was no change in total crow numbers as non-breeding individuals moved in when territorial birds were removed. Overall, no consistent effect of predator control on the survival of over 3,000 lapwing nests was found. However, the impact of control on nest survival varied considerably between sites (see Figure 5), and analyses showed that predator control did result in significant improvements in nest survival at sites where predator densities were high (Bolton *et al.* 2007).

Radio-tracking of nearly 500 chicks on a selection of these sites similarly showed no consistent effect of predator control on chick survival. However, by chance, the sites selected for radio-tracking generally held low densities of foxes and crows, so control measures tended to be unnecessary. At other sites, where radio-tracking was not undertaken and predator densities tended to be higher, the proportion of adults with young late in the season – an index of breeding success – was twice as high in years when predators were controlled (Bolton *et al.* 2007).

Overall, predator control had no impact on lapwing population trends across the 11 sites (Bolton *et al.* 2007). There are several explanations for this result. Perhaps the predators that were killed would, if present, merely have taken a similar number of lapwing eggs and chicks to those that would ultimately have died for other reasons, so foxes and crows had no impact on lapwing populations (i.e. mortality was not additive). Alternatively, lapwing populations might have been increased by killing these predators, but this effect was hidden by the mobility of adult lapwings: numbers settling to breed at a site will depend not only on breeding performance at that site in previous years, but also on the attractiveness of nesting conditions on neighbouring sites. Finally, an effect on lapwing populations might have been demonstrated had a higher proportion of predators been killed. However, fox densities following control in this experiment were similar to those reported in another experiment carried out by the Game Conservancy Trust (GCT) on Salisbury Plain, where an effect of predator control on grey partridge breeding numbers was found (Tapper *et al.* 1996; *see p.21*).

This study shows how it is possible, by experimental removal, to demonstrate an impact of predators on some measures of breeding success of their prey, but demonstrating an unequivocal impact on subsequent prey population size is rarely straightforward.

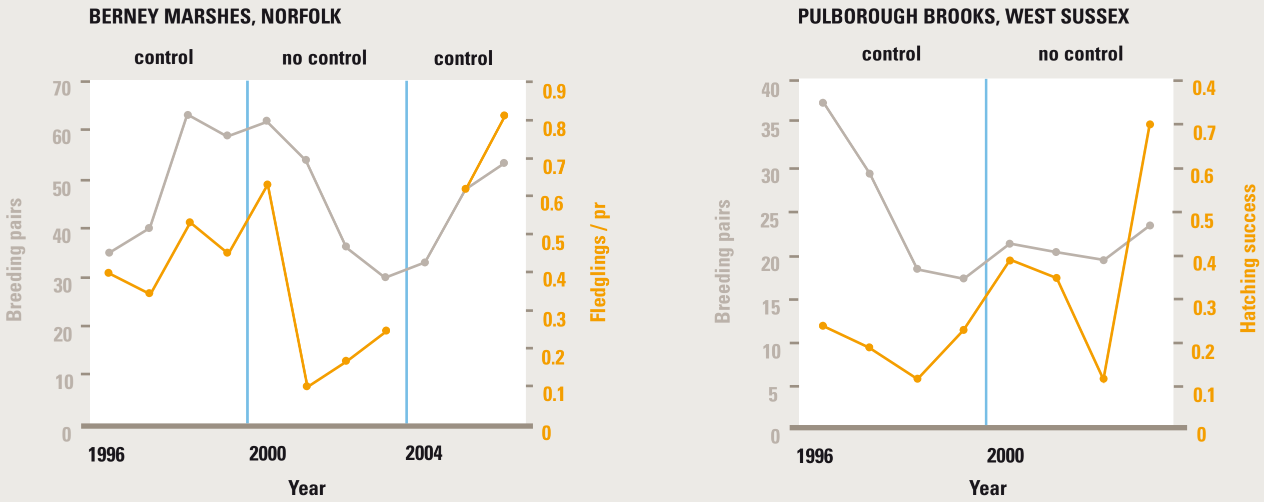


Figure 5 **Lapwings and predator control.**

Fox and crow control had no consistent effect on hatching or fledging success of lapwings, nor on their subsequent population trends, across eleven RSPB lowland wet grassland nature reserves. However, there was great variation between reserves. On some, such as Berney Marshes (above left) that suffered high levels of predation, predator control was effective. Breeding success (orange line) improved over the first period of fox and crow control, deteriorated dramatically when control stopped, and improved once again when control was restarted. The number of pairs of lapwings at Berney followed a similar trajectory (grey line). By contrast, on other sites, such as Pulborough Brooks (above right), fox and crow control had no clear effect on hatching success (a contributor to breeding success), nor on the number of lapwing pairs. If anything, hatching success tended to be lower when foxes and crows were controlled, and the number of breeding pairs tended to decline early on in the period of control, but remained stable thereafter and once control ceased.

Images clockwise from top left: a fox filmed at a lapwing nest on an RSPB reserve; a week-old lapwing chick; RSPB biologists Richard Allcorn and Laura Hurt radio-tracking lapwing chicks; adult lapwing alarm-calling.

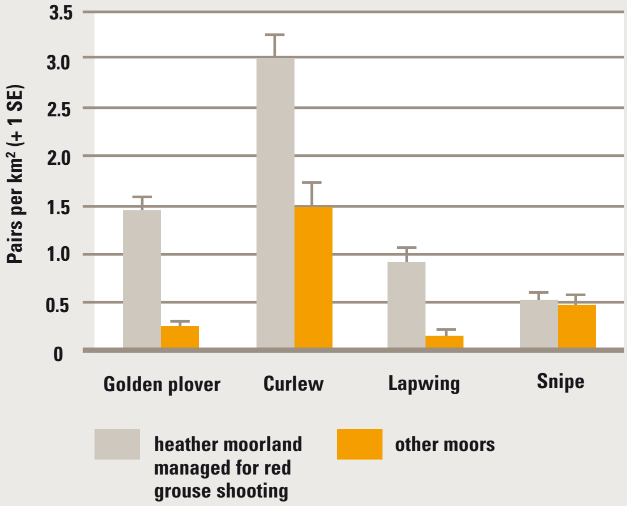


Figure 6 Golden plover, curlew, lapwing and snipe densities on heather moorland.

Densities of breeding golden plovers, curlews and lapwings, but not snipe, were higher on heather moorland managed for red grouse shooting than on other moors (Tharme *et al.* 2001). These results held even when habitat and other differences between the moorland types were taken into account.

Digger Jackson

Hedgehogs introduced to the Western Isles of Scotland have become predators of the eggs of wading birds, such as lapwings.

Sport shooting and wading bird densities in the uplands

Intensive control of some predators, principally foxes and crows, on moorland is a traditional part of management for the driven shooting of red grouse. If predation during the breeding season were limiting populations of breeding waders, their populations would be expected to be higher on moors managed for red grouse shooting (Ewald *et al.* in prep; Haworth and Thompson 1990; Thompson *et al.* 1997). Such differences were found in a study undertaken by the RSPB and the GCT across extensive areas of the English and Scottish uplands, with densities of lapwings, golden plovers and curlews (though not snipe) higher on grouse moors than other moors (Tharme *et al.* 2001; see Figure 6). By contrast, four species of passerine birds (meadow pipit, skylark, whinchat and crow) were less abundant on grouse moors. Hen harriers, peregrines and golden eagles are also known to be less abundant on this type of moorland due to illegal persecution (Court *et al.* 2004; Etheridge *et al.* 1997; Whitfield *et al.* 2003, 2004).

While these findings might suggest that predator control benefits breeding waders, the differences may be due to other aspects of moorland management, particularly muirburn (heather burning), which creates the short vegetation preferred for nesting by these waders (Robson 1998; Whittingham 1996). However, the differences in wader and meadow pipit densities remained even when the extent of muirburn was taken into account. Furthermore, golden plover and lapwing densities were low when crow densities (a reasonable indicator of predator control) were high (Tharme *et al.* 2001). Taken together, these findings suggest that the differences were more likely to be due to predator control than to vegetation management. Despite this, to provide a more robust assessment of whether differences in wader densities are due to predator control specifically, the GCT is undertaking an eight-year experiment controlling foxes, corvids and mustelids on moorland in northern England. Initial findings suggest that predator control improves wader breeding success, but effects on breeding density in subsequent years are less clear and conclusions cannot be drawn before completion of the study in 2008 (Fletcher *et al.* 2005; Fletcher 2006).

Hedgehogs and wading birds on the Outer Hebrides

While the hedgehog is native to much of the UK, where it is a conservation priority, it is not native to the Outer Hebrides where it was introduced in 1974. Since its introduction there, populations of breeding wading birds that nest on the islands' coastal grasslands (machair), particularly dunlins, redshanks, snipe and lapwings, have declined markedly. These declines have been greatest on those parts of the island group to which hedgehogs have spread, and predation of the nests of these birds by hedgehogs has been sufficiently high to account for their declines (Jackson and Green 2000; Jackson *et al.* 2004). It seems likely that the relative lack of ground predators on these islands before the introduction of the hedgehog helped maintain the extraordinarily high, internationally important densities of these wading birds on the archipelago (Jackson *et al.* 2004).

Avocet

A long-term study of avocets at RSPB's Havergate Island reserve, Suffolk (Hill 1988), showed that as numbers of breeding black-headed gulls increased, the avocet

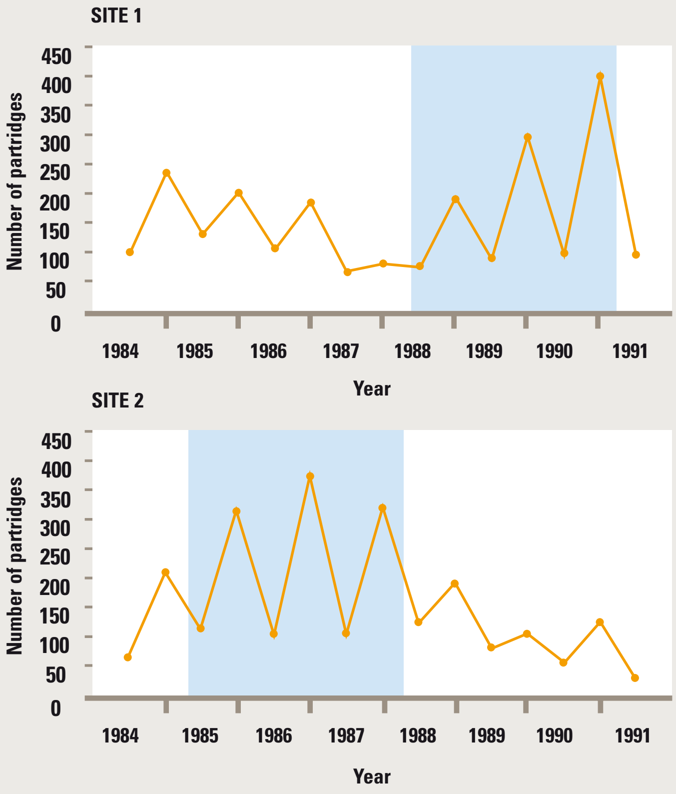


Figure 7 **The Salisbury Plain experiment.**

Changes in partridge populations at two sites on Salisbury Plain during years with (shaded) and without predator control. Spring and autumn stock are given for each year. (Redrawn from Tapper *et al.* 1996.)

🟦 **Predator control period**

population declined as gulls took their eggs and young. Avocet breeding success and numbers recovered following the onset of gull control in 1964, which substantially reduced the size of the gull population. However, after 1971, avocet breeding success deteriorated once more, apparently due to predation by kestrels. Gull control was initiated in 1966 at a second avocet colony, at the RSPB's Minsmere reserve, Suffolk, but had no impact on avocet breeding success. These examples illustrate the rather complex interactions that can occur among various predator species and the difficulty of generalisation from one study site to another, even for the same species of predator and prey.

Gamebirds

Grey partridge

Grey partridges on the South Downs, Sussex, have been studied by the GCT since 1968 (Aebischer and Ewald 2004; Potts 1980, 1986). Grey partridges have declined dramatically across the UK, and the population on the South Downs has suffered a similar fate. Here, densities per km² on the farmland study area dropped steeply from about 20 pairs, stabilised at about 4.5 in the early 1990s, and fell again to under two pairs in the late 1990s. Three plausible causes for the decline were identified (Aebischer *et al.* 2000a; Potts 1980, 1986). First, and most importantly, invertebrates important in chick diets have declined due to the use of herbicides, leading to reduced chick survival. Second, brood production has declined due to predation by foxes and corvids. Third, nesting cover has been lost as field boundaries have been removed to improve farming efficiency. It was also recognised that shooting losses could be contributory where grey partridge densities were low.

In 1984, the GCT started a six-year experiment looking at the second of these causes, specifically testing whether control of predators could increase partridge stocks. The experiment was conducted on two large areas of Salisbury Plain with similar initial partridge densities. Foxes, corvids, stoats and rats were controlled in one area in the first three years, with treatments switched between plots in the second. Numbers of foxes, carrion crows and magpies were all markedly reduced during the partridge nesting period (Tapper *et al.* 1996).

More partridge pairs bred successfully when these predators were controlled, and they produced larger broods. Consequently, after three years, autumn populations were 3.5 times higher with predator control than without. Moreover, as well as being sufficient to sustain some shooting, the population level was maintained until the following spring, and after three years, spring densities were 2.6 times higher with predator control than without (Tapper *et al.* 1996; see Figure 7).

This study showed clearly that mortality due to predation was, at least in part, additional to all other forms of mortality, rather than simply replacing it, and that predation limited the grey partridge population on this site.

By the late 1990s, the GCT advised that a combination of in-field management techniques, particularly set-aside strips, conservation headlands and beetle-banks, could provide the nesting and brood-rearing habitats required to stabilise the grey partridge population, though predator control could help speed its response to habitat management.

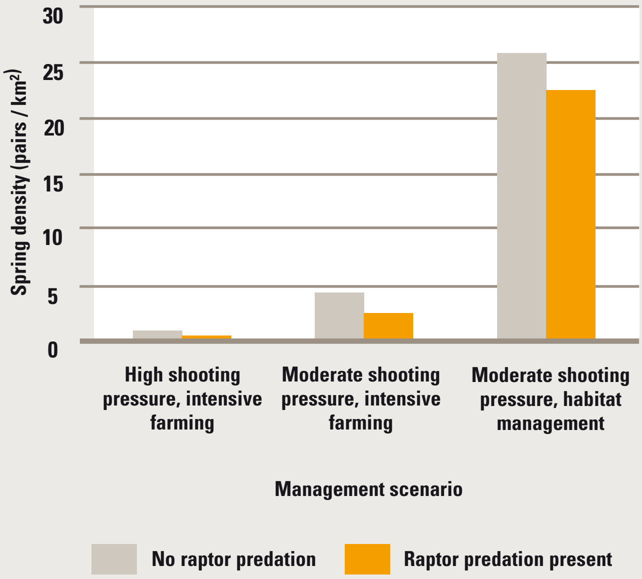


Figure 8 **Predicted spring densities of grey partridge in Sussex under different management scenarios (from data in Watson 2004a).**

Habitat management includes provision of nest cover and legal control of nest predators. At low partridge densities, raptor predation has a relatively large impact on spring densities. Where populations are boosted by habitat management, raptor predation has relatively little impact.

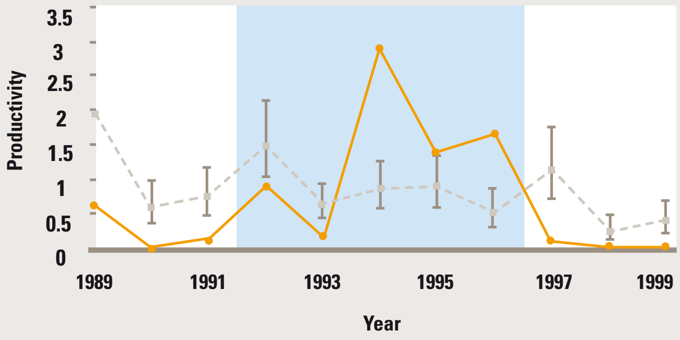


Figure 9 **Capercaillie productivity at Abernethy and elsewhere in Scotland.**

Productivity of capercaillie (chicks per female) at Abernethy during years when predators were (shaded) and were not controlled there, and at reference sites elsewhere. The vertical lines are 95% confidence limits for the reference sites. (Data from Summers *et al.* 2004b)

● **Abernethy** ▨ **Other reference sites**
▨ **Predator control period**


Ron Summers

A predated hen's egg A hen's egg from an artificial clutch predated by a crow. The rate at which these clutches were predated gave a measure of predator activity in Abernethy Forest. Some eggs were carried 2 km away from the clutch site.


Philip Newman (rspb-images.com)

A male capercaillie displaying.

