

**The indirect effects of increased nutrient inputs on
birds in the UK: a review**

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RSPB Research Report 21

ISBN Number 1 901930 77 7

Royal Society for the Protection of Birds
The Lodge, Sandy, Bedfordshire

October, 2006

Summary

Introduction

1. The past fifty years have seen declines in a range of bird species, notably those of farmland habitats, in the United Kingdom.
2. These declines have occurred alongside changes in human activities that have increased anthropogenic inputs of nutrients to the environment.
3. The most important anthropogenic sources of nitrogen and phosphorus are agriculture, sewage and domestic waste, while combustion of fossil fuels by industry and transport is a major source of reactive atmospheric nitrogen.
4. Around 60% of human nitrogen production, and about 80% of phosphate use are associated with fertiliser production for agriculture.
5. Both nitrogen and phosphorus are essential nutrients for plant growth and strongly influence the productivity of habitats. The use of inorganic fertilisers has allowed massive increases in agricultural production.
6. While all three major sources of nutrient pollution (fertiliser, fossil fuel combustion and sewage effluent) have declined over the past two decades, they still vastly increase the pool of available nutrients.
7. There is strong evidence that increased anthropogenic inputs of nutrients has altered the vegetation of the United Kingdom over the past century, with species typical of high-nutrient situations favoured.

Farmland

Vegetation

1. Increased fertiliser use generally reduces plant species richness in farm fields. Management practices associated with or driven by increased fertiliser use, notably silage production and intensive grazing, also reduce plant species richness.
2. Fertiliser application affects sward structure by promoting faster and earlier spring growth, leading to taller, denser swards. In grassland, both cutting for

silage and intensive grazing lead to short (although still dense) and heterogeneous swards.

3. Silage production probably has the most radical effects on vegetation of any form of farmland management, and silage production has replaced hay production over much of the UK. Early and frequent cutting affects sward structure, and reduce the amount of seed set by grass swards.
4. The use of inorganic fertilisers has led to changes in landscape configuration by releasing farmers from the need to graze stock for manure production and/or to rotate leguminous crops. There has been a loss of mixed farming landscapes and a polarisation of agriculture in the United Kingdom towards arable farming in the south and east, and pastoral farming in the north and west.

Invertebrates

5. Invertebrates, notably earthworms, may be killed by heavy applications of organic and inorganic fertiliser, due to toxic ammonia concentrations, salinity and desiccation. The effects are not usually long-term.
6. Invertebrate species richness is frequently positively related to plant species richness, due to increased opportunities for specialist species. However, the relationship does not always hold, nor is invertebrate abundance necessarily positively related to plant species richness.
7. Plant-eating invertebrates may be favoured by the increased nutritive content of fertilised crops, although there may be shifts in community composition. They are also favoured by the increased shoot growth resulting from fertiliser application.
8. The reduced root:shoot ratio resulting from increased foliar growth can be detrimental to soil invertebrates, although invertebrates feeding on roots may benefit from increased nutritive content.
9. Invertebrates that require specific sward structure, even those that eat plants, will be affected by the changes to sward structure arising from fertiliser application and associated management practices. Orthoptera (grasshoppers and crickets) are an example of this, as their habitat requirements are poorly met in intensively managed improved grassland.

10. Invertebrates may be affected by disturbance arising from grazing and cutting. Large insects are disproportionately affected, as their longer life cycles and relatively low recolonisation ability mean that they are more likely to disappear from intensively managed farmland.
11. Intensive grazing, and earlier and more frequent cutting associated with silage production directly remove invertebrates, and also remove much of the primary productivity.
12. Changes to sward structure probably have the greatest effects on invertebrate abundance, and these effects are most clearly observed in grassland under intensive grazing and/or cutting regimes.

Birds

13. Birds may be affected by fertiliser use via several mechanisms. The strongest effects are seen in pastoral landscapes, because fertiliser use has been the main driver of habitat changes in grassland, while the shift to autumn-sown cereals is a more important cause of habitat changes in arable landscapes.
14. Wintering geese graze preferentially on fertilised grass, and management for these important species includes fertiliser application and grazing.
15. Several species have suffered from reduced abundance and/or availability of surface-dwelling invertebrates. Species reliant on large invertebrates, such as circl bunting and red-backed shrike, are especially sensitive. Loss of large invertebrates is also suggested as a major cause of reduced productivity of breeding waders in grassland.
16. Species that feed on soil invertebrates may be affected by reduced availability in dense swards. Snipe, starling and chough are examples of these. Although desiccation also reduces the ability of birds to feed on soil invertebrates, increased crop growth can contribute to this.
17. Seed resources are also reduced in intensive agriculture, and this can affect several species of seed-eating passerines. The loss of winter stubbles due to more efficient harvesting and autumn-sown cereals is probably the strongest driver of this.
18. More intensive grazing can lead to increased nest trampling in ground nesting species such as skylark and lapwing. These species may also suffer higher

predation rates in intensively managed fields because sward homogeneity may make their nests easier to locate.

19. Nest destruction during silage cutting is a major cause of reduced productivity in ground nesting birds such as whinchat and corncrake.
20. The shift to silage production has probably had the greatest effect on bird populations in farmland, as it operates via three pathways: reduced invertebrate food due to frequent cutting; reduced seed resource as it is cut before setting seed; destruction of nests.
21. Birds may also have been affected by the polarisation of farming landscapes. Species such as starling and lapwing that prefer the juxtaposition of arable fields and pasture will have been disadvantaged by this process.
22. Organic farms are generally better for birds than conventional farms, but the causes of this are complex and cannot be simply ascribed to use of organic rather than inorganic fertiliser.

Aquatic habitats

Vegetation

1. Shallow freshwater lakes are especially susceptible to eutrophication. They tend to exist in either a clear-water state dominated by large plants (macrophytes), or a turbid-water state dominated by floating microscopic plants (phytoplankton).
2. Lakes shift between the states relatively suddenly. Switching can be triggered by a variety of processes, including changes in fish community and physical disturbance of vegetation, but the likelihood of switching is strongly influenced by nutrient levels. Both states are buffered against switching, so that a clear-water state can persist at high nutrient levels, and a turbid-water state may persist after nutrient levels are reduced.
3. Reedswamp vegetation has declined across areas of western and central Europe. Although there is some coincidence between reed decline and eutrophication, no cause and effect has been proven. In the Norfolk Broads,

there was a spatial relationship between water nitrate concentration and the decline of a particular floating form of reed, known as hover.

4. Upland lakes in the UK are mostly oligotrophic in the absence of anthropogenic inputs of nutrients. These lakes can be susceptible to minor increases in nutrient loadings.
5. Estuaries and coastal waters are generally better flushed than freshwater lakes, and so the effects of eutrophication are generally less persistent. However, where eutrophication occurs it typically leads to a decline in rooted plant communities such as seagrass and eelgrass beds, and their replacement by macroalgal mats and phytoplankton blooms.

Invertebrates and fish

6. In freshwater, large zooplankton such as cladocerans (water fleas) are favoured by a clear-water state, as the presence of submerged macrophytes provides shelter from fish that prey on such zooplankton.
7. Freshwater invertebrate communities are sensitive to nutrient inputs, with shifts in community composition frequently driven by changes to substrate rather than food abundance or availability. Anoxic conditions also affect both invertebrates and fish. Molluscs are especially sensitive to eutrophic conditions, while annelid worms are favoured.
8. Fish communities both respond to the stable state of fresh water bodies and buffer stable states from changes, through processes such as disturbance of sediments and predation of zooplankton.
9. Eutrophication of shallow lakes leads to a reduction of fish diversity, with roach and bream becoming dominant at the expense of perch, rudd and tench. The size structure of fish communities in upland lakes can be altered by nutrient pollution, leading to fewer but larger individuals.
10. Immediately adjacent to point sources of nutrient pollution, invertebrate biomass is reduced by extreme conditions. However, in surrounding areas it can be much higher, although the community is very different from low-nutrient waters.
11. In estuarine and coastal areas, where sewage outfalls are removed, or where treatment is implemented, invertebrate biomass usually falls, although species

richness increases and species composition more closely approximates natural conditions.

12. In intertidal mudflats, the presence of macroalgal mats forces invertebrates closer to the surface to evade anoxic conditions. If the mats persist invertebrate biomass may drop severely.
13. The mud-shrimp *Corophium volutator* and the sandworm *Nereis diversicolor* are more tolerant of eutrophic conditions and can provide abundant food resources to shorebirds.

Birds

14. The indirect effects of eutrophication can be complex and highly localised in aquatic systems, and local changes in bird populations may be affected by changes at larger scales. Increased nutrient loading may be beneficial to birds up to a point at which radical changes to habitat occur.
15. The negative effects of nutrients on birds are most consistent in freshwater lakes, where a shift in stable states results in a decline in food plants for herbivorous and omnivorous waterfowl.
16. Eutrophic conditions also radically change the bottom-dwelling invertebrate fauna, leading to a loss of sensitive elements such as molluscs. Diving birds that feed on these invertebrates suffer from reduced food supply.
17. Roach, a fish species tolerant of eutrophic conditions are thought to compete with tufted duck for food resources in Lough Neagh.
18. Fish-eating birds that chase their prey may be negatively affected by eutrophication, as water transparency tends to be reduced. Nutrient enrichment may also alter the size class of fish prey, reducing the abundance of suitable (small) individuals.
19. Eutrophication may affect birds reliant on reedbed by accelerating seral succession and by reducing the amount of open water present. Reedbed decline in Europe has been coincident with eutrophication, but no causality has been proven.
20. The red-listed bittern may be affected by reduced food supply. One of its major food items in Britain, rudd, performs poorly in eutrophic conditions.

21. In north-western Europe, marsh tern decline has been linked to eutrophication because its preferred nesting substrate, water soldier, is sensitive to increased nutrient loading.
22. Shorebirds in tidal areas generally benefit from anthropogenic nutrient inputs. Although the invertebrate community composition may shift radically, abundance is increased. Historically, bird populations have risen in estuaries where sewage inputs have increased, although population declines have not been observed in all situations where inputs have been reduced.
23. Species with specific prey requirements or foraging habits, such as shelduck, may not benefit from nutrient inputs.
24. In conditions of extreme eutrophication, where extensive macroalgal mats form, the anoxic conditions may force the mud-dwelling fauna to the surface, providing a short-term flush of food. If the mats persist, the food supply will be reduced in the long term.
25. Diving ducks in coastal waters also benefited from the increased food supplies around sewage outfalls, and their numbers have decline where outfalls have been removed.

Upland moor and lowland heath

Vegetation

1. There has been a decline in the extent of heather (*Calluna vulgaris*) cover in both heath and moorland in the United Kingdom in recent years. Causes of the decline include afforestation, conversion to farmland, invasion of grasses, and seral succession.
2. Atmospheric deposition of nitrogen increases the foliar nitrogen content of *Calluna* and decreases the root:shoot ratio. This increases sensitivity to desiccation, and dieback has been observed especially during winter droughts in upland moor and lowland heath.
3. Heath beetle outbreaks also cause *Calluna* dieback, and larval growth increases with foliar nitrogen content. It is suggested that nitrogen deposition increases the probability of beetle outbreaks.

4. *Calluna* is not competitively disadvantaged by increased nitrogen inputs in the absence of disturbance. Dieback resulting from heather beetle attacks or desiccation may cause disturbance sufficient for grasses to invade. Both of these mechanisms may be increased by nitrogen deposition.
5. Grazing disturbance has effects on the cover of heather and grass in moorland independent of the effects of nutrient inputs. Grazing intensity has increased over time in upland areas, although the drivers of this have mostly been agricultural subsidy policies. Nitrogen deposition may have facilitated this by increasing the forage quality of moorland, but this is difficult to determine and is likely to be a minor contributor.
6. These mechanisms are also suggested as causes for the loss of lowland heath in western Europe. However, lack of management is also implicated, so that succession to scrub and lack of burning have also resulted in loss of heath.

Invertebrates

7. Maintenance of invertebrate communities in moorland requires a mosaic of grass and heather of varying ages. Invertebrate biomass is generally lower in heather moorland than in grass moorland, although wet areas in moorland may support an abundant invertebrate fauna.
8. Plant-eating invertebrates may be favoured by nitrogen deposition and increased nutritive value of *Calluna*. However, intensive grazing will remove foliage to the detriment of these invertebrates.

Birds

9. The importance of nitrogen deposition in driving changes to bird populations in the uplands, relative to other causes (such as afforestation, climate change, land management), is difficult to determine. The evidence for links between increased nitrogen deposition (and associated processes) and bird populations is examined.
10. In upland moorland, the shift from heather to grass moorland over a large scale is likely to be the most important indirect effect of nitrogen deposition on

birds. For fifteen species there was sufficient evidence of such effects to estimate sensitivity to heather loss.

11. Two species (red grouse and merlin) are classed as sensitive to heather loss, because they are strongly associated with mature heather cover for breeding and foraging.
12. Seven species (black grouse, golden eagle, hen harrier, meadow pipit, stonechat, ring ouzel and twite) are classed as moderately sensitive to heather loss. These species require a mosaic of heather and grass cover, and the effects of heather loss on birds will depend on the extent of initial heather cover and its spatial distribution.
13. Six species (golden plover, curlew, snipe, skylark, whinchat, wheatear) are classed as having low sensitivity to heather loss. Some of these species are likely to benefit from the conversion of heather moorland to either grass or bracken, while for others the structure of moorland vegetation is more important than its floristic composition.
14. For almost all species, an appropriate mosaic of upland habitats is required to supply suitable resources (eg nesting and foraging sites). In many cases, vegetation structure is more important than species composition, and very few bird species benefit from continuous heather cover.

Acknowledgments

Ken Smith and Andy Evans co-ordinated the production of this report. Various people have commented on drafts and provided specific comments. They are Ken Smith, Andy Evans, Will Peach, Richard Bradbury, Murray Grant, James Pearce-Higgins, and Len Campbell.

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1. Introduction

1.1 Rationale

The alterations to nutrient cycles that have accompanied and enabled the post World War II boom in agriculture and industrialization are causing long-term and broad-scale threats to the environmental health of the planet. Post World War Two population declines have been observed in a wide range of bird species in the United Kingdom. This period has also seen a massive increase in the amounts of nitrogen and phosphorus released into the environment as a result of the increased use of fertilisers as part of the intensification of agriculture, and the increased rate of fossil fuel combustion. Radical changes have been documented in many habitats as a result of such increases in available nitrogen and phosphorus. The purpose of this review is to present the evidence for indirect effects of phosphorus and nitrogen on UK bird populations.

Increased productivity in response to inputs of nitrogen and phosphorus might be expected to increase the number of birds, and in fact this is the case in many instances. However, an increase in overall bird abundance may be at the expense of species that are adapted to oligotrophic habitats or that require specific resources that are negatively affected by nutrient pollution. This review does consider the positive effects of nutrient inputs on birds, but I place more emphasis on negative effects, as bird declines are of particular concern. I also recognise that nutrient inputs may benefit bird populations while simultaneously lowering overall environmental health. The responses of birds to changes in nutrient availability are likely to be complex and to rely on the effects of nutrients on lower trophic levels, as well as the ability of bird populations to respond to those effects (Furness and Greenwood, 1993).

1.2. Review Structure

The aims of the review are:

- To review current knowledge of the impacts of nitrogen and phosphorus inputs on ecosystems generally.
- To identify mechanisms by which bird populations may be affected by nutrient pollution.
- To document observed changes in bird populations resulting from nutrient pollution.

To achieve this, I will examine the evidence for indirect effects of nutrient inputs in three major habitats, in which I consider there to be the greatest likelihood and the best documentation of such effects. These are farmland (grassland and arable land), aquatic habitats (inland freshwater and coastal), and heather-dominated habitats (lowland heath and upland moor). Each of these habitats is dealt with in a separate section, in which I consider the evidence for changes in bird populations, the impact of nutrient loading on vegetation and food items, and the evidence for indirect effects of increased anthropogenic inputs of nitrogen and phosphorus on birds.

The present review restricts itself to the effects of nutrient inputs on productivity, and does not consider other effects, which may have important consequences of their own. For example, nitrogen oxides contribute to greenhouse gas emissions; nitrates are a human health issue; and atmospheric deposition of nitrogen can cause acidification of terrestrial and aquatic habitats. These problems are important, but are beyond the scope of this review, which is already wide-ranging. Similarly, I do not attempt to describe means of reducing emissions or mitigating their effects.

In this introductory section, I present a brief background on nitrogen and phosphorus, describe the means by which humans have increased their entry to the environment, and document the changes in anthropogenic inputs in the UK over time. The information presented here is intended as background information for the review. The nature and cycling of nitrogen and phosphorus, and the effects of anthropogenic inputs, including many that are beyond the scope of this review, are much more completely discussed in other publications (Marrs, 1993; Heathwaite et al., 1996;

Vitousek et al., 1997; Galloway, 1998; Bennett et al., 2001; NEG-TAP, 2001; Dalton and Brand-Hardy, 2003; Biffaward, 2005; Johnston and Dawson, 2005).

1.3. A brief description of nitrogen and phosphorus

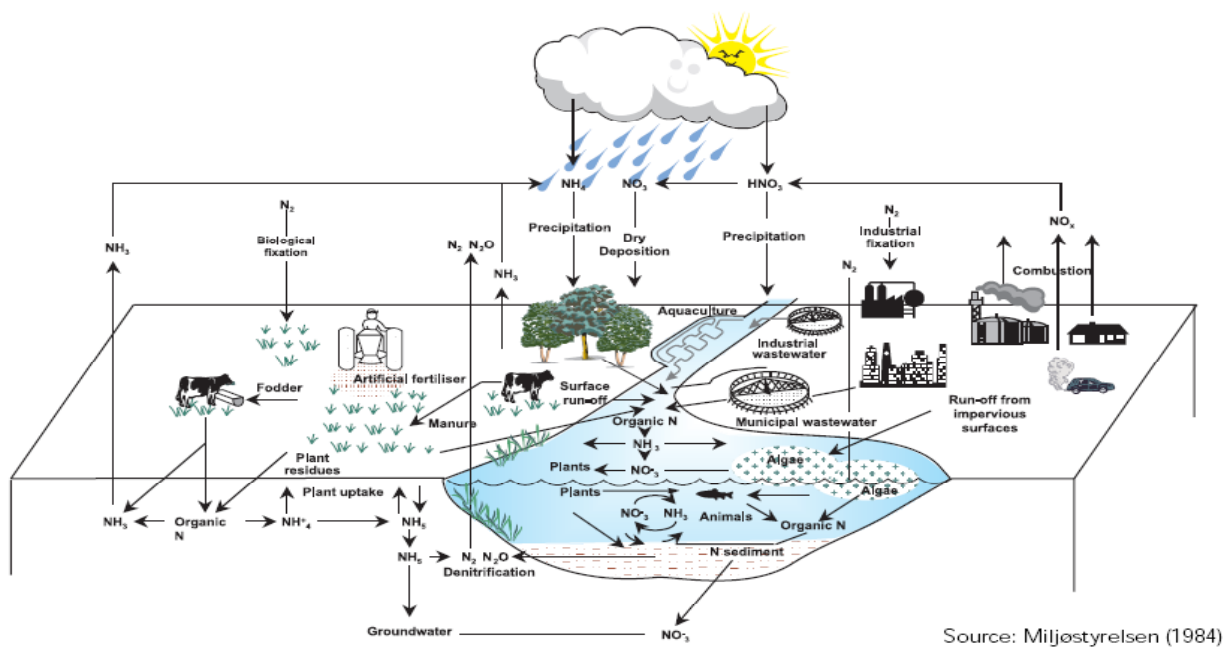
Phosphorus is an important part of cell membranes, and is a component of nucleic acids. Nitrogen is required for the formation of amino acids, proteins and nucleic acids. These elements are frequently the limiting factors for plant growth. Phosphorus and nitrogen are both major limiting factors on the distribution of plant species and communities.

1.3.1. Nitrogen

The earth's atmosphere is approximately 80% nitrogen, in the form of nitrogen gas (N_2), which is unavailable to most organisms. Even excluding nitrogen gas, only about 1% of nitrogen present is in biologically available (reactive) form (Biffaward, 2005). However, nitrogen is also present in other forms, which are linked by a number of processes known as the nitrogen cycle (Fig. 1.1).

Biologically available forms of nitrogen are nitrate (NO_3^-), nitrite (NO_2^-), ammonia (NH_3), and ammonium (NH_4^+). Two natural processes transfer nitrogen gas to biologically available forms: lightning and biological fixation by microorganisms. In natural and semi-natural (very low management) ecosystems, plant nitrogen requirements are met from soil reserves or from atmospheric nitrogen inputs. Rates of nitrogen transformation in soils are dependent on microbial populations and a range of soil conditions including pH, temperature, aeration and water content.

Nitrate is one of the main forms by which plants obtain nitrogen, and it is produced by nitrification of ammonia to nitrate via nitrite. The reverse process, known as denitrification, converts nitrate to nitrogen gas and nitrous oxide. Nitrite, which is very reactive and is also toxic, usually forms a small proportion of the nitrogen component in soil.



Source: Miljøstyrelsen (1984)

Figure 1.1. Illustration of the nitrogen cycle

Ammonia is produced by volatilisation of organic nitrogen and by the fixation of nitrogen gas by bacteria. Ammonia is taken up by plants, released into the atmosphere as a gas, or is converted to nitrate (via nitrite) by nitrification. Ammonia is highly soluble, oxidises readily to nitrate in water, and readily forms ammonium compounds in the atmosphere, whence it may be deposited as a gas or as part of ammonium compounds in rainfall. Other nitrogen forms present in the atmosphere, in addition to nitrogen gas, are nitrous oxide, nitric oxide, nitrogen oxide and nitrogen dioxide, the last two collectively known as nitrogen oxides (NO_x). Nitrous oxide is produced during the breakdown of organic matter. Nitrogen oxides are produced by soil bacteria and by combustion of fuels.

Nitrogen is also found in the soil as a component of organic material. Microbial decomposition (mineralisation) of organic nitrogen releases inorganic nitrogen (ammonia, nitrate and ammonium), which plants can use. Mineralisation rates are increased by cultivation, drainage, and burning. Dissolved organic nitrogen has recently been established as an important component of the atmospheric nitrogen load (Cornell et al., 2002).

In aquatic systems, inorganic nitrogen occurs as nitrate (which generally dominates), nitrite and ammonium. Dissolved organic nitrogen can comprise up to 85% of total nitrogen, and is typically 40-50% (Willett et al., 2004); it is released by mineralisation and nitrification (Heathwaite et al., 1996). Nitrate concentrations are highest in winter and spring due to replenishment from soil-water sources. Nutrients in lake systems may be recycled many times, and depending on the flushing rate may be incorporated into the sediments. The anoxic soil conditions in some wetlands hinder the decomposition of organic nitrogen and favour denitrification, thus leading to loss of nitrogen from wetlands (Morris, 1991).

1.3.2. Phosphorus

Phosphorus is an essential element for plant growth. Phosphorus occurs in phosphate (P_2O_5) bearing rock, and in soil via erosion. Phosphorus has low solubility and binds

strongly to soil particles (Johnston and Dawson, 2005). Phosphorus occurs in soils as inorganic phosphate or as part of the organic matter. In water, phosphorus occurs as soluble reactive phosphate (PO_4^{3-}), which is available to living organisms, and bound to soil particles, which is not biologically available, although it may become so. Phosphorus is readily precipitated with soil particles in the water, but this bound phosphorus can be released into the water column in reducing conditions or when sediments are disturbed (Sharpley et al., 1995). Dissolved organic phosphorus is released through mineralisation (Heathwaite et al., 1996). The phosphorus cycle is simpler than that of nitrogen (Fig. 1.2).

1.4. Anthropogenic sources of nitrogen and phosphorus

The major sources of anthropogenic nutrient inputs are agriculture, sewage and domestic waste (for both nitrogen and phosphorus), and combustion of fossil fuels by industry and transport (for nitrogen). Other sources include the planting of legumes as nitrogen-fixing crops, and the mobilisation of nitrogen from long-term nitrogen storage pools via burning, land clearance and drainage (Vitousek et al., 1997). Sources of pollution may be described as point or non-point (also referred to as diffuse); these terms are particularly used in reference to aquatic systems. Point sources have a fixed discharge point, although the amount of nutrient pollution may vary, while non-point sources follow a range of routes to their destination (Heathwaite et al., 1996). Atmospheric sources of nutrient pollution can also be thought of as diffuse; for example, ammonia is emitted from a number of sources over large areas (Dalton and Brand-Hardy, 2003).

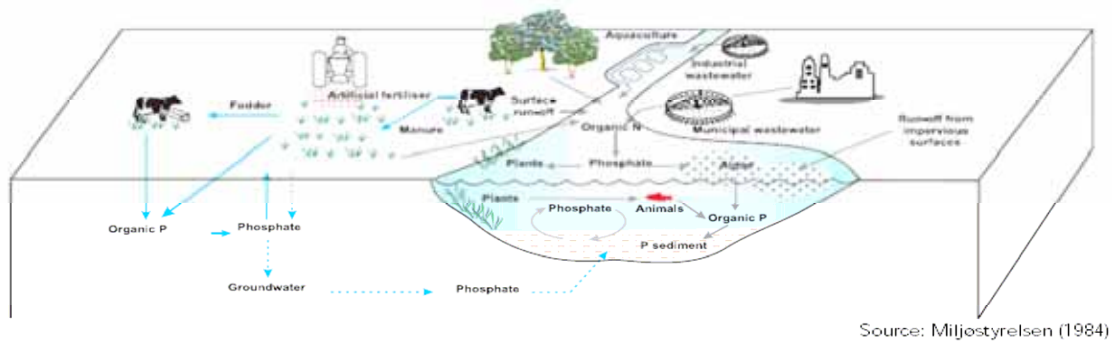


Figure 1.2. Illustration of the phosphorus cycle.

1.4.1. Agriculture

The major anthropogenic input of nutrients to agricultural land is the direct application of fertilisers. About five eighths of anthropogenic nitrogen production is associated with the production and use of inorganic fertilisers (Dalton and Brand-Hardy, 2003), and nitrogenous fertilisers are the largest source of nitrogen to agriculture in the UK (Fig. 1.3). Mineral fertilisers account for approximately 80% of phosphates used worldwide, with the remainder used in detergents, animal feeds and miscellaneous uses. Historically, the main plant nutrients, nitrogen and phosphorus, were recycled in agricultural communities. Food was consumed close to its place of production and the resulting animal and human manures were applied to the same land. In modern times, inorganic fertilisers are applied to provide plant nutrients that are naturally lacking or that have been removed by harvesting or grazing, or by physical processes such as leaching or erosion. The use of fertilisers has been instrumental in increasing agricultural output, and has enabled the production of sufficient food for the world's population, which might otherwise not have been possible. For example, in the absence of nitrogenous fertiliser, grass and forage crops typically yield up to 3 tonnes of dry matter per hectare, but this increases by about 20 kg of dry matter for each kg of nitrogen applied per hectare, up to around 300 kg/ha, beyond which response diminishes (Raymond et al., 1986).

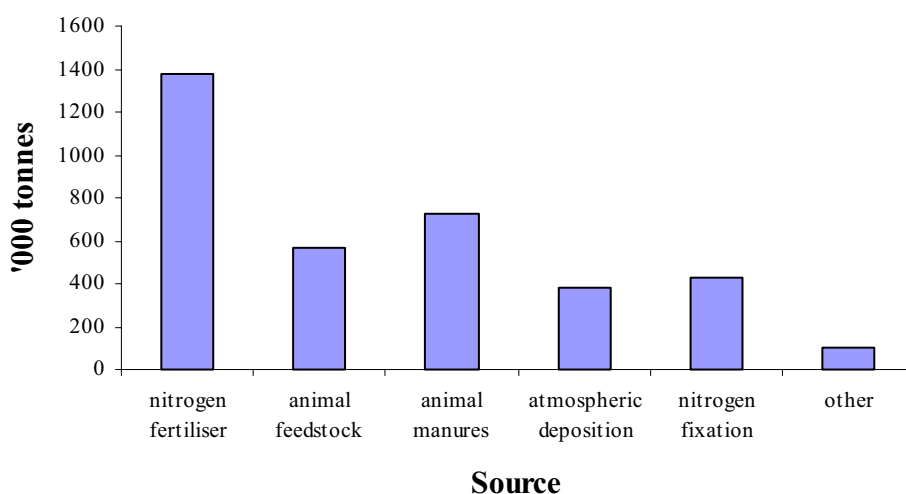


Figure 1.3. Sources of nitrogen to agriculture in the UK (Biffaward, 2005).

Popular inorganic fertilisers include anhydrous ammonia, urea, superphosphate, and diammonium phosphate, while organic fertiliser is applied as manure or slurry. Animal feeds may contribute significantly to the total import of phosphorus into agricultural landscapes (Johnston and Dawson, 2005). Fertilisers may be spread over the soil surface or plowed or drilled into the soil. Agriculture is also a major source of ammonia emissions, with the great majority arising from livestock wastes. In 2003, emissions of ammonia were estimated to be 300 000 tonnes, down from a high of 343 000 tonnes in 1991; of this almost 90% was from agriculture (DEFRA, 2006a). Agricultural areas may also receive nutrients from diffuse sources when they are flooded. In these cases, the ultimate source of nutrients is largely agricultural fertilisers, but the nutrient loading will be in addition to any fertilisers applied at the site.

1.4.1.1. Organic versus inorganic fertilisers

Fertilisers can be either inorganic, derived from phosphate mining and nitrate production, or organic, in the form of manure or liquid slurry. Organic manures apply already fixed nitrogen, and thus do not represent a net increase in global anthropogenic nitrogen fixation (Vitousek et al., 1997), although they can still have important local effects. When mixed farming systems were more prevalent, organic manures were more common. The polarisation of farming into pastoral or arable systems has removed sources of manure from potential receivers. Use of inorganic nitrogen suppresses nitrogen-fixing soil bacteria, making agriculture increasingly dependent on artificial fertilizer.

Organic manure contains available nitrogen in the form of ammonium nitrate, but also undigested proteins that release nitrogen slowly for plant uptake (Jones and Haggard, 1997). The use of organic fertilisers has been suggested as a means of reducing the nutrient inputs to the environment. A study comparing biodynamic, bioorganic and conventional farming in Switzerland over 21 years found that while crop yield in the organic systems was 20% lower than conventional, nutrient inputs were 34-51% less (Mäder et al., 2002). However, excessive mineralisation and loss of nutrients can be a problem with organic manures, due to difficulties in tailoring the applications to the needs of the crop (Stoate et al., 2001; Dalton and Brand-Hardy, 2003). Manure

application rates are frequently based on nitrogen content, but this can lead to excessive phosphorus application (Eck and Stewart, 1995).

1.4.2. Atmospheric pollution

The burning of fossil fuels releases fixed nitrogen to the atmosphere, as well as fixing atmospheric nitrogen via the combustion process (Campbell and Lee, 1996; Vitousek et al., 1997). This nitrogen is in the form of nitrogen oxides and ammonia. Over 80% of nitric oxide emissions and approximately 40% of nitrous oxide emissions are from anthropogenic sources (Vitousek et al., 1997); these come mostly from industry and motor vehicles. The remainder consists of natural emissions from the soil as a result of nitrification. Emissions of ammonia from road transport, although relatively small, are increasing as a result of the increasing number of three way catalysts in the vehicle fleet. Prior to 1950, burning of coal for domestic purposes was an important component of anthropogenic emissions of ammonia (Fowler et al., 2004), but now the major source is livestock farming, as detailed above. Nitrogen oxides are also released by soil microbial activity.

1.4.3. Point-source pollution

Domestic sewage and industrial effluent are the major point sources of nitrogen and phosphorus. In England and Wales, liquid effluent discharged to rivers comprises about 80% of domestic and industrial wastes (Heathwaite et al., 1996). At times these may form a high proportion of river flow. Much of the effort and expenditure to address nutrient pollution has aimed to reduce loadings from point-sources (such as sewage treatment works), with some success (Johnston and Dawson, 2005).

1.5. Transport of nutrients

1.5.1. Loss from agricultural landscapes

In agricultural systems, the major means of nutrient transport are surface runoff, soil erosion and subsurface flow in the case of phosphorus, which binds closely to soil particles, and leaching of soluble nitrate (McGechan, 1998). All of these processes are affected by weather and season. Nitrogen is lost from soil through the production of nitrogen oxides by denitrification and the production of ammonia through volatilisation (Stoate et al., 2001). Nutrients are also removed when crops are harvested or via grazing by livestock, and these nutrients may be released into the environment elsewhere (for example, via sewage following human consumption). Compensating for these losses has contributed to the need for fertiliser application in agricultural land.

The application of nitrogen to crops is cost-effective; the increased crop production pays more than the fertiliser costs (Goulding, 2000). However, the application of excessive amounts of nitrogenous fertiliser creates a surplus and increases the risk of loss through leaching of nitrate and dissolved organic nitrogen. About 33% of fertiliser nitrogen applied in the UK is lost through leaching (Heathwaite et al., 1996). Because nitrate is soluble, water movement is effectively translated into nitrate movement. Nitrate leaching occurs mostly in autumn, when the crop is unable to exploit it fully, and after ploughing, when organic nitrogen is mineralised (Bloem et al., 1994; Stoate et al., 2001). Nitrate from mineralisation of organic nitrogen can form a large proportion of leached nitrate, particularly at low levels of fertiliser application, and thus some leaching will occur regardless of fertiliser inputs (Stoate et al., 2001). The rate of leaching depends on soil type, crop type, time of fertiliser application and weather (Goulding, 2000). Grassland also releases nitrogen when ploughed, with quantities depending on the length of ley (Heathwaite et al., 1996).

Phosphorus is transported in soluble form (inorganic orthophosphate and organic phosphorus compounds and complexes), and as particulate phosphorus. The latter constitute 75-90% of the phosphorus transported from cultivated land, as phosphorus binds strongly to soil (Sharpley et al., 1995). In some areas, phosphorus has been added over a period of time at levels exceeding crop uptake, and soils have accumulated phosphorus, which is then at risk of being lost during runoff. However, loss of soluble phosphorus can also be important, as it is in this form that it is required by plants, and because the loss of small amounts can lead to eutrophication of water

bodies (Johnston and Dawson, 2005). Phosphorus loss from arable land is typically 0.8-2.0 kg/ha per year, while for improved grassland it is 0.4 kg/ha per year, and for semi-natural vegetation less than 0.1 kg/ha per year (Marsden et al., 1998).