However, the more recent decline on the Sussex study site in the late 1990s was not associated with changes in chick survival or brood production, but instead with increased over-winter losses of adults. While preliminary analyses showed that partridges had declined most in areas where raptors, especially buzzards, had increased (Aebischer 2000), a more comprehensive study (Watson 2004a; Watson *et al.* 2007) concluded that shooting pressure was largely responsible for this recent decline, not raptor predation. In two areas, where shooting pressure was relaxed or removed, grey partridge numbers stabilised even in the presence of raptor predation. The initial findings were explained when it was discovered that raptor densities were greatest in areas of high shooting pressure. In addition, buzzards rarely prey on grey partridges (Smart 2002; Swann and Etheridge 1995; Watson 2004a and b).

Using data on partridge survival rates from radio tracking and estimates of raptor density from 20 study sites in England, it has been calculated that partridge populations above five pairs per km² would be little affected by raptor predation (Watson 2004a and b). However, raptor predation could accelerate the decline of populations already reduced to this low density by, for example, farming practices. Populations boosted by sympathetic habitat management to increase breeding productivity would be little affected by typical levels of raptor predation (Figure 8).

Capercaillie

Notwithstanding a very recent change in its fortunes, by the mid 1990s, the capercaillie had become one of the fastest declining species in the UK (Wilkinson *et al.* 2001). Possible causes of this decline were low breeding success associated with a changing pattern of spring temperatures and reduced chick survival in wet summers, aggravated by fully grown birds colliding with deer fences (Moss 1986; Moss *et al.* 2000, 2001).

An 11-year study (1991–2001) across 14 forest areas in Scotland investigated the causes of this poor breeding success (Baines *et al.* 2004), and concluded that capercaillie reared more young in forests with more bilberry bushes and fewer predators. Bilberry provides good cover, while its leaves and berries, and the invertebrates it supports, are an important component of capercaillie chick diet (Picozzi *et al.* 1996; Summers *et al.* 2004a). The main predators were carrion crows, foxes and, to a lesser extent, raptors, although the effects of each could not be readily distinguished. Although pine martens are known predators of capercaillie eggs and chicks, they had no discernable effect on breeding success in this study. The study recommended that management of these forests should favour bilberry and include control of foxes and crows. However, it also suggested that marking or removing fences, thus reducing adult mortality from fence collisions, could compensate for losses of chicks and eggs to predation.

In the late 1980s, the RSPB acquired the Abernethy Forest reserve in Scotland. Capercaillie chick production in the forest was poor, and it was thought possible that predation on capercaillie nests by crows might be the cause, because crow-predated eggs were found. However, it was not known if predation alone was sufficient to cause the poor productivity.

To investigate the effect of crows on capercaillie productivity, RSPB carried out a study from 1992 to 1996, in which crows were killed. Capercaillie productivity during this period was compared to years when there was no control (1989–1991 and 1997–1999), and also with several other sites at which there were no abrupt changes in levels of predator control. Because capercaillie nests are hard to find, predation pressure was estimated from the rate of predation on artificial nests containing domestic hens' eggs.

The results showed that during the latter part of the predator control period (1994–1996), productivity at Abernethy improved and was greater than productivity elsewhere; at other times, productivity at Abernethy was lower than elsewhere (Summers *et al.* 2004b; see Figure 9). On the face of it, then, predator control did increase capercaillie productivity. However, rainfall was lower during the years of predator control than at other times, confounding these results somewhat. Nevertheless, analysis showed that capercaillie productivity was high when both predation and rainfall (in June) were low. High June rainfall probably caused chicks to become wet and die from hypothermia. It therefore seems likely that crow control can improve capercaillie productivity, but only in years when June is dry. Although fox control was attempted, there was no detectable change in fox numbers, and no association between capercaillie productivity and fox abundance, based on counts of droppings.

Based on these results, and knowing that numbers of full-grown capercaillie are determined by breeding productivity at Abernethy (Summers *et al.* in prep), it seems likely that crow predation there can limit capercaillie numbers, at least in years when June is dry. Because of this, the RSPB has reinstated crow control at Abernethy to benefit the population of capercaillie.

Ultimately, however, habitat management is likely to be a more sustainable form of long-term management (Summers *et al.* 2004b), both to provide for the needs of capercaillie and to deter generalist predators, for example by reducing the fragmented nature of the pine woodlands (Andrén 1992; Kurki *et al.* 1998; Summers *et al.* 2004b). Discarded viscera of culled red deer are a substantial winter food source for crows and foxes (RSPB, unpublished data). At Abernethy, these remains are now disposed of rather than being left for scavengers.

Black grouse

The black grouse has declined across much of Europe since the late 19th century. Ultimately, this decline is largely a consequence of habitat loss, fragmentation and degradation (Warren and Baines 2004). In Perthshire, its recent decline has been largely due to the maturation of conifer plantations (Pearce-Higgins *et al.* 2007), while in northern England it has been attributed to the loss and fragmentation of moorland fringe habitats (Baines 1994; Warren and Baines 2004). Appropriate conservation management has led to the recovery of black grouse populations in England and Wales (Calladine *et al.* 2002; Lindley *et al.* 2003).

Black grouse fall prey to a variety of predators, and predation is a major cause of mortality and breeding failure. A study by the GCT in northern England showed that 37% of black grouse died during autumn and winter 1998–2000, with most deaths attributed to predation by raptors and stoats in equal numbers, and mortality highest for young birds (Warren and Baines 2002). Similarly, studies in the Scottish Highlands and continental Europe have found predation, largely by raptors and foxes, to be the main cause of death amongst black grouse (Angelstam 1984; Caizergues and Ellison 1997; Picozzi and Hepburn 1986; Willebrand 1988). Predation also tends to be the main cause of nest failure (Brittas and Willebrand 1991; Storass and Wegge 1987). A study in Wales by the RSPB between 1998 and 2001 showed that three-quarters of chicks died between hatching and 50 days of age, with about 60% of deaths attributable to predation, mostly by birds (Johnstone and Lindley 2003; see Figure 10).

Given that predation rates are quite high in black grouse, several studies have investigated whether or not black grouse populations in the UK are limited by predation.

In a study in Wales, 66% of adults but only 18% of juveniles survived between September and February (Bowker *et al.* 2007). Although this low survival, reportedly due to predation, may have contributed to a short-term decline in black grouse numbers between 2000 and 2003, numbers nevertheless increased dramatically over the longer term, from 1994 to 2007.

In an experimental study (Summers *et al.* 2004b) at RSPB's Abernethy Forest reserve (see under capercaillie), crow control did improve black grouse productivity, but only in years when rainfall was low in June. Because black grouse numbers at Abernethy are largely determined by productivity (Grant and Dawson 2005; Summers *et al.* in prep), crow control here would be likely to improve black grouse numbers too, but only in dry years.

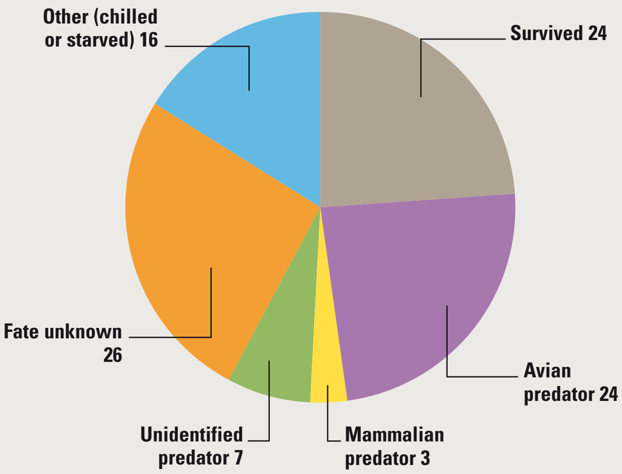
In a study by GCT in northern England and Scotland, black grouse densities and breeding success measured across 20 moors did not differ between those with gamekeepers (who undertake management including predator control) and those without (Baines 1996). However, both were higher on moors with light, rather than heavy, grazing, and these places had more chick food and tall vegetation to provide shelter from predators (Figure 11). In a subsequent experiment, male black grouse numbers increased by nearly 5% per year at sites on which sheep grazing was reduced, yet declined by nearly 2% per year on sites where it was not (Calladine *et al.* 2002).

As part of a recovery project in Wales run by the RSPB, habitat management was undertaken on several black grouse sites to stimulate the regeneration of heather and bilberry, important chick feeding habitats. This management included conifer thinning, and mowing and burning on adjacent dry heath. Fox, crow and stoat control took place on some of these sites as part of shooting management. By the end of the project, male black grouse numbers had risen by 85% (Lindley *et al.* 2003). Analyses are underway to clarify the relative contributions of habitat management and predator control to this increase in black grouse numbers.

The evidence that black grouse populations in the UK are limited by predation is thus equivocal; in some circumstances they may be, while in others they seem more limited by the availability of suitable habitat.

Capercaillie and black grouse on Baltic islands

In an experiment undertaken on two islands in the Baltic (Marcström *et al.* 1988), foxes and pine martens were killed on one island over a five-year period, and the breeding success and trends of black grouse and capercaillie compared with those on a second. The



Values given are percentages.

Figure 10 The fates of 75 black grouse chicks from 41 broods radio-tracked by the RSPB in Wales, 1998–2001 (Johnstone and Lindley 2003).

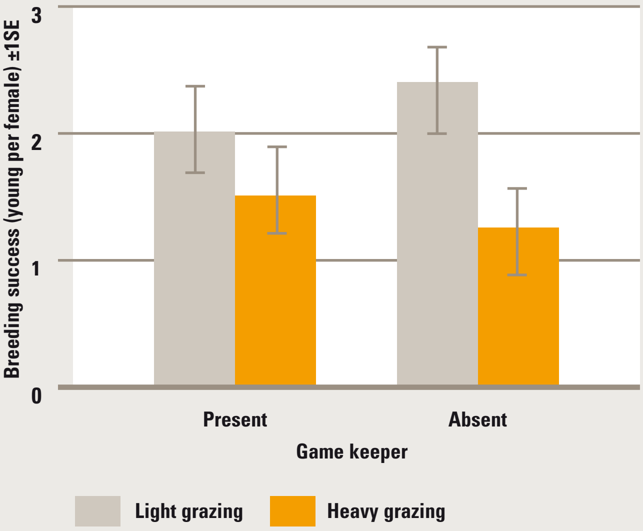


Figure 11 Black grouse breeding success on moors with and without game keeping.

In N England and Scotland, there was no difference in black grouse breeding success between moors with and without game keeping. However, breeding success was higher on moors with light grazing, as these had more chick food and tall vegetation to provide shelter from predators. (Adapted from Baines 1996).


Andy Hay (rspb-images.com))

A black grouse chick being measured to determine its age.


Pat Lindley

Moorland management Mowing dry heather moorland creates good habitat for breeding black grouse.

treatments were then switched for a further four years. When these predators were killed, the average brood size of capercaillie and black grouse combined was 5.5 and 77% of females had chicks. By contrast, when foxes and pine martens were not killed, average brood size was 3.3 and 59% of females had chicks. Numbers of breeding grouse increased after two years of predator removal. Thus, predation was limiting population size and predator control improved breeding success and population sizes of both grouse species.

This otherwise straightforward story was slightly complicated by the presence of alternative prey for foxes and martens. When voles were abundant, predation on grouse was reduced and their brood sizes and percentages of females with chicks were higher. This suggests that predator control is less useful when vole numbers are high, usually one year in three or four.

Red grouse

Over large upland areas of the UK, red grouse populations are managed at high densities to sustain driven shooting of grouse on private estates. This management includes legal control of generalist predators of grouse such as foxes, corvids and mustelids (Thirgood *et al.* 2000b). While this form of management is widespread, surprisingly few studies have attempted to determine the impact of predation on red grouse populations (Redpath and Thirgood 1997).

Early studies of high density grouse populations found that predators, principally foxes and peregrines, concentrated on non-territorial grouse in winter (Jenkins *et al.* 1967; Watson 1985) with most territorial grouse surviving, suggesting that predation was unlikely to limit red grouse breeding populations. By contrast, a study of a low-density population found that over-winter survival rates of territorial and non-territorial grouse were similar, and suggested that at least part of the winter predation was additive, thus reducing the density of breeding grouse in the spring (Hudson 1992). Two studies have investigated whether red grouse densities are higher where generalist predator numbers are lower. The first, undertaken by GCT, looked only at the numbers of grouse shot – a measure of post-breeding densities – and showed that bags were larger on moors with the highest densities of gamekeepers, probably because these moors had the highest levels of fox and crow control (Hudson 1992). The second study, undertaken by RSPB and GCT across extensive areas of the English and Scottish uplands, found that breeding red grouse densities were twice as high on moors managed for grouse shooting as on other moors (Tharme *et al.* 2001). This difference remained, though at a reduced level, after taking account of differences in habitat between the two types of moor. Gamekeepers – whose densities were three times higher on grouse moors – burn heather as well as legally killing foxes, crows and mustelids; both forms of management were shown to independently enhance red grouse density. Taken together, these more recent studies suggest that generalist predators can limit breeding red grouse densities.

Historically, predator control was routinely extended to raptors, and this drastically reduced the range and abundance of many species (Newton 1979). Although now illegal, the killing of raptors continues (UK Raptor Working Group 2000) and limits, in particular, the range and abundance of three species that are in the greatest perceived conflict with grouse management: hen harrier, peregrine and golden eagle (Etheridge *et al.* 1997; Whitfield *et al.* 2003, 2004).

The 1992–97 Joint Raptor Study (JRS) sought to measure whether predation by raptors could limit red grouse numbers at a level substantially lower than would occur in the absence of raptors (Redpath and Thirgood 1997). The study took place at Langholm, in Dumfries-shire, and five other moors across Scotland. Raptors were protected throughout the study and, at Langholm, hen harriers increased from two to 20 breeding females and peregrines from three to six pairs with protection.

The JRS found that hen harrier numbers were determined not by red grouse, but rather by numbers of alternative small prey, particularly meadow pipits. Where meadow pipit density was high, so was that of hen harriers. In addition, fluctuations in harrier numbers between years paralleled variations in the abundance of small mammals (Redpath and Thirgood 1999). Both of these prey species were favoured by heavy sheep grazing, which converted many areas of heather to grass.

Overall, spring raptor predation at Langholm removed 30% of breeding grouse and, by the end of the study, hen harriers were removing 45% of grouse chicks annually. These losses were probably additional to other forms of mortality, and together reduced the post-breeding grouse stock by half. Over winter, raptors killed 30% of grouse, though it was unknown to what extent this mortality was additive.

A population model predicted that, in the absence of raptors, grouse numbers would increase over two years

Red grouse Mark Hamblin (rspb-images.com)

by 1.9 times and post-breeding numbers by 3.9 times (Thirgood *et al.* 2000c). The impact of raptor predation was sufficient to dampen the usual cyclical changes in grouse populations, and prevented these increases from occurring, whilst numbers did recover from cyclical lows on neighbouring moors where raptors were not protected (Redpath and Thirgood 1997).

The short-term limitation of red grouse numbers by raptors does not explain long-term grouse declines recorded at Langholm and more widely across upland areas of the UK (Thirgood *et al*. 2000a). These were associated with the deterioration of heather moorland due to afforestation and increased grazing by sheep and deer (Thompson *et al.* 1995), as well as by increased populations of foxes and crows, and reductions in heather burning following the long-term decline in gamekeeper numbers (Hester and Sydes 1992; Hudson 1992).

The densities of hen harriers observed at Langholm in the latter years of the JRS are amongst the highest recorded anywhere on the Scottish mainland (UK Raptor Working Group 2000). The JRS included five other moors where raptor populations were protected, and red grouse populations there did not respond as they did at Langholm, nor did raptor numbers increase as much. However, driven grouse management was not in place at four of these, and raptors remained at low density at a fifth (Redpath and Thirgood 1997). For all these reasons, we do not know the general applicability of the Langholm findings. However, we do know that meadow pipit densities at Langholm are probably representative of grouse moors across upland areas of the UK (Smith *et al.* 2001), and thus that other moors could potentially attract nesting hen harriers at densities comparable to those at Langholm during the JRS.

The JRS was not a controlled experiment and cannot establish cause and effect. Nonetheless, its results imply that while raptors were not responsible for long-term declines in red grouse bags, predation can limit grouse populations at low density and reduce shooting bags to the point at which driven grouse shooting becomes untenable. This is most likely where raptors breed at high density because of the abundance of alternative prey (the Langholm experience) and where grouse populations are low, either due to low points in cyclic population change, or poor management over the longer term (Thirgood *et al.* 2000a).

Songbirds

Songbirds are found in a wide variety of habitats, but are most numerous in farmland and woodland, with some important populations in other habitats, including urban areas. Numbers of some species of songbird have declined in each of these habitats (Gregory *et al.* 2002). This section considers the impacts of predators on songbird populations, principally in farmland and woodland, but sets this against a backdrop of other widespread environmental changes, starting with the well-researched impacts of agricultural intensification on birds.