Balancing fertiliser use for crops with environmental goals may be difficult to achieve. For example, arable farms in the Netherlands that took measures to reduce loss to the environment still had average surpluses of 117 kg/ha/year of nitrogen, and 14 kg/ha/year of phosphorus (Schröder et al., 1996). Organic farming uses lower amounts of nutrients per unit area, but similar amounts per unit of production, meaning that nutrient losses to the environment from organic systems may be comparable to those from conventional farms for an equivalent agricultural output (Dalton and Brand-Hardy, 2003).

1.5.2. Transport to aquatic systems by hydrological processes

The major source of nutrient pollution to aquatic habitats in the UK is agricultural runoff and groundwater flow (McGechan, 1998). In the UK, over 70% of nitrates in surface and ground water originate in agricultural land (Dalton and Brand-Hardy, 2003). Dissolved organic nitrogen also reaches aquatic systems predominantly by hydrological processes, although much of this may be stored in sediments (Willett et al., 2004). Similarly, diffuse agricultural pollution in the form of runoff and subsurface water flow, are the major means of transport of increased particulate and soluble reactive phosphorus (Johnston and Dawson, 2005). However, human and household wastes can contribute considerably to phosphorus entering surface waters in the UK, partly because of the phosphorus content of detergents (Foundation for Water Research, 2000). Domestic and industrial wastes remain important, albeit decreasing, sources of organic material to aquatic habitats. Atmospheric sources of nitrogen (as described below) can be important for aquatic systems, especially in waterbodies with little fluvial input (Sharpley et al., 1995).

Other sources of nutrients in water that can be important locally include direct defecation by livestock into streams, discharge from sewage outlets, and release from sediments due to disturbance (Johnston and Dawson, 2005). Organic fertiliser is more

likely to cause phosphate pollution, because applications at the appropriate rates for nitrogen will include more phosphorus than is required by the crop.

In marine waters, phosphorus is naturally relatively abundant. In addition, coastal waters receive nutrient inputs from run off, aquaculture, sewage discharges and atmospheric deposition (of nitrogen); their effects are greatest where tidal flushing is low. Inorganic nitrogen concentrations in coastal waters are largely determined by inputs from fluvial discharges and mineralisation of organic nitrogen in sediments (Herbert, 1999). The rate of phosphate exchange between sediments and the water column is greater in anaerobic conditions, and thus the anoxic conditions that can result from eutrophication will further increase the soluble phosphorus proportion (Nienhuis, 1993). Phosphorus and nitrogen concentrations in coastal waters receiving water from agricultural catchments may be higher in winter, due to increased run-off, and to increased release of nutrients from soil (Raffaelli et al., 1989).

1.5.3. Atmospheric deposition

Deposition of atmospheric nitrogen can occur via wet deposition of nitrate and ammonium in rain or snow; via dry deposition of nitrogen dioxide, ammonia and nitric acid; and via “occult” deposition of cloud or fog droplets (Campbell and Lee, 1996). Wet deposition also includes a significant component of dissolved organic nitrogen (Cornell et al., 2003). While atmospheric concentrations of ammonia and rainfall concentrations of ammonium are highest in the south and east of Britain, deposition is highest in the north and west, due to higher rainfall. The amount of wet deposition is determined by the amount of rainfall, and is more important in locations removed from the pollutant sources (Bobbink and Heil, 1993). The amount of dry deposition is strongly determined by the nature of the deposition surface, is more important close to sources, and is highest in the south and east of Britain.

Atmospheric deposition of nitrogen near farmland can be higher than other areas due to localised ammonia volatilisation and re-deposition. Oxidised nitrogen persists for a longer time in the atmosphere, and as a result, a greater proportion of it is exported from the UK.

Atmospheric deposition of nitrogen to agricultural landscapes is small compared to the application of nitrogenous fertilisers. For semi-natural habitats (e.g. upland moorland and alpine areas) the situation is very different. These areas, covering 46.3% of the land cover of the UK, receive a large proportion of the nitrogen deposited, in excess of that which they lose by re-emission (Fowler et al., 2004). They are often naturally infertile, and leach relatively small amounts of nitrogen, which therefore accumulates in the soil. Semi-natural grasslands in the Peak District accumulated up to 89% (in calcareous grassland) and up to 38% (in acidic grassland) of experimental nitrogen deposition treatments (Phoenix et al., 2003).

Atmospheric deposition can also make a considerable contribution to the nutrient loading of aquatic systems (Morris, 1991; Paerl et al., 2002). Generally speaking, the importance of atmospheric nitrogen deposition increases with the proportion of the water budget comprised by rainfall.

1.5.4. Losses through burning

Fire as a management tool and accidental fire can release nutrients. The process of periodic burning of upland moor and lowland heath is used as a management tool to maintain these disclimax communities, to maintain their low nutrient status and to improve their utilisation by humans. Burning removes the standing crop and some of the accumulated litter, the amount depending on the severity of the burn. Burning of a lowland heath resulted in the loss of 95% of nitrogen and 26% of phosphorus from vegetation and litter combined (Chapman, 1967). This represented a net loss of both nutrients over a 12 year burning cycle, with rainfall inputs insufficient to replace the losses. Older heaths may have replaced the nitrogen and phosphorus lost in the previous fire.

1.6. Trends in nutrient pollution in the UK

On a global scale human activities have more than doubled the fixation of nitrogen gas to biologically available forms of nitrogen (Vitousek et al., 1997; Haygarth and

Jarvis, 2002). Global anthropogenic emissions of nitrogen have been estimated at 140 million tonnes per year (Haygarth and Jarvis, 2002), and 160 million tonnes per year (Dalton and Brand-Hardy, 2003). The principal means by which humans have increased biologically available nitrogen are by industrial fixation for fertilisers, combustion of fossil fuels, and planting of legumes as crops. Humans have increased the amount of biologically available phosphorus by mining phosphatic ore reserves for fertiliser, detergents and other uses, thus intercepting the natural geological and geomorphological processes by which these reserves would eventually have become available.

1.6.1. Fertiliser use

The application of phosphate-based fertiliser began in the 1800s and increased greatly following the industrial production of superphosphate in 1842 (Johnston and Dawson, 2005). Prior to 1860, farmers relied on natural biological fixation to provide soil nitrogen; early in the twentieth century, the Haber-Bosch method of synthesising ammonia was developed (Dalton and Brand-Hardy, 2003). Until the 1950s total nitrogen application was less than that of phosphorus, because until phosphorus deficiency was addressed, plants did not respond to nitrogen. Indeed, rates of application of phosphate per unit area continued to be higher than those of nitrogen in many areas until at least the 1960s, but the area of land dressed with nitrogen was greater (Yates and Boyd, 1965).

The major trends in the use of fertilisers in the United Kingdom from the turn of the twentieth century have been an increase in the amount of fertiliser used per hectare and an increase in the area receiving fertilisers. Phosphate application rose sharply from the 1940s, exceeding 400 000 tonnes annually by 1950 and remaining fairly steady following this before dropping slightly in the 1990s (Fig 1.4). Total nitrogen use began to rise sharply from the early 1950s, with the increase steepening in the 1960s, peaking in the 1980s before falling. The reductions in phosphorus and nitrogen applications have arisen from an increase in set-aside, and more efficient fertiliser use.

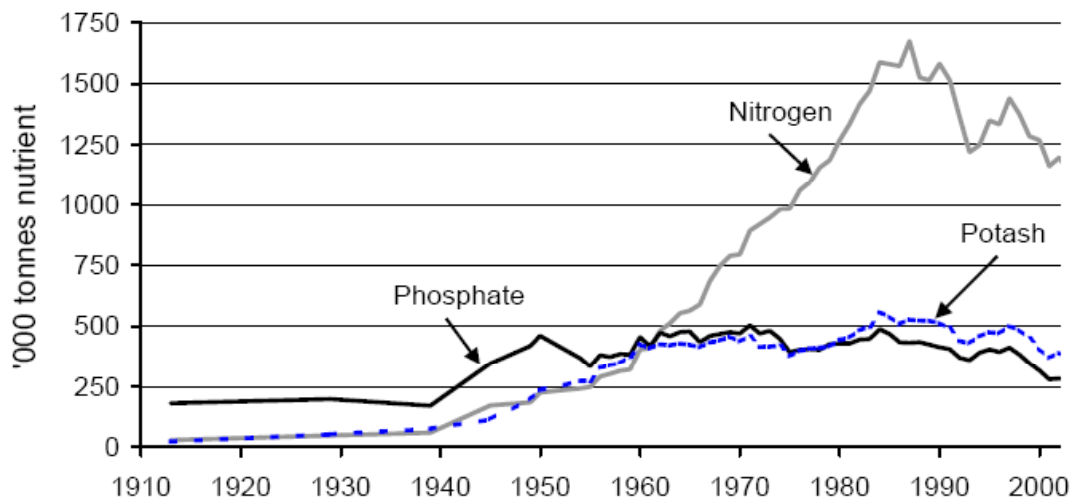


Figure 1.4. Quantities of nutrients applied as fertilisers in UK agriculture 1913-2000 (data from Rothamsted Research and MAFF; graph originally appeared in Johnston and Dawson, 2005).

Application rates of fertiliser per hectare vary according between crops, with the highest rates on winter cereals and on grassland silage fields, but generally speaking they also rose sharply post Second World War before declining slightly in recent years (Fig. 1.5). In the period 1969-1988 nitrogen application rates increased five-fold on arable fields and three-fold on grassland (Chalmers et al., 1990). Phosphate application rates were already quite high on cereal crops by the 1940s, while on grassland the steepest increases occurred between the 1940s and the 1960s (Yates and Boyd, 1965; Johnston and Dawson, 2005). Application rates have declined on both arable crops and on grassland since the 1980s, but the falls have been greatest on grassland (British Survey of Fertiliser Practice, 2004). The grassland nitrogen application rate (England and Wales data only) was the lowest since the mid-1970s. Changes in the proportions of crops, and their different fertiliser requirements, account for some of the changes in application rates (British Survey of Fertiliser Practice, 2004).

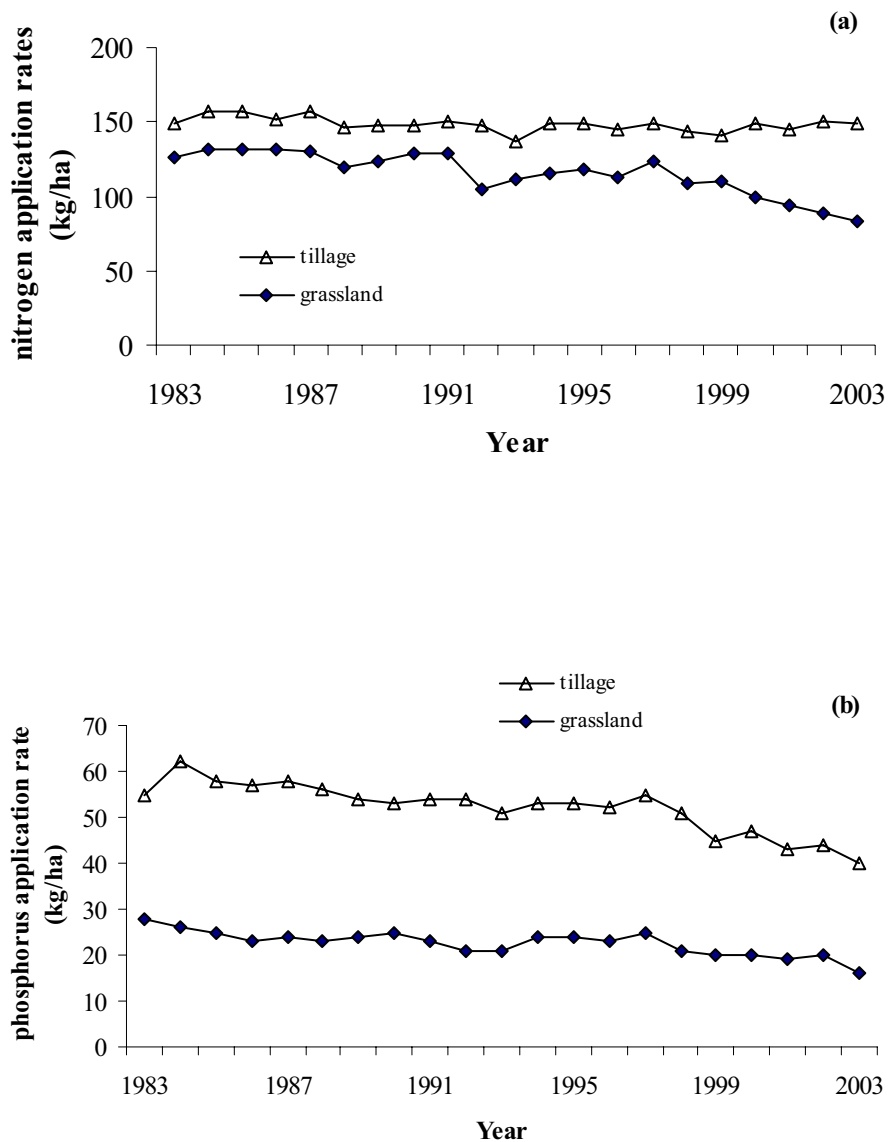


Figure 1.4. Application rates of (a) nitrogen and (b) phosphorus on tillage and on grassland in Great Britain, 1983-2003 (British Survey of Fertiliser Practice, 2004).

The area treated with fertiliser has also increased since the turn of the twentieth century. Fertiliser use was already widespread on cereal crops by the 1940s, and by the 1960s a large majority of cereal crops received fertiliser applications (Yates and Boyd, 1965). In 2003 99% of winter wheat in Great Britain received nitrogenous fertiliser and 81% received phosphate (British Survey of Fertiliser Practice, 2004). Grassland area treated was still quite low in the 1960s, with proportions receiving

fertiliser in England and Wales differing depending on district, but ranging from 22% to 62% for nitrogen, and from 20% to 47% for phosphate (Yates and Boyd, 1965). In 2003 in Great Britain the proportions of grassland over 5 years old treated with fertiliser were 67% for nitrogen and 55% for phosphate (Goodlass et al., 2003). However, the proportions for grassland under 5 years were 85% for nitrogen and 69% for phosphate, and young grass has become much more prevalent in the landscape.

Despite the decreases in overall fertiliser use and in application rates over the past two decades, the application of nitrogen and phosphorus to farmland remains very widespread and high (averaging around 200 kg/ha for winter wheat). While fertiliser application may be necessary for profitable agricultural production, its use affects the fertility of agricultural areas as well as the likelihood and magnitude of losses of nutrients to other habitats.

1.6.2. Levels in aquatic systems

Nutrient levels of any waterbody have a background level, which is comprised of natural soil erosion and leaching, animal excreta and plant residues, and fixation of atmospheric nitrogen by bacteria; these are determined by the natural fertility of the sources. However, in human-altered systems, which effectively comprise the whole of the UK, nutrient levels are additionally influenced by heightened concentrations in runoff and leachate, plus the increased levels of nutrients in the soil from fertiliser applications, and direct inputs from domestic waste, human sewage and atmospheric deposition.

In fresh water, phosphorus (in the form of phosphate) is usually the limiting nutrient/ In marine environments, phosphate is naturally present at higher concentrations, and so nitrogen tends to be the limiting nutrient; nitrogen-fixing cyanobacteria are uncommon in the sea. In estuaries, phosphorus tends to be the limiting nutrient at the head of the estuary, while nitrogen becomes increasingly important closer to the sea. Nitrogen is present in aquatic systems in soluble form, usually nitrate, although ammonia may also be present in conditions of low oxygen or where there is a large organic component to the nutrient pollution. In some circumstances nitrogen may the

limiting nutrient (Maberly et al., 2002; Gonzalez Sagrario et al., 2005). Human inputs of phosphorus also typically reduce the nitrogen:phosphorus ratio in freshwater, which leads to the development of nitrogen-fixing cyanobacteria (Harper, 1992).

Both nitrate and phosphate levels in UK rivers showed upward trends from the 1930s and 1940s, when records began to be kept (Heathwaite et al., 1996). Similar trends have been found for nitrate in groundwater and in lakes in the UK. Over recent decades nitrate levels in rivers have fluctuated but showed no clear trend, while orthophosphate (inorganic phosphate) levels have declined from a high in the 1980s (Fig. 1.5.). Nitrate levels in rivers in Britain have not changed markedly since the 1970s, and nutrient concentrations in some rivers have declined following tighter controls on effluent discharges (Green et al., 1990; Foundation for Water Research, 2000). This has led in some places to an overall decline in nutrient pollution, and in others to a shift in the relative contributions of point-source (with a large organic component) to diffuse (predominantly inorganic) pollution, with agriculture as the major source (Johnston and Dawson, 2005). Despite success in reducing point-source pollution, levels of nitrogen and phosphorus in aquatic systems have risen dramatically in many places in recent decades (Harper, 1992; Marsden et al., 1998). Palaeolimnological evidence from shallow coastal lakes in Wales, and from shallow lakes in the Norfolk Broads, suggests that eutrophication has increased over the last fifty years of the twentieth century as a result of agricultural and sewage inputs (Moss, 1980; Haworth et al., 1996).

There has been a reduction in the loadings of phosphorus to surface waters from sewage treatment works, largely due to the reduced use of phosphates in detergents (Foundation for Water Research, 2000). In the period 1990-2003, inputs of orthophosphates to UK coastal waters fell from 37 920 to 21 000 tonnes, before rising to 41 660 tonnes in 2004, and the proportion from direct inputs fell from 58% to 26% (DEFRA, 2006b) (lower limits). Total nitrogen inputs fell slightly from 321 640 tonnes to 286 550 tonnes from 1990 to 2004, and the proportion from direct inputs fell from 37% to 22% (lower limits).

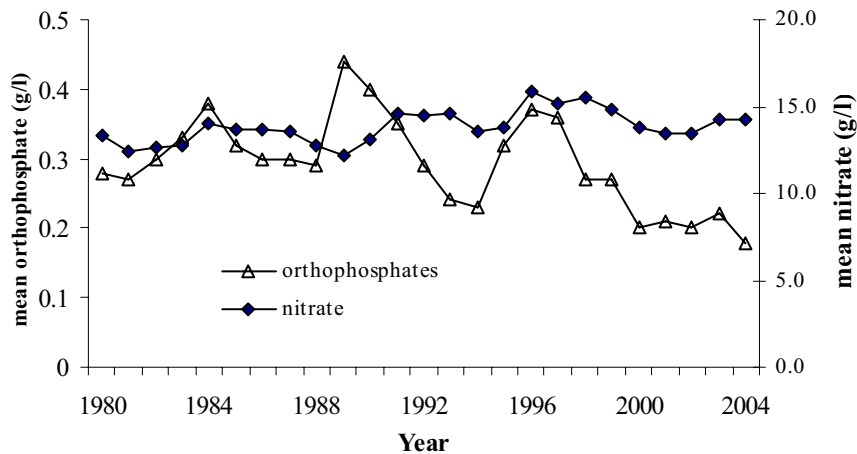


Figure 1.5. Nutrient concentrations in British rivers 1980-2004 (DEFRA statistics).

1.6.2.1. Classification of water bodies

The trophic status of inland standing waters has been classified by the Organisation of Economic Co-operation and Development according to phosphorus content, as follows (Foundation for Water Research, 2000).

	Total P ($\mu\text{g/l}$)
Ultra-oligotrophic	<4
Oligotrophic	<10
Mesotrophic	10-35
Eutrophic	35-100
Hypertrophic	>100

Classifications are also based on concentration of chlorophyll (the major photosynthetic component of plants) and water transparency. For flowing waters, classification is based on macrophyte surveys rather than phosphorus concentrations (Foundation for Water Research, 2000).

The UK Biodiversity Action Plan (available via www.ukbap.org.uk) states that eutrophic waters in Great Britain cover approximately 845 km², with 80% of waters in

England eutrophic, compared with 15% in Scotland; plus another 940 km² of eutrophic standing waters in Northern Ireland. Many of these waters would be hypertrophic by the above classification. Thus it can be seen that eutrophication is widespread in the United Kingdom, although some of the waters listed above would be naturally eutrophic. In recent decades efforts have been made to reduce the anthropogenic nutrient load reaching aquatic systems. As with agriculture, recent slight declines in nutrient inputs still leave levels in many places much higher than they would be in the absence of anthropogenic inputs.

1.6.3. Atmospheric nitrogen

Annual emissions of oxidised nitrogen in the UK were estimated to have been 312 000 tonnes of nitrogen in 1900, rising to a high of 787 000 tonnes in the 1980s, then falling to 460 000 tonnes by 2000 (Fowler et al., 2004). Annual emissions of reduced nitrogen were estimated to be 168 000 tonnes in 1900, when the major source was coal combustion, increasing to 263 000 tonnes in 2000, by which time they were dominated by agricultural sources (Fowler et al., 2004). Nitrogen oxide emissions have been falling due to the introduction of catalytic converters on vehicles and controls on emissions.

Less nitrogen is deposited in the UK annually than is emitted, meaning that the UK is a net exporter of nitrogen. One estimate of nitrogen deposition claims that about 380 000 tonnes (43% nitrogen oxides 57% ammonia) of nitrogen are deposited in the UK (NEG-TAP, 2001). Another estimate suggests that deposition of oxidised nitrogen (wet deposition of nitrate and dry deposition of nitrogen dioxide and nitric acid) increased from 66 000 tonnes in 1900 to 191 000 tonnes in 2000, while over the same period deposition of reduced nitrogen (wet deposition of ammonium and dry deposition of ammonia) increased from 163 000 tonnes to 211 000 tonnes (Fowler et al., 2004). Rates of atmospheric deposition of fixed nitrogen rose in Europe in the two decades to 1995 from 2-6 kg/ha/year to 15-60 kg/ha/year (Pitcairn et al., 1995). These vary geographically; in the UK the highest amounts are in areas of high rainfall, such as the Pennines, Lake District and parts of Wales, where wet deposition dominates. These areas receive up to 80 kg/ha/year of nitrogen, which approaches the amounts applied

by farmers to crops. Wet deposition is dominant in these areas. Current rates of atmospheric deposition of nitrogen are 5-20 times pre-industrial levels (Haygarth and Jarvis, 2002).

1.7 Historical changes to the vegetation of the UK

Anthropogenic nutrient inputs would be expected to affect the vegetation of the United Kingdom by several pathways. Farming and grazing are the major land uses in Britain, and much of this farmland receives fertiliser, as described above. Diffuse and point source nutrient pollution is transported by hydrological processes to aquatic habitats. Terrestrial habitats may be subject to fertiliser drift from farmland. And all habitats receive nitrogen via atmospheric deposition. Increased nutrient availability shifts the balance from below-ground competition for resources to above-ground competition for light and leads to dominance of species with a competitive advantage at high nutrient levels (Pennings et al., 2005). Indirect effects of fertilisers, notably shading from competitive species, may also cause the declines of some plant species (Robinson and Sutherland, 2002).

There is evidence that these increases in nutrient inputs have indeed had effects on the vegetation of the UK. Changes in vegetation co-occur with long term increases in nutrient (especially nitrogen) inputs. Agricultural intensification, including the increased use of fertilisers, is suggested as a major cause of historical shifts in the flora of farmland (Green, 1990; Wilson, 1992; Sotherton and Self, 2000). Similar declines have also been observed in Europe since the 1940s (Wilson, 1999). Flower-rich farmland habitats in Great Britain have largely disappeared, and many plant species (including some previously considered weeds) showed range declines in the 1950s and 1960s (Robinson and Sutherland, 2002). The BSBI Monitoring Scheme assessed changes in the vascular plant record between 1960 and 1987-88 in England and Scotland, and collected baseline data for future studies (Rich and Woodruff, 1996). At least 24% of the flora changed significantly in England, and 12% in Scotland, and species and communities typical of low soil fertility were especially hard hit. Of 179 native species whose UK distribution declined, 38% were species of calcareous, unimproved or acidic grassland (Rich and Woodruff, 1996).

The Countryside Survey 2000 examined changes in cover of broad habitats and in habitat quality (Haines-Young et al., 2000). Widespread nutrient enrichment from nitrogen was considered to be a major driver of changes in habitat quality in terrestrial habitats between 1990 and 1998. A repeat of a survey of British and Irish flora found that species with high Ellenberg indices (a measure of their preference for fertile sites) were more successful in the late twentieth century than they had been in the 1950s (Preston et al., 2002). An examination of the changes in abundance of vascular plants in Northamptonshire from pre-1930s to 1995 showed that species associated with higher soil nitrogen status generally increased (McCollin et al., 2000). In vegetation types associated with low fertility, changes in the distribution of vascular plants between 1978 and 1998 were consistent with increased nutrient availability and the responses of plant species to soil fertility (Smart et al., 2005). Heather cover in the UK has declined, mostly replaced by unimproved grassland or grass moor (Bunce, 1989; Cadbury, 1992); the mechanisms by which nutrient pollution may have contributed to this are described later.

The documented changes in the vegetation of the United Kingdom strongly suggest that increased nutrient availability has had effects over a wide scale. These changes will also be affected by other environmental factors; climate is one that has also changed over a similar time scale and could have effects over a similar spatial scale. In farmland, other aspects of agricultural intensification, including herbicide use and simplification of cropping systems, will also have affected the vegetation (Campbell et al., 1997; Stoate et al., 2001). Elsewhere, changes to grazing regimes, forest management, and land drainage will have altered the vegetation. Despite the difficulty in distinguishing the effects of nutrients from other drivers, I consider that the evidence that species favoured by high-nutrient conditions have generally increased in abundance and distribution over the past century is strong enough to conclude that increased availability of nutrients from anthropogenic sources is a major driver of changes in UK vegetation. In the forthcoming sections I will describe some of these changes in more detail, with particular reference to means by which they could affect bird populations in a variety of habitats.

2. Farmland habitats

2.1. Introduction

Agriculture is the major land use in the United Kingdom, and therefore trends in the management of farmland can have enormous impacts on the landscape and biota, including birds. In fact, lowland farmland birds as a group have declined considerably since the 1970s, both in the UK and across western Europe (Fuller et al., 1995; Schifferli, 2000; Gregory et al., 2004). These declines have accompanied large changes to farming systems, referred to generally as agricultural intensification, which have resulted in enormous changes to the landscape and biodiversity of the United Kingdom. These changes and the effects they have had on bird populations are discussed at length in many publications (Chamberlain et al., 2000; Fuller, 2000; Stoate et al., 2001; Robinson and Sutherland, 2002; Shrubbs, 2003; Newton, 2004; Vickery et al., 2001), and do not need to be discussed in detail here. As well as increased use of inorganic fertilisers, they include: increased mechanisation; increased drainage; increased use of pesticides; a switch from spring-sown to autumn-sown crops; and a polarisation of farming with pasture-based farms (including dairying) becoming concentrated in the west and north of Britain, and arable farms in the east and south, and a concomitant loss of mixed-farming landscapes. Disentangling the effects of both organic and inorganic fertilisers from the overall effects of agricultural intensification, while difficult, is one of the goals of this review.

The historical trends in use of nitrogen- and phosphorus-based fertilisers have been discussed in Section 1. However, the use of fertilisers is also associated with other changes in farming practices that have also had important effects on the landscape and biota. These include the large-scale switch from hay to silage, earlier and more frequent cutting, increased stock rates, reduced mixed-farming and rotation. These changes, and their effects on flora and fauna, will be described below.

For the purposes of this review, farmland consists of: enclosed arable and horticultural land; improved grassland; and semi-natural grassland. This constitutes around 18.5 million hectares, over 70% of the land area of the United Kingdom, and within this

area there is enormous variability due to geography, geology, climate, and cultural factors. The responses of some plant species to increased nitrogen inputs is partly determined by community context (Pennings et al., 2005), and thus the direct effects of fertiliser application, and the indirect effects arising from it, may differ between different types of farmland and different geographical areas.

The effects of fertiliser application (as well as other agricultural practices) on birds in lowland neutral grasslands have already been the subject of one review (Vickery et al., 2001). Another review, of lowland farmland birds, suggested that there was strong evidence that increasing fertiliser use was a component of the decline of several species (Anderson et al., 2001). The current review attempts to synthesise the state of knowledge about such effects on all agricultural land in the United Kingdom.

2.2. The population trends of farmland birds and the possible mechanisms by which increased use of fertilisers may contribute to these

Most bird species have been recorded from farmland at some time, but this review concentrates on those for which farmland is a significant habitat for part of their life cycle. A review of the indirect effects of pesticides on birds in lowland farmland considered 42 species, most of which bred on lowland farmland (Campbell et al., 1997). The current review includes all agricultural land in the UK, and therefore some species that breed outside lowland farmland, or that only winter in the UK, also come within the remit of this review. In particular, I consider the effects on wintering geese and on breeding waders. Table 1 summarises the species subject to review, their population trends, and some life history characteristics. While it would be desirable to systematically determine the susceptibility of all species to the indirect effects of increased nutrient inputs, in reality some species have been the subject of more thorough research (these species are likely to be those of conservation interest), and I concentrate on those species for which the links between nutrient inputs and bird populations can be established.

Table 2.1. Birds considered for review of the effects of fertiliser application in farmland in the UK.

Species ¹	listing ²	Trend ³ 1970-2003	Trend ³ 1994-2004	Diet ⁴	Nesting habit	Migratory status ⁵
bean goose	amber			f	n/a	w
pink-footed goose	amber			f	n/a	w
white-fronted goose	amber			f	n/a	w
greylag goose	amber			f	n/a	r + w
brent goose	amber			f	n/a	w
grey partridge	red	-87	-30	f, s, i	ground	r
quail	red			s, ei	ground	s
kestrel	amber	-26	-19	v	hole, ledge	r
corncrake	red	14	64a	s, ei	ground	s
oystercatcher	amber			si	(nidifugous) ground	r + w
golden plover	green			si	(nidifugous) ground	r + w
lapwing	amber	-45	-13	ei	(nidifugous) ground	r + w
dunlin	amber			ei	(nidifugous) ground	r + w
snipe	amber			si	(nidifugous) ground	r + w
curlew	amber			si	(nidifugous) ground	r + w
redshank	amber			ei	(nidifugous)	r + w
stock dove	amber	100	30	s	hole	r
woodpigeon	green	99	12	f, s	shrubs/trees	r
collared dove	green	100	30	s	shrubs/trees	r
turtle dove	red	-80	-45	s	shrubs/trees	s
green woodpecker	amber	108	34	ei	hole	r
skylark	red	-53	-10	ei	ground	r
barn swallow	amber	11	22	ei	buildings	s
yellow wagtail	amber	-62	-27	ei	ground	s
pie wagtail	green	58	21	ei	ground	r
whinchat	green		-15	s, ei	ground	s
blackbird	green	-17	17	si, b	shrubs/trees	r
fieldfare	amber			si, b	n/a	w
song thrush	red	-50	14	si, b	shrubs/trees	r
redwing	amber			si, b	n/a	w
mistle thrush	amber	-37	-2	si, b	shrubs/trees	r
grasshopper warbler	red		59	ei	shrubs/trees	s
sedge warbler	green	-14	15	ei	shrubs/trees	s
reed warbler	green	123	48	ei	shrubs/trees	s

¹ a list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends derived from CBC/BBS surveys (Eaton et al., 2005): a = 1997-2004, b = 1995-2003.

⁴ broad diet in farmland: b = berries, ei = epigeal and foliar invertebrates, f = foliage, o = omnivorous, s = seeds, si = soil invertebrates, v = vertebrates.

⁵ migratory status in the UK (species may be included in more than one category due to partial migration): r = resident, s = summer migrant, w = winter migrant.

Table 2.1. (cont.) Birds considered for review of the effects of fertiliser application in farmland in the UK.

Species ¹	listing ²	Trend ³ 1970-2003	Trend ³ 1994-2004	Diet ⁴	Nesting habit	Migratory status ⁵
red-backed shrike	red	decline	extinct	ei	shrubs/trees	s
magpie	green	101	-1	o	shrubs/trees	r
chough	amber			o	cliffs/ledges	r
jackdaw	green	89	19	o	buildings	r
rook	green		3	o	trees	r
					trees,	
carrion crow	green	78	11	o	buildings	r
raven	green		91	o	ledges	r
starling	red	-71	-30	si	holes	r
house sparrow	red	-64	-3	s, ei	holes	r
tree sparrow	red	-93	48	s, ei	holes	r
chaffinch	green	32	8	s, ei	shrubs/trees	r
brambling	green			s, ei	n/a	w
greenfinch	green	26	37	s, ei	shrubs/trees	r
goldfinch	green	49	28	s, ei	shrubs/trees	r
linnet	red	-48	-14	s	ground	r
yellowhammer	red	-54	-22	s, ei	shrubs/trees	r
cirl bunting	red	118	54b	s, ei	shrubs/trees	r
reed bunting	red	-43	4	s, ei	shrubs/trees	r
corn bunting	red	-89	-24	s, ei	shrubs/trees	r

¹ a list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends derived from CBC/BBS surveys (Eaton et al., 2005): a = 1997-2004, b = 1995-2003.

⁴ broad diet in farmland: b = berries, ei = epigeal and foliar invertebrates, f = foliage, o = omnivorous, s = seeds, si = soil invertebrates, v = vertebrates.

⁵ migratory status in the UK (species may be included in more than one category due to partial migration): r = resident, s = summer migrant, w = winter migrant.

2.2.1. Concordance of bird trends with trends in the use of fertilisers

Population trends of breeding birds in the United Kingdom have been monitored, initially by the Common Birds Census (CBC), and more recently by the Breeding Bird Survey (BBS) (Raven et al., 2005). Because of the wide geographical range of farmland, population trends of some species, notably those of uplands, will not have the same length of records, due to the lack of CBC plots in these areas. This has been addressed to some extent in the BBS, but it means that some population trends prior to 1994 are difficult to determine. This is especially relevant to the present review, as changes as a result of agricultural intensification (including increased fertiliser use) may be expected to have occurred primarily in the 1970s and 1980s, as was observed in lowland farmland. However, even when the data on bird trends are relatively comprehensive for recent decades, it is still the case that the increased use of fertilisers (particularly those based on phosphates) pre-dates the widespread bird monitoring schemes. Therefore, the substantial effects of increased fertiliser use on some bird species may have occurred before monitoring schemes were underway, and

the data presented in this review may be representing advanced stages of such effects. Finally, bird species may display population trends that differ regionally, or between habitats in the same region, and thus national population trends may not reflect the effects of increased nutrient levels on smaller scales.