Impacts of agricultural intensification

Many species of bird associated with farmland habitats, mainly songbirds, have declined dramatically in range and numbers in the UK and Europe (Donald *et al.* 2001; Fuller *et al.* 1995; Marchant *et al.* 1990; Tucker and Heath 1994; Siriwardena *et al.* 1998). In the UK, these declines occurred most rapidly during 1970–90 (especially 1975–85) and some species continue to decline (Raven and Noble 2006). Specialists of farmland have declined more than generalists (those that occur on farmland, but elsewhere, too), while species living in other habitats have been less affected (Fuller *et al.* 1995; Shultz *et al.* 2005; Siriwardena *et al.* 1998). Farmland plants and invertebrates, on which birds depend for food, have also declined (Donald 1998; Sotherton and Self 1999; Benton *et al.* 2002).

Over the same period, agricultural intensification dramatically increased as a result of production subsidies and technological development. Tellingly, farmland birds declined most in those European countries with the most intensive agriculture (Donald *et al.* 2001). Intensive ecological studies have provided compelling evidence that agricultural change is the major cause of the declines of many farmland species (Aebischer *et al.* 2000b; Anderson *et al.* 2001; Benton *et al.* 2002; Chamberlain *et al.* 2000; Potts 1991; Robinson and Sutherland 2002; Stoate *et al.* 2001; Vickery *et al.* 2004). A review of the large body of work accumulated over the last decade or so (Newton 2004) concluded that 27 out of 30 farmland species were affected by loss of nest sites, lack of winter food, lack of summer food or a combination of these factors. For at least 15 of these species, the cause of their declines was confirmed by experiment.

Has sparrowhawk and magpie predation influenced changes in songbird numbers?

Various attempts have been made to test whether increases in numbers of predators, such as magpies and sparrowhawks, have been a major cause of songbird declines. These tests have been undertaken at both local and national scales.

One of the most powerful, UK-wide studies involved analyses of songbird population changes recorded over 30 years on nearly 300 lowland farmland and woodland sites (Thomson *et al.* 1998). From the early 1960s until 2000, the BTO organised the Common Birds Census (CBC) in which volunteer birdwatchers conducted surveys of bird populations on these sites. Because the CBC recorded avian predators as well as songbirds, it was possible to test whether the presence or absence of sparrowhawks and magpies influenced changes in songbird numbers at those sites. If these predators were affecting songbird populations, we might expect songbird numbers to fall (or increase less) when predators were present and vice versa. The study considered 23 songbird species that fall prey to sparrowhawks, or whose eggs or chicks are taken by magpies. In only two out of the 46 comparisons made (23 songbird species, two predators) did a songbird species decline more when a predator was present than when absent. This number is fewer than expected by chance alone (Figure 12). Thus, it is very unlikely that sparrowhawks or magpies could have caused these songbird population declines (Thomson *et al.* 1998).

Sparrowhawk predation on songbirds

Two local studies of woodland birds confirm the general conclusion that sparrowhawks tend not to depress breeding densities of their songbird prey.

Songbirds breeding in an oak wood on Bookham Common, Surrey, were surveyed each summer between 1949 and 1979. Sparrowhawks were present in this area during the early part of the study (1946–59), then disappeared for 13 years during the organochlorine pesticide era, before recovering and re-colonising the area in the 1970s. If sparrowhawks were affecting songbird populations, we might expect songbird numbers to increase as sparrowhawks disappeared, then decline when they re-colonised. Nine out of 13 songbird species increased in numbers over the course of the study, but only one of these (song thrush) showed any signs of decline in numbers following re-colonisation of the wood by sparrowhawks (Newton *et al.* 1997). The study concluded that sparrowhawks had not reduced densities of breeding songbirds in this wood.

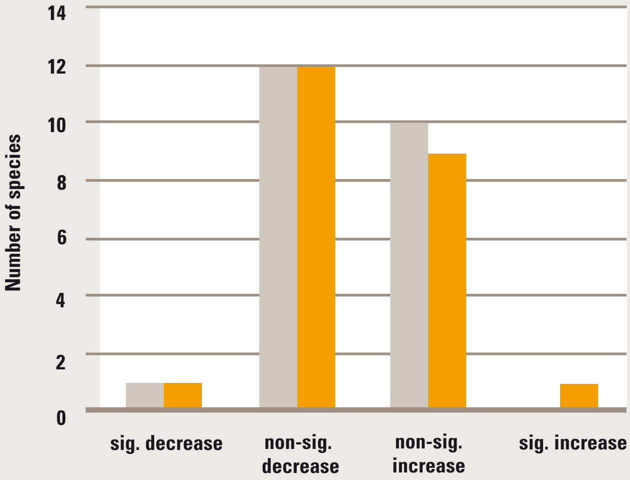


Figure 12 Numbers of songbird species whose populations increased or decreased on CBC plots when magpies or sparrowhawks were present (Thomson *et al.* 1998).

The species are grouped into those whose trends were significant (very few) or non-significant (most). The number of significant trends was fewer than expected by chance alone.

▨ Magpie ▨ Sparrowhawk

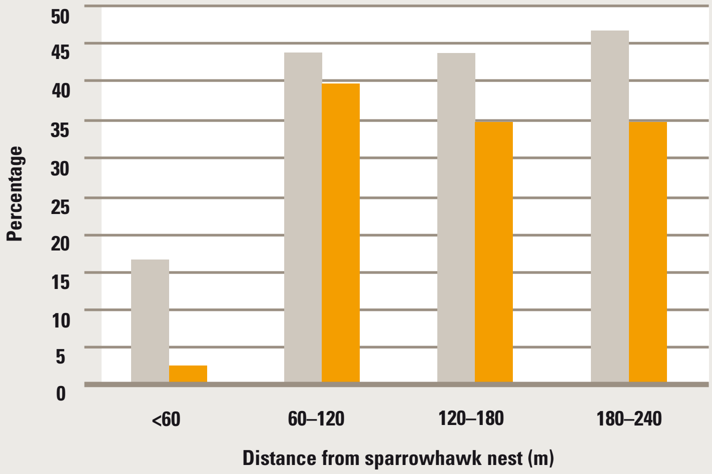


Figure 13 The percentages of tit nestboxes occupied and nests that were successful at increasing distances from sparrowhawk nests in Wytham Woods, Oxfordshire (data from Geer 1978).

▨ Percentage of boxes occupied

▨ Percentage of nests successful

A famous long-term study of great and blue tits in Wytham Woods, Oxfordshire, showed similar results and provided further insights into the effects of sparrowhawks on their prey. The presence of a successful sparrowhawk nest markedly reduced both nestbox occupancy and the nesting success of tits within 60 m of a sparrowhawk's nest (Geer 1978), probably because sparrowhawks took parent tits (Figure 13). However, most tits were unaffected because sparrowhawk nests were typically 800 m apart. Despite sparrowhawks taking up to a third (18–34%) of all recently fledged tits during summer, fluctuations in tit populations were unrelated to changes in sparrowhawk numbers (Perrins and Geer 1980). Tit numbers gradually increased over a forty-year period as the wood matured.

Magpie predation on songbirds

Two studies investigated whether songbird nests were more likely to fail when (or where) densities of magpies and other corvids were high. Both studies were based on the BTO's collection of nest record cards, covering many thousands of nests over many years from across the UK. The first study found no evidence that nest failures of 15 potentially vulnerable songbird species increased over a 20-year period (1966–86) when magpie numbers were increasing rapidly (Gooch *et al.* 1991). In addition, songbird nests in regions with high magpie densities did not suffer higher failure rates than elsewhere.

The second study, by contrast, showed that failure rates of blackbird and song thrush nests during incubation, but not chick rearing, were higher in areas in which magpies and jays were more widespread (Paradis *et al.* 2000). However, there was no evidence that high failure rates were actually caused by high corvid numbers, not least because the predator species responsible for nest failures were unknown.

Magpie densities in urban parkland in Manchester in the late 1980s were higher than had previously been recorded in other urban areas, and during the same period fewer than 5% of the blackbird nests in the parkland produced fledged young (Groom 1993). Although the cause of most nest failures was unknown, predation was the most important cause where it was known, and most of this was attributed to magpies. Despite the dramatically high level of nest failure, blackbird populations remained stable

Grey squirrel Roger Wilmshurst (rspb-images.com)

during the study, though low compared with other urban areas, and it was likely that the blackbird population was only maintained by immigration from elsewhere.

A study at Loddington in Leicestershire, run by the GCT, investigated the effects of removing magpies and crows on songbird nesting success and population levels (Stoate and Szczur 2001). Game management began in 1993 and involved a range of habitat improvements and predator control. Predation by corvids was the main cause of nest failure, and nesting success of four out of six open-nesting songbird species was higher in areas with fewer corvids (Stoate and Szczur 2001). In addition, numbers of five out of six songbird species increased following the start of game management. Thus, while corvids probably did influence songbird nesting success, it is unclear whether predator removal or habitat improvements (or both) were responsible for the songbird population increases.

In an attempt to disentangle these possibilities, predator control ceased at Loddington in 2002. While songbird numbers did decline in 2002 and 2003, they subsequently increased in 2004 and 2005, leading to the conclusion that '...the benefits of predator control for songbirds are not as clear as they are for game' (Stoate 2006). The increase in numbers may have resulted from improved artificial feeding of birds in the winter (Stoate 2005), the introduction of which has made it more difficult to tease apart the effects of predator control and habitat improvements. Although the Loddington study will continue for several more years before further conclusions can be drawn, for the spotted flycatcher, at least, predator control may have been beneficial. Flycatcher numbers increased in woodland, though not in gardens, between 1992 and 2001 – the period of predator control – and declined after 2002 once predator control stopped. It seems that predation reduced flycatcher breeding success at Loddington, perhaps accounting for fewer breeding birds in subsequent years (Stoate and Szczur 2006a, b). The identity of the predators was unknown.

Predation on woodland songbirds by squirrels and woodpeckers

Many species of woodland birds have declined over the last 30 years (Amar *et al.* 2006; Fuller *et al.* 2005; Hewson *et al.* in press). While several hypotheses have been proposed to account for these declines, the Repeat Woodland Birds Survey (RWBS) – which investigated changes in bird numbers over 20 years on more than 400 woodland sites in the UK – concluded that the most likely cause was changes in woodland structure (Amar *et al.*

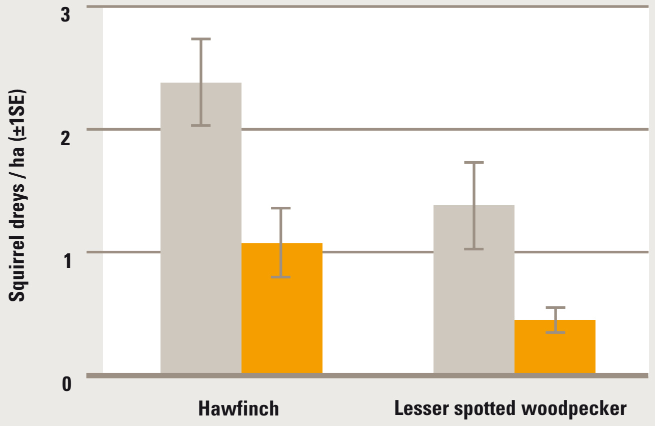


Figure 14 Grey squirrel drey densities.

Grey squirrel drey densities were higher in woodlands where numbers of hawfinches and lesser spotted woodpeckers declined than in those where they remained stable or increased between the mid-1980s and 2003–04. (Data from Amar *et al.* 2006).

2006). These changes were themselves probably a consequence of the ageing of woodland stands, a reduction in active management and, possibly, increased deer browsing and consequent reduction of under-storey vegetation (Amar *et al.* 2006). Despite this, there may be a few species for which predation from increased numbers of nest predators – such as great spotted woodpeckers or introduced grey squirrels – is responsible (Fuller *et al.* 2005).

A review of the impacts of the introduced grey squirrel on birds in the UK (Hewson *et al.* 2004) found only anecdotal evidence to suggest that they were major predators of birds. While the RWBS showed that changes in woodland structure was the most likely cause of population declines among woodland birds, populations of two out of 35 species studied, hawfinch and lesser spotted woodpecker, declined more at sites with relatively high densities of squirrel dreys (Amar *et al.* 2006; see Figure 14). While squirrels may thus be implicated in their declines, this study by no means proves that they were responsible. However, it is possible that canopy-nesting species, such as hawfinch, are particularly vulnerable to predation by grey squirrels (Fuller *et al.* 2005). Overall, though, population changes of the great majority (33 out of 35) of woodland bird species were apparently unaffected by squirrels.

One of the UK's most rapidly declining woodland species, the willow tit, nests in soft dead wood, and their nests are thought to be particularly vulnerable to predation by great spotted woodpeckers (Fuller *et al.* 2005), whose numbers have increased dramatically over the last 30 years (Baillie *et al.* 2005). However, willow tits did not decline any more rapidly on woodland CBC plots where great spotted woodpeckers increased most (Siriwardena 2005), and while they did on farmland, this is a relatively unimportant habitat for willow tits in the UK. A similar analysis investigated marsh tit trends and found no relationship with great spotted woodpecker numbers on CBC plots (Siriwardena 2006).

Cats and house sparrows

There are an estimated nine million domestic cats in the UK, and there is increasing concern about their possible impact on native wildlife. By no means are all cats hunters, but extrapolations from prey returns by relatively small samples of cats (May 1988; Woods *et al.* 2003) indicate that, nationally, they kill millions of birds each year. The house sparrow, whose numbers have halved in the UK since the mid 1970s, is one of the species most frequently killed by cats. However, house sparrows are short-lived and have high reproductive rates, and whether cats impose an additional mortality on sparrows or simply kill similar numbers to those that would have died anyway – for instance by taking young or weak individuals (Møller and Erritzøe 2000) – is unclear. Populations of some other birds commonly killed by cats, for example greenfinches, have increased (Raven and Noble 2006).

Declines of house sparrows in the countryside have been attributed to agricultural intensification (Hole *et al.* 2002). However, there have also been spectacular declines (>90%) in several UK cities (Crick *et al.* 2002; Summers-Smith 1999) and a high proportion of their population occurs in gardens (Bland *et al.* 2004). In an area of Bristol, cats killed at least 45% of the estimated post-breeding population of house sparrows annually (Baker *et al.* 2005). A recent study, however, has shown that nestling starvation – sometimes of whole broods – has played a major role in reducing house sparrow breeding success in Leicester (Vincent 2005). A large-scale experimental test of whether lack of invertebrate food for chicks limits house sparrow populations is currently being run by the RSPB in London.

Whether cat predation has contributed to house sparrow declines remains unclear. Nevertheless, it is prudent to adopt a precautionary approach to the impact of this non-native predator, and to design and adopt methods that reduce the numbers of sparrows, and other animals, killed by cats.

Seabirds

Seabirds tend to live for a long time, do not breed until several years old and lay small clutches (Croxall and Rothery 1991; Lack 1968; Weimerskirch 2002), and so are poorly adapted to compensate for losses of eggs, chicks or adult birds to predation. In addition, they breed in large colonies that can be extremely attractive to predators. For this reason, seabirds often favour nesting on predator-free islands or cliff ledges. Predators can thus limit seabird populations – and indeed other bird populations – simply by preventing them from breeding in areas that would otherwise be suitable (e.g. adjacent to a rich food supply), or by creating competition for predator-free nest sites (Birkhead and Furness 1985).

Although the best examples of limitation of seabirds by predators come from overseas, such processes also operate in the UK. Here, introduced brown rats are probably the main predators to render islands unsuitable for nesting seabirds, particularly burrow-nesting petrels. When rats have colonised islands, seabirds have disappeared and stayed away, only re-colonising when the rats were removed (Ratcliffe 2004a). For example, in one study in Orkney and Shetland, storm petrels were found to breed on 42 out of 142 islands surveyed in the archipelagos, while brown rats were present on 29; on only a single island did they co-occur, strongly suggesting that storm petrels are largely limited to rat-free islands (de Leon *et al.* 2006). So far, around a dozen rat eradication programmes have been implemented on UK islands (Ratcliffe 2004a). On Ailsa Craig, for example, an island in the Firth of Clyde, the introduction of rats in the 19th century caused the extinction of a puffin colony numbering several tens of thousands of birds. During the early 1990s rats were eradicated, and puffins bred for the first time in 50 years in 2002 (Zonfrillo 2002).

Rats are not the only introduced predator having an impact on seabird populations. The breeding success of small gulls and terns on sea-loch islets was reduced to almost zero when introduced American mink colonised the Scottish west coast (Craik 1995). When mink were controlled on a sample of islands, breeding productivity was restored and colonies grew due to immigration of birds from elsewhere, whereas islands not subjected to mink control continued to suffer breeding failure and were ultimately abandoned (Craik 1997). Following mink eradication, the survival of tern nests on the Uists, in the Western Isles, was better than on nearby Lewis where mink remained (Figure 15). Despite this, overall breeding success was unrelated to mink presence or absence (Clode and McDonald 2002; Ratcliffe *et al.* 2005). This was because during the study years, food availability was poor throughout the Western Isles, so that nesting attempts that failed due to mink were destined for failure due to starvation anyway. Further monitoring of terns is required here to assess whether mink eradication promotes improved productivity in years where food supply is favourable. Where introduced American mink were removed from small islands in the Baltic, populations of a range of seabirds (skuas, terns and auks) and other species increased (Nordström *et al.* 2003). Overall, populations of 14 out of 22 seabirds and other species on this archipelago increased following mink removal (Nordström 2003).