Many of the trends in species' declines show strong temporal and spatial association with agricultural intensification. Many species declined most steeply between 1975 and 1980, approximately six years after the greatest rates of change in agricultural practices (Chamberlain et al., 2000). A higher proportion of farmland species in the UK are in decline than are woodland species (Fuller et al., 1995). Declines have been recorded both in abundances and in range (Chamberlain and Fuller, 2000). Seven species showed range declines in lowland farmland of over 5% (on the scale of 10 km squares) between the late 1960s and the early 1990s: grey partridge, lapwing, turtle dove, corn bunting, yellow wagtail, tree sparrow and reed bunting. Local extinctions of these species were more likely in landscapes dominated by grassland, compared with arable or mixed landscapes, even in those species that decreased in abundance more in arable landscapes (Chamberlain and Fuller, 2001).

2.2.2. Ways in which fertiliser use may affect farmland birds

The three major ways in which any process can have an impact on bird populations are: alterations to nesting success, which affects productivity; alterations to predation levels, which affects survival; and alterations to food abundance or availability, which can affect both survival and productivity. The three major resources that birds require over the course of the year are winter food resources, summer food resources (for adults and chicks), and nesting habitat in summer. Ways in which increased fertiliser use may be expected to indirectly affect bird populations are presented schematically in Figure 1.

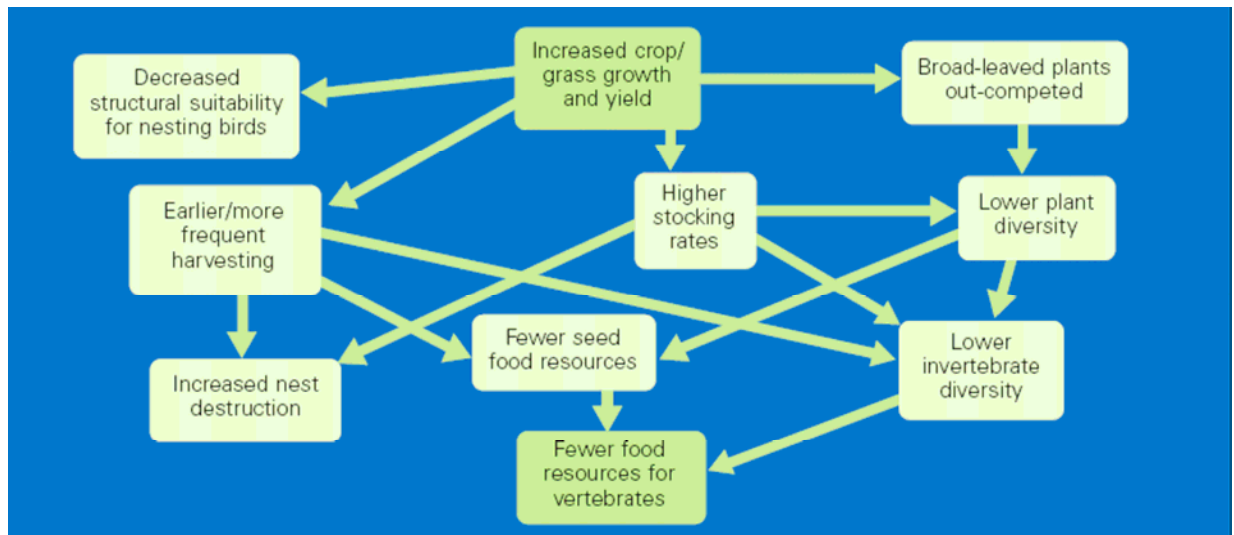


Figure 2.1. Flow diagram illustrating expected mechanisms for indirect effects of nutrient inputs on birds in farmland.

Important food sources for farmland birds are described in detail by Wilson et al (1999). Invertebrate groups that are key food sources for farmland birds include Orthoptera, Hymenoptera, Arachnida, Coleoptera, Lepidoptera, Hemiptera and Diptera (Wilson et al., 1999). Orthoptera, Coleoptera and Lepidoptera are of particular importance to bird species currently experiencing population declines in farmland habitats. Plant species that are important food sources for farmland birds include cereal crops, *Polygonum* (knotgrasses and persicarias), *Stellaria* (chickweeds) and *Chenopodium* (goosefoots), Asteraceae, Fabaceae and Brassicaceae (the latter two including crop components) (Wilson et al., 1999). Broad nest and food requirements for farmland birds are summarised in Table 1. Other more specific food requirements of particular species are mentioned in the text where appropriate.

2.3. Effects of fertiliser use on vegetation

A short background to some of the historical trends in vegetation in the United Kingdom is provided in Section One. There is an extensive literature on the effects of fertiliser applications on plant communities, including crops, in farmland habitats in the UK and elsewhere. I do not attempt to comprehensively review the entire

literature, but objectively review the results of those studies that I consider are relevant to the processes by which fertiliser use could ultimately have an impact on bird species.

In both grassland and arable land, the purpose of fertiliser application is to increase the crop yield, regardless of the ultimate use of the crop. Application of fertilisers also increases the nutritive value of the crop. Increased above-ground production can have profound effects on the structure and composition of the vegetation, even in intensively managed systems, where the goal is to maximise the production of a single crop. The effects of increased fertiliser applications on vegetation are summarised in Table 2.

2.3.1. Changes in plant species richness and composition

The amounts of nitrogen and phosphorus available are primary in determining plant species composition, and differential responses to nitrogen in particular are suggested as major causes of the decline of some arable species and the increases of others (Wilson, 1999). Within arable fields, plant species that are now uncommon performed better in the absence of nitrogen fertiliser applications, although shading by nitrogen-responsive winter cereals may be more important than the reaction of non-crop plant species to nitrogen (Wilson, 1999). Field margins have traditionally been an important location for weeds, but fertiliser drift may have effects on the flora of field margins (Boatman, 1994; Rew et al., 1992; Tsiouris and Marshall, 1998). In arable land in the Netherlands, levels of phosphorus and nitrogen were correlated with reduced plant species richness in the field margins (Klein and Verbeek, 2000). Weed species richness in Czech barley fields was reduced when nitrogenous fertiliser was applied, and the weed community was affected both directly by the fertiliser and indirectly by increased competition with the crop (Pyšek and Lepš, 1991). Erect weeds were able to take advantage of the increased nitrogen supply, whereas prostrate weeds were shaded by the dense cover of the crop.

Table 2.2. Some effects of fertiliser application and associated management practices on the vegetation of farmland.

Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
arable fields	Southern England	nitrogen fertiliser applications (none, 75 kg/ha and 150 kg/ha); uncommon arable species sown	9/14 weed species most abundant where no fertiliser applied	shading of non-crop plants by fertilised wheat; differential responses to increased nitrogen	1	Wilson, 1999
arable fields	Southern England	unfertilised patches within arable farms	15/29 weed species more abundant in unfertilised patches than in paired fertilised patches	shading of non-crop plants by fertilised wheat, differential responses to increased nitrogen	2	Wilson, 1999
barley fields	Czechoslovakia	application of nitrogenous fertilisers (0, 70 or 140 kg/ha)	lower species richness and diversity at both levels of fertiliser; change in species composition (also affected by type of fertiliser)	direct effects of fertiliser, and indirect effects mediated by competition with the crop	2	Pyšek and Lepš, 1991
arable field margins	Netherlands	spatial relationships between species richness and nutrient levels	inverse relationship between species richness and both nitrogen and phosphorus soil concentrations; inverse relationship between plant biomass and nitrogen soil concentration	competitive exclusion of weed species in fertile conditions	2	Klein and Verbeek, 2000
field margins	UK	fertiliser drift	altered botanical composition. no effect in seedling establishment experiment, but dominance of nitrophilous <i>Bromus sterilis</i> in established plant competition experiment	community already adapted to fertile conditions; time frame of study	2	Boatman et al., 1994
grassland field margins	Gloucester	simulated fertiliser drift	forb component reduced by inorganic fertiliser application only; species richness and abundance maintained in plots treated with organic fertiliser	competitive responses to fertilisation	1	Tsiouris and Marshall, 1998
grassland field margins	Wales	application of inorganic fertiliser (0, 100 or 300 kg N/ha/year), farmyard manure (30-42 kg N ha/year) or diluted slurry (27-72 kg N/ha/year) over five years	higher species richness at low levels of nitrogen input, but similar sward structure	slower release of N content of organic manures and more efficient uptake by plants	2	Jones and Haggard, 1997
lowland grassland	Devon and Bucks.	species richness in relation to nitrogen levels (as a surrogate of management intensity)	higher species richness in mowed plots; various responses to fertiliser but lowest species richness in plots receiving N, P and K	competitive exclusion, also effects of management	2	Tallowin et al., 2005
lowland grassland	Hampshire	experimental applications of fertiliser (N, P, K and lime) separately or in combination plus different mowing regimes	relationship between vegetation and management intensity (defined by nitrogen inputs) and sward structure	loss of poor competitors in unmowed plots	1	Fenner and Palmer, 1998
lowland grassland	Devon and Bucks.	management intensity (defined by nitrogen inputs) and sward structure	no effect on total seed head production; increased grass seed head production with management intensity	increased productivity of grasses in response to fertiliser	2	Atkinson et al., 2005

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 2.2. (cont.). Some effects of fertiliser application and associated management practices on the vegetation of farmland.

Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
acid grassland	Britain	spatial relationships between species richness and nutrient levels	lower species richness at more fertile sites	competitive exclusion by species able to take advantage of higher nutrient levels	2	Stevens et al., 2002
hay meadow	Somerset	application of nitrogenous fertiliser	lower species richness	competitive exclusion by species favoured by fertile soils	1	Mouniford et al., 1993
hay meadow	Somerset	species diversity in relation to rates of fertiliser application	lower species diversity, dominance by <i>Lolium perenne</i> , <i>Holcus lanatus</i> and <i>Rumex acetosa</i>	interactions with grazing	2	Kirkham et al., 1996
subalpine meadows	Switzerland	gradient of management intensity (grazing and fertiliser use)	highest species richness in lightly grazed, unfertilised meadows	competitive balance between species	2	Erhardt, 1985

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

High species richness is associated with low soil fertility across a range of semi-natural lowland grasslands (Janssens et al., 1998), and phosphorus is considered the key limiting nutrient in semi-natural grassland (Gough and Marrs, 1990; Walker et al., 2004). Fertiliser additions can lead to the dominance of grass species such as *Lolium perenne* and *Holcus lanatus* at the expense of sedges, rushes and forbs (Mountford et al., 1993), although interaction with grazing or other disturbance may affect the impacts of fertiliser addition (Kirkham et al., 1996). For example, in a Somerset hay-meadow, plots receiving nitrogen and modest rates of phosphorus plus aftermath grazing maintained dominance by *Lolium perenne*, but in the absence of aftermath grazing *Agrostis canina* dominated similarly fertilised plots (Kirkham et al., 1996). In Devon and Buckinghamshire grasslands there was a significant inverse relationship between nitrogen inputs and plant species richness (of both grasses and forbs); only fields receiving less than 50 kg/ha of fertiliser per year were likely to support more than 12 higher plant species (Tallowin et al., 2005). Cover of non-grasses decreased with higher nitrogen applications. Sown species dominated young grasslands (less than 4 years old), and there was a strong relationship between pasture age and fertiliser application.

In farmland, weed seeds are important as food sources for birds and as food sources for invertebrates that are bird prey items. As harvesting efficiency has increased, and fewer seeds from crops are available for birds, weeds become even more important for birds, but these broad-leaved species have declined in British farmland with increased agricultural intensification. While the use of herbicides and other forms of intensive management are the main causes of the decline, the application of inorganic fertiliser contributes to the loss of less competitive species, especially forbs, which are important sources of seeds (Jones and Haggard, 1997; Tallowin et al., 2005). Some weed species, such as goosefoots, oraches, chickweed and composites probably benefit from fertiliser applications (Wilson et al., 1999), although other elements of agricultural intensification, including some connected to fertiliser use, may reduce their abundance. Creeping thistle (*Cirsium arvense*), an important food source for some bird species, is out-competed in fertilised ungrazed grasslands, but benefits from competitive release in rabbit-grazed areas, as it is relatively unpalatable (Edwards et al., 2000).

Fertiliser use over time can leave a legacy of fertile soil, blocking the re-establishment of stress-tolerant species, which may hinder the restoration of species-rich communities that prefer low nutrient environments (Walker et al., 2004; Tallowin et al., 2005). Reductions in soil fertility can be slow, due to continued atmospheric input, and thus reversion to natural grassland communities may take many years, even though there is a general trend towards increased species diversity and reduced yield after the cessation of fertilisation (Walker et al., 2004). A combination of cutting and aftermath grazing appears to accelerate the reduction of soil fertility and to improve conditions for establishment of target species.

2.3.2. Changes to vegetation structure

The purpose of applying fertiliser is to promote crop growth, and thus the natural result of fertiliser application is taller and denser vegetation, and frequently earlier growth. Crop structure is frequently more important to higher trophic levels than species composition. Agricultural intensification has increased crop density, and simplified and homogenised sward structure (Wilson et al., 2005). Drainage, herbicide use and other elements of intensification contribute to these changes, but increased fertiliser use is central to the changes to crop structure. Fertiliser applications affect crop structure directly, by increasing growth, and via changes in management, which are described below. Birds may be affected by changed crop structure if it alters: the degree to which they are concealed or able to perceive predators; the degree to which they are exposed to weather extremes; or the availability or abundance of food items (Wilson et al., 2005).

2.3.3. Effects on management practices

The increases in crop yield as a result of fertiliser applications (along with other factors such as improved crop varieties) have been instrumental in changing farmland management practices in the UK, and these changes are documented in several publications (O'Connor and Shrubbs, 1986; Fuller, 1987; Chamberlain et al., 1999; Fuller, 2000; Anderson et al., 2001; Donald et al., 2001).

Some of the changes associated with agricultural intensification have been directly related to the increased inputs of fertilisers on arable and grassland. The use of nitrogenous fertilisers has removed the need for clover to be grown within rye grass (Raymond et al., 1986). A similar shift in forage composition has occurred in hay production. This has released farmers from the need to include nitrogen-fixing legumes in their rotations, and also from the need to include pasture on farms as a food source for herbivores producing organic fertiliser, thus triggering a move away from mixed-farming systems towards either pasture (in the north and west) or arable (in the south and east) (Fuller, 2000; Robinson and Sutherland, 2002). For example, the proportion of tilled land in Wales fell from 17% to 4% between 1945 and 1992 (Lovegrove et al., 1995).

There has been a massive shift from hay to silage production in the UK. Silage production involves several cuts (generally not more than three) of the grass crop before it has set seed, at approximately 6 week intervals beginning as early as late April (English Nature, 2006). Hay production involves a single cut later in the season, as late as July. Seed set is also undesirable for hay digestibility, but because this process requires much more moisture reduction in the crop, there may be benefits in cutting after some seed set has occurred, or this may be enforced due to weather conditions. The shift in cutting methods has been occurring for over a century (Wilman, 2002), but there was a particular increase in silage production in the 1970s and early 1980s. Silage comprised about 10% of preserved forage in 1970, rising to 70% in 1985 (Raymond et al., 1986), and is currently around 90% (Vickery *et al.* 2001). The desire to move from hay to silage production has been driven by socioeconomic and climatic factors, and has been enabled by increased mechanisation and improvements in ensilage techniques (Wilman, 2002). It might be expected that artificial fertilisers would be used in the production of silage but not essential in the change from hay to silage production. However, silage making involves high machinery, labour and fuel costs, and requires high grass yields to be profitable. Successive high yields can normally only be achieved with the application of artificial fertilisers (English Nature, 2006). Silage production has further effects on management of grassland, due to the earlier cutting and generally multiple cuts.

Increased grass yield has also allowed higher stocking rates on grassland, for longer periods of the year (Stoate, 1996). There has been a large increase in sheep numbers in the period 1970-1990 (Fuller and Gough, 1999), although the cattle herd has decreased (Vickery et al., 2001). In Devon and Buckinghamshire, stock rate was significantly related to nitrogen fertiliser input (Tallowin et al., 2005). Age of grass sward was also related to fertiliser input; swards in a majority of fields with low or moderate nitrogen input (<200 kg/ha/year) were over 20 years old, while those in one third of fields with higher applications were less than four years old, and less than a quarter were over 20 years old. Similar relationships between sward age and fertiliser inputs were recorded in a survey of grassland in south-west England (Hopkins et al., 1985). Improved grassland is more frequently re-sown, and although *Trifolium repens* is included in many seed mixtures, it disappears in response to high fertiliser inputs.

2.3.3.1. Effects of changes in management practices on vegetation

Changes to management that arise from increased fertiliser input can have major impacts on farmland vegetation. Indeed, the evidence from Tallowin et al., (2005) suggests that management has more impact on sward structure than fertiliser inputs *per se*. The increase in grazing pressure on more productive pastures can affect the floristics and structure of the grass sward. While moderate grazing levels are considered beneficial to sward heterogeneity and species richness, by providing disturbance necessary for some species to establish, at extreme levels it depresses both measures (McCracken and Tallowin, 2004). High stocking density, particularly by sheep, can greatly increase the density and uniformity of grassland swards, while reducing diversity (Vickery et al., 2001).

Mowing is non-selective, so while the reduction in biomass may be similar to that resulting from grazing, the nature of the defoliation is different, and has different effects on different species. When compared with hay meadows or grazed pastures, grasslands used to produce silage have a denser and taller sward, particularly early in spring (Vickery et al., 2001; Atkinson et al., 2004), and lower abundance and diversity of forbs (Atkinson et al., 2004). The cutting regime associated with silage production radically alters the disturbance regime in grassland and the vegetation structure following cutting. In Devon and Buckinghamshire, there was an inverse relationship between grassland sward height (in June) and nitrogen inputs, but this

was influenced by low input fields being hay meadows, and high input fields having been cut for silage (Tallowin et al., 2005). When hay meadows were removed from analysis, there was no significant relationship between nitrogen inputs and sward height, mass or density; stage of regrowth was probably the major determinant of these variables.

Even where hay production has persisted, use of fertiliser may have affected management regimes. In the North Pennines, the duration of hay cutting has reduced in recent years, due to earlier finish dates (Smith and Jones, 1991). This may be due to climate change and technological improvements, but faster growth of fertilised pastures is likely to have contributed. If this trend is nationwide, the number of fields with mature grass in late summer, and the amount of grass setting seed, is likely to be reduced by changes to hay making as well as the shift towards silage production. Another development in management that is associated with increased use of fertilisers is the exclusion of weed species by competitive crops. Improved grasslands are relatively young, as they are frequently reseeded, typically with high yielding grass species, particularly *Lolium perenne* and other grasses, with relatively few forbs (Hopkins et al., 1985; Rodwell, 1992; Tallowin et al., 2005). Several weed species, including thistles and buttercup, were associated with old grassland, as well as low intensity management, in south-west England (Hopkins et al., 1985). Changes in management have also reduced the amount of seed that is set in farmlands. The combination of changes in management resulting from agricultural intensification favour certain grass species, notably *Poa* spp., which are important in the diet of farmland birds; however, increases in grazing and in cutting for silage, combined with improved harvesting efficiency, mean that the proportion of grasses setting seed has reduced (Wilson et al., 1999).

2.3.3.2. Organic vs non-organic farming methods

Some of the differences between organic and inorganic fertilisers are described in Section 1. Organic fertiliser may have different effects on vegetation and higher trophic levels than inorganic fertiliser. For example, in Welsh grassland field margins, application of inorganic fertiliser led to a loss of the forb component of the margin,

but organic manure maintained species richness, while still producing a relatively high yield and nutrient-rich sward (Jones and Haggard, 1997). A meta-analysis of studies of organic against conventional farming systems in Europe found that plant species richness and weed abundance were generally favoured by organic systems (Bengtsson et al., 2005). Soil microbial activity has been observed to be much greater in organic systems compared with conventional farming (Mäder et al., 2002). However, the former are managed in several ways apart from fertiliser type that may be beneficial to biodiversity, such as maintenance of non-crop habitats, and lack of pesticide use. Thus while I touch upon the differences between organic and conventional farming systems, I recognise the difficulty of distinguishing fertiliser type from these other management practices.

2.4. Effects on invertebrates of fertiliser use, vegetation changes, and changes to management practices

Invertebrates are a vital food source for farmland birds, particularly in summer, for both adults and chicks (Moreby, 2004). A review of indirect effects of pesticide use on birds considered that of 36 farmland bird species, only eight were not dependent on invertebrates at some point during the life cycle (Campbell et al., 1997). It has been suggested that farmland bird abundance may be linked to changes in farming practice at least partly via changes in insect abundance (Benton et al., 2002). Therefore, changes in the abundance and availability of invertebrates can have significant impacts on birds, especially during the breeding season.

Studies of long term trends in insect abundance are relatively few. However, the Rothamsted Insect Survey documented decreases in moth abundance and diversity between 1933-1950 and 1960-1989 (Woiwod and Thomas, 1993, in Sotherton and Self, 2000), and in Scotland, insect abundance has been monitored since 1972, showing non-linear trends over time (Benton et al., 2002). The Game Conservancy Trust's Sussex Study has found declines in invertebrate numbers in cereal fields since 1970 (Barker, 2004). Not all groups declined, but several groups that are important in chick diets showed declines, including Araneae (spiders), Lepidoptera (moths and

butterflies), Tenthredinidae (sawflies), Coleoptera (beetles) (excluding carabids and elaterids), Chrysomelidae (leaf beetles) and Curculionidae (weevils) (Barker, 2004). Such declines are consistent with changes due to agricultural intensification, and it is possible that increased fertiliser use has played a role, but the main path of research has been into the effects of pesticide use, which has been another major component of agricultural intensification (Campbell et al., 1997). The effects of increased fertiliser inputs on invertebrates are summarised in Table 2.3.

Invertebrate biomass increases in some cases where fertiliser is applied, especially manures and slurry. This is not unexpected, as increased fertiliser use increases primary productivity, and the nutritive value of foliage, and would be expected to increase the abundance of higher trophic levels. However, high levels of fertiliser application are associated with changes in vegetation structure and with management practices that can reduce invertebrate species richness, average body size and even overall biomass, as described below. Compositional shift of invertebrate communities may also occur in response to fertiliser applications, as the plant biomass becomes concentrated in the foliage rather than below-ground.

2.4.1. Direct effects

Invertebrates may be directly affected by the application of fertilisers. Earthworms are especially responsive to fertiliser, and may be killed by large volumes of fresh slurry due to high ammonia and salt concentrations (Curry, 1976; Curry, 1994). Collembola (springtails) may also be killed by heavy applications of slurry (Curry, 1994). However, intermediate applications of fertiliser, especially organic fertiliser, may increase earthworm numbers and/or biomass. In South Wales grassland (some being rehabilitated from opencast mining, some undisturbed), while overall earthworm abundance was not affected by the application of either manure or inorganic NPK fertiliser, surface activity increased in response to manure and decreased in response

Table 2.3. Effects of increased fertiliser application on invertebrates in farmland

Level of removal from fertiliser use	Mechanism	Group	Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Effects of fertiliser on invertebrates	Direct toxicity	earthworms	grassland	South Wales	application of poultry manure/inorganic fertiliser (approx. 100-150 kg/ha N)	no change in abundance; increase in surface activity with manure, decrease with inorganic fertiliser	reduction in one surface-active species under inorganic fertiliser, possibly due to soil salinity	1	Scullion and Ramshaw, 1987
		earthworms	grassland	Poland	NPK application (680 kg/ha)	decrease in biomass of earthworms	reduced soil moisture due to fertilisation	2	Nowak, 1976
		earthworms	grassland	Ireland	experimental applications of cattle slurry at various rates with varying reapplications	absent after application of highest levels, but return to pre-application abundance 14 months later, higher numbers and/or biomass at intermediate levels	toxicity (ammonia and salts) causes initial decline at high levels of application, increase in organic material increases abundance	1	Curry, 1976
Effects of fertiliser on vegetation	Nutritive value	lumbricid earthworms	arable	Bucks.	relationship to manure application	lumbricid numbers positively related to manure application	increased organic material	2	Tucker, 1992
		Collembola	grassland	Ireland	application of cattle slurry	reduction in abundance	toxicity (ammonia and salts)	1	Curry, 1994
		Auchenorrhyncha	grassland	Poland	mowing and fertiliser (NPK) application	initial decline, then increase in abundance; simpler community composition	nutritive value of regrowing grass; simplified vegetation structure following mowing	2	Andrzejewska, 1979
	Biomass	Tipulidae (Diptera)	grassland	western Scotland	abundance in relation to management	higher abundance where organic fertiliser applied; no effect of inorganic fertiliser	increased sward productivity and nutrient content	2	McCracken et al., 1995
		phytophagous insects	oat-grass meadow	Poland	application of fertiliser (N, P and K)	decline in soil larvae biomass; increase in numbers of insects emerging	reduction in root biomass and increase in turf biomass	2	Andrzejewska, 1976a
		Auchenorrhyncha	natural meadow	Berks.	experimental addition of nitrogen (100-1200 kg/ha) alone and with other fertiliser	increase in abundance, decrease in diversity (but not total species richness)	improved food quality and more beneficial sward architecture	1	Prestidge, 1982
		Auchenorrhyncha	oat-grass meadow	Poland	application of fertiliser (N, P and K)	increase in biomass, change to community structure	increase in green plant biomass	2	Andrzejewska, 1976b
soil dwelling larvae	grassland	Poland	NPK application (680 kg/ha)	decrease in soil-dwelling phytophagous insect larvae	reduced root biomass	2	Nowak, 1976		
all insects	grassland	Poland	abundance in fertilised and unfertilised plots	general increase in biomass of insects	increased primary production	2	Olechowicz, 1976		

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Table 2.3. (cont.) Effects of increased fertiliser application on invertebrates in farmland

Level of removal from fertiliser use	Mechanism	Group	Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Effects of fertiliser on vegetation	Plant species richness	Lepidoptera; Araneae; Carabidae; Staphylinidae (Lepidoptera)	arable field margins	Cambs. and Hants.	relationship between abundance and species richness in plots sown with diverse seed mixtures	Correlation (+) between species richness and abundance of carabids and butterflies only	requirements of butterflies and carabids for particular host plants	2	Kirkham et al., 1999
		Auchenorrhyncha; Heteroptera; Coleoptera; Araneae	arable field margins	Hants.	relationship between abundance of 3 species and habitat variables	positive effects of shelter and abundance of flowers, including bramble and thistle	importance of stable microclimate; availability of nectar resources	2	Dover, 1996
			arable	western England	abundance and diversity in relation to plant species richness	Correlation (+) between plant species richness and abundance of Heteroptera, Auchenorrhyncha, and Araneae, (and diversity of phytophagous Coleoptera)	more opportunities for specialist species	2	Asteraki et al., 2004
		surface invertebrates	grassland	Hants.	experimental applications of fertiliser (N, P, K and lime) separately or in combination plus different mowing regimes	lower species richness in mown and in fertilised plots; higher proportion of phytophages and lower proportion of predators/parasitoids	increase in food for phytophages in fertilised plots; homogeneous habitat structure in mowed plots	1	Fenner and Palmer, 1998
Effects of management associated with fertiliser use	Sward structure	Lepidoptera	subalpine meadows	Switzerland	gradient in management intensity (grazing and fertiliser inputs)	high species richness in lightly grazed, unfertilised, and newly abandoned meadows; very low in intensively managed meadows	related to plant species richness and specialisation of Lepidoptera fauna	3	Erhardt, 1985
		Orthoptera	grassland	Netherlands	species richness and abundance in plots to which different levels of inorganic nitrogenous fertiliser were applied (none, 50 kg/ha/year, 155-400 kg/ha/year)	low species richness and abundance at high levels of fertiliser (compared to both none and low levels); species composition explained by temperature, vegetation biomass, light extinction and management intensity	unsuitable habitat created by dense swards	1	van Wingerden et al., 1992
		sward invertebrates (various groups)	grassland	Ireland	various management systems (grazing and cutting)	most similar invertebrate composition where management was most similar in terms of sward height	adaptation of invertebrate fauna to short swards (eurytopy, mobility, short life cycle, high reproductive rate)	2	Curry and O'Neill, 1979

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Table 2.3. (cont.) Effects of increased fertiliser application on invertebrates in farmland

Level of removal from fertiliser use	Mechanism	Group	Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference	
Effects of management associated with fertiliser use	Sward age	Auchenorrhyncha; Heteroptera; Coleoptera; Hymenoptera	grassland	Germany	species richness and abundance in fields of different grazing intensity or time since grazing	higher abundance in long-term ungrazed grassland than grazed pastures (regardless of grazing intensity)	greater primary productivity and habitat complexity in ungrazed grasslands	2	Kruess and Tschamtké, 2002	
		lumbricid earthworms; Coleoptera arthropods	grassland	Bucks.	Relationship with sward age	positive relationship	lack of physical disruption in old grass fields; positive effects of organic manure	2	Tucker, 1992	
	Intense grazing and/or frequent mowing			grassland	Netherlands	total and mean individual biomass in relation to nitrogen applications (0, 50 and 400 kg N/ha/year) in grazed and mown plots	total and mean individual biomass decreased with increasing fertiliser use in mown plots; relatively little change in grazed plots (some evidence of an increase in mean individual biomass)	life history characteristics of large arthropods; compensatory effects of dung in grazed grasslands	2	Siepel, 1990
			large insects	grassland	Netherlands	abundance in fertilised, mown and grazed pastures	reduced abundance in more intensively managed pastures	inability to complete life cycle	2	Beintema et al., 1990
			phytophagous insects	calcareous grassland	Germany	abundance in relation to experimental mowing and grazing	various effects on different species, depending on life history	direct removal, ability to recolonise site, microclimate changes	1	Volkl et al., 1993
			Auchenorrhyncha; Heteroptera	chalk grassland	Beds.	Abundance in relation to cutting and grazing regimes	decline in abundance when cut in July; less so in May	ability to complete life cycle	2	Morris and Lakhani, 1979
			Carabidae (Coleoptera)	lowland farmland	Dumfries	cutting and grazing regimes of various intensity compared with one unmanaged grassland plot	larger average bodyweight of carabids in unmanaged grassland	presence of species in unmanaged grassland due to ability to complete life cycle	2	Blake et al., 1996
			Carabidae (Coleoptera)	upland grassland	northern Britain	relationship between management intensity (including fertiliser application) and body size	body size decreased with increasing management intensity	requirement of large species for longer periods without disturbance	2	Blake and Foster, 1998
	Auchenorrhyncha; Heteroptera; Coleoptera; Hymenoptera	grassland	Germany	species richness and abundance in fields of different grazing intensity or time since grazing	lower species richness in intensively grazed pasture than extensively grazed or ungrazed pasture	disruption of insects feeding by grazing cattle	2	Kruess and Tschamtké, 2002		
	Curculionidae (Coleoptera)	chalk grassland	Beds.	Abundance of two species in response to grazing exclusion	increase in both species	increase in flowers and fruit of larval food plants	2	Morris, 1967		

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Table 2.3. (cont.) Effects of increased fertiliser application on invertebrates in farmland

Level of removal from fertiliser use	Mechanism	Group	Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Effects of management associated with fertiliser use	Plant species composition and vegetation structure	Heteroptera; herbivorous Coleoptera	grassland	Oxon.	Controlled grazing (none, short-period spring, short-period autumn, spring and autumn, and heavy autumn), samples taken in August over two years	composition determined by grazing effects on plant species richness; abundance lower under most grazing treatments in one year, but less clear results in other year	specialist feeders requiring plants dependent on particular grazing regimes	1	Gibson et al., 1992
		Gracillariidae (Lepidoptera); Araneae; Auchenorrhyncha	grassland	Oxon.	Controlled grazing (none, short-period spring, short-period autumn, spring and autumn, and heavy autumn), samples taken in August over two years (Gracillariidae in one year only)	composition determined by sward structure; abundance severely reduced under all grazing treatments for spiders and Gracillariidae, and Auchenorrhyncha in one year only	structural requirements for phytophages and predators	1	Gibson et al., 1992
		Carabidae (Coleoptera)	grassland	Dumfries	experimental cutting regimes (uncut, one cut per year, three cuts per year)	lower diversity in cut plots, but no change in abundance (possible function of sample method)	habitat requirements of various species; increased activity in cut plots due to lower prey density	1	Haysom et al., 2004
	Tipulidae (Diptera)	grassland	western Scotland	abundance in relation to habitat characteristics	higher abundance of larvae in single-cut silage fields compared with uncut or multiple cut	life cycle characteristics of tipulids	2	McCracken et al., 1995	
	Microclimate	Orthoptera	grassland	Netherlands	species richness and abundance in plots to which different levels of inorganic nitrogenous fertiliser have been applied (none, 50 kg/ha/year or 155-400 kg/ha/year)	reduced species richness and abundance at high levels of fertiliser (compared to none and low levels); species composition explained by temperature, vegetation biomass, light extinction and management intensity	inability of slow developing species to complete life cycle at cool ground temperatures created by dense sward	1	van Wingerden et al., 1992
		Carabidae (Coleoptera); Araneae	arable	Switzerland	abundance in paired farms using organic and low-input Integrated Crop Management (including inorganic fertilisers)	higher abundance of spiders and carabids (including large bodied species sensitive to agricultural intensification) in organic fields	proximity of semi-natural habitats on organic farms; microclimate of denser crops on non-organic farms; increased prey abundance	3	Pfiffner and Luka, 2003

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Table 2.3. (cont.) Effects of increased fertiliser application on invertebrates in farmland

Level of removal from fertiliser use	Mechanism	Group	Habitat	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Effects of management associated with fertiliser use	Landscape context	Pergidae (Hymenoptera)	lowland farmland	southern England	abundance in grass and cereal crops; performance of larvae on various host plants; effect of cultivation on over-winter survival	abundance higher in grass fields; larvae grew better on <i>Lolium perenne</i> than cereal crops; reduced over-winter survival in cultivated fields	loss of grassland in arable landscapes	2	Barker et al., 1999
		Carabidae (Coleoptera)	arable	Germany	relationship with non-arable landscape features	increased species richness and abundance (independent of farm management)	exchange of species that use multiple habitats during life cycle; increased species pool	3	Purtauf et al., 2005
		Araneae	arable	Germany	abundance and species richness in organic and conventional farms; also related to landscape features	higher abundance on organic farms; species richness positively related to non-arable landscape features	more prey due to organic applications, crop rotations and lack of pesticide use; ability to recolonise from non-arable features	2	Schmidt et al., 2005
	Organic vs conventional farming	earthworms	arable	Canada	abundance and diversity in plots treated with inorganic fertiliser or manure over 14 years	higher abundance and diversity in manure-treated plots compared to both untreated plots and plots treated with inorganic fertiliser	increased organic material in the soil	1	Estevez et al., 1996
		Auchenorrhyncha; Heteroptera; Coleoptera; Araneae nocturnal insects	arable	western England	abundance in organic and conventionally-managed plots	higher abundance except for larval Coleoptera	more diverse plant community	2	Asteraki et al., 2004
		Araneae	Mixed and pastoral farms arable	England and Wales	abundance and species richness on organic compared to paired conventional farms	both measures higher on organic farms	variety of factors associated with organic farms, including diversity of habitats, and lack of pesticide and herbicide use	2	Wickramasinghe et al., 2004
		Araneae	arable	western England	abundance and species richness in organic and conventional farms; relationship with understorey vegetation within crop	increased abundance in organic farms; abundance and species richness positively related to understorey density in both farming types	web building opportunities and presence of prey items; effects of organic management practices	2	Feber et al., 1998
earthworms, Coleoptera, Araneae	arable	Switzerland	comparison of abundance between organic and non-organic farming systems over a 21 year study	higher abundance of all groups in organic systems	more diverse plant community	2	Mäder et al., 2002		

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to NPK fertiliser (Scullion and Ramshaw, 1987). This is thought to be due to a decrease in one species, *Aporrectodea caliginosa*, considered responsible for the majority of surface casting, possibly due to soil salinity. Other groups may also be directly affected by osmotic salt effects following fertiliser application, especially if dry conditions follow application. This was suggested as the cause for reduced numbers of Collembola and Acari (ticks and mites) in treated cereal fields in Sweden in the first year of application (Andren and Lagerlof, 1983). However, numbers of these groups were either higher in fertilised fields, or showed no difference, the following year, when weather conditions were more amenable. Soil desiccation associated with increased plant growth in response to fertilisation has also been suggested as a cause of the negative response of earthworms to inorganic fertilisers (Nowak, 1976).

2.4.2. Changes to plant species composition, vegetation structure and nutritive value

2.4.2.1. Responses to plant species richness

Invertebrate groups may have higher diversity and/or abundance in more diverse plant communities, probably because of increased opportunities for specialist species (Curry, 1994; Atkinson et al., 2004). For example, in field margins of southern England, butterfly and predatory beetle species richness and abundance were positively correlated with plant species richness (Kirkham et al., 1999).

Auchenorrhyncha (leafhoppers, etc.), Heteroptera (true bugs) and Araneae abundance, and phytophagous Coleoptera diversity, were positively correlated with plant species richness in field margins in western England (Asteraki et al., 2004). In subalpine Swiss meadows, Lepidoptera species richness showed a strong association with plant species richness, and both increased along a decreasing gradient of fertilisation, from early abandoned meadow towards intensively grazed meadows (Erhardt, 1985). The replacement of flower-rich, perennial field boundaries with pernicious annual weed species, has been suggested as a possible cause for the decline of some satyrid butterfly species (Dover, 1996). However, the link between plant and invertebrate species richness is not universal, or may be negative. In lowland grassland in Hampshire, mowing maintained plant species richness, but the presence of taller plants in relatively species-poor unmowed and fertilised plots supported more species

of invertebrates (Fenner and Palmer, 1998). In German lowland grassland, plant species richness did not differ between intensively and extensively grazed pasture, but insect species richness was higher on extensively grazed pastures (Kruess and Tschardtke, 2002).

2.4.2.2. Responses to increased sward height and density

Sward architecture may affect invertebrates more than species composition (Southwood et al., 1979; Curry, 1994). Sward height rather than floristic composition influenced the invertebrate fauna in Irish grasslands, with similar treatments (in terms of effect on sward) having more similar invertebrate fauna; eurytopic, mobile species with short life cycles and high reproductive rates were favoured by high grazing and mowing regimes (Curry and O'Neill, 1979). Sward structure appears to have been important in determining the composition of the invertebrate fauna of experimental plots in grassland in Hampshire (Fenner and Palmer, 1998). Phytophagous invertebrates formed a greater (and predators and parasitoids a lesser) proportion of the fauna in mowed and fertilised plots. The lack of predators and parasitoids in response to sward structure in mowed plots would have increased the percentage of phytophages, while increased plant biomass in fertilised plots would have benefited phytophages, again increasing their relative component of the fauna, even though absolute abundance of predators and parasitoids may have been higher in these plots. In dry grasslands in the Netherlands, high levels of fertiliser application decreased the species richness and abundance of Orthoptera (grasshoppers and crickets), with the change partly attributed to increased sward density (van Wingerden et al., 1992). Slow developing species may be unable to complete their life cycle in the cooler ground conditions created by dense swards. Grasshoppers require low vegetation in spring and autumn, to increase egg development rate, but more vegetation in summer, to increase survival of nymph and imago stages (van Wingerden et al., 1992). The fast growth of grass in response to fertilisers may not provide these. Auchenorrhyncha are also sensitive to changes in sward structure (Curry, 1994).

2.4.2.3. Responses to changes to host plant abundance/biomass

Invertebrates may benefit from increased biomass of host plants in response to fertiliser additions. Auchenorrhyncha abundance increased in response to experimental nitrogen additions to lowland grassland in Berkshire, due to increased

food quality and availability of living area, although diversity decreased and species composition changed (Prestidge, 1982). The study site was not subject to the management regimes that are usually in place on improved grassland: cutting, grazing or both. Similar results were recorded in Polish meadows, where emergent Auchenorrhyncha biomass was higher in fertilised plots; this was ascribed to an increase in green plant biomass (Andrzejewska, 1976b). Community composition changed, with species typical of simplified habitats more abundant in fertilised plots. Saprophagous Diptera abundance was also greater in fertilised fields, because the greater primary productivity was translated into decomposing material in the absence of grazing or cutting (Olechowicz, 1976). In Dutch hay meadow of differing ages post-fertiliser treatment (7, 11, 24 and 29 years), Diptera, Araneae, Hymenoptera and Coleoptera, were more abundant in more recently fertilised plots (Hemerik and Brussaard, 2002). Abundance and diversity of isopods, centipedes and millipedes increased over the sequence of plots, except that the least recently fertilised plot had the lowest abundance and diversity of almost all groups, which may reflect long term oligotrophication (Berg and Hemerik, 2004).

Fertiliser use may not benefit all invertebrate groups, as the increase in plant biomass is concentrated in the above-ground parts of the plant. In a Polish meadow, addition of mineral fertiliser (nitrogenous, phosphatic and potassic) led to a decrease in root biomass, and a corresponding decrease in the biomass of soil invertebrates (Coleoptera larvae and Lepidoptera larvae) (Andrzejewska, 1976a). Abundances of some other groups (Orthoptera, Auchenorrhyncha, Aphididae [aphids] and above-ground Lepidoptera larvae) were not greatly different between fertilised and unfertilised plots, but many more insects emerged from unfertilised plots. Also in Poland, soil-dwelling phytophagous insect larvae decreased in numbers in a fertilised meadow compared to a control, which also had higher root biomass (Nowak, 1976). Conversely, increased nitrogen input to semi-improved grassland in Scotland led to higher biomass of soil microarthropods (Acari [mites] and Collembola) (Cole et al., 2005).

Species that are host-plant specific will obviously be affected if these host plant species increase or reduce in abundance due to changes associated with fertiliser input and management practices (Curry, 1994). This has been observed in Swiss meadows

(di Giulio et al, 2001). In the absence of grazing, two species of seed weevil increased in abundance on chalk grassland in Britain, in response to increased abundance of their larval food plants, *Lotus corniculatus* and *Campanula rotundifolia* (Morris, 1967).

2.4.2.4. Responses to changes in nitrogen content of vegetation

Invertebrate populations may also be directly affected by the available nitrogen in host plants (Curry, 1994). Phytophages are likely to be favoured by the increased foliar nitrogen content of the vegetation. In fertilised grasslands in Poland, Auchenorrhyncha were more abundant post-cutting (after an initial decline), due to the higher nutritive value of the regrowing grass, although the community composition differed greatly from that of semi-natural grasslands (Andrzejewska, 1979). Invertebrate phytophages supplied with nitrogen-rich food had shorter larval development, larger body size, and increased fecundity. Root-feeding tipulid (crane fly) and bibionid (march fly) larvae both increased in grassland where organic fertilisers were applied, probably due to increased sward productivity and nutrient content (D'Arcy-Burt and Blackshaw, 1991; McCracken et al., 1995). Inorganic fertiliser application appears to have no effect on tipulid larvae abundance (Linzell and Madge, 1986; McCracken et al., 1995; Paoletti, 1999). Emergent diptera larvae biomass was higher in heavily fertilised Polish meadow plots (Olechowicz, 1976), as was that of Apterygota from the same plots, although Acari declined considerably (Zyromska-Rudzka, 1976).

2.4.3. Changes to mowing/grazing regime

Increased productivity associated with fertilisers may not increase invertebrate biomass, or may vary in its effects between groups, because much of the primary production is removed from the site through grazing or cutting. There can be benefits of both grazing and cutting to biodiversity. Regrowth of grazed or cut plants provides young and nutrient-rich plant tissue, while selective grazing will lead to structural heterogeneity. Grazing and mowing may help to maintain floral diversity. However, intense grazing or frequent cutting of grasslands dominated by few plant species has very different effects. One of the major effects of fertiliser use on management

practices is the trend towards higher stocking rates, the preponderance of ensilage, and more frequent and earlier cutting of silage fields. The effects of grazing and cutting on invertebrates include direct physical disturbance, such as defoliation and trampling. Both reduce the size and complexity of the habitat that is available to invertebrates in grassland, and also the plant biomass, and tend to lower insect biomass as well (Curry, 1994). Increased stocking rates may compact soil and reduce availability of soil invertebrates, as well as altering their populations (McCracken and Tallowin, 2004; Tallowin et al., 2005). In the long term, grazing and cutting regimes may alter the plant species composition of pastures, which can have additional effects on vegetation structure.

Mowing is similar to grazing in that defoliation alters the above-ground biomass, but it is non-selective and therefore does not result in sward heterogeneity. It also does not result in trampling or compaction, processes that may be beneficial for some aspects of invertebrate life histories, such as Orthoptera oviposition (Curry, 1994). There may be a temporary flush of invertebrates following cutting, but the frequent and early cutting of silage fields leads to a general reduction in organic matter and hence soil invertebrate biomass (Vickery *et al.* 2001). Silage fields are also often heavy rolled early in the season, which leads to a marked decline in leatherjacket numbers (Clements and Cook, 1996). Improved fields are also likely to be reseeded more frequently, and therefore are younger on average than unimproved fields (Hopkins et al., 1985; Tallowin et al., 2005). Lumbricid earthworm and adult Coleoptera numbers both showed positive relationships with grass age in southern England farms (Tucker, 1992), while in German lowland grasslands, abundance of insects was greater in long-term ungrazed grassland than grazed pastures, probably due to increased resource productivity and habitat complexity (Kruess and Tschardtke, 2002). It can be difficult to distinguish the contribution of the various components of agricultural intensification, especially when studies use a gradient of management intensity. For example, in subalpine Swiss meadows Lepidoptera species richness decreased with management intensity in the form of grazing and fertiliser inputs (Erhardt, 1985). Ultimately both are associated with increased use of fertilisers, but the mechanisms driving the changes in Lepidoptera are not certain.

2.4.3.1. Direct destruction and removal

Mowing and grazing can have a direct effect on invertebrates, by killing them or removing them from the site. The life history characteristics of the invertebrates play an important role determining the impact. Species reliant on the aerial structures of plants are the most likely to be affected (Morris, 1967). In calcareous semi-natural grassland in Germany, univoltine phytophagous insect species developing in knapweed (*Centaurea scabiosa*) seed heads, which grow 80 cm tall, were effectively removed by mowing (Volkl et al., 1993). By contrast, bivoltine insects, and species dependent on dwarf thistle (*Cirsium acaule*) seed heads, which only grow 10 cm tall, were not directly affected by mowing or grazing. In German lowland grassland, differences in insect species richness could not be attributed to floristic or vegetation changes, and it was suggested that cattle grazing affected trophic interactions by disturbing insects feeding on pasture (Kruess and Tschardtke, 2002). Long-term (more than five years) ungrazed grassland did show differences in sward height (but not species richness) that could explain the greater abundance of insects on such grasslands compared with grazed pastures.

Increased rates of cutting, or higher stocking rates, increase the possibility that even invertebrates reliant on relatively small grassland plants will be unable to complete their life cycle. Larger species, with longer life cycles, are more sensitive to mowing and intensive grazing, and are therefore replaced by smaller species (Siepel, 1990). Large insects are less abundant in intensively managed grasslands, with high inputs of fertilisers (Beintema et al., 1990; Blake et al., 1994; Blake et al., 1996). In northern Britain, carabid beetles on intensively managed grassland (judged by sward age, fertiliser application, grazing and cutting) were on average only 40% as heavy as those under the least intensive management (Blake and Foster, 1998). Large beetles generally breed in autumn and are flightless, and are therefore susceptible to the rapid removal of grass by intensive grazing or cutting (Kegel, 1990, in Blake and Foster, 1998), both of which are facilitated by the application of fertiliser. While abundances of almost all invertebrate groups were higher in a cut grass field in Berkshire, biomass was lower (Southwood and van Emden, 1967). However, some surface-layer invertebrates can recover quickly after an initial dramatic decline following cutting (Curry and Tuohy, 1978; O'Neill, 1991, in Curry, 1994).

In semi-natural grasslands in Bedfordshire, cutting in July consistently reduced the abundance of Auchenorrhyncha and Heteroptera (Morris and Lakhani, 1979), as it disrupted the development of species in which adults emerge in late summer. Not all species were equally affected, as some species are typical of short grass. Coleoptera in the same habitat were much less affected by cutting, probably because this group is less vertically stratified within the sward (Morris and Rispin, 1987). Disturbance by cutting, along with changes to sward structure, were more important than plant species composition in determining the abundance of Hemiptera in Swiss meadows (di Giulio et al., 2001). Even phytophagous species that might otherwise be expected to benefit from the applications of nitrogen to meadows can be negatively affected by disruptions to their life cycles (Wilson et al., 1999; di Giulio et al., 2001).

2.4.3.2. Changes to plant species richness and vegetation structure

Grazing tends to increase plant species richness while reducing structural diversity, and the responses of invertebrates to grazing depend on their biology. In Oxfordshire grassland, the assemblages of groups that include a high proportion of feeding specialists, such as Gracillariidae (leaf miners) and herbivorous Coleoptera, were strongly determined by the effects of grazing on plant species composition (Gibson et al., 1992). The community composition of Auchenorrhyncha, Heteroptera and Araneae, which require particular sward structures, were determined by structural measures related to grazing. Abundance of all groups was lower under at least one grazing treatment in at least one year (of two), but the effects were strongest for Araneae and Gracillariidae (which were only examined in one year) (Gibson et al., 1992). Arachnids are in decline in farmland, and are affected by the loss of diverse structure that results both from dense swards as a result of fertilisation, and intensive grazing and cutting regimes (Wilson et al., 1999).

The impact of cutting on epigeal invertebrates depends on the nature and timing of the cutting, and their own life history characteristics, and can be difficult to distinguish from the effects of destruction and disturbance described above. In grassland field margins in Dumfries, carabid diversity was higher in plots that were uncut than in those that were cut for silage (either once or three times per year) (Haysom et al., 2004). Abundance did not differ between the treatments, although this may reflect increased activity of predatory species in short grass where prey density was lower.

Silage cutting regime had a marked effect on tipulid larvae abundance in western Scottish pastures, with single-cut pastures supporting more larvae than either uncut or multiple-cut pastures (McCracken et al., 1995). This was explained with reference to the life cycle of the tipulid, as the presence of long grass during the egg laying period, and the lack of disturbance following the single cut favoured oviposition.

2.4.3.3. Microclimate changes

Mowing and grazing alter microclimate; short swards are less humid and experience more extreme day/night temperature differences. Populations of insect species not affected directly by grazing or mowing may increase or decrease in response to either depending on their response to microclimatic changes (Volkl et al., 1993).

Xerothermophilic bugs benefit from the warm, dry microclimate provided by heterogeneous vegetation in extensively-managed meadows, while the homogeneity introduced by heavy grazing or frequent cutting may be detrimental to these species (di Giulio et al., 2001). Grasshoppers are affected by microclimate changes in intensively managed grasslands, as the denser swards arising from grazing and/or cutting result in cooler temperatures that do not allow them to complete their life cycles (van Wingerden et al., 1992). Microclimatic effects due to denser vegetation on non-organic arable farms in Switzerland was proposed as an explanation for the reduced abundance of xerothermophilic carabid and lycosid beetles (Pfiffner and Luka, 2003). Microclimate was considered to affect tipulid larvae abundance in western Scottish pastures, with longer and denser swards supporting more larvae in winter (McCracken et al., 1995).

2.4.4. Loss of mixed farming systems and changes to traditional crop rotation

The polarisation of farming into arable and pastoral systems can have effects on invertebrate communities and abundances, although the effects are complex and may be difficult to distinguish. The loss of mixed farming landscapes in the UK has contributed to the decline of Coleoptera (Wilson et al., 1999). Pergidae (sawfly), the larvae of which are important food items for several declining farmland species, are also affected by the loss of mixed farming systems and the loss of traditional crop

rotation (Barker et al., 1999), although the reduction in under sowing has also affected this group, as the emerging larvae are destroyed by ploughing or have little food. In German arable farmland, spider species richness was higher where non-arable landscape features were present in the landscape (Schmidt et al., 2005), and a literature review found that spider abundance was increased by agricultural diversification in 63% of studies (Sunderland and Samu, 2000). All but one of 26 spider species in Germany were more abundant in perennial habitats (including fertilised hay meadows subject to mowing three times per year) than arable (Schmidt and Tschardt, 2005), suggesting that the presence of perennial habitats within the landscape could improve spider populations at the landscape scale. Parasitoid wasps, ladybirds and ground beetles also benefit from landscape diversification (Purtauf et al., 2005; Schmidt et al., 2005). The increase in carabid species richness and abundance in mixed landscapes was independent of any effect of organic against conventional farming in at least one study (Purtauf et al., 2005). This effect was pronounced for spring breeders, which migrate into the fields from surrounding hibernation sites, and the exchange of species that use multiple habitats during their life cycle is suggested as one cause for the increased carabid species richness in diverse landscapes (Purtauf et al., 2005). Winter tillage means that only arthropods that can tolerate winter cultivation, or those that can escape to neighbouring areas to overwinter (opportunities for which are less in the absence of mixed farming systems), can persist (Holland, 2004).

2.4.5. Organic vs non-organic farming methods

Organic and inorganic fertilisers may have similar effects in terms of nutrient enrichment, but organic fertilisers provide food for decomposing elements of the invertebrate community, and the effects on invertebrates are more frequently beneficial (Vickery et al., 2001). Earthworms generally benefit from moderate levels of mineral fertilisers in grassland, but at high levels numbers can be depressed (Edwards and Lofty, 1975; Nowak, 1976; Edwards, 1983; Curry, 1994). Where organic fertiliser is applied, there is a shift in composition (Edwards and Lofty, 1982; Curry, 1994), and effects on behaviour. Application of organic manure grassland encouraged earthworm casting and burrowing to the surface, while inorganic fertiliser

discouraged these activities (Scullion and Ramshaw, 1987). Adverse chemical conditions in the soil may offset the increased food supply associated with inorganic fertiliser application, while organic applications contribute both directly and indirectly to earthworms' food supply. Most studies have compared organic and non-organic systems, but a study in Canada found that long-term (14 years) manure application improved soil earthworm populations and density compared to both untreated plots and plots treated with inorganic fertiliser (Estevez et al., 1996).

Organic arable farms in Germany had higher spider density, which could not be entirely ascribed to lack of insecticide use (Schmidt et al., 2005), and may also be due to greater abundance of saprophagous insects, especially Collembola and midges (Diptera) in regimes that use crop rotations and organic fertilisers. Spreading organic manure had positive effects on the abundance and diversity of carabid faunas of arable land (Hance and Gregoire-Wibo, 1987). In Switzerland, a long term comparison of organic and conventional farming found higher biomass and abundance of earthworms, and abundance of carabids, staphylinids and spiders in organic plots (Mäder et al., 2002). In western England, invertebrate abundance (except for larval Coleoptera) was higher in organically managed field margin plots than in conventionally-managed ones (Asteraki et al., 2004). In paired farms in southern England and Wales, nocturnal insect abundance and species richness were significantly higher on organic than conventionally-managed farms (Wickramasinghe et al., 2004).

The relatively beneficial nature of organic compared with conventional farming is not universal. Farm management was of relatively little importance in explaining species composition of carabids and butterflies in Swedish farms, compared with habitat type and surrounding landscape features (Weibull and Östman, 2003). A meta-analysis of the effects of organic agriculture on biodiversity found that predatory insects and soil earthworms generally responded well to organic farming systems, but that non-predatory insects did not (Bengtsson et al., 2005). At any rate, the benefits of organic farming for invertebrates may arise from characteristics of organic farming such as lack of pesticide and herbicide use and greater landscape and structural diversity (Pfiffner and Luka, 2003; Wickramasinghe et al., 2004). Despite this, I feel that it is reasonable to conclude that the use of organic fertilisers in moderate quantities is

likely to be more beneficial to the abundance of a range of invertebrates than either inorganic fertilisers or no application.

2.4.6. Summary

Few invertebrates suffer direct mortality from the application of fertilisers, although some soil invertebrates, notably earthworms, are sensitive to heavy applications. Many phytophagous insects are favoured by the increased growth and nutritive value of fertilised crops, although diversity may be reduced if plant species required by specialist invertebrates are lost. The denser growth of fertilised crops may have effects on invertebrates that require bare ground or particular sward structure. Intense grazing and frequent cutting directly disturb and remove invertebrates, and the resulting sward structure disadvantages a wide range of species. Reduced abundance and/or diversity of phytophagous invertebrates can have effects on higher trophic levels. Changes to sward structure probably have the most significant effects on most invertebrate groups, and the role that fertiliser applications ultimately plays in determining sward structure is greatest in grassland in the United Kingdom. Table 4 summarises the responses of some important invertebrate groups to fertiliser applications.

Table 2.4. Summary of effects of fertiliser application on invertebrate groups

Group	Effects
Earthworms (Lumbricidae)	high levels of organic and inorganic fertilisers toxic, but positive long-term response to organic fertiliser
Spiders (Araneae)	favoured by processes that increase prey abundance, but affected by intensive management that reduces the suitability of sward architecture
Moths and butterflies (Lepidoptera)	abundance and species richness reduced by loss of host plants and changes to microclimate
Beetles (Coleoptera)	specialist species disadvantaged by loss of host plants; some large species unable to complete life cycle under intensive management
Craneflies (Tipulidae: Diptera)	favoured by increased organic content and nutritive value of sward (following application of organic fertiliser); sensitive to cutting regime
Leafhoppers etc. (Auchenorrhyncha)	favoured by increased nutritive value and primary productivity, but specialists disadvantaged by loss of plant species; removed by intensive management
True bugs (Heteroptera)	favoured by increased nutritive value and primary productivity, but specialists disadvantaged by loss of plant species; removed by intensive management
Grasshoppers and crickets (Orthoptera)	unsuitable habitat caused by growth of dense grass sward; inability to complete life cycle due to cutting regime and microclimate

2.5 Evidence for indirect effects of increased fertiliser use on birds

Some bird species can be categorised in terms of the evidence for their responses to the indirect effects of fertilisers. In this section I provide details of ways in which the processes described above can have impacts on bird populations in the UK. More detail is supplied on some bird species under the different mechanisms. This is done when (a) I consider that among the various ways in which fertiliser applications may affect the population of this species, this mechanism is the most important, and (b) I consider that this species provides a good example of the ways in which this mechanism can affect birds, and which thus may be applicable to species with similar requirements. However, this does not mean that this is the only way in which increased fertiliser applications can affect populations of this species, and in particular I stress that (unless otherwise stated) this does not necessarily mean that the effects of increased fertiliser applications are the major factor affecting the populations of these species. The evidence for indirect effects of increased fertiliser use on birds is presented in Table 2.5.

2.5.1. Increased nutrient content of grass (wintering waterfowl)

The most direct relationship between fertiliser use and bird populations concerns wintering waterfowl, particularly geese, which graze on grass. As this topic is thoroughly reviewed elsewhere (Vickery and Gill, 1999), I present only a brief summary. Wintering waterfowl are important from a conservation point of view, but are also on the increase, to the extent that they have become agricultural pests. A major management issue is how to draw them away from agricultural crops, and one means of doing this is to add fertiliser to grass, as it improves the nutritional value and increases foraging by wintering geese (Vickery and Gill, 1999). Geese also show a preference for short grass swards, as these have a higher nitrogen content than long swards, although this can be counteracted by the addition of fertiliser (Hassall et al., 2001). Grazing and cutting regimes are employed to maintain short swards for goose grazing in parts of Britain (Vickery and Gill, 1999). The management of grasslands for wildfowl grazing may lead to some of the indirect effects on birds described

below, and as such illustrate potential conflicts conservation efforts. This is not the forum to discuss those conflicts, and I simply point out that application of fertiliser and intensive sward management are generally beneficial to wintering geese in the United Kingdom.

2.5.2. Changes to abundance/availability of epigeal invertebrates

A review of the indirect effects of pesticides concluded that over three quarters of farmland bird species examined were partly or wholly reliant on invertebrate food at some point in their life cycles (Campbell et al., 1997). Increased plant growth in response to fertiliser applications can increase the abundance of invertebrates, provided the crop is not removed by cutting for silage or by grazing. For common invertebrate feeders in grassland, there is evidence that nitrogen inputs and grazing pressure are beneficial in winter, and in summer there is a generally negative relationship with sward height (Atkinson et al., 2004). The reasons for this may be increased availability of food, even if at lower abundances, and better detection of predators (Butler and Gillings, 2004; Whittingham and Evans, 2004). Corvids such as magpie, carrion crow and rook are common in grazed fields, probably in response to invertebrate availability as well as abundance due to the presence of dung (Tucker, 1992). However, foliar invertebrates, which are particularly important to several passerine species as food for nestlings, are less abundant in more intensively managed grassland, and this is probably an important mechanism in the decline of these passerines (Atkinson et al., 2004). In Scotland, farmland bird numbers were positively related to insect abundance, often that of the previous year, suggesting that arthropod availability may influence bird populations via breeding success or over-winter survival (Benton et al., 2002).

Species such as yellow wagtail that feed largely on invertebrates (Nelson et al., 2003), may have been affected by reduced prey abundance under management regimes such as silage production, which reduces their abundance. This species establishes territories within fields with sparser vegetation and more bare ground (Bradbury and Bradter, 2004). Other species that feed chicks on invertebrates, may have reduced

Table 2.5. Indirect effects of fertiliser in birds in farmland habitats.

Habitat	Species	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
lowland farmland	farmland birds	USA	comparison of organic and non-organic farms	higher abundance and species richness of birds on organic farms; no species more abundant on non-organic farms	foraging opportunities due to more uncropped habitat	2	Beecher et al., 2002
	farmland birds	England and Wales	changes in abundance and occurrence in 10 km squares between late 1960s and early 1990s	local extinction more likely in grassland-dominated landscapes for seven species, even where population changes were lowest	unsuitability of lowland grassland for several species requiring elements of arable farms	2	Chamberlain and Fuller, 2001
	farmland birds	England and Wales	abundance of birds on paired organic and conventional farms in spring/summer, autumn and winter over three years	8 out of 18 species more abundant in organic farm field boundaries in at least one season/year; breeding skylark more abundant on organic fields in one year	provision of non-crop habitat; crop rotations associated with organic farming	2	Chamberlain et al., 1999
	farmland birds	Bucks.	winter occurrence of birds in fields in relation to habitat and management variables	in grass fields, three species positively related to inorganic fertiliser application and four positively related to frequency of manure application; in cultivated fields, two species positively related to frequency of manure application; various other relationships, including some positive and some negative with grazing	abundance of invertebrate food items, notably lumbricid earthworms and adult Coleoptera	2	Tucker, 1992
	turtle dove	England	radio tracking and examination of diet	increase in proportion of wheat and rape seed from 1960s	loss of weed seeds due to agricultural intensification	3	Browne and Aebischer, 2003
	turtle dove	England	examination of nest records	no decline in success of individual attempts; possibly fewer nest attempts	loss of weed seeds due to agricultural intensification	3	Browne et al., 2005
	skylark	southern England	relationships between distribution/breeding success and habitat variables/management	density higher in organic fields and set aside than intensively managed fields; no nesting in fast-growing broad-leaved crops; predation the main cause of nest failures, but nests also destroyed by silage cutting and trampling	insufficient time to nest in fast growing crops; loss of mixed farming systems to provide variety of field types for multiple nesting	2	Wilson et al., 1997

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 2.5. (cont.) Indirect effects of fertiliser in birds in farmland habitats.

Habitat	Species	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
lowland farmland	lapwing	England and Wales	reduction in mixed farming	reduced foraging efficiency	change in management	3	Sheldon et al., 2004
	starling	Oxon.	field foraging preferences	preference for short sward	increased visibility of prey and potential predators, easier soil probing	2	Whitehead et al., 1995
	tree sparrow	central England	loss of winter seed resources, and lack of invertebrate food resources during breeding season	reduced breeding success and winter survival	loss of mixed farming landscapes	3	Field and Anderson, 2004
	yellowhammer	Oxon. and Lincs.	foraging patch selection in relation to habitat variables in cereal crops	patches used for foraging had sparser vegetation, and more invertebrates	increased abundance and accessibility of food	2	Morris et al., 2002
	yellowhammer	southern England	foraging patch selection in grass margins related to habitat variables	margins with sparse sward selected	increased abundance and accessibility of food	2	Perkins et al., 2002
	farmland birds	Devon and Bucks.	relationship between bird occurrence and management intensity (defined by nitrogen inputs), sward structure, and seed and invertebrate food resources	higher occupancy of intensively managed fields in winter by species feeding on soil invertebrates; many species avoided fields with tall swards in summer	increased abundance and accessibility of food	3	Atkinson et al., 2005
	farmland birds	western England	summer occurrence in relation to grazing and sward height	various responses, but generally decreased frequency with higher sward height	availability of food items	2	Buckingham et al., 2004
	farmland birds	southern England	winter occurrence of birds in fields in relation to habitat and management variables	various relationships including positive between thrush occurrence and bare earth	greater prey availability	2	Perkins et al., 2000
	corn bunting	Sussex	nest success in relation to habitat variables and invertebrate prey abundance	negative correlation between invertebrate prey abundance and nest survival	increased predation risk due to adults spending longer away from the nest; lack of invertebrate food due to agricultural intensification	3	Brickle et al., 2000
	yellowhammer and reed bunting (winter)	western England	winter abundance in experimental plots (treatment = grass left to go to seed); grazed or ungrazed	strong preference for plots with grass left to set seed, and for ungrazed plots left to set seed over grazed	preferences for tall swards and high seed density	1	Buckingham and Peach, in press
	yellow wagtail	East Anglia	breeding territories in relation to habitat variables	territories associated with fields with short, sparse swards and high proportion of bare earth; nests associated with taller swards within same field	abundance/accessibility of invertebrate prey; need for heterogeneous grass sward	2	Bradbury and Bradter, 2004

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 2.5. (cont.) Indirect effects of fertiliser in birds in farmland habitats.

Habitat	Species	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
lowland farmland	chough	Calf of Man	historical population trends in relation to sheep and rabbit numbers	inverse relationship with sheep; positive relationship with rabbits in winter, positive with and nitrogen inputs but negative with sward height; in summer, negative with sward height	rabbit grazing is important in the creation of suitable habitat	2	McCanch, 2000
	starling	western England	relationships between occurrence and management	positive relationship with rabbits in winter, positive with and nitrogen inputs but negative with sward height; in summer, negative with sward height	increased productivity in response to nutrients; food availability	2	Fuller et al., 2003
	breeding waders	Netherlands	historic increases in nitrogen fertiliser application (1920-1975)	earlier breeding	earlier food availability and/or selection of earlier nesters through later nest losses	2	Beintema et al., 1985
upland farmland	lapwing chicks and starling	Scotland	sward height	increased foraging success	increased prey detection, improved mobility, predator detection	2	Devereux et al., 2004
	five passerine species (whinchat, tree pipit, yellowhammer, skylark and red-backed shrike)	Switzerland	relationships between abundance and land use and farming intensity	all except skylark were more abundant in less intensively farmed landscapes; foraging effort for red-backed shrikes feeding young was higher in more intensively farmed landscapes	various effects of intensive farming, including nest/brood destruction of ground nesting whinchat, use of arable land (related to farming intensity) by skylark, reduced abundance of insect prey for red-backed shrike	2	Schifferli et al., 1999
	whinchat	Switzerland	fledging success in intensively and traditionally managed grassland	higher fledging success in traditionally managed grassland	lower abundance of large invertebrates	2	Britschgi et al., 2006
	red-backed shrike	Austria	relationships between abundance and habitat variables	abundance most closely related to a mixture of grazed grassland and scrub	accessibility of insect prey; nest and perch sites in scrub	2	Vanhinsbergh and Evans, 2002
	lapwing	Peeblesshire	relationship between field occupancy and land-use; changes over time	declines in numbers over time; preference for nesting on unimproved grassland and arable land over improved grassland	loss of suitable nesting habitat due to grassland improvement (strongly linked to drainage)	2	Taylor and Grant, 2004
	lapwing	northern Britain	relationship between occurrence and sward height	preference for short sward	increased foraging efficiency and predator detection	2	O'Brien, 2002
	waders	northern England	abundance in improved and unimproved fields	significantly higher abundances of snipe, redshank, curlew and lapwing in unimproved fields	changes in plant communities and loss of heterogeneous swards in improved fields; also drainage and associated loss of invertebrates	2	Baines, 1988
kestrel	Wales	population related to increased historical stocking rates	10% decline 1968-72 to 1988-91	loss of vole prey due to heavy grazing pressure and loss of mixed farming systems	3	Shrubbs et al., 1997	

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

breeding success when they are less abundant. Corn bunting nest survival in west Sussex was negatively correlated with abundance of chick-food invertebrates close to the nest, apparently due to increased predation rates as the parents spent longer away from the nest (Brickle et al., 2000). Availability of invertebrates may be more important than abundance, as both yellowhammer and skylark have been found to forage more in areas of fields (margins and tramlines) where vegetation is shorter and sparser (Odderskaer et al., 1997; Wilson, 2001; Morris et al., 2002; Perkins et al., 2002). Yellow wagtail Orthoptera, Hymenoptera and Arachnida, and at a higher level of classification, Araneae, Acrididae (grasshoppers) and Symphyta (sawflies) were considered important components in the diet of a significantly higher proportion of declining than non-declining farmland birds in northern Europe (Wilson et al., 1999). Large invertebrates appear to suffer disproportionately in intensively managed and heavily fertilised farmland (Beintema et al., 1990; Blake and Foster, 1998); this has been implicated in the disappearance of stonechat from Dutch grasslands (Siepel, 1990). The evidence presented above suggests that each of these groups is disadvantaged by some mechanism associated with increased use of fertilisers.