Little terns have declined by 39% in the UK since 1971, and this is at least partly explained by their habit of nesting on beaches where they are vulnerable to high tides, human disturbance and fox predation (Ratcliffe 2004b). Electric fencing has been used to reduce fox predation at most colonies, but breaches of such defences can occur, sometimes resulting in serious predation in a single night (Pickerell 2004). Predation by kestrels is also high at a few colonies, and while diversionary feeding to minimise the impact of kestrels has so far proved inconclusive (Smart and Ratcliffe 2000), further tests are underway.

Great skuas are efficient predators of other seabirds, and may be partly responsible for declines of some prey species. When changes in fishery practices led to reductions in the availability of sandeels and in the quantity of dead fish discarded from trawlers, great skuas switched increasingly to seabird prey, probably contributing to declines of kittiwakes (Heubeck *et al.* 1997; Oro and Furness 2002) and Arctic skuas. The rapidly growing great skua population on St Kilda preys mainly on seabirds, especially Leach's petrels (Phillips *et al.* 1999), and recent surveys on the main colony of Dun suggest a rapid decline of Leach's petrels there (JNCC, unpublished data).

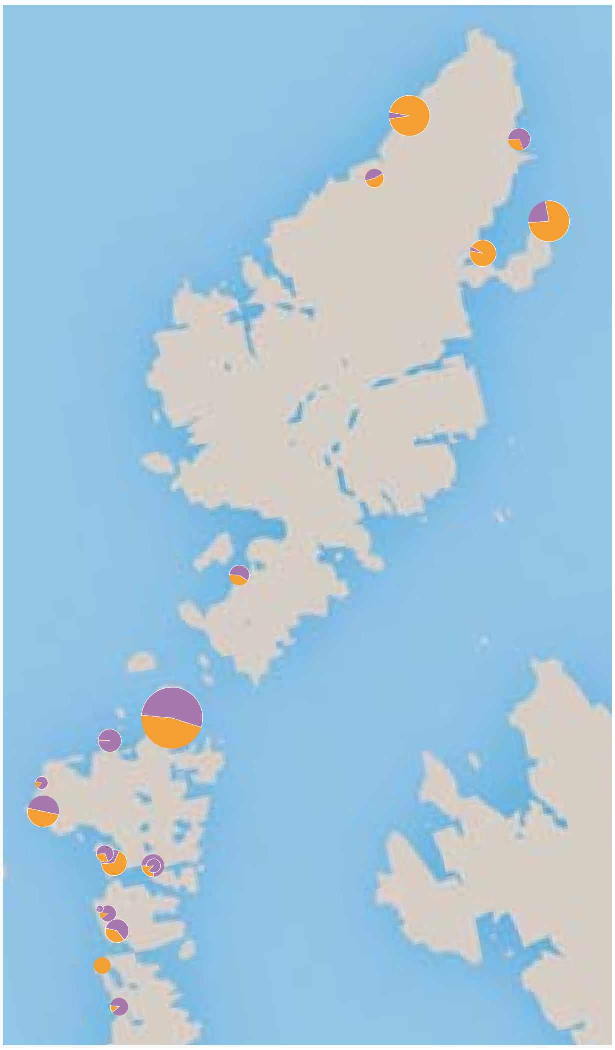


Figure 15 **Survival of tern nests in the Western Isles of Scotland in 2004–05 (Ratcliffe *et al.* 2005).**

Symbol size is related to colony size, with the proportion that hatched in purple, and proportion that failed in orange. Following mink eradication on the Uists (bottom left island group) the survival of tern nests there was better than on nearby Lewis (top right) where mink remained.

3.d. Summary of the impacts of predation on bird populations

A summary of the studies included in this review that investigated the effects of predation on bird populations in the UK is given in Table 3. For each prey species studied (some studies covered multiple species), the table outlines the predator species involved, whether or not there was evidence that predation limited the prey species' breeding population and the type of evidence obtained, broadly classified into 'fair', 'good' or 'best'. None of these studies simply measured levels of predation on prey; even those with the lowest type of evidence (fair) determined whether the level of predation measured was high enough to have caused the observed declines. Nevertheless, studies that compared prey numbers when (or where) predators were present and then absent, or varied widely in abundance, provided better evidence. Within these studies, those that were undertaken as formal predator removal experiments provided the best evidence, with those that relied on 'natural' variation in predator numbers yielding good evidence.

While this table does not attempt to be a comprehensive summary of all relevant studies, it does give a useful overview. In particular, it shows the growing evidence from the UK that populations of some ground-nesting birds, such as breeding waders (e.g. curlews, golden plovers, lapwings, avocets) and gamebirds (grey partridges, capercaillie, black grouse, red grouse), are more likely to be limited by predation than other groups; in the table, most studies of these species fall in the left hand 'evidence' columns. The reason for this is currently unclear, but may be that their nests or young are more vulnerable to predation. Similar results have recently been found in Germany (Langgemach and Bellebaum 2005) and the Netherlands (Teunissen *et al.* 2005).

In addition, the table shows that the evidence that songbird numbers are limited by predation is weak, with most studies falling in the right hand 'no evidence' columns. In particular, a classic study of the impact of sparrowhawks and magpies on nearly two dozen species of songbird over three decades on several hundred sites found no evidence that either predator influenced trends in songbird numbers. Rather, there is compelling evidence that changes in farming practices have led to the declines of many farmland songbirds, and emerging evidence, particularly from the RWBS, that numbers of some woodland songbirds have declined due to long-term changes in woodland structure.

Table 3 Impacts of predators on bird populations in the UK; a summary of evidence presented in this review

For each prey species the following are given: the studies that investigated predation, whether there was any evidence that predation limited prey numbers, and the type of evidence obtained. Only studies that looked at impacts of predators on prey numbers, densities and trends in the UK are included. Those that looked at measures of breeding success only and those from outside the UK are excluded.

Key:
Evidence Evidence that predation limited prey numbers
No evidence No evidence that predation limited prey numbers

Each numeral in the evidence / no evidence columns refers to an individual study, whose authors and date are given below. The complete reference for each study is given at the back of this report.

Predators whose names are given in bold are not native and were introduced to the area studied; with the exception of grey squirrels, these predators were introduced onto islands in all studies referred to. The individual studies of introduced predators are also given as numerals in bold.

Type of evidence
Fair High level of predation and further evidence that this is unsustainably high or likely to have reduced the prey population.
Good Comparison of prey trends or numbers in places (or at times) where (or when) predators were present or absent, or varied in abundance*.
Best Formal experiments; i.e. comparison of prey numbers in areas (or in years) from which predators were experimentally removed, with those where (or when) they were not.

Each number refers to a particular reference, thus:
1 De Leon *et al.* 2006
2 Petty *et al.* 2003
3 Hudson 1992
4 Tharme *et al.* 2001
5 Thirgood *et al.* 2000c
6 Grant and Dawson 2005; Summers *et al.* 2004; Summers *et al.* in prep
7 Baines 1996
8 Baines *et al.* 2004
9 Summers *et al.* 2004; Summers *et al.* in prep
10 Watson 2004a, Watson *et al.* 2007
11 Tapper *et al.* 1996
12 Hill 1988
13 Harding *et al.* 1994; Parr 1992
14 Thompson *et al.* 1994
15 Jackson and Green 2000; Jackson *et al.* 2004
16 Bolton *et al.* 2007
17 Grant *et al.* 1999
18 Craik 1997
19 Heubeck *et al.* 1997
20 Oro and Furness 2002
21 Ratcliffe 2004b
22 Amar *et al.* 2006
23 Thomson *et al.* 1998
24 Newton *et al.* 1997
25 Groom 1993
26 Stoate and Szczur 2006a, b
27 Siriwardena 2006
28 Siriwardena 2005
29 Newton 1998
30 Bowker *et al.* 2007

a Breeding success rather than breeding numbers were measured, but it is known that capercaillie and black grouse numbers in one year are often strongly linked to productivity the previous year.
b Raptor predation limited grey partridge populations, but only when they were at low densities.
c Shooting pressure, not raptor predation, was responsible for the recent decline of grey partridges on this Sussex study site.
d At one site (Havergate Island) only, but not at another (Minsmere).
e Higher return rates in well-keepered area.
f Possible evidence of impact of sparrowhawk predation, but could not be separated from several alternative causes.
g Results from this study suggest predation may limit this species, but only in woodland, not gardens; the identity of the predator was unknown.
h Apparently high levels of predation may have contributed to a short-term decline in black grouse numbers, though the population increased dramatically over the longer-term.
m Magpie analysis from reference 23.
s Sparrowhawk analysis from reference 23.

***Examples are:**
Comparison of prey numbers on land where predators were controlled for game management with those on land where they were not. Comparison of prey trends at times when predators were present with those when absent. Comparison of prey trends in areas onto which predators have been introduced, with those onto which they have not. Comparisons of prey numbers across areas with differing predator numbers.

Prey species	Predator species studied	Evidence			No evidence		
		Fair	Good	Best	Fair	Good	Best
Storm petrel	**Brown rat**		**1**				
Kestrel	Goshawk		2				
Red grouse	Carrion crow, fox, hen harrier, peregrine	3	4, 5				
Black grouse	Goshawk, carrion crow, fox	30^{h}		6^{a}		7	
Capercaillie	Carrion and hooded crow, raptors, fox		8^{a}	9^{a}			
Grey partridge	Carrion crow, magpie, buzzard, sparrowhawk, fox		10^{b}	11		10^{c}	
Avocet	Black-headed gull			12^{d}			12^{d}
Golden plover	Carrion crow, common gull, fox		4, 13				
Lapwing	Carrion crow, fox, **hedgehog**		4, 14^{e}, **15**				16
Dunlin	**Hedgehog**		**15**				
Snipe	Carrion crow, fox, **hedgehog**		**15**			4	
Curlew	Hooded/carrion crow, lesser black-backed gull, fox	17	4				
Redshank	**Hedgehog**		**15**				
Black-headed gull	**American mink**		**18**				
Common gull	**American mink**		**18**				
Kittiwake	Great skua	19, 20					
Common tern	**American mink**		**18**				
Little tern	Fox	21					
Woodpigeon	**Grey squirrel**					**22**	
Green woodpecker	**Grey squirrel**					**22**	

Prey species	Predator species studied	Evidence			No evidence		
		Fair	Good	Best	Fair	Good	Best
Great spotted woodpecker	**Grey squirrel**					**22**	
Lesser spotted woodpecker	**Grey squirrel**		**22**				
Skylark	Sparrowhawk, magpie					23^{s}, 23^{m}	
Tree pipit	**Grey squirrel**					**22**	
Meadow pipit	Carrion crow, sparrowhawk, magpie, fox					4, 23^{s}, 23^{m}	
Wren	Sparrowhawk, magpie, **grey squirrel**		23^{m}			**22**, 23^{s}, 24	
Dunnock	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}	
Robin	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Redstart	**Grey squirrel**					**22**	
Blackbird	Sparrowhawk, magpie, **grey squirrel**	25				**22**, 23^{s}, 23^{m}, 24	
Song thrush	Sparrowhawk, magpie, **grey squirrel**		23^{s}, ?24^{f}			**22**, 23^{m}	
Mistle thrush	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}	
Garden warbler	**Grey squirrel**					**22**	
Blackcap	Sparrowhawk, **grey squirrel**					**22**, 24	
Wood warbler	**Grey squirrel**					**22**	
Chiffchaff	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Willow warbler	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Goldcrest	**Grey squirrel**					**22**	
Spotted flycatcher	Unknown, **grey squirrel**		26^{g}			**22**	
Pied flycatcher	**Grey squirrel**					**22**	
Long-tailed tit	**Grey squirrel**					**22**	
Marsh tit	Great spotted woodpecker, jay, **grey squirrel**					**22**, 27	
Willow tit	Great spotted woodpecker, jay, **grey squirrel**					**22**, 28	
Coal tit	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Blue tit	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24, 29	
Great tit	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24, 29	
Nuthatch	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Jay	**Grey squirrel**					**22**	
Jackdaw	**Grey squirrel**					**22**	
Starling	Sparrowhawk, magpie					23^{s}, 23^{m}, 24^{f}	
Tree sparrow	Sparrowhawk, magpie					23^{s}, 23^{m}	
Chaffinch	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}, 24	
Greenfinch	Sparrowhawk, magpie					23^{s}, 23^{m}	
Goldfinch	Sparrowhawk, magpie					23^{s}, 23^{m}	
Siskin	**Grey squirrel**					**22**	
Linnet	Sparrowhawk, magpie					23^{s}, 23^{m}	
Lesser redpoll	**Grey squirrel**					**22**	
Bullfinch	Sparrowhawk, magpie, **grey squirrel**					**22**, 23^{s}, 23^{m}	
Hawfinch	**Grey squirrel**		**22**				
Yellowhammer	Sparrowhawk, magpie					23^{s}, 23^{m}	
Reed bunting	Sparrowhawk, magpie					23^{s}, 23^{m}	

4. Mitigating the impacts of predators

If predation is thought to be reducing nest survival, breeding success, survival of young and adults or breeding numbers, then Game or Conservation Managers may wish to intervene to minimise the impact of predators on the prey species they are concerned about. However, the objectives of Game and Conservation Managers differ. A Conservation Manager would intervene if the prey population were rare or had declined, and would seek to ensure that the size of the breeding population increased, or at least stopped declining. Game Managers in addition need to ensure that sufficient young are produced each year to provide a surplus of birds in the autumn and winter for shooting.

Interventions could be of various sorts, and several approaches are considered here; removal of predators (most commonly by killing them), exclusion of predators, management of habitat to reduce predation, diversionary feeding, conditioned taste aversion and methods that warn prey of approaching predators.

4.a. Predator removal

One of the most convincing ways to determine whether a predator is limiting a population of its prey is to remove the predators, or reduce their numbers, and see if prey populations increase. Such studies will also show whether predator removal is a useful management tool. Ideally, these studies should be done as formal experiments, with predators removed in some areas or years, but not in others, and the impact on prey measured (Newton 1998). Some of the most informative studies involve a switch, in which the same parcels of land have periods of several years with and without predator removal. Generally, predator removal is achieved by shooting or trapping and killing, though live predators can be removed and translocated elsewhere (e.g. Molony *et al.* 2006).

Several examples of such experiments on birds in the UK have already been mentioned, for example on lapwings, avocets, capercaillie, black grouse and grey partridges. However, many more have been undertaken elsewhere, and here we summarise the results of two reviews that looked at their success. It is worth bearing in mind, however, that such experiments are more likely to have been undertaken on populations of species thought to be limited by predation.

The first review (Newton 1993, 1998) considered 30 studies and found that predator removal resulted in improved nest survival of prey in 23 of 27 studies (85%), increased post-breeding population size ('autumn densities') in 12 of 17 studies (71%), and increased subsequent breeding numbers in 10 of 17 studies (59%). A recent update of this review (Nordström 2003) considered eight more studies, and found, unsurprisingly, very similar results (improvements in nest survival, post-breeding population and subsequent breeding population sizes of 84%, 70% and 61%, respectively). Thus, it appears that in more than half of all studies, the prey populations concerned had been limited by predation, and once predators were removed, prey populations rose. Most of the species studied were ground-nesters, specifically gamebirds or waterfowl, which may be more vulnerable to predation than other birds that nest in safer sites. Alternatively, the precocial young of ground-nesting birds may be more vulnerable to predation than those of other species. Among gamebirds, only four out of 10 experiments led to increases in breeding numbers (Nordström 2003; Valkama *et al.* 2005). Few experiments have attempted to remove predators of songbirds.

By contrast, the second review (Côté and Sutherland 1997), a more formal statistical analysis, took account of the magnitude of the effect of predator control (i.e. not just whether nest survival changed or not, but by how much) and found that reducing predator numbers did not reliably increase breeding bird populations. This review examined 20 individual predator control experiments, incorporating many of those from the first review. It concluded that, while predator control resulted in marked increases in nest survival and autumn densities, the effects on the size of the breeding population the following year were less consistent. While there was a tendency for them to be larger following predator control, this effect fell just short of statistical significance. Some studies showed increased breeding populations following predator removal, whereas others showed no effect or even decreases.

There are a range of reasons why predator control experiments might not always increase subsequent prey breeding populations. First, predation might not have been limiting the populations of prey studied and so killing predators would not lead to increases in prey breeding numbers. Several examples of this have been given earlier; predator control was ineffective for capercaillie when June was wet (Summers *et al.* 2004), for capercaillie and black grouse when vole numbers were high (Marcström *et al.* 1988) and for terns when chick food availability was low (Ratcliffe *et al.* 2005).