2.5.2.1. Cirl bunting

The cirl bunting is a red-listed species, having suffered a major population decline and range contraction during the twentieth century (Evans, 1997b). In summer, chick survival is much higher later in the season, concomitant with an increase in the amount of Orthoptera in the chick diet (Evans et al., 1997). Cirl bunting have been affected indirectly by fertiliser applications in two ways. First in the loss of Orthopteran prey in summer. Grasshoppers like a mosaic of long and short grass, and nitrogenous fertilisers lead to uniform, species-poor swards that reduce Orthoptera numbers (van Wingerden et al., 1992), as do high stocking densities (van Wingerden et al., 1991). Cirl bunting select semi-improved grassland for breeding territories to increase food items for chicks (Stevens et al., 2002). Second, there has been a decline in the extent of winter stubbles as a result of winter sown cereals and the loss of arable habitats within grassland-dominated landscapes. Low intensity mixed farming provides adequate winter stubble, and rough grass that harbours invertebrates in summer (Evans 1997b; Peach et al., 2001). While there are other causes for the decline of cirl bunting (e.g. more efficient harvest leaving less seed over winter, removal of hedges), there is strong circumstantial evidence that nitrogenous fertilisers

have affected nest productivity and over-winter survival. This evidence is strengthened by the fact that the implementation of recovery programs, including rough grass field margins, has seen a recovery in the ciril bunting population (Peach et al., 2001).

2.5.2.2. Red-backed shrike

Large insects, especially Coleoptera and Orthoptera, make up the major part of the red-backed shrike's diet (van Nieuwenhuysse et al., 1999). The decline of large insects, which are more sensitive to intensive management (Siepel, 1990; Blake et al., 1996), in response to inorganic fertiliser applications is suggested as the major cause of the decline of this species in Europe (van Nieuwenhuysse et al., 1999). The use of pesticides reduces the number of insects, but Orthoptera are notably sensitive to fertiliser application (van Wingerden et al., 1992). In Europe, red-backed shrike abundance was higher in low intensity upland farming areas (Schifferli et al., 1999). Ground hunting on freshly-cut meadows and aerial hunting on taller grassland were important foraging techniques, and foraging distance from the nest was higher in more intensive farmland (Schifferli et al., 1999). Grazed grassland (with some scrubland for nest and perch sites) provided better habitat than ungrazed grassland in Austria (Vanhinsbergh and Evans, 2002). In France, reproductive success was higher on unimproved pasture than on meadows or fallow land; fertilised grass becomes too dense for soil surface invertebrates, and so prey items become less abundant and less available (Lefranc, 1997). This species appears to be disadvantaged by the reduction of low intensity pastoral agriculture (Bignal and McCracken, 1996), in which low or moderate grazing pressure provides a patchy sward which facilitates foraging (Vanhinsbergh and Evans, 2002), and moderate inputs of manure have a positive or neutral effect on insect prey abundance.

2.5.2.3. Skylark

The skylark is an example of a species disadvantaged by changes in crop structure due to agricultural intensification (Donald et al., 2002; Donald and Morris, 2005). In arable farmland, crops now grow too tall and dense too early in the breeding season, and this restricts both nesting opportunities and availability of invertebrates due to the lack of bare ground (Donald and Morris, 2005). The provision of undrilled patches within arable fields improved skylark productivity, and this is thought to relate to

increased accessibility of prey items, rather than increased abundance (Morris et al., 2004). Elsewhere skylark foraged in tramlines and experimentally unsown plots in barley fields more than in the main crop, even though arthropod abundance was greater in the main crop (Odderskaer et al., 1997). The major cause of the structural changes is the switch to autumn-sown cereals, and although increased fertiliser use may contribute to the denser and taller growth, it is probably a relatively minor component. However, changes in grassland crop structure and management resulting from increased fertiliser use are implicated in the decline of skylark in this important breeding habitat. Nest survival in southern England was much lower in grassland than in arable, and the cause of nest failure differed, being mostly predation in arable land, but trampling and agricultural operations in grassland (Donald et al., 2002). Destruction of nests by silage production is thought to be a major factor in the decline of skylark in lowland Britain (Donald and Morris, 2005).

2.5.3. Changes to abundance/availability of soil dwelling invertebrates

Increased application of fertiliser to farmland may increase the biomass of soil invertebrates, while at the same time reducing their availability due to the increased density of the vegetation in spring. This is especially noticeable in grassland, but it can also happen in arable land, although there the major driving force has been the development of winter-sown cereals. Drainage is probably the major cause of reduced accessibility to soil invertebrates, but fertiliser application can also reduce soil penetrability in grasslands due to denser grass swards, and the desiccating effects in increased plant growth (Nowak, 1976). Earthworms, which form the major part of many bird species' diets, are sensitive to heavy applications of inorganic fertilisers in the short term (Curry, 1994). Earthworms and tipulid larvae (another important bird food item) generally benefit from the application of organic fertilisers, and the latter seem to be unaffected by inorganic fertilisers (McCracken et al., 1995). Their availability to birds may be affected by the presence of a dense and/or tall grass sward, but in grasslands in the Netherlands black-tailed godwit and lapwing abundance increased in response to management (including organic fertiliser) that increased earthworm biomass (Brandsma, 2004).

Grazing can be beneficial to bird species such as chough, starling, and lapwing, by providing access to soil invertebrates, and by increasing the numbers of dung-dwelling invertebrates (Vickery et al., 2001). Mowing to simulate grazing has been used to create appropriate winter feeding habitat in lowland grassland (Milsom et al., 1998). It has been suggested that increased access to earthworms determines the selection of short grass in grazed meadows by nocturnal foraging woodcock (Duriez et al., 2005). Foraging behaviour also reflects predation risk and this may explain preferences for short grass swards in species such as lapwing and starling (Devereux et al., 2004).

2.5.3.1. Starling

In grassland, starling show a strong preference for short grass swards (Whitehead et al., 1995; Devereux et al., 2004). Tipulid larvae are a major prey item for this species, and this may be the reason for the preference for short swards. Tipulids are relatively unaffected by grassland improvement, and starlings are common in improved pasture (Crick et al., 2002). However, the spread of silage production may have affected starling numbers negatively; silage fields are cut frequently, reducing organic matter and invertebrate biomass, and are rolled early in the season, which reduces tipulid numbers (Clements and Cook, 1996). The major cause of starling decline may be the use of insecticides and antihelminthics, but fertiliser application via the shift to silage production is likely to have negative effects.

2.5.3.2. Chough

In the United Kingdom chough are confined to western coasts and cliffs, where they display a complicated relationship with grassland management. Choughs feed predominantly on surface-active soil (and dung-associated) invertebrates, and rely on appropriate vegetation structure to find their prey (McCracken and Bignal, 1994). They therefore also rely on management regimes that maintain suitable vegetation structure, particularly extensive grazing. On Islay, chough forage preferentially in pastures in which tall swards grow in autumn, encouraging high numbers of tipulid larvae, but which are heavily grazed by stock or geese in winter and spring, allowing access to these prey items (Bignal and McCracken, 1996). In north Wales, foraging choughs selected short swards and minor habitats with elements of bare earth (Johnstone et al., 2002). On the Calf of Man, chough abundance was significantly

related to both sheep and rabbit numbers for the period 1969-1994, and a model combining density of both herbivores explained considerably more of the variation in chough breeding success than models containing a single herbivore as a predictor variable (McCanch, 2000). The complete cessation of grazing in parts of Britain coincided with declines in chough populations (Bullock et al., 1983), and is likely to be detrimental where it occurs (Johnstone et al., 2002). However, earlier and denser spring growth in improved pastures, and the prevalence of multiple-cut silage, are likely to reduce abundance and availability of prey items for chough. Given the relationships that this species shows with grassland vegetation structure and grazing regime, it seems highly likely that increased fertiliser use, and the changes in management associated with it, have contributed to the decline of chough, although not in isolation from other elements of agricultural intensification.

2.5.3.3. Breeding waders

Changes associated with agricultural intensification have seen significant reductions in many wader species (Smith, 1983; Wilson et al., 2005). Waders rely on farmland for both breeding and foraging habitat, and both of these are affected by increased fertiliser use. In upland England, abundances of snipe, redshank, lapwing and curlew were significantly lower in improved than unimproved grassland (Baines, 1988). Nidifugous wader chicks rely heavily on carabids at the earliest stages of their lives, and the shift in body size in carabids in intensively managed grasslands may affect their energy budgets (Beintema et al., 1990; Blake and Foster, 1998). Indeed, the energy budgets of self-feeding chicks may become impossible in improved grasslands, where large invertebrates are lost (Siepel, 1990; Beintema, 1991). Changes to grassland structure may also affect the ability of wader chicks to feed. Black-tailed godwit chicks feed predominantly on invertebrates from relatively tall vegetation, including many flying insects (Beintema, 1991). Faster growth promoted by fertilisers may increase the abundance of such species, but intense grazing on improved pastures will be detrimental, and the use of much grassland for silage will affect the abundance of invertebrates in the sward.

Historical changes to earlier breeding (as measured by ringing dates of chicks) by waders in Dutch meadows have been positively related to historical inputs of nitrogen in fertilisers, which in turn allow earlier grass cutting and cattle grazing (Beintema et

al., 1985). Two mechanisms are suggested: earlier availability of food resources; and selection against later nests, which was observed to be the case in one spring season (Beintema and Müskens, 1987). Both mechanisms have potentially negative effects: earlier laying in response to food availability may lead to unfavourable conditions at the chick stage; while selection for earlier nests at the chick stage may lead to unfavourable conditions at the laying stage (Beintema et al., 1985). For example, nest predation on snipe in lowland grassland was higher early in the breeding season (Green, 1988).

Beintema et al. (1997) stated that changes in wet grassland bird species composition in the Netherlands follow a pattern in response to fertiliser input. Increases in fertiliser use initially make meadows suitable habitat for a given species, probably by an increase in food resources. Increases in fertiliser may improve habitat for the species up to a point, but earlier mowing dates and increased stocking may affect reproductive output. Finally, intensive management reaches a point at which the species cannot reproduce sufficiently to replace its population, and the population declines. In the Netherlands, and in parts of Britain, dairy farming developed on wet soils, unsuitable for crops. Wet conditions cause slow annual development of the sward and therefore grazing and mowing is late, even where the soil is fertile. But fertilisers (and drainage) allow early mowing and grazing, affecting nesting success. Although there is evidence of increased chick mortality in the Netherlands, due to changes in invertebrate community composition (Siepel, 1990; Beintema, 1991), Beintema et al. (1997) suggested that a major cause of decline is egg destruction from increased stock rates.

Breeding waders in Britain have different habitat requirements, and will be affected differently by changes caused indirectly by increased fertiliser inputs. Snipe feed largely on earthworms, insect larvae and snails, by probing in soil and mud, and the use of feeding sites is affected by the density of prey items and the force required to probe the soil (Green et al., 1990). The female incubates alone, and therefore relies on suitable foraging habitat near the nest. The length of the breeding season is affected by the soil penetrability (Green, 1988), and the breeding season of snipe in the Netherlands was truncated between the 1940s and 1980s, which has been ascribed to agricultural improvement (Beintema et al., 1997). Snipe leave their breeding areas

when soil penetrability becomes too low (Düttmann and Emmerling, 2001, in Plum, 2005). In English wet grassland, nest failure was high (mostly due to predation and trampling), but the number of chicks hatched per female was also determined by the duration of the breeding season, which was related to soil penetrability (Green, 1988). Water levels are the main determinant of soil penetrability, and drainage of wet grassland is probably the major cause of the decline of snipe (Wilson et al., 2004) and drainage has consequences for breeding waders generally (Ausden et al., 2003). However, increased sward density early in the breeding season as a result of the application of fertilisers, also decrease prey accessibility, increased growth contributes to soil desiccation.

2.5.4. Changes to abundance and availability of plant food resources

Seed food is an important food resource for many species, especially granivorous passerines, and especially over winter. Most declining farmland bird species in lowland Britain are granivorous during winter, and over-winter survival is considered a key driver of the declines (Buckingham and Peach, in press). Changes to management associated with increased fertiliser use contribute to the reduction of seed resources, although there are other factors, particularly the use of herbicides, that may be more important. Higher seed abundance in stubble fields was associated with greater occupancy by linnet, corn bunting, grey partridge, reed bunting, yellowhammer and chaffinch (Moorcroft et al., 2002). However, seed density is not the only factor affecting winter foraging by birds in farmland. There were few associations between bird occurrence and food abundance (seeds and invertebrates) in Devon and Buckinghamshire grasslands (Atkinson et al., 2004). Seed availability and vegetation structure (and its effects on foraging behaviour) may be as important as seed abundance (Butler et al., 2005; Wilson et al., 2005).

The loss of winter seed food due to the loss of stubbles has been associated with the declines in many farmland birds in the UK (Chamberlain et al., 2000). While I consider that the loss of winter stubbles, through increased winter sowing and the loss of mixed farming landscapes, is likely to have had the greatest effect on farmland bird populations via this pathway, there are mechanisms by which increased fertiliser

application can contribute. Within grassland, cutting for silage prevents seed being set, which could provide a valuable food source for winter granivorous birds (Buckingham and Peach, in press). Reduced botanical diversity associated with increased fertilisation may reduce seed availability for species such as linnet and turtle dove (Vickery et al., 2001). However, there were no significant differences in the proportions of declining farmland bird species for which any plant taxon was considered present or important in the diet (Wilson et al., 1999).

2.5.4.1. Turtle dove

Turtle dove have declined in the UK by 77% between 1970 and 2001 (Eaton et al., 2004), with decreases in range and abundance most notable in grassland-dominated landscapes (Chamberlain and Fuller, 2001). This species is entirely granivorous, and was recorded feeding primarily at 'man-made sites' (spilt grain, grain stores, etc.) (Browne and Aebischer, 2003). Wheat and rape seeds have grown as a component of the diet, from 5% in the 1960s, when weed seeds comprised 90% of the diet, to 61%. Reduced weed abundance, to which application of fertiliser contributes, is suggested as a major cause of the decline of turtle dove (Browne and Aebischer, 2003). There has also been a loss of preferred feeding sites such as hayfields and clover leys, the former through the switch to silage production and the latter through the use of inorganic fertilisers in place of crop rotation. The loss of food resources might be expected to affect breeding. However, there has been no decline in individual nest success, and if breeding productivity is the cause of the decline, then it must be due to a reduction in the number of nest attempts, which has indeed been documented (Browne et al., 2005).

2.5.4.2. Granivorous passerines

There is a group of seed-eating passerines that are in decline in the UK, including reed bunting, yellowhammer, linnet and corn bunting (Eaton et al., 2005). In experimental plots on grassland, yellowhammer and reed bunting showed a strong preference in winter for grass that had been left to go to seed instead of being cut for a third silage crop (Buckingham and Peach, in press). Of plots left to go to seed, they preferred ungrazed plots. Many granivorous passerines also take invertebrate food in the breeding season, especially when feeding chicks, and those that do are more likely to

be in decline. The decline in chick food (notably sawfly larvae) has been implicated in reduced productivity in corn bunting (Barker, 2004).

2.5.5. Reduced breeding success due to increased grazing/cutting intensity or denser spring vegetation

Nest predation may increase in homogeneous landscapes, although there are tradeoffs between detection and concealment (Whittingham and Evans, 2004). Agricultural intensification increases homogeneity at several scales (Benton et al., 2003; Wilson et al., 2005). Nest predation and trampling has been found to be a major cause of nest failure in several ground nesting species, including skylark in southern England (Wilson et al., 1997), snipe on wet grassland in southern England (Green, 1988), and curlew in Northern Ireland (Grant et al., 1999). Complete absence of grazing can lead to a deterioration of habitat for grassland birds by allowing grass to grow too tall or dense (Laiolo et al., 2004), and fertiliser application has a similar effect in both arable land and pasture by increasing crop growth in spring. Concealing vegetation may increase predation risk of adult birds from predators that use olfactory detection and hinder anti-predator behaviour (Wilson et al., 2005). Several ground nesting birds, such as lapwing and skylark select short swards, which improves foraging and predator detection (Wilson et al., 1997; O'Brien, 2002). However, the uniform sward structure associated with heavy grazing may increase the detection of nests by predators; corvids, common nest predators, may increase in response to greater availability of invertebrates in short swards (Vickery et al., 2001). Magpie and crow occurrences in winter have both shown positive relationships to application of inorganic fertiliser (Tucker, 1992). Increased grazing density may also affect nesting success of birds that require different vegetation structure for nesting. Redshank in salt marshes in the Wash were more abundant where moderate grazing created variable sward density, while intensive sheep grazing created uniform swards unsuitable for nesting (Norris et al., 1997; Norris et al., 1998). Increased grazing also increases the rate of nest destruction through trampling, although the type of stock and the timing of grazing will determine the magnitude of the effect.

2.5.5.1. Lapwing

The lapwing population has been in steep decline since the 1980s in all areas, but particularly in lowland farmland (Wilson et al., 2001; Chamberlain and Crick, 2003; Sheldon et al., 2004). The causes of the decline are complex, but have been attributed mainly to reduced productivity (Galbraith, 1988; Baines, 1990). Preferred nesting habitat is arable land (particularly spring-sown crops) and unimproved grassland (Galbraith, 1989; Wilson et al., 2001; Taylor and Grant, 2004). Lapwings have suffered from loss of nesting habitat due to changes in vegetation structure and in landscape-level changes to land use. The increased spring height and density of winter crops or the enhanced growth of improved grassland is detrimental, as nesting lapwings depend on short swards (O'Connor and Shrubbs, 1986; Shrubbs and Lack, 1991; Hudson et al., 1994; O'Brien, 2002). Foraging chicks also prefer short grass, probably because it facilitates prey detection, improves mobility and increases foraging time by altering vigilance patterns (Devereux et al., 2004). However, lapwings avoid silage grass, and they may have been forced into nesting in less suitable habitat by its spread (Shrubbs, 1990). Arable nesting habitat is more suitable when it is close to pasture, where the chicks are taken to forage (Galbraith, 1988), and thus this species suffers from the polarisation of landscapes into arable or grassland (Wilson et al., 2001; Sheldon et al., 2004).

Lapwings suffer from nest failure via several routes indirectly related to fertiliser application. Grazing is beneficial, as it reduces the sward height, although the type of grazing is important; lapwings are more associated with horses or sheep than cattle (Shrubbs and Lack, 1991). However, nest trampling due to increased stocking density, has been suggested as a major cause of nest failures (Shrubbs, 1990). Nest failure due to predation was higher in Britain in the 1990s than in the three preceding decades, and was the greatest cause of nest failure in that decade in arable and mixed farmland (but not in pasture) (Chamberlain and Crick, 2003). Lapwing breeding success was lower on improved than unimproved pasture in northern England, and the reduced breeding success was largely accounted for by increased predation (Baines, 1989; Baines, 1990). On a coastal grazing marsh, grazing intensity was associated with increased predation risk, possibly because disturbance of incubating birds left nests unattended for longer (Hart et al., 2002). Corvids and foxes are suggested as major predators of lapwing nests in the UK, although fox predation was considered

‘incidental’ in a study in North Yorkshire (Seymour et al., 2003), and predation pressure may relate to cycles of alternative prey (Beintema and Müskens, 1987). Predation of first broods may be a more serious problem due to the loss of suitable nesting habitat later in the season, again as a result of taller and denser vegetation. The indirect effects of increased fertiliser application have contributed to lapwing decline in the UK via pathways associated with productivity.

2.5.6. Nest/brood destruction due to changes in grass cutting regime

Mowing is a destructive event, which often takes place over a large area in a short space of time. Birds nesting at the time when silage is cut will have their nests destroyed (Wilson et al., 1997). Silage is cut earlier and more frequently than hay, leading to more nest and chick destruction (Beintema and Müskens, 1987). Nest destruction by cutting for silage may have contributed to the decline of yellow wagtail in British upland grassland (Nelson et al., 2003). For this species and others with similar breeding and food preferences, silage cutting not only destroys nests, but also reduces availability of foliar invertebrates, which would be expected to reduce productivity. Some wader species require tussocky areas for nest concealment while breeding, but may avoid uniform dense swards, such as those present in areas of silage production (Vickery et al., 2001).

2.5.6.1. Whinchat

Whinchats have virtually disappeared from Swiss lowland farmland, suffering from high brood losses in intensively managed grassland, as the mowing interval is shorter than the period between nesting and fledging (Schifferli et al., 1999). Between 1988 and 2002, meadow cultivation changed markedly, with the onset of mowing brought forward by around 20 days and pastures cut for silage replacing hay meadows (Müller et al., 2005). Mowing date strongly predicted the proportion of successful broods, and in some areas breeding success was too low to compensate for mortality. In addition to nest destruction, whinchat have suffered from a decline in arthropod abundance, particularly of large insects, in intensively managed subalpine meadows in Switzerland (Britschgi et al., 2006). Fledging success was lower in these intensively managed meadows, which were mostly silage fields, than in traditionally managed

hay meadows, which were cut less frequently and later in the season. Whinchat began to decline in lowland Britain in the first half of the twentieth century, and it is now considered a bird typical of upland areas (Mead, 2000). It has also disappeared from lowland Europe in the past half century (Müller et al., 2005). Whinchats, along with other ground nesting birds, have declined at sites in British pastoral uplands in more recent years, concomitant with improvement of most sites (Henderson et al., 2004). The decline of this species in lowland Britain has probably been at least partly caused by the indirect effects of fertiliser application, specifically improvement and earlier cutting of grasslands, and it may undergo further declines in upland areas.

2.5.6.2. Corncrake

As early as the 1940s, more rapid and earlier grass cutting as a result of mechanisation were proposed as the causes of historical population declines of the corncrake (Norris, 1945; Norris, 1947). In the second half of the twentieth century the introduction of new varieties of grass and the increased use of fertilisers has advanced cutting dates for hay and silage (Green, 1995). This has been compounded by an increase in the proportion of land allocated to silage, which may be cut multiple times in a summer. A study of site occupancy found that corncrakes continued to occupy sites with a greater area of hay meadow, and where silage was not the dominant method of grass management (Stowe et al., 1993). Corncrake population density was positively related to the area of tall marshland vegetation in spring, and to area of grass taller than 20 cm in summer, but only where the mean date of mowing was in late July (Green, 1996). The mechanism behind the decrease in corncrake populations is increased nest and brood destruction during grass cutting (Green and Stowe, 1993). In the absence of mowing clutch and brood survival are high (Green et al., 1997), and the decline of corncrakes has been reversed by a series of corncrake-friendly measures, including a delay in mowing (Aebischer et al., 2000). Other changes associated with agricultural intensification but independent of increased fertiliser use, notably mechanisation, have been involved in the decline of corncrake. However, enhanced grass growth in response to increased fertiliser use has led to increased nest and chick destruction. And increased land used for silage production, which is economically viable when grass yield is high in response to fertiliser applications, has led to habitat loss. There remains the possibility that conditions on the wintering and staging grounds may also

affect corncrake numbers (Green and Gibbons, 2000), but there is very strong evidence for the causal role of indirect effects of increased fertiliser use on corncrake.

2.5.7. Changes to landscape configuration

Reduced habitat heterogeneity on the landscape, between-field and within-field scale has been suggested as a major consequence of agricultural intensification and a major cause of the decline of farmland birds (Benton et al., 2003). Many ground nesters require a combination of longer swards for nesting and short swards for foraging. Intensive management of farmland leads to a homogenous sward, which may be either taller and denser than previously (in early spring due to increased growth) or shorter than previously (after cutting or heavy grazing). In arable fields, fertiliser application encourages a dense crop structure, and modern varieties respond vigorously to fertilisers (Stoate et al., 2001). This can reduce the suitability of the field for both nesting and foraging. For example, lapwings prefer spring cereals for nesting, but rear their chicks on grassland, and thus require the juxtaposition of these habitats (Galbraith, 1988). Increased rates of local extinction of seven red- or amber-listed bird species in grassland-dominated landscapes suggests that lowland grassland is suboptimal habitat for birds, and the loss of arable components has had a negative impact on farmland birds of conservation concern (Chamberlain and Fuller, 2001).

The polarisation of pastoral and arable farming, and the loss of crop rotations, which have occurred as farmers have been able to rely on inorganic fertilisers, have led to a reduction in mixed agriculture in Britain (Evans, 1997a). Mixed farming landscapes are likely to provide the greatest diversity and abundance of seed foods in intensive farming landscapes, as some plant species require cultivation and others thrive in fertilised grasslands and field margins (Wilson et al., 1999). Mixed farming habitats can be especially important to birds in winter. Some species that are insectivorous in the breeding season, and therefore utilise pastoral systems, switch to seed over winter, and utilise arable landscapes (Atkinson et al., 2002). Included in this group are stonechat, starling, pied wagtail and meadow pipit. Thus the shift in landscapes may have contributed to the decline of farmland bird species in Britain. The effect is difficult to quantify, and as a driver of this process, inorganic fertiliser use probably

only applies to loss of pasture (with livestock to provide organic manure) in arable landscapes, and not the loss of arable land in pastoral landscapes. Mixed farms tend to use less intensive management practices and maintain uncropped habitats such as hedgerows, and this may also play a role in determining the distribution of birds in British farmland (Atkinson et al., 2002). The loss of mixed farming systems, and the variety of habitats, has been suggested as contributing to the decline of skylark (Wilson et al., 1997) and starling (Whitehead, 1994, in Anderson et al., 2001). Swallows in arable landscapes are thought to have suffered from a loss of pasture, as many of the insects they feed on rely on animal dung (Evans, 2001, in Anderson et al., 2001).

2.5.8. Organic versus conventional farming

The results of studies presented above suggest that organic fertilisers are more likely to be beneficial to invertebrates that are important food items of birds than are inorganic fertilisers (Vickery et al., 2001; Wickramasinghe et al., 2004). There is some evidence that bird populations on organic farms are higher than those on conventional farms, although the differences are not necessarily consistent between years and seasons (Chamberlain et al., 1999; Bengtsson et al., 2005). Skylark density in southern England was higher in organically-cropped fields (and set-aside) than in intensively cropped fields or grazed pasture (Wilson et al., 1997). On maize farms in the USA, bird abundance was higher on organic fields than paired conventional farms, and organic farms held more species (Beecher et al., 2002). No species (of 54) was more abundant on non-organic farms. The differences between organic and conventional farms include the use of fertilisers and herbicides, the nature of cultivation, and crop rotations, and all of these may contribute to organic farms supporting more birds. Physical management of farms, and the provision of non-crop vegetation on organic farms, may be more important in determining the abundance of birds than the type of fertiliser used (Chamberlain et al., 1999; Beecher et al., 2002).

Nevertheless, the positive response of earthworms in particular to moderate applications of farmyard manure should provide increased food resources for birds. In southern England, the distribution of four species (lapwing, starling, fieldfare and

redwing) in grass fields in winter was positively related to the frequency of application of farmyard manure (Tucker, 1992). Lapwing and black-headed gull showed similar relationships in cultivated fields. The frequency of occurrence of three species (starling, magpie and crow) was higher where inorganic fertiliser was applied. Starling and magpie both feed on tipulid larvae, which are not adversely affected by inorganic fertilisers.

2.5.9. Summary

A list of farmland bird species for which I consider use of fertilisers to have indirectly contributed to the decline is shown in Table 2.6. Birds may be affected by more than one process associated with fertiliser use, and the proximate causes of decline may be at more than one remove from the ultimate cause. In addition, more than one component of agricultural intensification can have the same ultimate effect on birds. The negative effects of increased inputs of fertiliser are most apparent in pastoral landscapes. This is because fertiliser use has driven agricultural intensification in this habitat, whereas the changes in arable farmland have been more strongly affected by shifts to winter-sown cereals. Fertiliser use has contributed to the magnitude of these changes, by increasing growth rates and crop yield, but changes of this nature would likely have happened anyway. However, I feel that there is strong evidence for fertiliser use as one driver of decline of farmland birds in the United Kingdom.

Table 2.6. Summary of suggested ways in which application of fertilisers has indirectly affected farmland birds in the United Kingdom

Species	listing	Mechanism by which fertiliser use may have indirectly affected bird species ¹							
		reduced abundance of epigeal/foiar invertebrates	reduced abundance/availability of soil invertebrates	reduced abundance availability of seed food resources	reduced sward suitability for nesting birds	nest trampling	nest destruction by cutting for silage	increased predation in homogeneous swards	loss of mixed farming landscapes
corncrake	red						P		
lapwing	amber	C+			P	C		C	C+
snipe	amber		C					C	
curlew	amber	C+						C	
redshank	amber	C+							
turtle dove	red			C					
skylark	red	P-		C-	P	C	C	C-	
barn swallow	amber								C
yellow wagtail	amber		C		C+		C		
whinchat	green	C+					C+		
red-backed shrike	red	C+							
chough	amber		C+						
starling	red		C+						C
tree sparrow	red	C		C-					
linnet	red			C-					
yellowhammer	red	C		C-					C
cirl bunting	red	P		C-					C+
reed bunting	red	C		C-					C
corn bunting	red	C		C-			C		C

¹ P = proven (e.g. by recovery or experimental study), P- = proven, but fertiliser use is secondary to other cause(s) of mechanism, C = correlation, C+ = strong correlation, C- = correlation, but fertiliser use is secondary to other cause(s) of mechanism

3. Aquatic habitats

3.1. Introduction

Increased nutrient supply to natural ecosystems has been recognised for many years as a major environmental problem in aquatic ecosystems. Much of the discussion of the issue has centred on the threat to the natural functioning of aquatic systems, and ways to prevent and mitigate this threat. However, while the effects on vegetation and some animal groups are relatively well known, the indirect effects on birds have not been addressed in a comprehensive way. This review attempts to collate evidence for such effects in the United Kingdom.

The term eutrophication was coined to refer to the elevated nutritional status of waters. The Environment Agency (2000) defined eutrophication as:

The enrichment of water by nutrients, stimulating an array of symptomatic changes including increased production of algae and/or higher plants, which can adversely affect the diversity of the biological system, the quality of the water and the uses to which the water may be put.

But the Urban Waste Water Directive, defines it as “the enrichment of water by nutrients, especially compounds of nitrogen and/or phosphorus, causing an accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present in the water and to the quality of the water concerned.” (European Union Directive 91/271/EEC on Urban Waste Water).

Both of these definitions indicate that eutrophication is usually considered in terms of its physical manifestation, rather than the actual levels of nutrients in the water and sediments. Waters have naturally different nutrient levels, due to geographical factors, and may undergo natural eutrophication. However, eutrophication as a result of human activities within catchments (known as cultural eutrophication) is the subject of this review.

The effects of nutrient increases on flora and fauna are documented in an enormous literature (eg Pearson and Rosenberg, 1978; Harper, 1992), and I consider that the case for extensive cultural eutrophication of aquatic habitats has been made forcefully by other authors. Some background information about the sources and transport of nutrients is included in Section One, but an effort to review all the literature on all plant and animal groups would be unwieldy and detract from the main purpose of this review; to assess the known and potential impacts on birds. Therefore, I include a limited number of examples of effects of eutrophication on habitat, flora and non-avian fauna, particularly where effects on birds have also been documented. Other aspects of human activity have also had major effects on the wetland habitats of the UK; land drainage is one example. This review restricts itself to the effects of nutrient inputs, and attempts to distinguish such effects from others that may be strongly associated.

3.2. Birds of aquatic habitats in the UK

The United Kingdom holds internationally important populations of waterfowl and waders, especially over winter (Kershaw and Cranswick, 2003; Rehfish et al., 2003; Collier et al., 2005). The combination of relatively mild climate and high tidal amplitude provide suitable foraging conditions in estuaries, while species such as waders and wildfowl also feed extensively inland. Wetland habitats in the UK are also important breeding habitats for many species; some species such as reed and sedge warblers migrate in spring and make use of reedbeds that cover large areas in parts of the country. The bird species considered for review, their conservation status, broad diets and use of aquatic habitats in the United Kingdom are summarised in Table 3.1. Some species that might be thought of as wetland species, such as swans and some waders, are not included, because in the UK they predominantly use non-aquatic habitats, notably wet grassland and upland moor, both of which are discussed in other sections of this review.

Table 3.1. List of bird species considered for review, conservation status, population trends, use of habitats, diet and migratory status.

Species ¹	Listing ²	Winter trend (long-term) ³	Winter trend (five-year) ⁴	Habitats ⁵ (breeding)	Habitats ⁵ (winter)	Diet ⁶	Migration ⁷
red-throated diver	amber			fl	cw	f	r + w
black-throated diver	amber			fl	cw	f	r + w
great northern diver	amber			fl	cw	f, db	w
Slavonian grebe	amber			fl	cw	f, db	r + w
black-necked grebe	amber			fl	e, fl	f, db	r + w
great-crested grebe	green	49	1	fl, r	fl, r	f	r
little grebe	green	42	4	fm, fl	fm, fl, e	f	r + w
cormorant	amber	67	3	fl, cw	fl, cw	f	r + w
bittern	red			rb	rb	f	r
grey heron	green			fl, rb, e	fl, rb, e	f	r
mute swan	amber	96	30	fl, fm	fl, fm, e	od	r
shelduck	amber	8	-59	e	e	bi	r + w
mallard	green	-32	-23	fl, fm	fl, fm, e	od	r
gadwall	amber	>1000	82	fl	fl	od	r + w
pintail	amber	80	-23	fl, fm	fl, fm, e	od	r + w
shoveler	amber	69	-5	fl, fm	fl, fm	od	r + w
wigeon	amber	53	17	fl	e, fl	od	r + w
teal	amber	148	6	fl, fm	e, cl, fl	od	r + w
garganey	amber	n/a	n/a	fm	n/a	od	s
pochard	amber	-13	-10	fl	fl, e	db, p	r + w
scaup	amber			n/a	e	db	w
tufted duck	green	36	15	n/a	fl	db	r + w
eider	amber			cw	e, cw	db	r + w
common scoter	red			fl	e, cw	db	r + w
velvet scoter	amber			n/a	cw	db	w
long-tailed duck	amber			n/a	cw	db	w
goldeneye	amber	86	-14	fl, r	fl, e	db	r + w
goosander	green	43	-20	fl, r	fl, e	f	r + w
red-breasted merganser	green	225	11	fl, cw	cw	f	r + w
water rail	amber			rb, fm	rb, fm	ai, f	r
spotted crane	amber			rb, fm	n/a	p, ai	s
moorhen	green			fl, r, fm	fl, r, fm	p, ai	r
coot	green	n/a	30	fl, fm	fl, fm	od	r + w
oystercatcher	amber	8	-15	e, cl	e, cl	bi	r + w

¹ a list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends of wintering waterfowl and waders in the UK over 25 years (or longest period for which data are available) (Eaton et al., 2005).

⁴ population trends of wintering waterfowl and waders in the UK 1998-2003 (Eaton et al., 2005).

⁵ use of aquatic habitats in the UK: b = beaches/shorelines, cl = coastal lagoons, cw = coastal waters, e = estuaries and tidal flats, fl = freshwater lakes, fm = freshwater marshes, r = rivers, rb = reedbed, sm = saltmarshes.

⁶ broad diets: ai = aquatic/foal/arerial invertebrates, bi = benthic invertebrates (by probing), db = benthic invertebrates (by diving), f = fish, o = omnivorous, od = omnivorous dabbling waterfowl, p = plant material.

⁷ migratory status in the UK (species may be included in more than one category due to partial migration): p = passage, r = resident, s = summer migrant, w = winter migrant.

Table 3.1. (cont.). List of bird species considered for review, conservation status, population trends, use of habitats, diet and migratory status.

Species ¹	Listing ²	Winter trend (long-term) ³	Winter trend (five-year) ⁴	Habitats ⁵ (breeding)	Habitats ⁵ (winter)	Diet ⁶	Migration ⁷
avocet	amber	>1000	354	e	fm, e, sl	bi	r + w
ringed plover	amber	-32	-26	cl, e, b	cl, e	bi	r + w
grey plover	amber	185	-4	n/a	e	bi	w + p
knot	amber	11	-3	n/a	e	bi	w
sanderling	green	7	21	n/a	e, b	bi	w
turnstone	amber	-17	-30	n/a	e	bi	w
dunlin	amber	-36	-23	e, cl, sm, fl	n/a	bi	r + w
green sandpiper	amber			n/a	e, fm	bi	s
common sandpiper	green			r, fl	fl, e	bi	s + w
redshank	amber	-2	-1	sm	e, sm, fm	bi	r + w
bar-tailed godwit	amber	5	-2	n/a	e	bi	w
black-tailed godwit	red	211	74	n/a	e	bi	w + p
curlew	amber	5	-17	sm	sm, e	bi	r + w
black-headed gull	amber			fm, e, sl	fm, e, sl	o	r + w
common gull	amber			fm, fl, cw	fl, cw	o	r + w
Mediterranean gull	amber			cl	cw	o	r + w
herring gull	amber			cw, b	cw, fl	o	r + w
lesser black-backed gull	amber			b	fl	o	r + w
great black-backed gull	green			cw, sm, fm	fl	o	r + w
kittiwake	amber			cw	n/a	f, bi	s
little tern	amber			b, fl	n/a	f	s
sandwich tern	amber			b	n/a	f	s
common tern	green			b, sm	n/a	f	s
black tern	green			fm, sm	n/a	f, ai	p
kingfisher	amber			r	r	f, ai	r
grasshopper warbler	red			fm, rb	n/a	ai	s
sedge warbler	green			fm, rb	n/a	ai	s
reed warbler	green			fm, rb	n/a	ai	s
aquatic warbler	red			fm, rb	n/a	ai	p
Cetti's warbler	green			fm, rb	fm, rb	ai	r
bearded tit	amber			rb	rb	ai	r
reed bunting	red			fm, rb	fm, rb	seeds, ai	r

¹ a list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends of wintering waterfowl and waders in the UK over 25 years (or longest period for which data are available) (Eaton et al., 2005).

⁴ population trends of wintering waterfowl and waders in the UK 1998-2003 (Eaton et al., 2005).

⁵ use of aquatic habitats in the UK: b = beaches/shorelines, cl = coastal lagoons, cw = coastal waters, e = estuaries and tidal flats, fl = freshwater lakes, fm = freshwater marshes, r = rivers, rb = reedbed, sm = saltmarshes.

⁶ broad diets: ai = aquatic/foliar/aerial invertebrates, bi = benthic invertebrates (by probing), db = benthic invertebrates (by diving), f = fish, o = omnivorous, od = omnivorous dabbling waterfowl, p = plant material.

⁷ migratory status in the UK (species may be included in more than one category due to partial migration): p = passage, r = resident, s = summer migrant, w = winter migrant.

While waterfowl, waders and other wetland species are the subject of several surveys intended to document changes in national populations (Mitchell et al., 2004; Collier et al., 2005), national measures of population changes are not necessarily the best way to document population changes resulting from anthropogenic nutrient inputs to aquatic habitats. These change are likely to operate on a much smaller scale than factors affecting global or British populations. So, although I include national population trends for those species where data are available, population changes in limited areas in response to measurable or observable changes in nutrient inputs and/or levels are a more appropriate way of examining the indirect effects of cultural eutrophication on birds. National trends and conservation status of species are more likely to be useful in determining the overall concern that might be felt about a species undergoing a population change in a specific location.

Ways in which changes to nutrient status might be expected to affect birds in aquatic habitats are largely through changes in food abundance and/or availability, although there could potentially be impacts on nesting resources. Increased primary productivity due to increased nutrient availability may increase the food resource for birds. However, changes to plant and animal community composition may positively or negatively affect food items of particular bird species. Extreme eutrophication can have massive effects on aquatic systems, which are also expressed in bird populations, as described below. There are several examples where nutrient inputs on a local scale have been reduced, and/or the physical state of eutrophication has disappeared. Thus this section of the review provides the opportunity to examine the effects of reduced as well as increased nutrient inputs, in some cases at the same site.

3.3. Effects of nutrient increases on vegetation

The most fundamental effect of increased nutrient availability is increased primary productivity. Increases in nutrient availability also change the competitive environment for the vegetation, and lead to changes in species composition. Nutrient status is a major determinant of the type of vegetation found at any site even in the absence of human influence. For example, nutrient requirements of constituent species play a large part in distinguishing the plant assemblages of British standing

waters (Palmer et al., 1992). Cultural eutrophication acts in addition to natural spatial and temporal variation in nutrient levels. While impacts of nutrient increases are habitat-specific, the general trend is a shift away from macrophyte vegetation towards dominance of phytoplankton and algae, which are able to exploit the eutrophic conditions and to create conditions favourable for their own persistence. However, the major changes are usually evident when a threshold is reached, at which point there is a radical shift in vegetation. This threshold depends on factors in addition to nutrient loading. Because naturally eutrophic conditions are uncommon, cultural eutrophication may not lead to benefits for specialists of naturally eutrophic conditions, as these will typically have other habitat requirements beyond high nutrient levels. Thus generalist species are more likely to be favoured. Increasing primary productivity can also have profound effects on the oxygen regime of a water body. The accumulation and decomposition of plant material depletes oxygen in the sediments and lower layers of water, which may become stratified (Harper, 1992). Nocturnal anoxia may also occur due to respiration by algae. The effects of eutrophication on the vegetation of aquatic ecosystems are summarised in Table 3.2.

3.3.1 Streams and rivers

The flushing process in rivers and streams should spare fluvial systems the spectacular effects of eutrophication seen elsewhere, unless flows are low. In addition to the effects of eutrophication, nitrogen plays a role in acidification of fresh water, and this role, including its impact on bird species such as dipper and yellow wagtail has been investigated (Ormerod and Tyler, 1989; Tyler and Ormerod, 1992). However, the current review restricts itself to the effects of nutrient status, and therefore acidification is not considered. Rivers generally do not develop phytoplankton, and eutrophic conditions are more often indicated by the presence of filamentous algae (which becomes established more easily in conditions of slower flow) and tolerant macrophytes such as *Potamogeton pectinatus* (Harper, 1992). Processes that reduce flow will increase the likelihood of changes to vegetation in rivers and streams.

Table 3.2. Effects of increased nutrient supply on vegetation in aquatic habitats

Habitat	Subject	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Shallow lake	phytoplankton	NW Europe	historical decline in external phosphorus loading over 13 years	decline in biomass in some seasons, with different groups showing individual seasonal variation	response to reduced phosphorus loading; increased grazing from zooplankton	2	Jeppesen et al., 2005b
	vegetation community	Netherlands	reduction in nutrient inputs to a lake undergoing restoration	shift from charophyte- to phytoplankton-dominated vegetation and return following restoration	changes in underwater light availability	2	Coops and Doef, 1996
	vegetation community	Netherlands	historical changes	switch from macrophyte- and charophyte-dominated to phytoplankton-dominated community, and recovery when phosphorus inputs reduced	switch of stable state (as described in main text)	2	Noordhuis et al., 2002
	vegetation community	Netherlands	reduction in phosphorus inputs	shift from phytoplankton to macrophyte domination	shift in stable state assisted by reduced nutrient loading	2	van den Berg et al., 1997
	vegetation community	Sweden	natural shifts of stable state	clear-water state dominated by macrophytes and charophytes; turbid state dominated by phytoplankton	buffering of stable state condition by positive feedback mechanisms	2	Blindow et al., 1993
	vegetation community	Norfolk Broads	historical changes	shift from charophyte-dominated vegetation to algae-dominated vegetation	increased phosphorus inputs (mostly from sewage treatment works); switch in stable states	3	Moss, 1980; Madgwick, 1999
	vegetation community	Norfolk Broads	experimental addition of P (0-5.3 g/m ³) and N (0, 29 and 63 g/m ³); other treatments involving fish control/addition and vegetation disturbance	no switch to phytoplankton-dominated state except where submerged plants physically removed	buffering of nutrient loading by submerged macrophytes	1	Balls et al., 1989
	reedswamp vegetation	Norfolk Broads	historical changes	reduction in distribution, especially of floating reed (hover)	various causes, including erosion, grazing and chemical pollution	2	Crook et al., 1983

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study

Table 3.2. (cont.) Effects of increased nutrient supply on vegetation in aquatic habitats

Habitat	Subject	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Experimental ponds	phytoplankton	UK	nutrient additions (500 mg/l N and 50 mg/l P every 3 weeks in winter, 170 mg/l N and 17 mg/l P every 2 weeks in summer); addition of fish; warming of water	increase in phytoplankton biovolume and chlorophyll a concentrations in response to nutrient additions but no switch to phytoplankton dominance	increased primary production in response to nutrients, but lack of other triggers to switch state	1	Moss et al., 2003
Lakeside vegetation	common reed (<i>Phragmites australis</i>)	central Europe	relationship between reed dieback and trophic status	no clear evidence that eutrophication is the general cause of reed decline	hypothesised relationship between eutrophication and culm architecture not present	2	Ostendorp et al., 2001
Lowland stream	vegetation community	Denmark	historical changes	decline in species richness; <i>Potamogeton</i> species adapted to eutrophic conditions increased relative to those adapted to oligotrophic conditions	eutrophication in lakes, leading to loss of propagules; turbidity in streams; more frequent disturbance	2	Riis and Sand-Jensen, 2001
Upland stream	vegetation community	Germany	spatial distribution of current plant species, and comparisons with previous records	decline in abundance and frequency of several pollution-sensitive species, but also some eutrophic species; loss of aquatic vegetation in lower reaches of some rivers	eutrophication, but also channelisation, spread of muskrats, and extreme floods	3	Schutz, 1995
	vegetation community	France	spatial distribution of plant species in relation to habitat variables	lower species richness in lower reaches, where filamentous algae increased in abundance	effects of eutrophication	2	Thiébaud and Muller, 1998
Estuarine	green algae	NW Europe	historical changes	large increase in abundance since 1950s	higher nutrient availability	2	Lotze, 2005
	red and brown algae	NW Europe	historical changes	decline in abundance and species richness	loss of eelgrass beds as substrate	2	Lotze, 2005
	eelgrass	NW Europe	historical changes	loss of eulittoral beds since 1960s	higher nutrient levels causing algal blooms, which inhibit eelgrass (also turbidity and effects of mussel fishery)	2	de Jonge et al., 1996
Upland lake	phytoplankton and periphyton growth	UK	spatial variation and experimental addition of P and N	phytoplankton yield limited by P in 20% of cases, N in 22% and both in 58%	inability of nitrogen-fixing cyanobacteria to live in upland lakes, leading to nitrogen limitation	1	Maberly et al., 2002

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

The composition of the vegetation of European streams has changed in recent decades, and one cited cause for this change is eutrophication (Schutz, 1995). In south-western German streams, comparison of current vegetation with previous herbarium material and records from previous studies showed decreases in abundance and frequency of several species over a forty year period, including pollution sensitive species, but also two macrophyte species, *Oenanthe aquatica* and *Butomus umbellatus* typical of naturally eutrophic conditions (Schutz, 1995). Filamentous algae, and the pondweeds *Zannichellia palustris* and *Potamogeton pectinatus*, increased in abundance, although the last decreased in distribution. In the lower reaches of some streams aquatic vegetation almost disappeared, and the temporal coincidence of the loss and changes in vegetation suggest that eutrophication may be the cause, although other possibilities are also put forward, including channelisation, spread of muskrat, and extreme floods in the 1980s (Schutz, 1995). In the Vosges Mountains of France, streams with high nutrient loads were characterised by low vascular plant species richness and by the presence of filamentous algae (Thiébaud and Muller, 1998).

Similar trends have been described in Danish lowland streams, where species richness of submerged plants has declined severely, particularly among the *Potamogeton* genus (Riis and Sand-Jensen, 2001). *Potamogeton* species adapted to eutrophic conditions have increased relative to those typical of oligotrophic conditions. The decline in species richness is partly ascribed to the loss of species in eutrophic lakes that are part of the stream system (thus reducing the source of propagules), and increasing turbidity in the streams (itself associated with eutrophication).

Lowland ditches at the Ouse Washes in southern England showed considerable increase in the mat-forming duckweeds *Lemna minor* and *Spirodela polyrhiza*, and *Lemna*-dominated community represented the climax community at high nutrient loadings (Cathcart, 2002). Between 1978 and 2002 the aquatic macrophyte community of the Ouse Washes deteriorated significantly. In the Ouse Washes, the shift from submerged macrophytes to duckweed dominance in ditches was different from the switch to phytoplankton observed in shallow lakes (Cathcart, 2002), which is described below.

3.3.2. *Inland standing water and fens*

3.3.2.1 Freshwater lakes

Lowland shallow lakes have received a good deal of attention in relation to eutrophication, perhaps because they best display some of the extreme effects of the condition. The accepted view is that two alternative stable states can exist: a clear-water state dominated by submerged macrophytes and charophytes; and a turbid, phytoplankton-dominated state (Blindow et al., 1993; Scheffer et al., 1993). Moss (1989, in Blindow et al., 1993) suggested an intermediate stable state, where macrophytes dominate but charophytes are absent, and phosphorus levels are intermediate. Spontaneous switches between the stable states have been observed in many shallow lakes: Lake Veluwemeer in the Netherlands (Noordhuis et al., 1997), where phytoplankton dominated from the 1960s due to increased nutrient levels, but which returned to a macrophyte-dominated state in the 1990s following a reduction in phosphorus inputs; Lakes Tåkern and Krankesjön in Sweden in response to water level changes (Blindow et al., 1993; Hargeby et al., 1994); and Hickling Broad in Norfolk (Armitage et al., 2000). In the last case, the shift to phytoplankton dominance in the 1970s was attributed to guano-trophication by black-headed gulls (Irvine et al., 1993).

Light is a key factor for the presence and abundance of submerged macrophytes (Blindow et al., 1993). The presence of macrophytes in water improves water clarity via several mechanisms, which include reduction in re-suspension of sediments, provision of refuges for herbivorous plankton against fish predators, suppression of algae due to reduction of nutrient availability, and release of substances toxic to algae (Scheffer et al., 1993). Phytoplankton-dominated states are buffered from switching back by shading (due to earlier growth and competition for resources), turbidity (affecting the depth at which other plants can grow), inhibition of herbivorous zooplankton, and promotion of planktivorous fish. While phosphorus has been considered the most important nutrient in determining the trophic status of shallow lakes, nitrogen may play a far more important role than previously thought (González Sagrario et al., 2005).

Nutrient levels play an important role in determining which stable state is present in a water body, but many other factors drive the switch from one state to the other (Phillips et al., 1978; Moss, 1990; Blindow et al., 1993; Moss et al., 2003). These include physical damage to vegetation, changes to fish community, changes to water level and changes to salinity. Thus a clear-water state may persist at high levels of nutrient concentration in the absence of triggers, and similarly, a phytoplankton-dominated state, once established, may persist at relatively low nutrient levels if conditions for a switch back are not present. For example, in experimental freshwater ponds, increased nutrient loadings did not lead to a switch to phytoplankton dominance, although phytoplankton biovolume and chlorophyll a concentrations did increase in response to both of these treatments (Moss et al., 2003). In the Norfolk Broads, experimental additions of phosphate and ammonium nitrate did not cause a switch to a phytoplankton-dominated state, even though nutrients were added in quantities larger than usually received by nearby lakes that had lost their submerged plants (Balls et al., 1989). Only where submerged macrophytes were manually removed did a turbid water state develop in response to nutrient additions, and it is suggested that macrophytes strongly buffered the effects of nutrient loading. Phosphorus levels may remain high even after inputs have been decreased, due to internal remobilisation from the hypolimnion and sediments (Moss et al., 2005).

The presence of planktivorous and benthivorous fish in lakes can trigger a switch to a phytoplankton-dominated state. Experimental enclosures containing fish in two eutrophic Swedish lakes exhibited the symptoms of eutrophication, including high chlorophyll concentrations, phytoplankton blooms, low transparency, and high nitrogen concentrations when compared with fish-free enclosures (Andersson et al., 1978). The understanding of the complexities involved with vegetation responses to nutrient levels has been driven by attempts to restore eutrophic lakes to clear-water states (Lauridsen et al., 1994; Coops and Doef, 1996; Perrow et al., 1999; Jeppesen et al., 2005a). This has also led to examination of the effects of increased nutrient levels concentrating on extreme eutrophication, with less attention to incremental effects that may occur even without a switch to a phytoplankton-dominated state. There is evidence suggesting that processes other than nutrient concentrations frequently

trigger the switch of stable state *per se*. However, the likelihood of switching depends strongly on nutrient levels, and in some cases phytoplankton biomass may respond quickly to changes in nutrient levels (Jeppesen et al., 2005b).

3.3.2.2. Reedswamps

Reedswamps dominated by common reed *Phragmites australis* are an important ecosystem in their own right and provide important habitat for many bird species. The Norfolk Broads is a particularly important region for reedswamp and has been the subject of several studies. The Broads have undergone historical changes to nutrient status, with sewage works a major source of those nutrients (Moss, 1980). There is some suggestion that in the nineteenth century the early stages of this process led to increased vegetation growth without wide-scale switches to phytoplankton-dominated states (Moss et al., 1996). Similar claims have been made for central Europe (Kubin and Melzer, 1997). In the second half of the twentieth century, negative effects to vegetation in the Broads have been linked to increased nutrient status (Moss, 1980; Crook et al., 1983; Moss, 1983; Madgwick, 1999). These include the loss of reed swamp, loss of submerged macrophytic vegetation, and shifts to phytoplankton-dominated vegetation, although these changes are also tied up with other factors, such as fen drainage, physical disturbance and increased sediment load. Much of the reed that disappeared was a floating growth form, known as hover, and there was a strong association between hover loss and nitrate concentrations in the water (Crook et al., 1983). It has been claimed that increased nitrogen availability can lead to a top-heavy growth form due to increased shoot biomass relative to root and rhizome (Klotzli and Zust, 1973, in Moss et al., 1996), and thus make hover more susceptible to disturbance in other forms such as recreational boat use.

Reedswamp in western and central Europe has undergone a decline in extent, and in quality where present (Ostendorp, 1989), which has been coincident with increases in cultural eutrophication, although showing a time lag (Kubin and Melzer, 1997). It has been suggested that eutrophication has been an important contributory factor to the dieback of common reed by altering the growth form as described above, and also by reducing the porosity of reed culms in the presence of high nitrogen levels (Votrubová and Pecháčková, 1996, in Fogli et al., 2002). However, in central European freshwater

lakes, where reed dieback has also been documented, Ostendorp et al. (2001) concluded that eutrophication did not affect culm architecture and was not a general cause in reed decline. Similarly, performance of reed populations in the Czech Republic and the Netherlands could not be related to habitat fertility (Clevering, 1998). Thus eutrophication is not considered to affect reeds directly, but there may be indirect effects, as increased productivity can increase litter accumulation, leading to anoxic conditions and to by-products toxic to reed (van der Putten, 1997). In brackish conditions in northern Italy, there was no difference in soil nutrient levels between healthy and declining reedbeds (Fogli et al., 2002), although this may reflect faster litter break down in warmer temperatures (van der Putten, 1997). While reed dieback and eutrophication have coincided in Europe, cause has not been proven. Indeed, despite the association of eutrophication and reed decline in Europe, a major threat from increased nutrient loading may be more rapid seral succession, which is a cause of reedbed loss (Bibby and Lunn, 1982).

3.3.2.3. Upland lakes

Upland lakes in Britain are usually naturally oligotrophic. These lakes receive nutrients from catchment runoff, but atmospheric deposition may be relatively more important, due to their position in high rainfall areas and the relatively poor nutrient status of soils in their catchments. Fertiliser runoff from forestry operations is another important source of nutrients, and fish farms in some lakes may raise nutrient levels. Phytoplankton biomass in fifteen Scottish lochs (mostly high quality waters) was dependent not only eutrophication pressure from the catchment, but also the attributes of the lochs themselves, such as water depth and flushing rate, that determine their sensitivity to nutrient inputs (Bailey-Watts, 1998). Even though most Scottish lochs are considered oligotrophic, they are still at risk from the effects of eutrophication, such as cyanobacterial blooms (Marsden et al., 1998).

3.3.3. Estuaries and coastal waters

Although the vegetation communities are different from those in freshwater, the effects of eutrophication can be similarly spectacular in saline situations. However,

most coastal waters are better flushed than similarly sized lakes, and eutrophication tends to be short-lived rather than persistent. Nevertheless, increased nutrient loadings, particularly of nitrogen, can have major effects on estuarine vegetation. Estuaries are naturally productive habitats, and under natural conditions in north-west Europe dense mats of vegetation can be important feeding areas for birds that either feed directly on the vegetation or on invertebrates found within the mats (Goss-Custard and West, 2004). Eutrophication typically leads to a decline in rooted phanerogam communities such as seagrass and eelgrass (*Zostera* spp.) beds, and their replacement by macroalgae and phytoplankton blooms (Nienhuis, 1993; Herbert, 1999). Densities of green macroalgae have increased in the Wadden Sea since the late 1950s in response to enhanced nutrient loading (Lotze, 2005). In the same area, eulittoral eelgrass has declined since the 1960s, and eutrophication and algal blooms (as a result of eutrophication) have been suggested as being major contributing factors (de Jonge and de Jong, 1993, in Lotze, 2005). In turn, the loss of eelgrass beds as substrate is considered to have been a contributing factor in the decline of red and brown algae (Wolff, 2000). Loss of seagrass beds has also been observed in response to eutrophication in a Portuguese estuary (Cardoso et al., 2005). Attempts to improve water quality by increasing water replacement in two brackish Danish lagoons saw a loss of seagrass beds due to changes in water level and salinity (Holm and Clausen, in press).

Macroalgal mats have been observed in many estuaries; they are a natural phenomenon, but one that is thought to be on the increase due to cultural eutrophication. Nutrient inputs from sewage effluent discharges in the 1970s were suggested as the cause of macroalgae mats found throughout Portsmouth Harbour (Soulsby et al., 1978) and Langstone Harbour (Tubbs, 1977). Sewage discharge was considered the main source of nitrogen for nuisance macroalgae in Dublin Bay (Jeffrey et al., 1995). Initially, nutrient enrichment increases overall productivity, but the anoxic conditions created in the water column, along with the release of toxic sulphides can have major effects on the flora and fauna (Herbert, 1999). Birds themselves may affect the manifestation of eutrophication in the vegetation of estuaries. In Canada, predation by waders on the amphipod *Corophium volutator*,

which feeds on diatoms and bacteria, resulted in substantial increases in algal cover (Hawkins, 1985, in Green et al., 1990).

3.4. Effects of nutrient increases on bird food items

The effects of nutrient inputs on bird food items are the most likely pathways for indirect effects on bird populations. Once again, although there are differences between habitats, there is a theme of increased primary productivity and faunal biomass with increased nutrient loading, and a point at which there is a community shift. In the most extreme cases of eutrophication, the increased primary productivity leads to high biological oxygen demand, and the resulting anoxia and sulphide concentrations can lead to mortality amongst aquatic animals. This can happen in any aquatic system, although it is inhibited where there is flushing of the system. However, at nutrient levels above normal, but in the absence of catastrophic anoxia or toxicity, abundance of food items will generally increase. The effects of increased nutrient levels on invertebrates in aquatic systems are summarised in Table 3.3.

3.4.1. Invertebrates in rivers and streams

The invertebrate communities of rivers and streams are sensitive to nutrient inputs. In the USA, the macroinvertebrate community was homogeneous along the longitudinal gradient of a stream flowing through agricultural land, despite geomorphological changes (DeLong and Brusven, 1998). Periphyton abundance was high, and functional grazers dominated the community, while many species common in the upper reaches of streams in the same drainage basin were absent. In a Mediterranean stream with longitudinal changes in nutrient levels, invertebrate community also varied longitudinally, with insects and gastropods dominant in the upper reaches, and oligochaetes, crustaceans and chironomids in the lower and polluted reach (Solimini et al., 2001). However, despite the change in community structure, the shape of the size structure differed little between reaches, and this has been observed elsewhere (Bourassa and Morin, 1995). Changes in taxonomic composition of the invertebrate

community may be driven by substrate availability as well as food abundance and availability. Thick periphyton cover in experimentally enriched streams in Canada saw a loss of filter feeders and chironomids and an increase in grazers (snails and oligochaetes), although overall invertebrate biomass did not change (Bourassa and Cattaneo, 2000). In lowland Britain, the distribution of several mollusc species in ditches was influenced by water nutrient levels, even where habitat was apparently suitable (Watson and Ormerod, 2004; Watson and Ormerod, 2005). The responses of these molluscs to anoxia and increased sedimentation rates associated with phytoplankton-dominated communities were suggested as possible mechanisms for their absence from some ditches. Slow-flowing drainage ditches share many characteristics with lakes and fens discussed below.

3.4.2. Lowland shallow lakes and fens

3.4.2.1. Vegetation

The switch to a phytoplankton-dominated stable state reduces food availability for herbivorous birds in freshwater lakes. Submerged macrophytes and charophytes are important food items, and these elements of vegetation are lost in the switch to a phytoplankton-dominated state, as described above. Food plants, such as stoneworts (*Chara* spp.) and pondweeds (*Potamogeton* spp.) have effectively disappeared from some lakes in the Netherlands, Sweden and the United Kingdom, as they have undergone eutrophication, and returned as lakes have recovered to a clear-water state (Hargeby et al., 1994; Armitage et al., 2000; Noordhuis et al., 2002). Macrophytes and charophytes are also important as food and habitat for invertebrates and fish that birds prey upon.

Table 3.3. Some effects of increased nutrient content on bird food items in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Estuarine	polychaete (<i>Capitella</i> sp.)	Australia	experimental addition of nutrients (and exclusion of shorebird predators)	increase but only in plots unaffected by macroalgal mats	increased food resources, but sensitivity to macroalgal mats	1	Morris and Keough, 2003
	epifauna and infauna (including whelks, crabs, sea anemones)	Netherlands	historical eutrophication	declines of many species	anoxia from decaying algal mats	2	Lotze, 2005
	pipefish and stickleback	Netherlands	historical eutrophication	decline in population	loss of eelgrass beds due to eutrophication	2	Lotze, 2005
	amphipods and polychaetes	Netherlands	historical eutrophication and pollution (1950s to 1980s)	decline in species richness but increase in abundance	increased nutrient availability, loss of predators (crabs and fish) due to pollution	2	van Impe, 1985
	gastropod (<i>Hydrobia ulvae</i>)	Portugal	eutrophication followed by restoration; spatial and temporal trends in abundance	decline in biomass and abundance during eutrophic conditions; recovery following restoration	association with seagrass beds that also recovered following restoration	2	Cardoso et al., 2005
	benthic infauna	NE England	increase in sewage effluent from point source	reduction in abundance of five taxa	localised hypoxia	2	Hall et al., 1997
	fish	NE England	increase in sewage effluent from point source	increase in small pelagic fish abundance, no change in benthic fish abundance, decline in flounder abundance	localised hypoxia, reduction in predation on small fish	2	Hall et al., 1997
	burrowing crustacean (<i>Corophium volutator</i>)	Scotland	spatial distribution	absent in sediments polluted by extreme nutrient enrichment	inability to survive anaerobic conditions	2	McClusky, 1968
Freshwater ditch	bivalve molluscs (cockles and tellins)	Scotland	observation of movements in an extremely enriched habitat	upwards into aerated sediments	inability to survive anaerobic conditions	2	Perkins and Abbott, 1972
	gastropods	south-east England	endangered species distribution in relation to habitat variables	two out of three species absent from ditches with otherwise suitable habitat where nitrate and nitrite levels high	responses to eutrophic conditions	2	Watson and Ormerod, 2004a
	sphaerid mussel (<i>Pisidium pseudosphaerium</i>)	south-east England	distribution in relation to environmental variables	scarcer at high levels of nitrogen	anoxia caused by eutrophication, greater sedimentation rates in phytoplankton dominated ditches	2	Watson and Ormerod, 2005

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 3.3. (cont.) Some effects of increased nutrient content on bird food items in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Small ponds	emergent insects	New York, USA	experimental additions of P and N (0.056 g/m ³ /year P, or 0.56 g/m ³ /year P and 12.1 g/m ³ /year N)	increased abundance in fertilised ponds	increased nutrient levels; independent effect of fish removal	1	McCarty, 1997
Shallow wetland	macroinvertebrates and small fish	Florida, USA	abundance and species richness in relation to nutrient gradient	both higher in enriched areas	increased nutrient availability, possible sampling bias	2	Rader and Richardson, 1994
Shallow lake	benthic fauna and cladocerans	Sweden	abundance in enclosures with and without fish	higher abundance in enclosures without fish	removed predation pressure	1	Andersson et al., 1978
	macroinvertebrates	Sweden	abundance in experimental plots with and without fish excluded	reduction in biomass (but not abundance) in plots with fish	predation pressure	1	Marklund et al., 2002
	benthic macroinvertebrates	Sweden	abundance over time (natural recovery from eutrophication)	increase in biomass and diversity following recovery; shift in composition towards snails and isopods	increased plant substrate and plant food; less bare sediment	2	Hargeby et al., 1994
	zebra mussels	Netherlands	historical changes in abundance in relation to trophic status	decline in population and recovery following reduction of phosphorus inputs	shift in stable state to macrophyte domination, clear water and increased food availability	2	Noordhuis et al., 2002
	macroinvertebrates	Netherlands	relationships with <i>Chara</i> spp biomass	positive relationship for total macroinvertebrate abundance; macrophytes strongly predicted invertebrate community composition	feeding habits of constituent invertebrate species	2	van den Berg et al., 1997
	zooplankton	Denmark	historical reductions in external phosphorus loading over 13 years	increase in average body weight of <i>Daphnia</i> and cladocerans	reduced predation on zooplankton and increased grazing on phytoplankton	2	Jeppesen et al., 2005b
	fish	Denmark	historical reductions in external phosphorus loading over 13 years	change in community structure (decrease in cyprinids, except rudd, which increased along with pike and perch)	improved foraging for piscivores	2	Jeppesen et al., 2005b
	fish	Norfolk Broads	cessation of anthropogenic nutrient inputs	increased diversity of fish community	changes in competitive environment of foraging fish at early life stages	2	Peirson et al., 1985
	fish	Norfolk Broads	historical changes associated with increased phosphorus concentrations (mainly from sewage treatment works)	collapse of pike fishery, dominance of roach and bream	loss of water plants	2	Perrow and Jowitt, 1997, Madgwick, 1999

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

3.4.2.2. Invertebrates

Invertebrates respond to nutrient status, and in the absence of a switch in stable state, increased nutrient availability should increase invertebrate biomass. In small ponds experimental addition of phosphorus and nitrogen increased abundance of emergent insects (McCarty, 1997). However, once lakes shift to a phytoplankton-dominated state, the radical changes to habitat generally lead to a decrease in invertebrate abundance and diversity due to adverse conditions, such oxygen depletion or loss of suitable substrate. There is also a shift in community composition away from sensitive species towards tolerant species such as annelid worms (Harper, 1992). In Lake Veluwemeer, zebra mussels, an important bird food item, declined from the 1960s, when algal blooms began to dominate the lake as a result of eutrophication (Noordhuis et al., 2002). Elsewhere in the Netherlands, *Chara* spp. biomass (an indicator of nutrient status) in shallow lakes recovering from eutrophication was a major determinant of macroinvertebrate community composition (van den Berg, 1997). In Sweden's Lake Krankesjön, recovery from phytoplankton-dominated conditions saw an increase in the biomass and diversity of the benthic macroinvertebrate fauna (Hargeby et al., 1994). There was also a shift away from dominance by chironomids and oligochaetes towards snails and isopods, which are associated with macrophyte cover. Invertebrate communities in eutrophic lakes of the Norfolk Broads are very low in diversity, typically dominated by oligochaetes and some chironomid larvae, with molluscs especially poorly represented (Harper, 1992). Despite the heightened primary productivity, these lakes do not provide suitable habitat for much of the invertebrate fauna typically present in such lakes.