Second, control efforts may not have removed all predators from the study areas; others may have moved

Gamekeeper Peter Cairns (rspb-images.com)

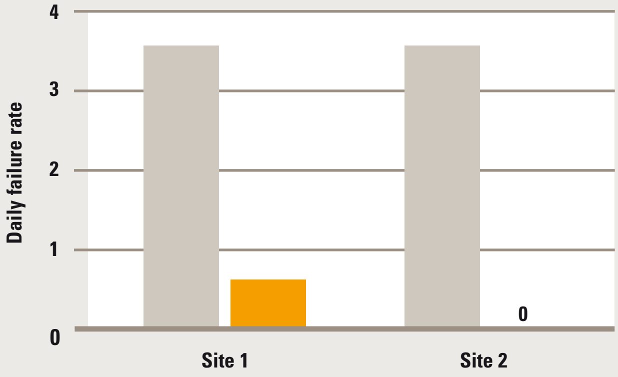


Figure 16 Daily failure rates of wader nests (% per day) to introduced hedgehogs on the Western Isles, Scotland, in fenced (orange bars) and unfenced (grey bars) plots for each of two study sites. (Data from Jackson 2001).

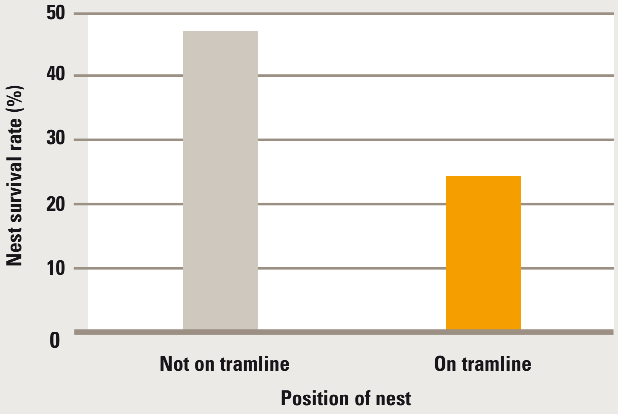


Figure 17 Skylarks forced to nest on tramlines in rapidly growing cereal crops suffer increased nest predation. (Reproduced from Donald 2004).

in to fill the habitat left by those that were removed, or populations of smaller predators may have increased as their own predators were removed. Finally, because birds and their predators are so wide-ranging, it is difficult to remove predators experimentally and hope to determine the impact on subsequent prey numbers. The examples of successful experiments of this kind (e.g. Tapper *et al.* 1996) tend to involve prey species that do not disperse far. If birds only disperse a short distance, then it is more likely that effects of local improvement in breeding productivity due to predator control will result in local increases in adult numbers.

Both reviews suggest that predator control may be an effective tool for Game Managers, as it often increases the production of young for shooting in the autumn and winter. However, it is less effective for Conservation Managers, whose goal is to maintain and even increase the size of the breeding population. Interestingly, in the second review, predator removal failed to stem the decline of three of the four formerly declining populations included in the study, while it tended to increase populations that had formerly been stable or rising. In most of these experiments, when control stopped, predators soon moved back and predation rates and population levels reverted to their former levels (Newton 1993, 1998). On islands, which are less likely to be naturally re-colonised by predators and on which there are fewer predator species anyway, the effects of control tend to be longer lasting (Myers *et al.* 2000; Nordström 2003).

Lethal control of predators should not be seen as a substitute for provision of good habitat and food supplies, and recovery of prey populations can be achieved through habitat-mediated measures alone (e.g. Gilbert *et al.* 2007; O'Brien *et al.* 2006; Peach *et al.* 2001). However, there are cases, particularly for some ground-nesting birds, where predator control can provide a valuable additional tool for Conservation Managers.

4.b. Predator exclusion

Physical barriers, such as fences, can greatly reduce the rate at which mammalian predators encounter their bird prey. While fencing is generally used to protect small areas of land with high densities of birds, much larger-scale exclusion projects have been implemented in Australia and New Zealand. Fencing designs vary, but are commonly electrified (Moseby and Read 2006). In the UK, fencing has been used to exclude mammals from tern colonies on mainland beaches (Smart 2004) and the avocet colony at the RSPB's Minsmere nature reserve, Suffolk.

Fences can be effective in reducing predation (Jackson 2001; Patterson 1967; Smart 2004). In a study by the RSPB on the Outer Hebrides, for example, when hedgehogs (which are not native to the islands) were removed from two fenced plots, the hatching success of breeding dunlins and lapwings doubled compared to that in two nearby areas with no fences (Jackson 2001; see Figure 16).

However, fences can sometimes be breached. On the Outer Hebrides, hedgehogs occasionally re-entered the fenced plots through burrows dug by rabbits under the fence. In tern colonies, even a single intrusion by a fox can cause severe losses of eggs and chicks (Smart 2004). Furthermore, the pacing of predators around a fenced perimeter at night can result in parent birds being disturbed from their nests with resultant loss of eggs or chicks to exposure. Fences are, of course, wholly ineffective at reducing predation by birds, and this may partially replace that by the excluded mammals. For example, fox predation at the Great Yarmouth little tern colony has been reduced by fences and nocturnal patrols by wardens, but subsequent kestrel predation has caused heavy losses of chicks in some years (Smart and Ratcliffe 2000). Fences may also delay or hinder chicks that may want to move away from their nests unless carefully managed (Isaksson *et al.* 2007).

An alternative to fencing entire colonies is to protect individual nests instead. One approach is to use nest exclosures. These are protective cages placed over nests that allow incubating adults free access to the nest and let chicks leave when they need to, yet hinder predators from reaching it. Although such nest exclosures have been widely used, their efficacy has rarely been tested and where it has been, results have been mixed (Johnson and Oring 2002; Mabeé and Estelle 2000). In a recent study in Sweden, protected lapwing and redshank nests had higher hatching success than unprotected nests, but incubating adult redshanks – although not lapwings – were more likely to be predated from protected nests (Isaksson *et al.* 2007). This increased predation on incubating adults was probably because redshanks tended to sit tight until predators were close by, and only then flushed. When flushed, they tended to fly to the top of the cage and may not have been able to escape the predator fast enough. This study suggests that nest protectors should only be used on shorebirds that flush early, when predators are still far away.

Predator-proof nestboxes can also be designed to prevent predation on hole-nesting species. Such boxes stopped weasel predation on tit nests in Wytham Woods, although this had little effect on tit population size (McCleery and Perrins 1991).

Sonic deterrents can also be used to reduce predator incursions. For example, in an experiment undertaken by the RSPB, 'Catwatch' units, which emit a high-pitched sound when a movement sensor is activated, reduced the number and duration of cat intrusions into gardens (Nelson *et al.* 2006).

4.c. Habitat management to reduce predation and its impacts

While it may be tempting to think that declines of bird populations are due either to predation or to other environmental causes, such as changes to their habitat, this view is too simplistic as these two potential causes are often interlinked. Even if the immediate cause of a species' decline in a particular area is predation, a broader habitat or environmental change may have, for example, led to increased predator numbers or prey vulnerability. In such circumstances, predation can become the proximate cause of a species' decline, while habitat change may be the ultimate cause. In this section, we discuss these inter-linkages (Evans 2004; Martin 1992; Newton 1998; Whittingham and Evans 2004), and consider ways in which habitats could be managed, or land-management changed, to reduce the impacts of predation on birds and, if declining, aid their recovery.

First, habitat change may alter the vulnerability of birds to predation. For example, because of the switch from spring to winter-sowing of cereals over the last few decades, skylarks are unable to nest successfully later in the season in the dense, winter-sown crop and so are forced to nest close to the more open tractor tramlines where they are often predated (Donald 1999; JD Wilson *et al.* 1997; see Figure 17). This happens less often in more open, later developing, spring-sown cereal crops, which have now been mostly replaced by winter-sown varieties. Lapwings may now nest at lower densities following their population and range contraction due to changes in farming practices. Lapwing nests are much more likely to be predated where nests are at a low density, probably because there are fewer adults to communally defend their nests against predators (Stillman *et al.* 2006).

In principle, birds and their nests could be made less vulnerable to predation by managing the habitat, to ensure that they are better hidden from predators or are in locations less favoured by predators. For a range

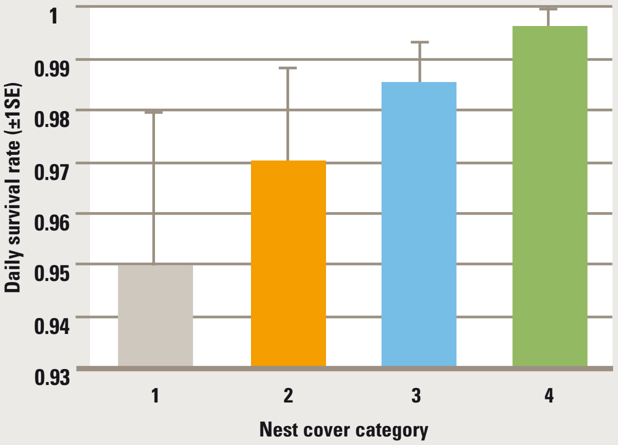


Figure 18 **Removal of unmanaged rank vegetation from farmland reduces the amount of nest cover.**

Reed bunting nests with less cover (lower category) suffered higher predation rates at the egg stage. (Reproduced from Brickle and Peach 2004).

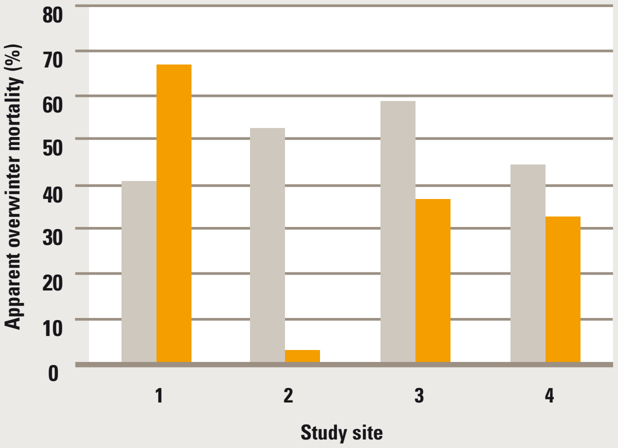


Figure 19 **Cover strips, designed to reduce predation on grey partridges actually increased their over-winter mortality at three out of four study sites in France. (Data adapted from Bro *et al.* 2004).**

of species, predation on nests is lower where there is more nesting cover (Gregg *et al.* 1994; Guyn and Clark 1997; Jiménez and Conover 2001). In the UK, for example, hedgerows provide nesting cover for grey partridges, and where these are more plentiful, nest predation is lower, particularly where there is a lot of dead grass in which to hide nests at the foot of the hedge (Potts 1980; Rands 1988). In Germany, dummy songbird nests in wide hedges were less often predated than those in smaller hedges (Barkow 2005). Lapwing nests may be less well concealed and thus more vulnerable to predation on the uniform short grass swards associated with intensive grassland management for livestock (Baines 1990). The general tidying up of farmland and consequent loss of rank unmanaged vegetation may have reduced the availability of safe nesting sites for reed buntings, as their nests are more often predated where there is little cover (Brickle and Peach 2004; see Figure 18).

The vulnerability of birds and their nests to predation can also be influenced by proximity to particular habitat features. For example, redshanks feeding close to cover are more likely to be killed by sparrowhawks who use cover to hide their approach from the redshank's view (Hilton *et al.* 1999; Quinn and Cresswell 2004). Similarly, lapwing nests close to field boundaries are more likely to suffer predation, probably because predators use these features to navigate or hunt (Sharpe 2006; Sheldon 2002; Stillman *et al.* 2006).

Such interactions can be yet more subtle. Where intensive land management favours high livestock densities, this can both increase losses of nests due to trampling (Beintema and Muskens 1987) and increase the chance that the nest will be predated as incubating birds are continually flushed off the nest (Hart *et al.* 2002). Any change in habitat that reduces food supplies for young birds may increase predation as hungry songbird nestlings are more vocal and may be more easily found by predators (Brickle *et al.* 2000; Evans *et al.* 1997). Alternatively, reduced food supplies may force birds to forage for longer, or in more dangerous places, making them more likely to be killed by a predator (Hilton *et al.* 1999; Martin 1992; Quinn and Cresswell 2004; Rands 1986). For example, bullfinches are more vulnerable to predation when food supplies decline in late winter forcing them to feed farther from cover (Marquiss 2007). Loss of seed food due to changes in agricultural practices could have contributed both directly, through starvation, and indirectly, through predation, to the bullfinch's decline in the UK (Newton 2004).

Second, some habitat and land-use changes may constrain a bird species' ability to compensate for losses to predation. For example, if deteriorating habitat quality were to shorten the breeding season, birds that would otherwise be well adapted to high levels of predation may have less time to re-nest if a previous nest is lost to predators. The switch from spring to autumn sowing of cereals has tended to curtail the skylark's breeding season (Chamberlain *et al.* 1999), while drying out of wet grasslands, exacerbated by drainage, makes them less suitable for breeding snipe later in the season (Green 1988). In one study, in an arable area of Essex, song thrushes stopped breeding earlier in the season than those in an area of mixed farming in Sussex (Peach *et al.* 2004), probably because food was less available in the arable site. In each of these cases, the breeding season had been curtailed due, in one way or another, to habitat change. Such changes may have made these species less able to compensate for losses to predation. Any approach – not simply predator control – that can boost overall productivity or enhance survival would improve a species' chance of compensating for any losses to predation. For example, a study of capercaillie in Scotland (Baines *et al.* 2004) suggested that marking or removing fences, thus reducing adult mortality from fence collisions, would help this species compensate for losses of chicks and eggs to predation.

Finally, changes to habitat or land management can increase predator numbers, thus potentially increasing predation on birds. Several examples of this have already been outlined. The deteriorating quality of heather moorland (Thirgood *et al.* 2000a; Thompson *et al.* 1995) favours hen harriers by increasing numbers of their preferred staple small prey, and thus predation pressure on red grouse. The fragmentation of native pinewoods may have increased the numbers of crows and foxes that would normally live at fairly low densities in pinewoods, increasing predation on capercaillie nests (Summers *et al.* 2004). Several studies have shown that numbers of generalist predators are higher in fragmented landscapes (Andrén 1992; Kurki *et al.* 1998), and that predation is more common in such landscapes near forest edges, or in small forest patches, than in the interior of large forests (Andrén 1992; Andrén and Anglestam 1988; Baines *et al.* 2004; Chalfoun *et al.* 2002; Hoover *et al.* 1995; Huhta *et al.* 1996; Kurki and Lindén 1995; Kurki *et al.* 1997; Newton 1998; Thompson *et al.* 2002). More broadly, the growing emphasis on large-scale rear and release of gamebirds for sport shooting has probably improved the food supply of generalist predators, such as the fox (GCT 2004), and may have increased predation pressure on a wide range of bird prey.

From each of these studies arise some potential solutions that could be implemented to reduce predation on birds. Hedgerows, grassland and cereal crops could be managed, and rank vegetation retained to make nests and chicks less likely to be found by predators. Bird-food rich habitats could be provided to ensure highly-vocal starving chicks do not attract predators, and that birds aren't forced to forage for longer and in more dangerous places. Potential breeding sites and perching places for predators could be removed in some open habitats that are important for threatened bird prey species. Woodland fragments could be joined together to reduce levels of predation that can be higher near forest edges than in their interiors. Food supplies that maintain populations of generalist predators could be controlled. More broadly, habitats could be managed in ways that boost productivity or enhance survival, thus improving a species' chance of compensating for any losses to predation. While some of these solutions could be quick fixes (e.g. providing food rich habitats), others clearly require a much longer-term investment (e.g. reducing forest fragmentation).

Unfortunately, many of these potential solutions remain untested. For example, although several studies in the US have shown that cover around nests reduces predation (Jiménez and Conover 2001), few studies have experimentally manipulated cover. However, in one study in the North American Prairies, the conversion of cropland to grassland contributed to recovery in wildfowl populations as predation on nests fell due to improved nesting cover and avoidance of the converted areas by some mammal predators (Greenwood and Sovada 1996; Phillips *et al.* 2003). In the UK, work is planned to test simple management solutions that can reduce predation on lapwing nests by persuading them to nest at high densities and away from field boundaries, both of which independently improve nest survival (Stillmann *et al.* 2006). Such rigorous testing is needed in order to develop practical solutions that work. An experiment in France, for example, designed to reduce grey partridge predation by raptors and mammals by planting crops to provide cover, backfired when it apparently increased over-winter mortality of partridges (Bro *et al.* 2004; see Figure 19). This was probably because these cover crops did not provide an effective refuge against predators for a species that relies on vigilance and crypsis as its main anti-predator strategies, rather than concealment in dense vegetation.

Little tern Chris Gomersall (rspb-images.com)

4.d. Diversionary feeding

The principle of diversionary feeding is simple; predators are provided with alternative food in the hope that less prey will be killed. The practice of diversionary feeding, however, is not so straightforward. Although commonly proposed as a method to reduce predation, there are few cases where it has been proven to work successfully (Graham *et al.* 2005; Jiménez and Conover 2001).