In the Florida Everglades, a naturally oligotrophic system, macroinvertebrate (particularly ostracod) and small fish abundance were greater in areas enriched by nutrients from agricultural runoff than they were in unenriched sloughs, and the trophic structure did not appear to differ along a nutrient gradient (Rader and Richardson, 1994). However, in the same area, Turner et al. (1999) did not record increased invertebrate biomass at enriched sites, although fish biomass did increase. In a eutrophic lake in Minnesota, USA, benthic macroinvertebrates, including the amphipod *Hyaella azteca*, significantly increased in abundance following the return to a clear water state as a result of fish removal (Hanson and Butler, 1994).

Cladoceran grazing on phytoplankton was a major cause of improved water clarity. This process, while not involving changes to nutrient levels, is analogous to that which can be achieved by oligotrophication.

3.4.2.3. Fish

Fish are sensitive to the nutrient status of the water, both directly, as they may be killed by anoxic condition and toxic compounds released by algal blooms, and indirectly, through changes in habitat and prey (Harper, 1992). Fish may also affect aquatic vegetation, the magnitude of which varies greatly depending on the fish species (Williams et al., 2002). Removal of fish reduces predation pressure on zooplankton, and can thus increase cladoceran grazing on phytoplankton, improve water clarity and promote growth of submerged macrophytes, and it is used as a management tool in lake restoration (Hanson and Butler, 1994). Fish have been shown to reduce the abundance of benthic fauna as well as that of large cladocerans (Andersson et al., 1978).

Roach are favoured in phytoplankton-dominated lakes as it is able to feed on blue-green algae (Blindow et al., 1993). Cyprinids in general benefit from water turbidity, as it decreases predation pressure and they are less hampered as they use tactile orientation. However, rudd appear to do poorly compared with roach, possibly due to their need for submerged macrophytes as spawning substrate (Noble, 2003) and because they graze on submerged macrophytes (van Donk et al., 1994; Garcia-Berthou and Moreno-Amich, 2000).

One result of accelerated eutrophication of shallow lakes is a reduction of fish diversity, with roach and bream becoming dominant at the expense of perch, rudd and tench (Leach et al., 1977). Fish populations in shallow lakes in the Norfolk Broads are affected by eutrophication (Moss et al., 1996). Alderfen Broad, a shallow lake suffering from eutrophication, was isolated from its major anthropogenic source of nutrient-rich water, and showed an increase in fish diversity, although not total species richness, reflecting lower dominance of roach (Peirson et al., 1985). This was ascribed to increased recruitment success of larvae and fry of fish other than roach. In turn, it is suggested that the competitive advantage that foraging roach have in the

early life stages decreases with increasing submerged macrophyte abundance. Rudd (along with pike and perch) also increased with oligotrophication in Danish shallow lakes, while other cyprinids declined (Jeppesen et al., 2005b). Total zooplankton biomass remained steady but average body mass of *Daphnia* and cladocerans increased, indicating that piscivorous fish were reducing the predation pressure from zooplanktivorous cyprinids.

Fish affect the state of shallow lakes through predation of planktivorous zooplankton (Irvine et al, 1989; Blindow et al., 1993; Perrow et al., 1999). This predation is more efficient in the absence of submerged macrophytes, and can result in the establishment or persistence of a turbid-water state. Fish also reduce macroinvertebrate biomass, even when fish density is low (Marklund et al., 2002). Cyprinids also cause sediment suspension through their foraging behaviour, thus maintaining water nutrient status and reducing light availability for macrophytes. Submerged macrophytes can inhibit the impact of cyprinids and maintain water clarity by preventing access to the lake bottom, favouring piscivorous fish, and harbouring zooplankton (Blindow et al., 1993; Scheffer et al., 1993).

3.4.3. Upland lakes

Upland lakes, which are mostly naturally oligotrophic, are susceptible to the effects of increased nutrient inputs, which may affect invertebrate and fish communities. Trout lakes, trout spawning is adversely affected by fertiliser runoff (which may be predominantly from forestry operations), which changes the size structure of the trout populations, resulting in fewer and larger fish, while fish-eating birds such as divers require abundant small fish. In addition, where fish farms are present, wild trout may consume food pellets intended for farmed fish, again increasing in size and reducing the availability of suitable prey for fish-eating birds. Availability of fish prey may also be affected by reduced water clarity in upland lakes as a result of nutrient inputs.

3.4.4. Estuaries and coastal waters

3.4.4.1. Invertebrates in intertidal areas

There is evidence that pollution, particularly sewage discharge points, while damaging to the integrity of the environment as a whole, may increase the populations of pollution indicator species, which can be valuable food sources for birds. Effects of eutrophication, especially from sewage point sources, on benthic communities are well documented (eg Crema et al., 1991; Green et al., 1990). In the Wadden Sea, eutrophication has led to an increase in mass blooms of green algae, with consequent mass mortality of epifauna and infauna due to the anoxic conditions resulting when algal mats decay (Lotze, 2005). However, there is evidence from elsewhere that eutrophication has led to an increase in the infauna (especially polychaetes) of mud and sand flats. In a Portuguese estuary, eutrophication saw the replacement of seagrass beds and the decline in abundance of the gastropod *Hydrobia ulvae* (Cardoso et al., 2005). Sites where sewage outfalls are removed, or where treatment is implemented, generally show a decrease in invertebrate biomass, although species richness increases and species composition changes to more closely approximate non-polluted sites (Green et al., 1990).

Changes in the abundance and availability of bird prey items in response to extreme nutrient pollution have been observed in intertidal habitats in Scotland (Pounder, 1976). In the Clyde estuary, anaerobic conditions led to the conversion of organic matter to sulphur compounds, leading to cockles (*Cerastoderma edule*) and tellins (*Macoma balthica*), moving upward into more aerated surface sediments (Perkins and Abbott, 1972). These shellfish are important food items for waders, especially oystercatchers, which would then have a temporarily increased food supply but potentially a longer-term loss in food supply. The amphipod *Corophium volutator*, an important food item for many shorebirds, is intolerant of the macroalgal mats that occur in response to eutrophication (Pounder, 1976), although it declined in abundance in the Clyde estuary following the reduction of sewage and industrial wastes (Furness et al., 1986). This species and the polychaete *Nereis diversicolor* may be most affected by the oxygen status of sediments, as they seem otherwise to be favoured by anthropogenic nutrient inputs (Green et al., 1990). Experimental

additions of nitrogen and phosphorus to plots in tidal mudflats in Australia resulted in increases in the polychaete *Capitella* sp., but only in plots unaffected by macroalgae (Morris and Keough, 2003).

3.4.4.2. Invertebrates in coastal waters

Benthic filter feeders control eutrophication of estuarine waters to some extent by depositing organic material from the water column onto the bottom sediments, and accelerating the regeneration of nutrients from this deposited organic matter (Nienhuis, 1993). If eutrophication causes organic matter to build up on the sediments faster than the process of aerobic mineralisation, anaerobic conditions will develop and lead to the death of the benthic fauna. In the Tyne estuary, reductions in the abundance of benthic infauna were observed close to a sewage output following an increase in sewage output (Hall et al., 1997). However, some benthic invertebrates, notably annelids, are abundant close to sources of nutrient pollution (Green et al., 1990), while others, notably molluscs are less abundant close to sewage outfalls (Rees et al., 1992). Experimental addition of nutrients has also changed the species composition and reduced its diversity, of the invertebrate fauna in coastal waters (Eleftheriou et al., 1982).

3.5. Indirect effects of aquatic eutrophication on birds

There is evidence for both positive and negative effects of aquatic eutrophication on birds. One possible, albeit unusual, effect is that of toxicity from algal blooms (stimulated by eutrophication), which were the cause of kittiwake mortality in northeast England (Coulson and Strowger, 1999). But most indirect effects operate at one or more further removes from the cause, via the food chain or habitat change. Increased productivity may lead to greater food availability. For example, tree swallows in North America fed more frequently on ponds with added nutrients, because of the increase in emergent insects in such ponds (McCarty, 1997). In fact, the effects of increased nutrient loading of aquatic systems are likely to be positive for birds as long as (a) there are no major shifts in the structure or composition of habitat, flora or fauna; or (b) such changes as occur are compensated by, for example, an

alternative food source. Birds are most likely to be negatively affected by changes to food supply, although in some cases there is evidence of effects on nesting sites. As the following descriptions will show, most negative effects of eutrophication on birds occur when there is a major shift in habitat, particularly towards the dominance of phytoplankton, but even in that event there may be circumstances where birds can exploit the situation. Figure 3.1 illustrates the most commonly observed patterns between birds and nutrient levels in aquatic habitats.

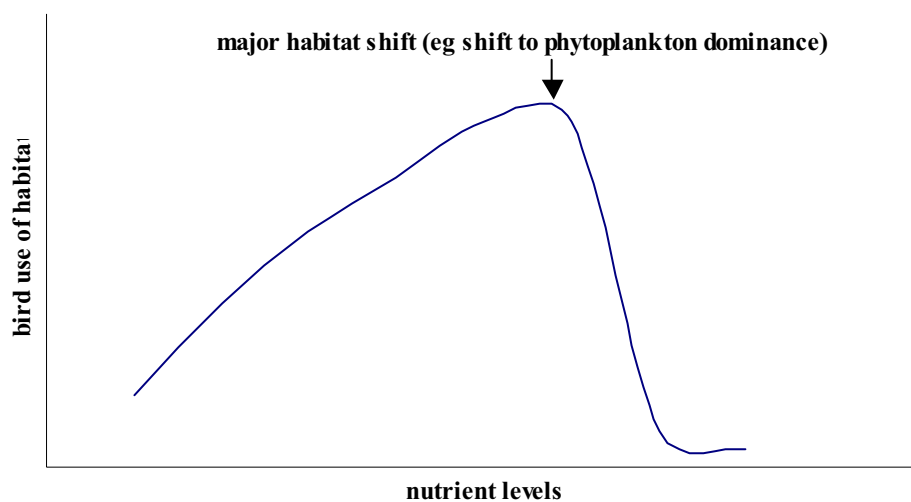


Figure 3.1. Typical effects of nutrient levels on birds in aquatic habitats.

I present the evidence for indirect effects of cultural eutrophication on birds in various habitats. Where appropriate I also present more detailed descriptions of ways in which anthropogenic nutrient inputs (or their removal) have affected, or could potentially affect, species or groups of birds. However, I stress that this does not necessarily mean that the indirect effects of eutrophication are the major drivers of population change for these species, and the effects may well be locality-specific, even within the same habitat. The indirect effects of cultural eutrophication on birds are summarised in Table 3.4.

Table 3.4. Indirect effects of nutrient increases and decreases on birds in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Small ponds	tree swallows	USA	experimental additions of nutrients	increase in foraging at high fertiliser levels	increase in emergent insects	1	McCarty, 1997
Shallow lake/marsh	waterfowl	Netherlands	recovery from eutrophication	recovery of bird numbers, especially diving ducks and long-necked waterfowl; strong relationships between bird abundance and food items (<i>Chara</i> spp. and zebra mussels)	recovery of food items due to reduction in phosphorus inputs	2	Noordhuis et al., 2002
	birds of open water	Sweden	multiple regression of species richness/abundance on environmental factors	species richness related positively to nitrogen (plus shore development and pH), density related positively to phosphorus (plus area of fen)	increased productivity (authors considered relationship with nitrogen possibly spurious)	3	Nilsson and Nilsson, 1978
	black-throated diver	Sweden	multiple regression of abundance on environmental factors	negative relationship with chlorophyll a and phosphorus	uncertain, no relationship with water transparency	2	Nilsson and Nilsson, 1978
	coot	Netherlands	temporal relationship between coot grazing, macrophyte biomass and lake restoration	coot removed around 70% of macrophyte biomass, without affecting lake restoration	replacement by macrophyte species able to take up nutrients from water column, thus reducing nutrient loading	2	Van Donk et al., 1994
	waterfowl	USA	restoration of clear-water state by fish removal	increase in waterfowl numbers	increase in food items (macrophytes and macroinvertebrates); reduced competition for food from fish	2	Hanson and Butler, 1994
	waterfowl	Sweden	recovery from eutrophication	marked increase in coot and mute swan numbers; less marked increase in dabbling ducks	increase in macrophyte and charophyte food for birds and of invertebrate prey items	2	Hargeby et al., 1994
	all birds	Florida, USA	nutrient gradient	higher total abundance at enriched sites; no trend in species richness; shift in species composition (some species only present at low nutrient sites)	greater food availability, but loss of some habitat features	2	Crozier and Gawlik, 2002

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 3.4. (cont.) Indirect effects of nutrient increases and decreases on birds in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Freshwater lake	staging waterfowl (autumn)	Sweden	historical eutrophication (in 1970s and 1980s) and recovery (in 1990s)	most species present at high numbers before eutrophication peak, then absent or at low numbers, before recovering following lake restoration	lack of food resources (submerged macrophytes, invertebrates and some fish)	2	Andersson and Nilsson, 1999
	all birds	Florida, USA	relationship between bird abundance/species richness and habitat variables	positive correlation between abundance and nutrient measures; species richness positively related to lake area and phosphorus levels	increased productivity	2	Hoyer and Canfield, 1994
	divers	Sweden	distribution in relation to habitat variables	black-throated diver preferred more transparent lakes (also relationships with shoreline development and perch density), red-throated diver sensitive to acidification (also positive relationship with lake surface area)	prey abundance and availability	2	Eriksson and Sundberg, 1991
	tufted duck	Northern Ireland	historical trends in wintering population in relation to roach populations; examination of diet abundance and species richness related to lake variables	decline in tufted duck population, then increase as roach populations dropped; large overlap in diet	competition for food	2	Winfield et al., 1992; Winfield and Murphy et al., 1984
	ducks	Alaska, USA	historical trends in wintering population in relation to roach populations; examination of diet abundance and species richness related to lake variables	nitrite and phosphate concentrations both included as positive variables in multiple regression; ammonia concentration negative for duck species richness; nitrate concentration negative for species richness	increased productivity in response to nutrient concentrations leading to increased food resources	2	Murphy et al., 1984
	common scoter	Ireland	breeding success on two lakes, one clear water, one eutrophic	no fledged young on eutrophic lake, 0.53 and 2.2 per pair on sections of other lakes; molluscs and mayfly larvae more abundant on clear lake	lack of food for ducklings	2	Partridge and Smith, 1988
	diving ducks	Ireland	historical population trends	three species feeding on eutrophication-sensitive chironomid larvae declining, one species feeding on tolerant chironomid larvae steady	food abundance	2	Allen et al., 2004
	common scoter	Lough Erne	historical population trends in relation to eutrophication	population reduced from 150 breeding pairs (1967) to almost none (1995)	loss of food items for ducklings	2	Partridge and Smith, 1988
	pursuit divers	Sweden	test of model predictions	positive relationship for both black-throated diver and goosander for lakes with high "prey detectability index"	improved prey detectability	2	Eriksson, 1985

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 3.4. (cont.) Indirect effects of nutrient increases and decreases on birds in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Canal	tufted duck and pochard	Manchester	spatial distribution of foraging in relation to site characteristics	foraging in areas with high total benthic organic content	high abundance of oligochaetes and other pollution-tolerant invertebrates	3	Marsden and Bellamy, 2000
Estuarine/tidal flats and coastal water	intertidal birds	Netherlands	historical eutrophication and pollution (between 1950s and 1980s)	increase in mean spring/summer numbers for 8 out of 10 species (7 by over 100%), 1 species steady, 1 species declined	increase in food items	2	van Impe, 1985
	shorebirds	Portugal	abundance in relation to habitat variables	positive relationship for black-backed gull (with presence of non-treated sewage discharges) and for grey plover (with presence of sewage discharge points); both species also showed relationship with other variables	increased productivity	2	Rosa et al., 2003
	shorebirds	Portugal	distribution in relation to habitat variables	negative relationship for three species with distribution of macroalgal mats, but positive (or no) relationship with feeding behaviour of those birds feeding on mats	no decrease in prey abundance in macroalgal mats, decrease of birds in these areas not explained	2	Cabral et al., 1999
	shorebirds	Scotland	historical changes in wintering populations in relation to increased nutrient loading and greater extent of macroalgal mats	increases in six (of nine) species, four against national trends; decline of shelduck	increased overall productivity of estuary	2	Raffaelli et al., 1989.
	shorebirds	Netherlands	distribution of foraging birds in relation to existing algal mats and experimentally moved mats	preference for newly placed algal mats, but not for existing mats	movement of sediment fauna to avoid anoxic conditions below mats, then depletion of food resource	1	Metzmacher and Reise, 1994
	shorebirds	Firth of Forth	reduction in effluent inputs between the 1970s and 1980s	reductions in both groups	reduction in food abundance for wildfowl; other factors for waders	2	Bryant, 1987
	shorebirds	Scotland	changes in populations before and after reduction of sewage and industrial effluent	declines of three species (dunlin, redshank, lapwing), but not of oystercatcher and curlew	declining species feed predominantly on prey that also declined following reduction in effluent	2	Furness et al., 1986

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study

Table 3.4. (cont.) Indirect effects of nutrient increases and decreases on birds in aquatic habitats

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Estuarine/tidal flats and coastal water	gulls	Tyne estuary	implementation of sewage treatment	over 90% decrease in two species; no change in two species; significant increase in two species	species reliant on sewage outfalls declined, but one species fed at a new location within the estuary; other species mostly fed outside the area	2	Raven and Coulson, 2001
	shelduck	Firth of Forth	spatial distribution in relation to <i>Hydrobia ulvae</i>	positive relationship	food abundance	2	Bryant and Leng, 1976
	light-bellied brent goose	Lindisfarn (England) and Denmark	changes in population and distribution	geese moved to nearby <i>Zostera</i> beds when local ones were depleted; where this was not possible they shifted food source or left the area	<i>Zostera</i> is the preferred food source	3	Clausen and Percival, 1998
Open coastlines	purple sandpiper and turnstone	Hartlepool	historical changes in bird populations in relation to introduction of sewage treatment	no decline in turnstone and no greater decline in purple sandpipers (declining nationally)	rapid dispersal of pollution prior to sewage treatment; insufficient time to detect changes	2	Eaton, 2000a
Coastal waters	seaducks	Firth of Forth	introduction of sewage treatment	two species declined and changed distribution in response to treatment, three species showed unclear patterns	loss of direct food items from outflows, and loss of food items depending on sewage outflows	2	Campbell, 1984
	seaducks	Firth of Forth	spatial distribution in relation to sewage outfalls	concentration of goldeneye and scaup near outfalls	increased benthic invertebrate populations and grain husks in the water column	2	Campbell, 1978

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

3.5.1. Rivers and streams

The effects of habitat change on birds of fast flowing streams has largely concentrated on acidification, and the present review does not discuss this issue. In slower flowing riverine habitats, the indirect effects of eutrophication on birds (at least for those birds for which there is evidence of effects) are likely to be similar to those in lowland shallow lakes and fens, as described below.

3.5.2. Lowland freshwater lakes

Increased nutrient loading in freshwaters can be beneficial to birds. In fifteen Alaskan freshwater lakes, nitrate and phosphate concentrations were positively related to duck species richness and abundance (Murphy et al., 1984). In a slow moving river system, the Manchester Ship Canal, feeding behaviour of wintering pochard and tufted duck was concentrated in areas with high benthic organic carbon resulting from sewage release (Marsden and Bellamy, 2000). These areas hold high densities of oligochaetes and other pollution-tolerant invertebrates. In eleven Swedish shallow lakes, waterbird density was positively related to chlorophyll a and phosphorus concentrations, while species richness was positively related to degree of shore development, area of fen and nitrogen concentration (Nilsson and Nilsson, 1978). Despite these relationships, there appeared to be no increase in waterbird species richness in culturally eutrophic lakes; the relationship with nutrient levels only held for lakes with naturally high nutrient levels. Mild eutrophication has been linked with increases in some species, such as moorhen and whooper swan in Finland, in response to increased aquatic vegetation, and of piscivorous birds such as great-crested grebe elsewhere in Europe (Harper, 1992). The major proximate cause of waterbird decline following nutrient increases in freshwater lakes is likely to be the loss of food items, both plant and invertebrate, when there is a shift to a turbid-water, phytoplankton-dominated state. Increases in nutrient inputs in the absence of shift in stable-state are more likely to be beneficial to birds of freshwater lakes, although in naturally oligotrophic lakes, piscivores may be affected by minor changes in transparency or shifts in fish size structure arising from relatively small changes in nutrient loading.

3.5.2.1. Herbivorous and omnivorous waterfowl

Submerged macrophytes and charophytes form an important part of the diet of many waterbirds, even those thought of as typically carnivorous. In winter, pondweeds (*Potamogeton* spp.) and wild celery (*Vallisneria americana*), along with oligochaetes, form important parts of the diets of scaup and goldeneye in North America (Jones and Drobney, 1986). When shallow lakes shift to phytoplankton-dominated states these food resources are lost to waterfowl, with consequences for their populations. Most studies relating bird numbers to eutrophication have concerned the results of restoration efforts and historical changes to bird numbers, plus spatial and/or temporal relationships with food resources. For example, anthropogenic restoration of a freshwater lake to a clear-water state in the USA, although achieved by fish removal rather than reductions in nutrient inputs, saw the recovery of macrophyte and macroinvertebrate populations, including an amphipod that is the preferred food of migrating lesser scaup in North America (Hanson and Butler, 1994). Lesser scaup, along with herbivorous waterfowl, recovered strongly following lake restoration.

In Lake Veluwemeer, a Dutch shallow lake, bird populations of several waterfowl species, some of conservation importance, declined when their food items (macrophytes, charophytes and zebra mussels) declined in response to eutrophication dating from the 1960s (Noordhuis et al., 2002). Following an improvement in its trophic status, waterbirds returned to the lake in large numbers. Abundances of eight species (Bewick's swan, mute swan, pochard, tufted duck, coot, gadwall, red-crested pochard and pintail) were significantly positively related to abundance of their primary food sources, which included pondweeds and filamentous macro-algae as well as mussels and charophytes. Short-necked, non-diving waterfowl did not show the same increase in numbers following lake recovery. In all cases except gadwall, *Chara* biomass was the most important predictor of abundance; however, this was also correlated with zebra mussel abundance. Macrophyte decline has been linked with the disappearance of mute swan, coot, teal and gadwall from Loch Leven (Allinson and Newton, 1974 in Harper, 1992). In Hickling Broad, Norfolk, swan, pochard and tufted duck all declined following the loss of Hickling Broad's submerged aquatic flora in response to eutrophication (Harper, 1992). Spontaneous

recovery to a clear-water state with abundant charophyte beds provided a food resource for herbivorous and omnivorous waterfowl (Armitage et al., 2000),

Historical eutrophication and recovery has also been associated with bird abundance in Lake Ringsjön, Sweden (Andersson and Nilsson, 1999). This moderately deep (mean depth 3 m, maximum depth 17 m) lake is an important staging area in autumn for migrating waterfowl. Eutrophication in the 1970s saw a large reduction in staging waterfowl populations. At the beginning of the 1980s, a programme to reduce nutrient inputs was initiated, and in 1989-1990 cyprinid fish reduction was implemented, as their behaviour can help to maintain the phytoplankton-dominated state. Following oligotrophication, bird numbers increased again. This trend is evident for herbivores (mute swan, whooper swan and coot), omnivores (teal, wigeon and others), benthivores (tufted duck, pochard and goldeneye), and one piscivore (goosander), while two other piscivores either showed no trend (great-crested grebe) or a general increase from the 1980s (cormorant). For most species, the changes at Lake Ringsjön did not mirror regional population changes, and thus were probably related to changes in food resources in the lake (Andersson and Nilsson, 1999). While numbers of most waterfowl species have recovered following restoration, in most cases abundance is less than that of the late 1960s. It is possible that bird numbers in the late 1960s had increased following enrichment prior to a shift to a phytoplankton-dominated state. A similar phenomenon has been observed in Lake Krankesjön, where bird numbers have mirrored the spatial increase in pondweed and stoneworts following recovery from eutrophic conditions (Hargeby et al., 1994). The increase in bird numbers was most marked for the predominantly herbivorous coot and mute swan, but dabbling ducks also increased in abundance. The increase in dabbling ducks probably reflects an increased availability of food, both plant and invertebrate, as the macroinvertebrate biomass and diversity increased following recovery from eutrophication (Hargeby et al., 1994).

Herbivory by birds has been considered to have the potential to halt the restoration of lakes to clear-water states by removing macrophytes. However, although coot consumed large quantities of submerged macrophytes in Lake Zwemlust, the lake's recovery was not affected (Van Donk et al., 1994). Coot grazing over winter may

have altered the composition of the macrophyte community, by removing *Elodea nuttallii*, which does not form dormant buds, and thus promoting *Ceratophyllum demersum*, which does (and which may also lower the nutrient loading of the water, as it mainly takes up nutrients from water). In Swedish eutrophic lakes, the risk of a reduction in submerged vegetation due to waterfowl herbivory was considered to be low (Marklund et al., 2002).

3.5.2.2. Benthivorous diving birds

Benthivorous diving birds may be negatively affected by eutrophication due to a reduction of invertebrate food items such as molluscs, which disappear in response to changes to substrate, and by the availability of prey that is present as water becomes turbid. A return to a clear-water state increases macroinvertebrate biomass and diversity, and improves water transparency, and populations of diving ducks generally increase following lake restoration (Hanson and Butler, 1994). Where such restoration does not reduce nutrient levels birds are likely to benefit from increased primary productivity compared to that in oligotrophic lakes with similarly clear water.

Eutrophication has been suggested as the ultimate cause of population declines of some diving ducks in Irish freshwater lakes. The breeding population of common scoter on Lough Erne fell from 152 pairs in 1967 to practically none in 1995 (Underhill et al., 1998), while phosphorus concentrations in the lake doubled between 1974 and 1997 (Zhou et al., 2000). Tufted duck and red-breasted merganser numbers also fell between the 1960s and 1980s (Partridge and Smith, 1988). In a study in the 1980s, no young were fledged on lower Lough Erne, while young were fledged from mesotrophic Lough Conn/Cullin (Partridge and Smith, 1988). Mollusc and mayfly abundance was significantly higher in the transparent waters of Lough Conn/Cullin, and submerged pondweed beds were a favoured feeding area. Freshwater mussels tend to be sensitive to shifts in stable state in lakes, and species that feed on them, such as pochard and tufted duck (Werner et al., 2005), are likely to be affected by the loss of food resources. While nest predation (by mink) was a possible cause of reduced productivity, lack of food for ducklings on Lough Erne was considered the most likely cause of the differences observed (Partridge and Smith, 1988).

Changes to food resources have also been suggested as a major cause of the decline of wintering diving ducks on Lough Neagh, a eutrophic water body. Chironomid larvae are a major food source for diving ducks, and three species that forage on similar size classes (pochard, tufted duck and goldeneye) are in decline (Allen et al., 2004).

Populations of scaup, which feeds on larger chironomids that are more tolerant of eutrophic conditions, have remained steady. However, there may be further explanations for the decline of tufted duck. Numbers fell in response to the introduction of roach in the 1980s, and then recovered following control of the roach population (Winfield et al., 1992; Winfield and Winfield, 1994). Great-crested grebe, which feed on young roach, showed the opposite trend. Roach generally benefit from eutrophication, and have a diet that overlaps with that of tufted duck more closely than do those of other fish species, as they take a large proportion of molluscs, which form an important part of the diet of tufted duck (Winfield and Winfield, 1994). Competition from fish may be more important than the loss of food abundance or availability for tufted duck. Common scoter also feed on molluscs, and it is possible that competition with roach for food may contribute to the decline of this species in freshwater lakes generally (Winfield and Winfield, 1994), or indeed of birds feeding on molluscs in eutrophic waters (containing roach) generally.

Local conditions in aquatic habitats may exert a strong influence over the indirect effects of eutrophication on bird populations, and species may show different responses in different circumstances. For example, nationally significant populations of tufted duck (and pochard) overwinter in the eutrophic Manchester Ship Canal, where they concentrate their feeding in areas with high total benthic organic carbon (Marsden and Bellamy, 2000). Improvements to the overall ecological status of this site may well reduce the populations of these species, although other bird species, such as goosander and goldeneye may be expected to benefit from improved water clarity and greater diversity of food sources. The physical characteristics of Lough Neagh help to determine the effects that eutrophication has on diving ducks via the food supply, and there may be no universal pattern of effects (populations of all four species are increasing globally).

3.5.2.3. Piscivorous diving birds

Birds that actively pursue fish, such as divers, will be affected both by water transparency and by populations of suitable prey. Transparency in lakes indicates lower productivity, but this may be offset by higher detectability of prey. Pursuit divers may benefit from lower fish density in oligotrophic lakes, as transparency increases due to reduced predation on zooplankton and thus changes in the phytoplankton community (Eriksson, 1985). Divers are typical of low-nutrient lakes, and in Britain breeding is restricted to upland lakes. Lake occupancy of breeding black-throated diver in Scotland was associated with a high abundance of small salmonid fish, the major food items of adults and well-grown chicks (Jackson, 2005). Diver productivity (chicks fledged) was lower on lakes without small fish (minnows and/or sticklebacks), where adults fed chicks on aquatic insect larvae. Lake occupancy was predicted by a water chemistry principle component, which in turn was weakly related to water transparency (Jackson, 2005). The results suggest that divers in Scotland prefer lakes with abundant and easily-hunted small salmonids. Brown trout growth is retarded in low nutrient conditions (and also at low water temperatures); thus fish tend to remain small (and appropriate diver prey), and abundant, because no brown trout individuals become large enough to prey on smaller individuals. Increased nutrient loading of oligotrophic lakes may affect prey for divers by increasing individual fish body size and by increasing piscivory by large fish. Nutrient loading may also reduce water transparency, reducing the ability of divers to catch prey, while high nutrient levels can interfere with brown trout spawning, which may also reduce prey items.

Elsewhere in Europe, black-throated diver may feed on different fish prey; perch and cyprinids are the main prey in Swedish lakes (Eriksson and Sundberg, 1991). In eleven Swedish shallow lakes, black-throated diver abundance showed a negative relationship with indicators of lake productivity (chlorophyll a and phosphorus concentrations), although no relationship with water transparency (Nilsson and Nilsson, 1978). However, in two other studies in Sweden black-throated diver preferred more transparent lakes (Eriksson, 1985; Eriksson and Sundberg, 1991). Red-throated diver did not show such relationships, possibly because they feed on pelagic fish rather than bottom-dwellers (Eriksson and Sundberg, 1991). However, the lakes

in question were oligotrophic, and increases in nutrient inputs may change water transparency sufficiently to affect red-throated diver foraging.

Sawbilled ducks are also pursuit divers, and as such may be indirectly affected by the effects of nutrient inputs on prey abundance and availability (Eriksson, 1985). However, these birds also forage by probing lake and river bottoms to locate hiding fish (Sjöberg, 1985), and thus may be less affected by water transparency. In Denmark, goosander abundance and diving behaviour were greater on hypertrophic Lake Sjaelsø than on eutrophic Lake Esrom (Woollhead, 1986), suggesting that greater abundance of prey was more important.

3.5.3. *Fens, marshes and reedbed*

Marsh, fen and reedbed are important habitats for several bird species, such as marsh harrier, water rail, Cetti's warbler, and bearded tit. As described above, eutrophication of fresh waters has coincided with reed dieback in Europe, and this has been linked to bird populations; for example, the decline of great reed warbler in the Netherlands due to reduced nesting opportunities (Graveland, 1998). However, causality has not been conclusively proven, although it will be interesting to see whether such a connection can be made in the future.

Eutrophication may be reducing the amount of marsh, fen and reedbed habitat by two other mechanisms, neither of which necessarily relies on a switch to a phytoplankton-dominated stable state. The first is an increase in the rate of seral succession to scrub and woodland and the desiccation of swamps and fens (Bibby and Lunn, 1982). The second is a decrease in the amount of open water due to increased primary productivity of macrophytes and the spread of vegetation, similar to that seen in the Everglades of Florida (Crozier and Gawlik, 2002). In this oligotrophic wetland, bird abundance generally increased with nutrient enrichment, although there was also a shift in species composition. Increases in food resources, and changes to habitat structure (typically the replacement of sawgrass marshes and open sloughs with dense stands of *Typha* spp. and little open water) were suggested as the main mechanisms

behind the changes in bird numbers (Crozier and Gawlik, 2002). Enriched sites had more rails and bitterns, which prefer heavily vegetated areas, while species that require open water (eg pied-billed grebe and some raptor species) were more common at non-enriched sites. Piscivores such as wood stork, great egret and great blue heron were more abundant at enriched sites. Although enrichment reduced the extent of open water, fish were more abundant in the open water that remained (Rader and Richardson, 1994; Turner et al., 1999). Other species, such as killdeer and black-necked stilt were only recorded in non-enriched areas. The presence of open water is important for many reedbed bird species (Bibby and Lunn, 1982), even for those that do not use it directly. If a switch to a phytoplankton-dominated state does occur in fens and swamps, then there would be expected to be change to the trophic structure similar to that observed in shallow lakes and described above.

3.5.3.1. Bittern

The red-listed bittern has suffered loss of its required habitat, extensive wet reedbed and reed fringed by open water. This has occurred due to drainage, direct clearance and seral succession (Bibby and Lunn, 1982; Tyler et al., 1998; Gilbert et al., 2005). Loss of reedbed habitat, specifically hover in the Norfolk Broads, has previously been attributed to the weakening effects of nitrates on reed stems (Crook et al., 1983), although this is in dispute (Ostendorp et al., 2001). However, eutrophication can have negative impacts on bitterns via another pathway. In Britain bittern feed largely on fish, particularly eel and rudd, and eutrophication can potentially reduce the abundance and availability of rudd (Gilbert et al., 2003; Noble, 2003). The shift from a macrophyte-dominated to a phytoplankton-dominated plant community can lead to direct fish kills due to hypoxia in extreme cases. In addition, rudd appear to be disadvantaged by eutrophic conditions, possibly due to their need for aquatic macrophytes as spawning substrate (Noble, 2003; Jeppesen et al., 2005b), while other cyprinids that are less suitable prey, such as roach, have less specific requirements. Given that eel populations in the UK are threatened by other processes, including habitat connectivity (Self, 2005), rudd may assume increased importance in the diet of bitterns at some sites. In any event, water turbidity associated with eutrophication, is presumed to have effects on foraging efficiency of bitterns. Both reduced abundance and reduced foraging efficiency may affect the ability of bittern to successfully raise

broods, and chick starvation is the most frequent cause of nest failure (Puglisi and Bretagnolle, 2005). Thus, while eutrophication may not be the major factor in determining abundance and distribution of this species, and management unrelated to nutrient status also affects fish prey (Noble et al., 2004), it is likely to be important at the local scale.