The best-known diversionary feeding trial in the UK – an attempt to reduce hen harrier predation on red grouse chicks – was carried out at Langholm Moor. Hen harriers delivered 86% fewer grouse chicks to their nests during the nestling period when provided with supplementary food (dead rats and cockerel chicks) in the spring and summer (Redpath *et al.* 2001). However, despite this, chick mortality remained high, perhaps because other predators took the grouse chicks (Redpath *et al.* 2001).

Another study of diversionary feeding in the UK, of kestrels predating little terns nesting on a beach at Great Yarmouth, proved inconclusive (Smart 2004; Smart and Ratcliffe 2000). While diversionary feeding may have reduced the level of kestrel predation in some years, variability in the weather and availability of alternative prey (voles) for kestrels made it difficult to draw firm conclusions.

More broadly, there is a risk that predator breeding success or density might be improved by supplementary feeding; this could serve to worsen the problem rather than solve it (Reynolds and Tapper 1996). This risk is increased if food is provided year round, rather than for a few weeks at a critical time in the breeding season.

Notwithstanding these complications, research into diversionary feeding is still at an early stage, and further developments could provide valuable tools to allow hen harriers to co-exist with driven grouse moor management, and kestrels with the conservation of little terns. Further tests of diversionary feeding to reduce predation of little tern chicks are already underway, and are planned for red grouse chicks.

Intriguingly, there may be merit in providing supplementary food to the prey rather than the predator (Quinn and Cresswell 2004) if this could be shown to reduce the vulnerability of prey, for example by reducing the amount of time they spend feeding in dangerous locations.

4.e. Conditioned Taste Aversion

One potential method to reduce predation is to provide individual predators with a bait that resembles their prey, but which is dosed with noxious chemicals to make them sick. Over time, the predator will learn to stop taking their real prey believing that they, too, will make them sick. This method, known as Conditioned Taste Aversion (CTA), has been shown to reduce predation on bird's eggs by corvids (Avery and Decker 1994; Bogliani and Bellinato 1998; Dimmock and Nicolaus 1990; Nicolaus 1987; Nicolaus *et al.* 1983) and mammals (Conover 1990) in the wild in the US. For example, up to 10 ravens were killed annually over a three-year period to protect a colony of Californian least terns. The following year, eggs injected with methiocarb were set out for ravens and, consequently, no tern eggs were predated and no ravens had to be killed (Avery *et al.* 1995).

Foxes have been successfully conditioned using bitter chemicals in small-scale laboratory trials (Macdonald and Baker 2004). Unfortunately, some mammals are able to detect the chemicals and so avoid the baits (Massei *et al.* 2003a), and there can be marked differences between individuals of the same predator species in their response (Anon 2001; Massei *et al.* 2003b). In addition, it can be difficult to exclude non-target mammals, because accurate dosing is problematic as individual predators vary in body size (Reynolds 2000), and this method is only really practical where predator numbers are low as each individual predator has to be conditioned.

No CTA trials designed to reduce predation have been successfully conducted in the wild in the UK, but experience from the US suggests that trials for some specific UK circumstances could be merited.

Some chemicals could deter predators simply by their smell – an innate aversion rather than a learnt one. While a number of products with particularly strong smells, such as creosote or lion dung, are promoted as alternative methods to deter ground predators, the efficacy of these products in reducing predation has not yet been tested experimentally.

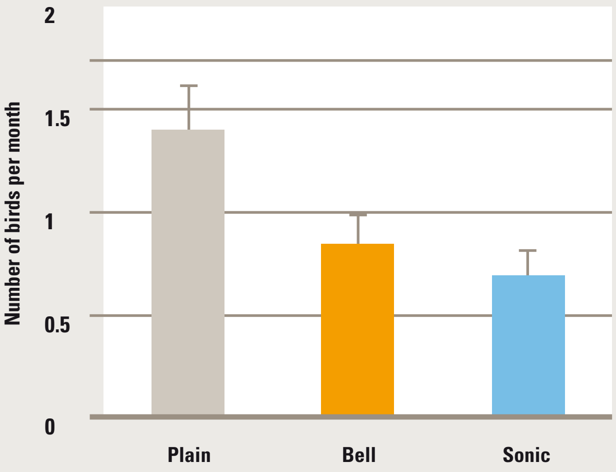


Figure 20 Average (+/- 1 SE) number of prey returned in a month by cats fitted with collars that had a sonic device, a bell or nothing (plain). (Data from Nelson *et al.* 2005).

Sonic device (CatAlert™) and bell on quick-release cat collars.

4.f. Warning prey of approaching predators

If prey could be warned of the approach of hunting predators, they could take avoiding action and reduce their chances of being killed. While it is hard to imagine how to do this in most circumstances in the wild, it may be practical for domestic predators.

Domestic cats undoubtedly kill a large number of birds in the UK every year, although it is unclear whether this constitutes a conservation problem. Nevertheless, management techniques to reduce the mortality caused by cats would be welcome and prudent. One option is to attach a collar-mounted warning device (a bell or electronic bleeper) to those cats known to hunt. Several studies (e.g. Woods *et al.* 2003) found no effect of bells on bird predation rates. However, in these studies volunteers were asked to record the prey brought back by their cats and note whether the cat was fitted with a bell. Owners of cats prone to kill birds may be more likely to fit their animal with a bell, so any effect of bells reducing predation may have already occurred, and would not be picked up by this type of study.

Experimental studies are more revealing. One recorded the prey brought back by individual cats during periods when they were, or were not, wearing a bell, and showed that bells reduced bird predation (measured by prey returns) by about half (Ruxton *et al.* 2002). A second experimental study by the RSPB tested both bells and electronic sonic devices that emit an audible ‘bleep’ every seven seconds. Bells and sonic devices reduced bird kills by 41% and 51%, respectively (Nelson *et al.* 2005; see Figure 20).

Clearly, collar-mounted warning devices offer a partial solution to cat predation, and more research could usefully be done to improve their efficacy. Because domestic cats obtain most of their food from their owners, making them less effective killers is unlikely to have an impact on their welfare or survival. This might not be the case with wild predators.

5. Future research needs

Most of the scientific evidence presented here has been collected over the last 50 or so years. Undoubtedly, further evidence will become available, and reviews such as this should be undertaken periodically to ensure that conservation policy and practice is underpinned by the most contemporary science.

Various suggestions for research have been highlighted throughout this review and these are summarised here to help focus any future work.

Further studies that provide clear evidence of whether predators limit populations of their bird prey are needed. While such evidence is best obtained from predator removal experiments, these are not always straightforward, so an alternative approach is to compare populations of bird prey in areas, or at times, with differing predator densities. So far, most studies have been of ground-nesting birds, and similar studies of songbirds are needed, for example in urban and suburban areas. In addition, some of the songbird studies that have been undertaken need updating. In particular, a classic study of the impacts of magpies and sparrowhawks on songbird populations (Thomson *et al.* 1998) is now a decade old, and trends of these and other predators and their songbird prey have changed.

An updated review of the effectiveness of removing predators to protect bird populations would be valuable, as the existing reviews (Côté and Sutherland 1997; Newton 1998) are now also a decade old, and additional removal studies have been undertaken in the interim. Such a review should seek to determine the circumstances in which predator removal is most often effective, thus allowing better targeting of this method.

The interactions between changes in habitat management and land-use practices and levels of predation need to be better understood, so that additional non-lethal solutions to reduce predation can be designed, tested and implemented. For example, can vegetation be managed to make predators less numerous and nests or chicks of prey less easily located? Similarly, can the right resources, such as food and nest sites, be provided to ensure breeding seasons of prey are not curtailed, allowing them to re-nest if predated to help compensate for losses to predation? Furthermore, to what extent have artificial food supplies and fragmented habitats boosted populations of generalist predators? For example, have fox numbers increased because of the growth in rear and release of gamebirds, and has this led to increased predation pressure on ground-nesting birds?


Sue Tranter (rspb-images.com)

Wren

Several other non-lethal methods need further development, despite only being applicable in quite specific circumstances. In particular, research is needed to improve the success of methods to exclude predators, to provide them with diversionary food and to condition them not to kill eggs and chicks.

Finally, more research to determine the identity of key predators and their foraging behaviour is needed, because both lethal and non-lethal solutions to reduce levels of predation can be markedly improved upon when these are known.

6. Implications for conservation

This extensive scientific review provides little evidence that songbird numbers in the UK are limited by predation. In particular, it shows that declines in songbird numbers over the last few decades should not be blamed on predation by sparrowhawks or magpies. Because of this, any attempt to recover the UK's songbird numbers by managing predator populations, such as those of sparrowhawks or magpies, is likely to prove ineffective. A great deal of conservation resource is currently being spent on recovering songbird populations by managing their habitats; the evidence presented in this review supports this approach.

By contrast, there is growing scientific evidence that breeding populations of some ground-nesting birds, such as waders and gamebirds, are more likely to be limited by predation than other groups, perhaps because their nests or young are more vulnerable to predation. Consequently, as well as managing habitats to provide food and nest sites, Conservation Managers should consider ways of reducing the impacts of predation on ground-nesting birds that have a poor conservation status. While reducing predator numbers by killing them is one option that can be successful, other, non-lethal solutions are available, though their efficacy is less well documented. Such options include placing electric fences around nesting colonies, diversionary feeding and managing habitats to reduce the chances of bird prey being killed.

Lapwings Mike Read (rspb-images.com)

7. References

Aebischer NJ (2000) Grey partridges, lowland raptors and the Sussex study. In: *Review of 1999*. Game Conservancy Trust, Fordingbridge: 61–65.

Aebischer NJ, Evans AD, Grice PV and Vickery JA (eds) (2000b) *The Ecology and Conservation of Lowland Farmland Birds.* British Ornithologists' Union, Tring, UK.

Aebischer NJ and Ewald JA (2004) Managing the UK grey partridge *Perdix perdix* recovery: population change, reproduction, habitat and shooting. *Ibis* 146 (Suppl. 2): 181–191.

Aebischer NJ, Green RE and Evans AD (2000a) From science to recovery: four case studies of how research has been translated into conservation action in the UK. In: Aebischer NJ, Evans AD, Grice PV and Vickery JA (eds) *Ecology and Conservation of Lowland Farmland Birds*. British Ornithologists' Union, Tring, UK: 43–54.

Amar A, Hewson CM, Thewlis RM, Smith KW, Fuller RJ, Lindsell JA, Conway G, Butler S and MacDonald M (2006) *What's happening to our woodland birds? Long term changes in the populations of woodland birds*. RSPB Research Report No.19 and BTO Research Report No.169. RSPB and BTO, Sandy and Thetford, UK.

Anderson GQA, Bradbury RB and Evans AD (2001) Evidence for the effects of agricultural intensification on wild bird populations in the UK. RSPB Research Report No.3. RSPB, Sandy.

Andrén H (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794–804.

Andrén H and Angelstam P (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69: 544–547.

Angelstam P (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica* 15: 123–134.

Anon (2001*) Identification and testing of potential CTA agents for use in Mammalian Pest Control*. MAFF report. Project code no: VC0408.

Avery ML and Decker DG (1994) Responses of captive fish crows to eggs treated with chemical repellents. *Journal of Wildlife Management* 58: 261–266.

Avery ML, Pavelka MA, Bergman DL, Decker DG, Knittle CE and Linz GM (1995) Aversive conditioning to reduce raven predation on California least tern eggs. *Colonial Waterbirds* 18: 131–245.

Baillie SR, Marchant JH, Crick HQP, Noble DG, Balmer DE, Beaven LP, Coombes RH, Downie IS, Freeman SN, Joys AC, Leech DI, Raven MJ, Robinson RA and Thewlis RM (2005) *Breeding birds in the wider countryside: their conservation status 2004*. BTO Research Report No.385. BTO, Thetford.

Baines D (1990) The roles of predation, food and agricultural practice in determining the breeding success of the lapwing *Vanellus vanellus* on upland grassland. *Journal of Animal Ecology* 59: 915–929.

Baines D (1994) Seasonal differences in habitat selection by black grouse *Tetrao tetrix* in the Northern Pennines, England. *Ibis* 136: 39–43.

Baines D (1996) The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *Journal of Applied Ecology* 33: 54–62.

Baines D, Moss R and Dugan D (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology* 41: 59–71

Baker PJ, Bentley AJ, Ansell RJ and Harris S (2005) Impact of predation by domestic cats in an urban area. *Mammal Review* 35: 302–312.

Baker H, Stroud DA, Aebischer NJ, Cranswick PA, Gregory RD, McSorley CA, Noble DG and Rehfisch MM (2006) Population estimates of birds in Great Britain and the United Kingdom. *British Birds* 99: 25–44.

Balharry EA, McGowen GM, Kruuk H and Halliwell E (1996) *Distribution of pine martens in Scotland as determined by field survey and questionnaire*. Unpublished report to Scottish Natural Heritage, Edinburgh.

Barkow A (2005) Predation on passerine nests in hedges: the impact of nest placement, hedge structure and predators. *Vogelwelt* 126: 346–352.

Battersby J (ed) and Tracking Mammals Partnership (2005) *UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership.* JNCC/Tracking Mammals Partnership, Peterborough.

Beintema AJ and Muskens GJDM (1987) Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology* 24: 743–758.

Benton TG, Bryant DM, Cole L and Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39: 673–687.

Berg A, Lindberg T and Gunnar K (1992) Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. *Journal of Animal Ecology* 61: 469–476.

Birkhead TR and Furness RW (1985) Regulation of seabird populations. In: Sibley RM and Smith RH (eds) *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Blackwell, London: 145–167.

Birks JDS and Kitchener AC (1999) *The Distribution and Status of the Polecat* Mustela putorius *in Britain in the 1990s*. The Vincent Wildlife Trust, National Museums of Scotland.

Bland RL, Tully J and Greenwood JJD (2004) Birds breeding in British gardens: an underestimated population? *Bird Study* 51: 97–106.

Bogliani G and Bellinato F (1998) Conditioned aversion as a tool to protect eggs from avian predators in heron colonies. *Colonial Waterbirds* 21: 69–72.

Bolton M, Tyler G, Smith K and Bamford R (2007) The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology* 44: 534–544.

Bowker G, Bowker C and Baines D (2007) Survival rates and causes of mortality in black grouse at Lake Vyrnwy, North Wales, UK. *Wildlife Biology.*

Brickle NW, Harper DGC, Aebischer NJ and Cockayne SH (2000) Effects of agricultural intensification on the breeding success of corn buntings *Emberiza calandra*. *Journal of Applied Ecology* 37: 742–755.

Brickle NW and Peach WJ (2004). The breeding ecology of reed buntings *Emberiza schoeniclus* in farmland and wetland habitats in lowland England. *Ibis* 146 (Suppl. 2): 69–77.

Brittas R and Willebrand T (1991). Nesting habitats and egg predation in Swedish black grouse. *Ornis Scandinavica* 22: 261–263.

Bro E, Mayot P, Corda E and Reitz F (2004) Impact of habitat management on grey partridge populations: assessing wildlife cover using a multisite BACI experiment. *Journal of Applied Ecology* 41: 846–857.

Caizergues A and Ellison LN (1997) Survival of black grouse *Tetrao tetrix* in the French Alps. *Wildlife Biology* 3: 177–185.

Calladine J, Baines D and Warren P (2002) Effects of reduced grazing on population density and breeding success of black grouse in northern England. *Journal of Applied Ecology* 39: 772–780.

Chalfoun AD, Thompson FR and Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16: 306–318.

Chamberlain DE and Crick HQP (2003) Temporal and spatial associations in aspects of reproductive performance of lapwings *Vanellus vanellus* in the United Kingdom, 1962–99. *Ardea* 91: 183–196.

Chamberlain DE, Fuller RJ, Bunce RGH, Duckworth JC and Shrubb M (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales *Journal of Applied Ecology* 37: 771–788.

Chamberlain DE, Wilson AM, Browne SJ and Vickery JA (1999) Effects of habitat type and management on the abundance of skylarks in the breeding season. *Journal of Applied Ecology* 36: 856–870.

Clode D and Macdonald DW (2002) Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. *Bird Study* 49: 118–123.

Conover MR (1990) Reducing mammalian predation on eggs by using a conditioned taste aversion to deceive predators. *Journal of Wildlife Management* 54: 360–365.

Côté IM and Sutherland WJ (1997) The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11: 395–405.

Court IR, Irving PV and Carter I (2004) Status and productivity of peregrine falcons in the Yorkshire Dales between 1978 and 2002. British Birds 97: 456–463.

Craik JCA (1995) Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland. *Seabird* 17: 3–11.

Craik JCA (1997) Long-term effects of North American mink *Mustela vison* on seabirds in western Scotland. *Bird Study* 44: 303–309.

Crick HQP, Robinson RA, Appleton GF, Clark NA and Rickard AD (2002) *Investigation into the causes of the decline of starlings and house sparrows in Great Britain.* BTO Research Report No.290. Defra, London.

Croxall JP and Rothery P (1991) Population regulation of seabirds; implications of their demography for conservation. In: Perrins CM, Lebreton J-D and Hirons GMH (eds) *Bird Population Studies. Relevence to Conservation and Management*. Oxford University Press, Oxford: 272–296.

Davis SE, Newson SE and Noble DG (2007) *The production of population trends for UK mammals using BBS mammal data: 1995–2005 update.* BTO Research Report No. 462. BTO, Thetford, UK.

De Leon A, Minguez E, Harvey P, Meek E, Crane JE and Furness RW (2006) Factors affecting breeding distribution of Storm petrels *Hydrobates pelagicus* in Orkney and Shetland. *Bird Study* 53: 64–72.

Dimmock CR and Nicolaus LK (1990) Efficiency of conditioned aversion in reducing depredation by crows. *Journal of Applied Ecology* 27: 200–209.

Donald PF (1998) Changes in the abundance of invertebrates and plants on British farmland. *British Wildlife* 9: 279–289.

Donald PF (1999) *The Ecology and Conservation of Skylarks* Alauda arvensis *on Lowland Farmland*. DPhil Thesis, University of Oxford.

Donald PF (2004) *The Skylark*. T & AD Poyser, London.

Donald PF, Green RE and Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B* 268: 25–29.

Eaton MA, Ausden M, Burton N, Grice PV, Hearn RD, Hewson CM, Hilton GM, Noble DG, Ratcliffe N and Rehfisch MM (2006) *The State of the UK's Birds 2005*. RSPB, BTO, WWT, CCW, EN, EHS and SNH, Sandy, Bedfordshire.

Eaton MA, Austin GE, Banks AN, Conway G, Douse A, Grice PV, Hearn R, Hilton G, Hoccom D, Musgrove AJ, Noble DG, Ratcliffe N, Rehfisch MM, Worden J and Wotton S (2007a) *The State of the UK's Birds 2006*. RSPB, BTO, WWT, CCW, EHS, NE and SNH, Sandy, Bedfordshire.

Eaton MA, Dillon IA, Stirling-Aird PK and Whitfield DP (2007b) Status of golden eagle *Aquila chrysaetos* in Britain in 2003. *Bird Study* 54: 212–220.

Eaton MA, Noble DG, Cranswick PA, Carter N, Wotton S, Ratcliffe N, Wilson A, Hilton GM and Gregory RD (2004.) *The State of the UK's Birds 2003*. BTO, RSPB and WWT, Sandy, UK.

Etheridge B, Summers RW and Green R (1997) The effects of illegal killing and destruction of nests on the population dynamics of hen harriers in Scotland. *Journal of Applied Ecology* 34: 1081–1106.

Evans AD, Smith KW, Buckingham DL and Evans J (1997) Seasonal variation in breeding performance and nestling diet of cirl buntings *Emberiza cirlus* in England. *Bird Study* 44: 66–79.

Evans KL (2004) The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* 146: 1–13.

Ewald JA, Kingdon N, Aebischer NJ, Tapper S and Graham NA (Unpublished ms.) *Quantification of Management for Shooting on Upland Estates, and Implications for Breeding Wader Distributions*. GCT, Fordingbridge.

Fletcher K (2006) Predator control and ground nesting waders. In: *The Game Conservancy Trust, review of 2005*. GCT, Fordingbridge, Hampshire: 80–83.

Fletcher K, Hoodless A, Foster R and Baines D (2005) Quantifying the impact of predator removal on moors managed for red grouse on other ground nesting birds – progress report. *Grouse News* 30: 14–16.

Fuller RJ, Gregory RD, Gibbons DW, Marchant JH, Wilson JD, Baillie SR and Carter N (1995) Population declines and range contractions among farmland birds in Britain. *Conservation Biology* 9: 1425–1442.

Fuller RJ, Noble DG, Smith KW and Vanhinsbergh D (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Birds* 98: 116–143.

Galbraith H (1988) The effects of territorial behaviour on lapwing populations. *Ornis Scandinavica* 19: 134–138.

Game Conservancy Trust (2004). *Review of 2003*. GCT, Fordingbridge, Hampshire.

Geer T (1978) Effects of nesting sparrowhawks on nesting tits. *Condor* 80: 419–422.

Gibbons DW, Reid JB and Chapman RA (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T & AD Poyser, London.

Gilbert G, Tyler GA, Dunn CJ, Ratcliffe N and Smith KW (2007) The influence of habitat management on the breeding success of the great bittern *Botaurus stellaris. Ibis* 149: 53–66.

Gooch S, Baillie SR and Birkhead TR (1991) Magpie *Pica pica* and songbird populations – retrospective investigation of trends in population density and breeding success. *Journal of Applied Ecology* 28: 1068–1086.

Graham K, Beckermann AP and Thirgood S (2005) Human predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159–171.

Grant MC and Dawson R (2005) Black grouse habitat requirements in forested environments: implications for conservation management. In: Anon (ed) *Proceedings of the 3rd European Black Grouse Conference, Ruthin, Wales*: 106–119.

Grant MC, Orsman C, Easton J, Lodge C, Smith M, Thompson G, Rodwell, S and Moore N (1999) Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. *Journal of Applied Ecology* 36: 59–74.

Green RE (1988) Effects of environmental factors on the timing and success of breeding of common snipe *Gallinago gallinago* (Aves, Scolopacidae). *Journal of Applied Ecology* 25: 79–93.

Greenwood RJ and Sovada MA (1996) Prairie duck populations and predation management. *Transactions of the North American Wildlife and Resources Conference* 65: 31–42.

Gregg MA, Crawford JA, Drut MS and DeLong AK (1994) Vegetational cover and predation of sage grouse nests in Oregon. *Journal of Wildlife Management* 58: 162–166.

Gregory RD, Wilkinson NI, Noble DG, Robinson JA, Brown AF, Hughes J, Procter D, Gibbons DW and Galbraith C (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: 410–448.

Groom DW (1993) Magpie *Pica pica* predation on blackbirds *Turdus merula* nests in urban areas. *Bird Study* 40: 55–62.

Guyn KL and Clark RG (1997) Cover characteristics and success of natural and artificial duck nests. *Journal of Field Ornithology* 68: 33–41.

Harding NJ, Green RE and Summers RW (1994) *The Effects of Future Changes In Land Use on Upland Birds in Britain.* RSPB, Sandy.

Harris S, Morris P, Wray S and Yalden D (1995) *A review of British mammals; population estimates and conservation status of British mammals other than cetaceans.* Joint Nature Conservation Committee, Peterborough.

Hart JD, Milsom TP, Baxter A, Kelly PF and Parkin WK (2002) The impact of livestock on lapwing *Vanellus vanellus* breeding densities and performance on coastal grazing marsh. *Bird Study* 49: 67–78.

Haworth PF and Thompson DBA (1990) Factors associated with the breeding distribution of upland birds in the south Pennines, England. *Journal of Applied Ecology* 27: 562–577.

Henderson IG, Wilson AM, Steele D and Vickery JA (2002) Population estimates, trends and habitat associations of breeding lapwing *Vanellus vanellus*, curlew *Numenius arquata* and snipe *Gallinago gallinago* in Northern Ireland in 1999. *Bird Study* 49: 17–25.

Hester A and Sydes C (1992) Changes in the burning of Scottish heather moorland since the 1940s from aerial photographs. *Biological Conservation* 60: 25–30.

Heubeck M, Mellor RM and Harvey PV (1997) Changes in the breeding distribution and numbers of kittiwakes *Rissa tridactyla* around Unst, Shetland, and the presumed role of predation by great skuas *Catharacta skua*. *Seabird* 19: 12–21.

Hewson C, Arjun A, Lindsell J, Thewlis RM, Butler S, Smith K and Fuller RJ (in press) Recent changes in British woodland bird populations derived from the Repeat Woodland Bird Survey. *Ibis*.

Hewson C, Fuller R, Mayle B and Smith K (2004) Possible impacts of grey squirrels on birds and other wildlife. *British Wildlife* 15: 183–191.

Hill D (1988) Population dynamics of the avocet (*Recurvirostra avosetta*) breeding in Britain. *Journal of Animal Ecology* 57: 669–683.

Hilton GM, Ruxton GD and Creswell W (1999) Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* 87: 295–302.

Hole DG, Whittingham MJ, Bradbury RB, Anderson GQA, Lee PLM, Wilson JD and Krebs JR (2002) Widespread local house sparrow extinctions. *Nature* 418: 931–932.

Holling M and the Rare Breeding Birds Panel (2007) Rare breeding birds in the United Kingdom in 2003 and 2004. *British Birds* 100: 321–367.

Hoover JP, Brittingham MC and Goodrich LJ (1995) Effects of forest patch size on nesting success of wood thrushes. *Auk* 112: 146–155.

Hudson PJ (1992) *Grouse in space and time: the population biology of a managed gamebird*. Fordingbridge: Game Conservancy Trust.

Huhta E, Mappes T and Jokimaki J (1996) Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography* 19: 85–91.

Isaksson D, Wallander J and Larsson M (2007) Managing predation on ground-nesting birds: the effectiveness of nest exclosures. *Biological Conservation* 136: 136–142.

Jackson DB (2001) Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *Journal of Applied Ecology* 38: 802–812.

Jackson DB, Fuller RJ and Campbell ST (2004) Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*). *Biological Conservation* 117: 151–166.

Jackson DB and Green RE (2000) The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on the machair in South Uist, Scotland. *Biological Conservation* 93: 333–348.

Jenkins D, Watson A and Miller GR (1967) Population fluctuations in the red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology* 36: 97–122.

Jiménez JE and Conover MR (2001) Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. *Wilson Society Bulletin* 29: 62–69.

Johnson M and Oring LW (2002) Are nest exclosures an effective tool in plover conservation? *Waterbirds* 25: 184–190.

Johnstone I and Lindley P (2003) The proximate causes of black grouse breeding failure in Wales. CCW Contract Science Report No.600.

Kurki S, Helle P, Lindén H and Nikula A (1997) Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos* 79: 301–310.

Kurki S and Lindén H (1995) Forest fragmentation due to agriculture affects the reproductive success of the ground nesting black grouse. *Ecography* 18: 109–113.

Kurki S, Nikula A, Helle P and Lindén H (1998) Abundance of fox and pine marten in relation to composition of the boreal forest. *Journal of Animal Ecology* 67: 874–886.

Lack D (1968) *Ecological adaptations for breeding in birds*. Methuen, London.

Langgemach T and Bellebaum J (2005) Predation and the conservation of ground-breeding birds in Germany. *Vogelwelt* 126: 259–298.

Lindley P, Johnstone I and Thorpe R (2003) The status of black grouse *Tetrao tetrix* in Wales in 2002 and evidence for population recovery. *Welsh Birds* 3: 318–319.

Mabeé TJ and Estelle VB (2000) Assessing the effectiveness of predator exclosures for plovers. *Wilson Bulletin* 112: 14–20.

Macdonald DW and Baker SE (2004) Non-lethal control of fox predation: the potential of generalised aversion. *Animal Welfare* 13: 77–85.

Macdonald DW and Baker S (2005) *The State of Britain's Mammals 2005*. The Mammals Trust UK, London.

Macdonald DW, Bunce RGH and Bacon PJ (1981) Fox populations, habitat characterization and rabies control. *Journal of Biogeography* 8: 145–151.

Marchant JH, Hudson R, Carter SP and Whittington P (1990) *Population Trends in British Breeding Birds.* British Trust for Ornithology, Tring.

Marcström V, Kenward RE and Engren E (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology* 57: 859–872.

Marquiss M (2007) Seasonal pattern in hawk predation on common bullfinches *Pyrrhula pyrrhula*; evidence of an interaction with habitat affecting food availability. *Bird Study* 54: 1–11.

Massei G, Lyon A and Cowan DP (2003a) Potential compounds for induction conditioned taste aversion in ferrets. *New Zealand Journal of Zoology* 30: 95–100.

Massei G, Lyon A and Cowan DP (2003b) Levamisole can induce conditioned taste aversion in foxes. *Wildlife Research* 30: 633–637.

Martin TE (1992) Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9: 163–197.

May RM (1988) Control of feline delinquency. *Nature* 332: 392–393.

McCleery RH and Perrins CM (1991) Effects of predation on the numbers of great tits *Parus major*. In: Perrins CM, Lebreton J-D and Hirons GMH (eds) *Bird population studies. Relevence to Conservation and Management*. Oxford University Press, Oxford: 129–147.

McDonald RA and Harris S (1999) The use of trapping records to monitor populations of stoats *Mustela erminea* and weasels *M. nivalis*: the importance of trapping effort. *Journal of Applied Ecology* 36: 679–688.

Milsom TP (2005) Decline of northern lapwing *Vanellus vanellus* breeding on arable farmland in relation to loss of spring tillage. *Bird Study* 52: 297–306.

Møller AP and Erritzøe J (2000) Predation against birds with low immunocompetence. *Oecologica* 122: 500–504.

Molony SE, Dowding CV, Baker PJ, Cuthill IC and Harris S (2006) The effect of translocation and temporary captivity on wildlife rehabilitation success: an experimental study using European hedgehogs (*Erinaceus europaeus*). *Biological Conservation* 130: 530–537.

Moseby KR and Read JL (2006) The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. *Biological Conservation* 127: 429–437.

Moss R (1986) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis* 128: 65–72.

Moss R, Oswald J and Baines D (2001) Climate change and breeding success: decline of the capercaillie in Scotland. *Journal of Animal Ecology* 70: 47–61.

Moss R, Picozzi N, Summers RW and Baines D (2000) Capercaillie *Tetrao urogallus* in Scotland – demography of a declining population. *Ibis* 142: 259–267.

Myers JH, Simberloff D, Kuris AM and Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 15: 316–320.

Nelson SH, Evans AD and Bradbury RB (2005) The efficacy of collar-mounted devices in reducing the rate of predation of wildlife by domestic cats. *Applied Animal Behavioral Science* 94: 273–285.

Nelson SH, Evans AD and Bradbury RB (2006) The efficacy of an ultrasonic cat deterrent. *Applied Animal Behaviour Science* 96: 83–91.

Newton I (1979) *Population ecology of raptors*. Poyser, London.

Newton I (1993) Predation and the limitation of bird numbers. *Current Ornithology* 11: 143–198.

Newton I (1994) Current population levels of diurnal raptors in Britain. *The Raptor* 21: 17–21.

Newton I (1998) *Population Limitation in Birds.* Academic Press, London.

Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579–600.

Newton I, Dale L and Rothery P (1997) Apparent lack of impact of sparrowhawks on the breeding densities of some woodland songbirds. *Bird Study* 44: 129–135.

Newton I and Wyllie I (1992) Recovery of a sparrowhawk population in relation to declining pesticide contamination *Journal of Applied Ecology* 29: 476–484.

Nicolaus LK (1987) Conditioned aversion in a guild of egg predators: implications for aposematism and prey defense mimicry. *American Midland Naturalist* 117: 405–419.

Nicolaus LK, Cassel JF, Carlson R and Gustavson C (1983) Taste aversion conditioning of crows to control predation on eggs. *Science* 220: 212–214.

Nordström M (2003) Introduced predator in Baltic Sea archipelagos: variable effects of feral mink on bird and small mammal populations. *Annales Universitatis Turkuensis*. Sarja – Ser AII Osa – Tom. 158.

Nordström M, Högmander J, Laine J, Nummelin J, Laanetu N and Korpimäki E (2003) Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biological Conservation* 109: 359–368.

O'Brien M (2004) Estimating the number of farmland waders breeding in the United Kingdom. *International Wader Studies* 14: 135–139.

O'Brien M, Green RE and Wilson J (2006) Partial recovery of the Corncrake *Crex crex* in Britain 1993–2004. *Bird Study* 53: 213–224.

Ogilvie MA and the Rare Breeding Birds Panel (2004) Rare breeding birds in the United Kingdom in 2002. *British Birds* 97: 492–536.

Oro D and Furness RW (2002) Influences of food availability and predation on survival rates of kittiwakes. *Ecology* 83: 2516–2528.

Paradis E, Baillie SR, Sutherland WJ, Dudley C, Crick HQP and Gregory RD (2000) Large-scale spatial variation in the breeding performance of song thrushes and blackbirds in Britain. *Journal of Applied Ecology* 37: 73–87.

Parr R (1992) The decline to extinction of a population of golden plover in north-east Scotland. *Ornis Scandinavica* 23: 152–158.

Parr R (1993) Nest predation and numbers of golden plovers *Pluvialis apricaria* and other moorland waders. *Bird Study* 40: 223–231.

Paton PWC (1994) The edge effect on avian nest success: how strong is the evidence? *Conservation Biology* 8: 17–26.

Patterson IJ (1967) The control of fox movement by electric fencing. *Biological Conservation* 11: 267–278.

Peach WJ, Lovett LJ, Wotton SR and Jeffs C (2001) Countryside Stewardship delivers cirl buntings (*Emberiza cirlus*) in Devon, UK. *Biological Conservation* 101: 361–374.

Peach WJ, Robinson RA and Murray KA (2004) Demographic and environmental causes of the decline of rural song thrushes *Turdus philomelos* in lowland Britain. *Ibis* 146 (Suppl. 2): 50–59.

Pearce-Higgins JW, Grant MC, Robinson MC and Haysom SL (2007) The role of forest maturation in causing the decline of black grouse *Tetrao tetrix*. *Ibis* 149: 143–155.

Perrins CM and Geer TA (1980) The effect of sparrowhawks on tit populations. *Ardea* 68: 133–142.

Petty SJ, Anderson DIK, Davison M, Little B, Sherratt TN, Thomas CJ and Lambin X (2003) The decline of common kestrels *Falco tinnunculus* in a forested area of northern England: the role of predation by northern goshawks *Accipiter gentilis. Ibis* 145: 472–483.

Phillips ML, Clark WR, Sovada MA, Horn DJ, Koford RR and Greenwood RJ (2003) Predator selection of prairie landscape features and its relation to duck nest success. *Journal of Wildlife Management* 67: 104–114.

Phillips RA, Thompson DR and Hamer KC (1999) The impact of great skua predation on seabird populations at St Kilda: a bio-energetics model. *Journal of Applied Ecology* 36: 218–232.

Pickerell G (2004) Little Tern. In: Mitchell PI, Newton S, Ratcliffe N and Dunn T (eds) *Seabird Populations of Britain and Ireland*. T & AD Poyser, London: 339–349.

Picozzi N and Hepburn LV (1986) A study of black grouse in North East Scotland. In: Hudson P and Lovel TWI (eds) *Proceedings of the III International Grouse Symposium*: 462–480.

Picozzi N, Moss R and Catt DC (1996) Capercaillie habitat, diet and management in a Sitka spruce plantation in central Scotland. *Forestry* 69: 373–388.

Potts GR (1980) The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* 11: 1–79.

Potts GR (1986) *The Partridge. Pesticides, Predation and Conservation*. Collins, London.

Potts GR (1991) The environmental and ecological importance of cereal fields. In: Firbank LG, Carter N, Darbyshire JF and Potts GR (eds) *The ecology of temperate cereal fields*. Blackwell Scientific Publications, Oxford: 3–21.

Quinn JL and Cresswell W (2004) Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology* 73: 143–154.

Rands MRW (1986) The survival of gamebird (Galliformes) chicks in relation to pesticide use on cereals. *Ibis* 128: 57–64.

Rands MRW (1988) The effect of nest-site selection on nest predation in grey partridges (*Perdix perdix*) and red-legged partridges (*Alectoris rufa*). *Ornis Scandinavica* 19: 35–40.

Ratcliffe N (2004a) Causes of seabird population change. In: Mitchell PI, Newton S, Ratcliffe N and Dunn T (eds) *Seabird Populations of Britain and Ireland*. T & AD Poyser, London: 407-437.

Ratcliffe N (2004b) Little terns in Britain and Ireland: estimation and diagnosis of population trend. In: Allcorn R (ed) *Proceedings of a symposium on little terns* Sterna albifrons. RSPB Research Report No.8, Sandy, UK; 4–18.

Ratcliffe N, Houghton D, Mayo A, Smith T and Scott M (2005) Breeding success of terns in the Western Isles in relation to mink distribution. RSPB report, Sandy, UK.

Raven MJ and Noble DG (2006) *The Breeding Bird Survey 2005*. BTO Research Report No.439. BTO, JNCC and RSPB, Thetford, UK.

Raven MJ, Noble DG and Baillie SR (2007) *The Breeding Bird Survey 2006*. BTO Research Report No. 471. BTO, JNCC and RSPB, Thetford, UK.

Redpath S and Thirgood S (1997) *Birds of Prey and Red Grouse*. Her Majesty's Stationery Office, London.

Redpath S and Thirgood S (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology* 68: 879–892.

Redpath S, Thirgood S and Leckie FM (2001) Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology* 38: 1157–1168.

Reynolds JC (2000) Conditioned Taste Aversion – the end of the line. *The Game Conservancy Review* 31: 57–60.

Reynolds JC and Tapper SC (1993) Are foxes on the increase? *The Game Conservancy Review* 25: 94–96.

Reynolds JC and Tapper SC (1996) Control of mammalian predators in game management and conservation. *Mammal Review* 26: 127–156.

Robinson RA and Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39: 157–176.

Robson G (1998) *The Breeding Ecology of Curlew* Numenius arquata *on North Pennine Moorland*. PhD thesis, University of Sunderland.

Ruxton GD, Thomas S and Wright JW (2002) Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of the Zoological Society of London* 256: 81–83.

Seymour AS, Harris S, Ralston C and White PCL (2003) Factors influencing the nesting success of lapwings *Vanellus vanellus* and behaviour of red fox *Vulpes vulpes* in lapwing nesting sites. *Bird Study* 50: 39–46.

Sharpe FE (2006) Productivity and population trends of northern lapwing (*Vanellus vanellus*) in Britain. PhD thesis, University of Bath.

Sheldon RD (2002) Factors affecting the distribution, abundance and chick survival of the lapwing. PhD thesis, Harper Adams University College.

Sheldon RD, Chaney K and Tyler GA (2005) Factors affecting nest site choice by northern lapwing *Vanellus vanellus* within arable fields: the importance of crop structure. *Wader Study Group Bulletin* 108: 47–52.

Shrubb M (1990) Effects of agricultural change on nesting lapwings *Vanellus vanellus* in England and Wales. *Bird Study* 37: 115–127.

Shultz S, Bradbury RB, Evans KL, Gregory RD and Blackburn TM (2005) Brain size and resource specialisation predict long-term population trends in British birds. *Proceedings of the Royal Society of London B* 272: 2305–2311.

Sim IMW, Dillon IA, Eaton MA, Etheridge B, Lindley P, Riley H, Saunders R, Sharpe C and Tickner M (2007) Status of the Hen Harrier *Circus cyaneus* in the UK and Isle of Man in 2004, and a comparison with the 1988/89 and 1998 surveys. *Bird Study* 54: 256–267.

Sim IMW, Gregory RD, Hancock MH and Brown AF (2005) Recent changes in the abundance of British upland breeding birds. *Bird Study* 52: 261–275.

Siriwardena GM (2005) Possible roles of habitat, competition and avian nest predation in the decline of the willow tit *Parus montanus* in Britain. *Bird Study* 51: 193–202.

Siriwardena GM (2006). Avian nest predation, competition and the decline of British marsh tits *Parus palustris. Ibis* 148: 255–265.

Siriwardena GM, Baillie SR, Buckland ST, Fewster RM, Marchant JH and Wilson JD (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology* 35: 24–43.

Smart J (2004) Managing colonies for little terns. In: Allcorn R (ed) *Proceedings of a symposium on little terns* Sterna albifrons. RSPB Research Report No. 8, Sandy, UK; 19–28.

Smart J and Ratcliffe N (2000) Monitoring the effects of supplementary feeding as a means of reducing kestrel predation on little tern chicks at the Great Yarmouth colony. RSPB report, Sandy, UK.

Smart S (2002) The diet of breeding sparrowhawks *Accipiter nisus* and common buzzard *Buteo buteo*. MSc thesis, University of Reading.

Smith AA, Redpath SM, Campbell ST and Thirgood SJ (2001) Meadow pipits, red grouse and the habitat characteristics of managed grouse moors. *Journal of Applied Ecology* 38: 390–400.

Sotherton NW and Self MJ (1999) Changes in plant and arthropod biodiversity on lowland farmland: an overview. In: Aebischer NJ, Evans AD, Grice PV and Vickery JA (eds) *Ecology and Conservation of Lowland Farmland Birds.* British Ornithologists' Union, Tring: 26–35.

Stanbury A, O'Brien M and Donaghy A (2000) Trends in breeding wader populations in key areas within Northern Ireland between 1986 and 2000. *Irish Birds* 6: 513–526.

Stillman RA, MacDonald MA, Bolton MR, le V dit Durell SEA, Caldow RWG and West AD (2006) Management of wet grassland habitat to reduce the impact of predation on breeding waders: Phase 1. CEH/RSPB report to Defra.

Stoate C (2005) Loddington game and songbirds. In: *The Game Conservancy Trust review of 2004*. GCT, Fordingbridge, Hampshire: 16–17.

Stoate C (2006) Loddington game and songbirds. In: *The Game Conservancy Trust review of 2005*. GCT, Fordingbridge, Hampshire: 16–17.

Stoate C, Boatman ND, Borralho RJ, Carvalho CR, Snoo GRD and Eden P (2001) Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63: 337–365.

Stoate C and Szczur J (2001) Could game management have a role in the conservation of farmland passerines? A case study from a Leicestershire farm. *Bird Study* 48: 279–292.

Stoate C and Szczur J (2006a) Spotted flycatchers at Loddington. In: *The Game Conservancy Trust,review of 2005*. GCT, Fordingbridge, Hampshire: 18–19.

Stoate C and Szczur J (2006b) Potential influence of habitat and predation on local breeding success and population in Spotted Flycatchers *Muscicapa striata. Ibis* 53: 328–330.

Storass T and Wegge P (1987) Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *Journal of Wildlife Management* 51: 167–172.

Summers RW, Dugan D and Proctor R (in prep) Numbers and breeding success of capercaillie and black grouse at Abernethy Forest, Scotland.

Summers RW, Proctor R, Thornton M and Avey G (2004a) Habitat selection and diet of the capercaillie *Tetrao urogallus* in Abernethy Forest, Strathspey, Scotland. *Bird Study* 51: 58–68.

Summers RW, Green RE, Proctor R, Dugan D, Lambie D, Moncrieff R, Moss R and Baines D (2004b) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology* 41: 513–525.

Summers-Smith JD (1999) Current status of the house sparrow in Britain. *British Wildlife* 10: 381–386.

Swann RL and Etheridge B (1995) A comparison of breeding success and prey of the common buzzard *Buteo buteo* in two areas of northern Scotland. *Bird Study* 42: 37–43.

Tapper SC, Potts GR and Brockless MH (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.

Taylor IR and Grant MC (2004) Long-term trends in the abundance of breeding lapwing *Vanellus vanellus* in relation to land-use change on upland farmland in southern Scotland. *Bird Study* 51: 133–142.

Teunissen WA, Schekkerman H and Willems F (2005) Predatie bij weidevogels. Op zoek naar de mogelijke effecten van predatie op de weidevogelstand. *Sovon-onderzoeksrapport* 2005/11. Sovon Vogelonderzoek Nederland, Beek–Ubbergen. Alterra–Document 1292, Alterra, Wageningen.

Tharme AP, Green RE, Baines D, Bainbridge IP and O'Brien M (2001) The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology* 38: 439–457.

Thirgood S, Redpath S, Haydon DT, Rothery P, Newton I and Hudson P (2000a) Habitat loss and raptor predation: disentangling long- and short-term causes of red grouse declines. *Proceedings of the Royal Society of London B* 267: 651–656.

Thirgood S, Redpath S, Newton I and Hudson P (2000b) Raptors and red grouse: conservation conflicts and management solutions. *Conservation Biology* 14: 95–104.

Thirgood S, Redpath S, Rothery P and Aebischer NJ (2000c) Raptor predation and population limitation in red grouse. *Journal of Animal Ecology* 69: 504–516.

Thompson DBA, Gillings SD, Galbraith CA, Redpath SM and Drewitt J (1997) The contribution of game management to biodiversity: a review of the importance of grouse moors for upland birds. In: Fleming V, Newton AC, Vickery JA and Usher MB (eds) *Biodiversity in Scotland: Status, Trends and Initiatives*. Stationery Office, Edinburgh: 198–212.

Thompson DBA, MacDonald AJ, Marsden JH and Galbraith CA (1995) Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* 71: 163–178.

Thompson DBA, Redpath SM, Fielding AH, Marquiss M and Galbraith CA (eds) (2003) *Birds of prey in a changing environment*. The Stationery Office, Edinburgh.

Thompson FR, Donovan TM, DeGraaf RM, Faaborg J and Robinson SK (2002) A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Studies in Avian Biology* 25: 8–19.

Thompson PS, Baines D, Coulson JC and Longrigg G (1994) Age at first breeding, philopatry and breeding site-fidelity in the Lapwing *Vanellus vanellus. Ibis* 136: 474–484.

Thomson DL, Green RE, Gregory RD and Baillie SR (1998) The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society of London, B* 265: 2057–2062.

Tucker GM and Heath MH (1994) *Birds in Europe: their conservation status*. BirdLife Conservation Series No.3. BirdLife International, Cambridge.

UK Raptor Working Group (2000) *Report of the UK Raptor Working Group*. DETR/JNCC, Bristol.

Valkama J, Korpimäki E, Arroyo B, Beja P, Bretagnolle V, Bro E, Kenward R, Mañosa S, Redpath SM, Thirgood S and Viñuela J (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biological Review* 80: 171–203.

Vickery JA, Evans AD, Grice PV, Aebischer NJ and Brand-Hardy R (2004) *Ecology and Conservation of Lowland Farmland Birds II: The Road to Recovery*. British Ornithologists' Union, Tring, UK.

Vincent KE (2005) Investigating the causes of the decline of the urban house sparrow *Passer domesticus* population in Britain. PhD thesis, De Montfort University.

Warren PK and Baines D (2002) Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England. *Wildlife Biology* 8: 129–135.

Warren PK and Baines D (2004) Black grouse in northern England: stemming the decline. *British Birds* 97: 183–189.

Watson A (1985) Social class, socially-induced loss, recruitment and breeding of red grouse. *Oecologia* 67: 493–498.

Watson M (2004a) The effects of raptor predation on grey partridges *Perdix perdix*. DPhil thesis, University of Oxford.

Watson M (2004b) The effects of raptor predation on grey partridges. In: *Review of 2003*. Game Conservancy Trust, Fordingbridge: 64–67.

Watson M, Aebischer NJ, Potts GR and Ewald JA (2007) The relative effects of raptor predation and shooting on overwinter mortality of grey partridges in the United Kingdom. *Journal of Applied Ecology*, 44: 972–982.

Webbon CC, Baker PJ and Harris S (2004). Faecal density counts for monitoring changes in red fox numbers in rural Britain. *Journal of Applied Ecology* 41: 768–779.

Weimerskirch H (2002) Seabird demography and its relationship with the marine environment. In: Schreiber EA and Burger J (eds) *Biology of Marine Birds*. CRC Press, Boca Raton: 115–135.

Whitfield DP, Fielding AH, MacLeod DRA and Haworth PF (2004) Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. *Biological Conservation* 119: 319–333.

Whitfield DP, McLeod DRA, Watson J, Fielding AH and Haworth PF (2003) The association of grouse moor in Scotland with the illegal use of poisons to control predators. *Biological Conservation* 114: 157–163.

Whitlock RE, Aebischer NJ and Reynolds JC (2003) *The National Gamebag Census as a Tool for Monitoring Mammal Abundance in the UK*. Research report to JNCC. The Game Conservancy Trust, Fordingbridge.

Whittingham MJ (1996) *Habitat Requirements of Breeding Golden Plover* Pluvialis apricaria. PhD thesis, University of Sunderland.

Whittingham MJ and Evans KL (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* 146 (Suppl. 2): 210–220.

Wilkinson NI, Langston RHW, Gregory RD, Gibbons DW and Marquiss M (2002) Capercaillie *Tetrao urogallus* abundance and habitat use in Scotland in winter, 1998-99. *Bird Study* 49: 177–185.

Willebrand T (1988) *Demography and ecology of a black grouse* Tetrao tetrix *population.* PhD thesis, Uppsala University, Sweden.

Wilson AM, Vickery JA and Browne SJ (2001) Numbers and distribution of Northern Lapwings *Vanellus vanellus* breeding in England and Wales in 1998. *Bird Study* 48: 2–17.

Wilson G, Harris S and McLaren G (1997) *Changes in the British Badger Population 1988–1997*. People's Trust for Endangered Species, London.

Wilson JD, Evans J, Browne SJ and King JR (1997) Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England.

Woods M, McDonald RA and Harris S (2003) Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review* 33: 174–188.

Zonfrillo B (2002) Puffins return to breed on Ailsa Craig. *Scottish Birds News* 66: 1–2.

Great spotted woodpecker Nigel Blake (rspb-images.com)

The RSPB

UK Headquarters
The Lodge, Sandy, Bedfordshire SG19 2DL
Tel: 01767 680551

Northern Ireland Headquarters
Belvoir Park Forest, Belfast BT8 7QT
Tel: 028 9049 1547

Scotland Headquarters
Dunedin House, 25 Ravelston Terrace, Edinburgh EH4 3TP
Tel: 0131 311 6500

Wales Headquarters
Sutherland House, Castlebridge, Cowbridge Road East, Cardiff CF11 9AB
Tel: 029 2035 3000

www.rspb.org.uk

The RSPB is the UK charity working to secure a healthy environment for birds and wildlife, helping to create a better world for us all. We belong to BirdLife International, the global partnership of bird conservation organisations.

Cover image: red fox by David Tipling (Alamy)
Back cover image: domestic cat on top of nestbox by Susanne Danegger (nhpa.co.uk)
Regd charity England & Wales no 207076, Scotland no SC037654 230-0134-07-08