3.5.3.2. Black tern

Eutrophication of marshlands has had an impact on black tern populations (which declined by 90% in the period 1950-2005) in the Netherlands, via two mechanisms (van der Winden, 2005). The first is the lack of nesting substrates, as the preferred species, water soldier (*Stratiotes aloides*) has declined in response to eutrophication (Barendregt et al., 1990, in van der Winden, 2005). Nymphaeids have replaced water soldier in many places, but provide unsuitable nesting habitat (van der Winden et al., 2004). The other mechanism is the loss of diversity of food items to feed chicks. Fish provide essential calcium, and their populations are most affected by water acidity (Beintema, 1997). However, fish may require excessive effort to catch, and large insects (notably water beetles) are also a major food item for chicks. Provision of breeding rafts has addressed the problem of nesting, and the population has stabilised (van der Winden, 2005). This species effectively disappeared from the UK as a regular breeder in the nineteenth century, and the cause of this is unknown. Nevertheless, it provides an example of the effects of eutrophication on nesting habitat, and its return to Britain may be affected by eutrophic conditions.

3.5.4. Estuaries and tidal flats

British estuaries and are important conservation areas, particularly for shorebirds and wildfowl in winter and during migration (Collier et al., 2005). The effects of organic inputs to estuaries on wintering birds in estuaries in Britain have been reviewed (Green et al., 1990), as have the effects of reduced organic and nutrient inputs on birds in estuaries and coastal waters in England and Wales (Burton et al., 2004). The effects of nutrient inputs to coastal systems depend on the time that such inputs remain in the system. In estuaries this may be considerable, but water currents on

open coastlines cause the rapid dispersal of sewage, which may explain the apparent lack of effect on birds in some estuaries and coastal ecosystems (Eaton, 2000a). Effects on the food chain in such environments may be very localised, and bird populations may be affected by processes elsewhere. Wintering brent geese fed preferentially on *Zostera* at Lindisfarne, northern England and in Denmark, and where this food source declined (in some places due to eutrophication) they either shifted to alternative food sources nearby or moved away. (Clausen and Percival, 1998).

Important food items for birds on intertidal flats include the gastropod *Hydrobia ulvae*, the cockle *Cerastoderma edule*, the polychaete *Nereis diversicolor*, the mussel *Mytilus edulis*, the amphipod *Corophium volutator* and the clam *Macoma balthica*, and several studies have found spatial associations between shorebirds and abundance of prey species (Green et al., 1990). Some of these prey items are negatively affected by eutrophication, especially at extreme nutrient loadings, but overall invertebrate abundance is likely to be greater, and birds that are able to be flexible in prey choice should benefit.

3.5.4.1. Shorebirds (waders and wildfowl)

Sewage outflows improve food availability for intertidal waders and other shorebirds, and historical increases in sewage inputs to estuaries and tidal waters have generally resulted in increases in bird populations. In Langstone Harbour, sewage effluent input increased from the 1950s to the 1970s, as did the extent of mats of the macroalgae *Enteromorpha* and *Ulva*, and eelgrass (*Zostera*) beds (Tubbs, 1977). In the same period winter numbers of oystercatcher, grey plover, black-tailed godwit, bar-tailed godwit, knot, dunlin, dark-bellied brent goose, teal and wigeon increased, while numbers of shelduck, redshank and possibly curlew declined. Brent goose and possibly wigeon would have benefited from extra grazing on *Enteromorpha* and *Zostera*, and although a reduction in invertebrate density may have been expected, most shorebirds did indeed forage on these (Tubbs, 1977). Under the mats *Capitella capitata* was the main invertebrate surviving, but within the mats *Hydrobia*, *Gammarus locusta* (amphipod), *Nereis diversicolor* and common shore crab (*Carcinus maenus*) were present.

In the Wadden Sea, the biomass of benthic organisms more than doubled between the 1970s and 1990s as a result of eutrophication, to the benefit of many species, such as eiders and oystercatchers (Meltøfte et al., 1994). However, changes due to eutrophication, particularly the loss of eelgrass beds, but also changed benthos communities and anaerobic sediments were considered to have contributed to the decline of some species. In the Scheldt estuary of the Netherlands, ecological deterioration (including pollution other than nutrients) between the 1950s and 1980s probably led to a greater food supply for intertidal birds; species richness of the macrobenthic community (polychaetes, amphipods, decapods and molluscs) fell, but numbers of polychaetes and amphipods increased (van Impe, 1985). Over the same period, several intertidal bird species (oystercatcher, grey plover, bar-tailed godwit, redshank, spotted redshank, avocet and black-headed gull) doubled their mean spring/summer abundance. Curlew increased to a lesser extent, while the common sandpiper remained stable, and only ringed plover declined. In the Ythan estuary in Scotland, phosphorus and nitrogen loadings increased between 1966-67 and 1980-84 (Raffaelli et al., 1989). Despite the inability of the amphipod *Corophium volutator* (one of the main prey items of birds in the estuary) to tolerate the macroalgal mats that developed, winter populations of six bird species increased over the period, four of them (mute swan, curlew, redshank and dunlin) contrary to national trends: only shelduck populations declined. An overall increase in productivity, and of invertebrates able to tolerate macroalgal mats, such as the polychaete *Capitella capitata*, was suggested as the reason for the observed increases (Raffaelli et al., 1989).

Removal of sewage discharges or improvement to sewage treatment is expected to reduce shorebird populations, although this has not been observed everywhere (Eaton 2000b; Burton et al., 2004). In the latter study, spatial changes in biological oxygen demand in several British estuaries were not related to waterbird numbers, although at the four sites with greatest reductions, a significantly higher proportion of species declined following improvements. The lack of change in bird populations may be due to difficulties in determining changes at an appropriate scale, or because insufficient time had elapsed to discern changes (Burton et al., 2004).

Elsewhere reduced anthropogenic inputs have had measurable impacts on bird populations. In the Clyde estuary winter numbers of dunlin, redshank and lapwing declined considerably following the reduction of sewage and industrial effluent in the 1970s (Furness et al., 1986). These species fed predominantly on the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor*, and loss of food items, or competition for food from increasing fish populations in the re-oxygenated waters are suggested as the cause of their declines, which were not consistent with national trends. Both food items are abundant in eutrophic conditions, although *Corophium volutator* is sensitive to the macroalgal mats; it may be that no (or few) such mats were present in the Clyde estuary during the period of nutrient enrichment. In Portugal, a study of the wader community of an increasingly urbanised estuary found the presence of sewage discharge points to be positively related to grey plover abundance, and the presence of untreated sewage points to be positively related to black-backed gull abundance (Rosa et al., 2003). Abundances of other species, including avocet, black-tailed godwit and common sandpiper were not related to the presence of sewage points. Wildfowl and waders in the Forth estuary between the 1970s and 1980s also showed large declines, attributed largely to reductions in effluent inputs (Bryant, 1987).

While eutrophication may provide more food resources for many bird species, in situations of extreme eutrophication those food resources may be lost. Where macroalgal mats develop on tidal flats they may reduce the abundance or availability of invertebrate food items. In tidal flats in Portugal macroalgal biomass was positively related to prey density and biomass (Cabral et al., 1999). However, macroalgal coverage was negatively related to the distribution of dunlin, ringed plover and grey plover (but not Kentish plover), although other variables were also identified in the multiple regression, notably a negative relationship with gull abundance for all species except for grey plover. The answer may lie in the effect over time on the abundance and availability of sediment fauna. On tidal flats in the Wadden Sea of the Netherlands, few foraging birds were observed in an area covered by green algal mats, but when algal mats were manually transferred to areas of bare mud dunlin, ringed plover and black-headed gull were attracted to them (Metzmacher and Reise, 1994). This is explained by the movement of sediment fauna moving upwards to avoid

anoxic conditions, while at long-established mats this source of food had already been depleted. The presence of algal mats may provide a short-term flush of food, due to increased availability, but if the mats persist then the food source will become exhausted. Thus nutrient pollution may have complex effects on bird abundance, reducing the abundance of some important food items (Pounder, 1976), but initially increasing abundance and availability of alternative food items before anoxic conditions remove this alternative food source. Ephemeral algal mats will be attractive to birds provided there is sufficient opportunity for recolonisation of invertebrates between periods of coverage by algal mats (Metzmacher and Reise, 1994).

3.5.4.2. Shelduck

Shelduck is one species typical of tidal waters for which there is evidence for sensitivity to the effects of eutrophication, although following improvement to waste discharges in British estuaries, they declined at more sites than they increased at (Burton et al., 2004). Nevertheless, they appear to be less able to exploit food resources where macroalgal mats are prevalent. The distribution of shelduck in several estuaries has been found to be positively related to *Hydrobia ulvae* abundance (Bryant and Leng, 1976; Green et al., 1990), which in turn is negatively affected by eutrophication, specifically macroalgal mat blooms (Lillebø et al., 1999; Cardoso et al., 2005). Shelduck do not appear to be able to exploit the flush of food created by the movement of infauna to the surface, and avoided feeding on macroalgal mats in Langstone Harbour, perhaps because they do not take alternative prey or because it hinders their foraging method (Tubbs, 1977; Raffaelli et al., 1989). British estuaries are important wintering locations for shelduck in Europe, and so reduced nutrient loadings ought to improve their food supply (Bryant and Leng, 1976).

3.5.4.3. Gulls

Gulls were one of the major beneficiaries of sewage outflows into British estuaries (Raven and Coulson, 2001). In the Tyne estuary, gull numbers (except for those of kittiwake) were expected to drop following the implementation of sewage treatment. Two species, common gull and great black-backed gulls declined by over 90% between 1969-70 and 1993-94, but numbers of herring gull and black-headed gull did

not change significantly, and those of lesser black-backed gull and kittiwake rose dramatically (Raven and Coulson, 2001). Black-headed gull appeared to have located an alternative food source within the estuary, while the other species that did not decline significantly fed predominantly outside the estuary.

3.5.5. Coastal waters (diving ducks)

Waterfowl, notably diving ducks, have been observed to be associated with sewage outfalls at various sites in Scotland, and have declined where sewage outfalls have been closed (Pounder, 1976; Fox and Salmon, 1988). In the 1970s, two species of diving duck (scaup and goldeneye) in the Firth of Forth were distributed in a manner that suggested that they were exploiting food resources (invertebrates and grain) from sewage outfalls (Campbell, 1978). Both species showed declines in numbers, as well as changes in distribution, following the introduction of sewage treatment in the late 1970s, that were consistent with changes in food abundance as a consequence of changes in nutrient levels. The effects on three other species (eider, common scoter and long-tailed duck) were less clear (Campbell, 1984).

3.5.6. Summary

The indirect effects of eutrophication on birds depend strongly on habitat type and locality. Some general trends of responses by bird populations to increased nutrient loading are included in Table 3.5. The most consistently negative effects on birds occur in freshwater lakes, where eutrophication leads to a shift in stable state to phytoplankton dominance and turbid water. In such circumstances food supplies for a range of waterbirds are drastically reduced, and historical censuses have shown strong relationships between the trophic status of lakes and bird populations. In naturally oligotrophic lakes, pursuit piscivores may be affected by relatively minor increases in nutrient status, as these may reduce water transparency and alter size distributions of prey species.

Shorebirds generally benefit from nutrient inputs to tidal areas, as the increased productivity provides food resources, even though the invertebrate community composition may differ. The exceptions are where there is extended eutrophication, such that macroalgal mats persist and the infauna declines, and some species that are unable to adjust foraging techniques and food preferences. Reduction of anthropogenic nutrient inputs is likely to reduce shorebird populations, at least locally, and this has been observed at some sites where sewage treatment has occurred. Similar trends have been observed in diving ducks of coastal waters where sewage outfalls have been closed.

Table 3.5. General trends of effects of nutrient increases on bird populations in aquatic habitats.

Group	Response	Typical species
dabbling herbivorous and omnivorous waterfowl	decline due to loss of food resources in phytoplankton-dominated state	mute swan, coot, wigeon, pintail
diving benthivores (fresh waters)	decline due to loss of food resources and reduced water transparency in turbid water conditions	goldeneye, pochard, tufted duck, scoters
diving benthivores (coastal waters)	increase due to greater food availability	scaup, goldeneye
pursuit divers (oligotrophic lakes)	decline due to reduced water transparency and changes to fish size distribution	red-throated diver, black-throated diver
pursuit divers (mesotrophic lakes)	possible increase due to increased prey abundance	goosander, red-breasted merganser, great-crested grebe
reedbed specialists	decline due to loss of habitat and reduced food resources	bittern, other possibilities include bearded tit and water rail
shorebirds (waders and wildfowl)	increase due to greater food availability, except where macroalgal mats are persistent; specialist feeders may decline	oystercatcher, dunlin, grey plover, knot, redshank (and other waders), wintering geese; shelduck (decline)
gulls	increase due to greater food availability	common gull, great black-backed gull

4. Upland moorland and lowland heath

4.1. Introduction

Upland moorland and lowland heath are both important habitats, from aesthetic, conservation and economic points of view. Both are distinguished by ericaceous dwarf shrubs, particularly heather *Calluna vulgaris* (henceforth referred to as *Calluna*), although grass-dominated plant communities also occur in heathland and moorland (Thompson et al., 1995). Both habitat types share other similarities, including a requirement for regular vegetation disturbance either at intermediate intervals (typically by fire) or at low intensity on a continual basis (typically by grazing) for their maintenance, and distribution on predominantly low nutrient soils. Upland moorland occurs in the submontane zone, above enclosed agricultural land. The lower altitude boundary varies geographically but typically occurs at around 300-400 m asl, although it can occur at much lower altitudes than this in the far north, while lowland heathland occurs below the submontane zone (Thompson et al., 1995). Upland moorland is a large-scale mosaic of heather moorland, dominated by *Calluna*, and grass moorland, dominated by *Agrostis* spp. *Festuca* spp. or *Nardus stricta*. It includes large areas of blanket bog, whilst marshy grassland and bracken are also present depending on geography and management. A considerable amount of upland moorland is managed for grouse, and is rotationally burned in patches to provide young shoot as food and older plants as cover (Brown and Bainbridge, 1995). Lowland heath similarly forms a mosaic of *Calluna*-dominated vegetation and grassland, typically dominated by *Deschampsia flexuosa* and *Molinia caerulea*. It has little economic use except for low intensity grazing and recreation.

Calluna is a seral dominant, passing through four phases in most circumstances in which it grows: pioneer, where it colonises and is associated with other species; building, the phase of maximum growth, where it forms a dense canopy and excludes other species; mature, where the canopy becomes uneven and signs of gaps appear; and degenerate,

when plants begin to die back and gaps become obvious (Gimingham, 1995). Heathland and moorland occur naturally where conditions are too severe for trees and tall shrubs, but the greatest part of these habitats present today is of anthropogenic origin (Heil and Aerts, 1993). Human management, particularly grazing and burning, plays a large part in the maintenance of heath and moorland communities. Moderate grazing will maintain heather in its productive phase, while stimulation of regeneration by appropriate fire management will virtually by-pass the pioneer phase (Gimingham, 1995).

There has been a decline in the extent of lowland heath in Europe, some of which has been the result of conversion to forestry and agriculture, but also due to transition to grassland, scrub and woodland (Bunce, 1989; Aerts and Heil, 1993). A similar decline has occurred in the UK (Rose et al., 1999; Smart et al., 2003). The decline of traditional management practices, such as woodcutting, burning and turf-stripping, has been suggested as a further cause for the transition (Diemont and Heil, 1984), along with nitrogen deposition, which will be discussed below. Upland moorland has also experienced a decline in the cover of heather in many areas, due to afforestation, conversion to grassland, from increased grazing levels and agricultural improvements, bracken encroachment and poor burning management (Miles, 1988; Cadbury, 1992; Bardgett et al., 1995; Gimingham, 1995; Mackey et al., 1998; Fuller and Gough, 1999; Haines-Young et al., 2000). In England and Wales, the land area covered by heather fell from 631,400 to 509,800 hectares between 1947 and 1980 (Thompson et al., 1995). In Scotland, heather cover declined by 23% (over 300 000 ha) in the period 1947-1988, over half of which was attributed to afforestation (Mackey et al., 1998). Causes of the decline are varied but include overgrazing (leading to invasion of grasses), afforestation (the cause of over half the heather loss in Scotland), conversion to farmland, and succession to scrub.

4.2. Bird population trends in moorland and heath

There has been considerable debate about what constitutes the avifauna of the uplands and several publications have attempted to compile lists depending on various criteria

(Thompson et al., 1988; Ratcliffe, 1990; Stillman and Brown, 1998; Beeston, 2005). Most of these lists include species typical of upland habitats other than moorland, and therefore I consider that the list of 40 species typical of upland heather moorland compiled by Thompson et al (1995) is the most appropriate for the current review. From this list I concentrate on species for which there is evidence linking atmospheric deposition of nitrogen to population changes, and/or mechanisms by which population changes could occur. However, in doing this it is important to note that there are many potential drivers of changes in populations of upland bird species, notably those related to changes to climate and land management. Although the relative importance of these different causes is often unknown, the evidence available from existing studies tends to indicate that factors associated with land management and climate change are likely to be of greatest importance in determining changes in bird abundance on moorlands (Hudson 1992; Etheridge et al., 1997; Fuller and Gough, 1999; Thirgood et al., 2000; Tharme et al., 2001, Calladine et al., 2002, Amar and Redpath 2005; Beale et al., 2006, Pearce-Higgins and Grant, 2006), although few/no studies have attempted to assess effects of increased nitrogen deposition directly.

Despite the debates about which species are included in a list of upland bird species, it is undeniable that the British uplands support internationally important populations of birds, and many of these use heather moorland either for breeding or feeding (Ratcliffe and Thompson, 1988; Thompson et al., 1995). The use of moorland by bird species is summarised in Table 4.1, along with population trends for some species. Population trends of upland breeding birds are generally less well known than are those for lowland birds, largely because of the extremely low coverage of upland areas in the CBC and the fact that they remain under-represented in the BBS. Therefore, where national population trends from these sources are presented for species that occur in both upland and lowland habitats the trends cannot be assumed to be representative of those for the moorland component of the population of that species, and may in fact be highly unrepresentative of it. Therefore, the most reliable evidence for population changes generally come from repeat surveys, some of which are national surveys with representative coverage, such as black grouse national surveys (Sim et al., unpubl. data), but most of which are derived

Table 4.1. Bird species considered typical of upland moorland or lowland heath and considered for review of effects of nitrogen deposition

Species ¹	Listing ²	Long term trend (1970-2003) ³	10-year trend (1994-2004) ⁴	Use of moorland ⁵	Migrant status ⁶	Nesting habit
white-fronted goose	amber			feeding habitat	w	n/a
teal	amber			major breeding habitat	r + w	ground
red grouse	amber		-4	confined	r	ground
black grouse	red	decline	-22 ^a	major breeding habitat	r	ground
red kite	amber			feeding habitat	r	tree
hen harrier	red		44 ^b	breed mainly on moorland	r	ground
buzzard	green			feeding habitat	r	tree/cliff
goshawk	green			feeding habitat	r	tree
golden eagle	amber			feeding habitat	r	tree/cliff
kestrel	amber	-26 ^a	-19	feeding habitat	r	hole/ledge
merlin	amber			breed mainly on moorland	r	ground
peregrine	amber			feeding habitat	r	cliff
oystercatcher	amber			locally important breeding habitat	r + w	ground
golden plover	green			breed mainly on moorland	r + w	ground
lapwing	amber	-45 ^a	-13	locally important breeding habitat	r + s	ground
dunlin	amber			major breeding habitat	r + w	ground
snipe	amber			locally important breeding habitat	r + w	ground
whimbrel	amber			major breeding habitat	s + p	ground
curlew	amber	-46 ^a	-34	major breeding habitat	r + w	ground
redshank	amber			locally important breeding habitat	r + w	ground
greenshank	green			major breeding habitat	s + w + p	ground

¹ a full list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends based on CBC/BBS or individual surveys (b-d) (Eaton et al., 2005). a = may be unrepresentative, b = 1970-2000, c = 1981-2004, d = 1970-1997

⁴ population trends based on BBS or individual surveys (a-e) (Eaton et al., 2005). a = 1995/6-2005 (Sim et al., unpub.data), b = 1998-2004, c = 1995-2000, d = 1992-2004, e = 1986-1997

⁵ use of moorland as described by Thompson et al. (1995).

⁶ migratory status of birds. r = resident, w = winter visitor, s = summer visitor, p = passage. Birds may have several listings, as migration may be partial. For example, many passerines leave moorland in winter, while wader populations in the UK are boosted in winter by migrants.

Table 4.1. (cont.) Bird species considered typical of upland moorland or lowland heath and considered for review of effects of nitrogen deposition

Species ¹	Listing ²	Long term trend (1970-2003) ³	10-year trend (1994-2004) ⁴	Use of moorland ⁵	Migrant status ⁶	Nesting habit
Arctic skua	green			major breeding habitat	s	ground
great skua	amber			major breeding habitat	s	ground
common gull	amber			major breeding habitat	r + w	ground
cuckoo	amber	-44 ^a	-19	major breeding habitat	s	parasitic
short-eared owl	amber			major breeding habitat	r + w	ground
skylark	red	-53	-10	major breeding habitat	r + s	ground
meadow pipit	amber	-32 ^a	-2	major breeding habitat	r + s	ground
wren	green	68	14	locally important breeding habitat	r	scrub/shrubs
whinchat	green		-15	major breeding habitat	s	ground
stonechat	amber		135	major breeding habitat	r	ground/shrubs
wheatear	green		7	locally important breeding habitat	s	ground cavities
ring ouzel	red			major breeding habitat	s	ground
grasshopper warbler	red		59	locally important breeding habitat	s	scrub/shrubs
whitethroat	green	-5	39	locally important breeding habitat	s	scrub/shrubs
willow warbler	amber	-45 ^a	0	locally important breeding habitat	s	scrub/shrubs
carrion crow	green	78	11	feeding habitat	r	trees/ledges
raven	green		91	feeding habitat	r	ledges
twite	red			locally important breeding habitat	r + w + s	ground
stone curlew	red	-15 ^b	54 ^c	lowland heath species	s	ground
Dartford warbler	amber			lowland heath species	r	low shrubs
nightjar	red	114 ^c	32 ^d	lowland heath species	s	ground
woodlark	red	704 ^d	544 ^e	lowland heath species	r + p	ground

¹ a full list of scientific names is included in Appendix 1.

² indication of conservation concern (Gregory et al., 2002).

³ population trends based on CBC/BBS or individual surveys (b-d) (Eaton et al., 2005). a = may be unrepresentative, b = 1970-2000, c = 1981-2004, d = 1970-1997

⁴ population trends based on BBS or individual surveys (a-e) (Eaton et al., 2005). a = 1995/6-2005 (Sim et al., unpub.data), b = 1998-2004, c = 1995-2000, d = 1992-2004, e = 1986-1997

⁵ use of moorland as described by Thompson et al. (1995).

⁶ migratory status of birds. r = resident, w = winter visitor, s = summer visitor, p = passage. Birds may have several listings, as migration may be partial. For example, many passerines leave moorland in winter, while wader populations in the UK are boosted in winter by migrants.

from selected sites (Hancock and Avery, 1998; Fuller et al., 2002; Sim et al., 2005). Re-surveys of a range of upland areas (including a mixture of upland habitats in addition to heather moorland) found declines in some species, particularly waders, but increases in others, with geographical variation in population trends (Sim et al., 2005). While lowland heath is used by a number of species, four species of high conservation concern are closely associated with the habitat: Dartford warbler, stone-curlew, woodlark and nightjar. Population trends and life history characteristics of these species are also included in Table 4.1.

4.3 Effects of nutrient increases on vegetation

In upland moorland, atmospheric deposition of nitrogen, particularly wet deposition of ammonium and nitrate, is the major source of nutrient inputs. This source of nitrogen is also important for other naturally low-nutrient vegetation types in upland areas, including ombrotrophic mires and unimproved grassland (Carroll et al., 2003; Tomassen et al., 2004). Increased levels of deposition may have impacts on all of these vegetation types, and has also been implicated in the decline of montane moss heaths (Ratcliffe and Thompson, 1988; Pearce and van der Wal, 2002). Atmospheric deposition of nitrogen is also important as a nutrient source for lowland heath, but dry deposition, especially of ammonia, dominates these areas (Carroll et al., 1999); Lowland heaths receive additional amounts of nutrients from sources such as fertiliser drift. The effects of increased nutrient levels on *Calluna*-dominated vegetation are summarised in Table 4.2. Much of the understanding of the effects of nutrient levels to *Calluna*-dominated ecosystems has arisen from attempts to restore the vegetation in the face of shifts towards grassland and scrub. There is evidence of the effects of nitrogen on *Calluna* relevant to both upland moor and lowland heath. *Calluna* foliar nitrogen concentrations in the UK show spatial relationships with levels of atmospheric nitrogen deposition (Pitcairn et al., 1995). Shoot growth is stimulated by the addition of nitrogen both in moorland and lowland heath (Power et al., 1995; Uren et al., 1997; Power et al., 1998a; Carroll et al., 1999), although the marked increases in shoot growth may not persist, possibly due to a shift to limitation

by other nutrients (Carroll et al., 1999). Additions of nitrogen are retained predominantly in vegetation and litter at lower levels of application (40 kg N/ha/year), but at higher levels (80 and 120 kg N/ha/year) considerable quantities of nitrogen accumulate in the soil (Pilkington et al., 2005). Management of heath and moor by grazing, turf cutting, and especially burning, is important to maintain low soil nutrient status by exporting accumulated nutrients (Barker et al., 2004).

Increased nitrogen content of heather leaves leads to higher sensitivity to winter desiccating conditions, although this was initially thought to be sensitivity to frost (Heil, 1984, in de Smidt, 1995; Power et al., 1998b). In upland moorland, addition of nitrogen improved *Calluna* frost hardiness in the first 4-5 years, but late winter browning was subsequently observed in fertilised plots, leading to gaps in the canopy (Lee and Caporn, 1998). As healthy shoots were not more sensitive to frost, a possible cause for the winter browning may be sensitivity to winter and early spring desiccating conditions (Carroll et al., 1999). Similar late winter/early spring sensitivity to drought was observed in Dutch lowland heath (van der Eerden et al., 1991). Summer drought has also caused dieback of *Calluna* in lowland heath, and water stress was greatest in nitrogen-rich conditions, because of the increased root biomass in the topsoil and increased water demand from the increased *Calluna* biomass (Berdowski et al., 1985, in Berdowski, 1993). The presence of competing grass species may exacerbate the problem by slowing the movement of water to deeper soil layers. In Scottish acid moorland, *Calluna* foliar nitrogen concentrations increased with both dry deposition of nitrogen (of ammonia) and wet deposition (of ammonium), whereas several other species, including important grass competitors, responded only to wet deposition (Leith et al., 2001). Autumn and winter water loss rates for *Calluna* increased with ammonia applications. Susceptibility to drought is considered more likely than reduced frost hardiness to be the cause of loss of *Calluna* in areas of heightened nitrogen deposition (Sheppard and Leith, 2002). A decrease in the root to shoot ratio observed in *Calluna* subjected to experimental applications of nitrogen may explain this sensitivity (van der Eerden et al., 1991).

In addition to its effects on drought sensitivity, addition of low levels of nitrogen to *Calluna* in lowland British heath increased larval growth rates and adult weights of heather beetles (*Lochmaea suturalis*) (Power et al., 1998b). Similar effects were observed in the Netherlands (Brunsting and Heil, 1985; van der Eerden, 1991). Heather beetles feed monophagously on *Calluna* and during outbreaks form high population densities that can have severe impacts on *Calluna* foliage and canopy cover, water transport in the xylem, and the ability to store carbohydrates in the fine roots (Berdowski, 1993). Physiological consequences of leaf damage seem to be a more important cause of heather dieback than defoliation (Pakeman et al., 2004). Increased nitrogen uptake by heather increases the nutritive value of its leaves, and this means that heather beetle can build up dense populations more quickly (de Smidt, 1995), although decreased bryophyte cover in response to fertiliser can reduce egg and pupal survival (Berdowski, 1993). Improved insect performance in response to increased foliar nitrogen content has the potential to increase insect damage and contribute gaps in *Calluna* canopy (Brunsting and Heil, 1985).

4.3.1. Upland moorland

Atmospheric deposition of nitrogen has been implicated as a major cause of the shift from *Calluna*-dominated to grass-dominated moors. However, increased nutrient levels alone generally do not lead to the decline of *Calluna*, and are in fact unlikely to be the main factors driving the conversion of heather to grass on moorlands. The interaction between increased nutrient levels and disturbance, particularly grazing, may be important. Nevertheless, some moorland elements are directly affected by nitrogen levels. Bryophytes are especially sensitive to increased atmospheric nitrogen deposition, and the loss of these elements from upland moors may lead to increased leaching of nitrogen from the soil (Carroll et al., 2003; Curtis et al., 2005). Fertilised plots in Wales lost moss and lichen cover over a period of several years (Lee and Caporn, 1998). Bryophytes may also be negatively affected by increased shading from shrub species that grow taller and denser in response to increased nitrogen deposition. Application of fertiliser can change

Table 4.2. Some effects of increased nutrient inputs on the vegetation of lowland heath and upland moor

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Lowland heath	cryptogams	Netherlands	application of nitrogenous fertilisers	loss of lichens and bryophytes, then increase in grasses and other invasive species	direct effect of fertiliser on cryptogams	1	de Smidt, 1995
	<i>Calluna</i> and <i>Deschampsia flexuosa</i>	Netherlands	experimental additions of N (10 or 50 kg/ha/year); other treatments (soil type, watering)	<i>D. flexuosa</i> reduced <i>C. vulgaris</i> yields when grown together, but no extra effects of N addition	addition of nitrogen does not alter competitive balance	1	Britton et al., 2003
	<i>Calluna</i> and <i>Festuca ovina</i>	Netherlands	experimental addition of N (up to 28 kg/ha) and P on heathland plots over 11 years	replacement of <i>Calluna</i> by <i>Festuca</i> at the highest rate of N application, no effect of P	competitive balance, also attack by heather beetle	1	Heil and Diemont, 1983
	<i>Calluna</i> , <i>Erica</i> and <i>Molinia caerulea</i>	Netherlands	experimental addition of N (0-20 g/m ² /year), P (0-4 g/m ² /year) and K (0-20 g/m ² /year)	when grown together, <i>Calluna</i> out-competed <i>Molinia</i> ; <i>Erica</i> out-competed <i>Molinia</i> in all but the highest nutrient treatment	superior competitive ability of <i>Calluna</i> and <i>Erica</i> for light	1	Aerts et al., 1990
	<i>Calluna vulgaris</i> and heather beetle	Netherlands	experimental addition of N	faster growth of larvae	nutrient content of foliage	1	Brunsting and Heil, 1985
	<i>Calluna</i> , grasses and heather beetle	Netherlands	experimental addition of ammonium and ammonia (applications ranged from 0-240 µg/m ³ of N)	larval growth of heather beetle increased with N addition; <i>Calluna</i> drought sensitivity increased with N addition	foliar nitrogen content; possibly increased transpiration and decreased root:shoot ratio	1	van der Eerden et al., 1991
	<i>Calluna vulgaris</i>	East Anglia	changes to vegetation in 11 heath sites 1983-1991	variety of changes, ranging from continued <i>Calluna</i> dominance to invasion by grasses	effects of N inputs, such as frost sensitivity, herbivory and competitive balance; most sites were unmanaged for this period	3	Marrs, 1993

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

Table 4.2. (cont.) Some effects of increased nutrient inputs on the vegetation of lowland heath and upland moor

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Lowland heath	<i>Betula</i> spp.	Dorset	experimental addition of P (0, 1, 2 or 3 additions of 17.6 kg/ha); manipulation of seed availability and disturbance	seed availability the greatest limitation to seedling density; P additions and disturbance also increased seedling density	greater ability of <i>Betula</i> to use inorganic P	1	Manning et al., 2004
	<i>Calluna vulgaris</i>	Surrey	experimental addition of nitrogen (7.7 or 15.4 kg/ha/year) to <i>Calluna</i> plots over 7 years	increased above-ground growth and litter production even at low levels of N addition; no shift in vegetation composition	increased productivity with increased nutrients; insufficient time for changes to take place	1	Power et al., 1998a
	<i>Calluna vulgaris</i>	Surrey	management by mowing or burning; application of 0 or 30 kg N/ha/year	lower positive effect of N on shoot growth with intensive management; <i>Deschampsia</i> invasion greater with N addition	greater export of nutrients in intensively managed plots; competitive advantage of grasses in disturbed and fertilised plots	1	Barker et al., 2004
Upland moor	<i>Calluna vulgaris</i>	Britain	spatial relationship between foliar N concentrations and rates of atmospheric N deposition	generally linear positive relationship	increased uptake of available nitrogen	2	Pitcairn et al., 1995
	<i>Calluna vulgaris</i>	Wales	experimental additions of N (0-20 g/m ² /year) over 9 years	stimulated growth and improved frost hardiness for first 4 years, then winter browning in plots receiving ≥ 8 g/m ² /year; loss of moss and lichen understorey	inability to maintain foliar water content under winter desiccating conditions	1	Lee and Caporn, 1998

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Table 4.2. (cont.) Some effects of increased nutrient inputs on the vegetation of lowland heath and upland moor

Habitat	Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
Upland moor	<i>Calluna</i> and grasses	NE Scotland	grazing exclusion and addition of fertiliser (7.5 g/m/year N, 2.5 g/m/year P, 5 g/m/year K)	effect (+) of fencing on <i>Calluna</i> height and growth, marginal effect (+) of fertiliser on height, interactive effect (+) on growth; generally positive effects of fencing on grasses (see text)	lack of direct negative effects of fertiliser on <i>Calluna</i>	1	Alonso et al., 2001
	<i>Calluna</i> and grasses	NE Scotland	grazing exclusion and addition of fertiliser (75 kg/ha/year N, 12.5 kg/ha/year P, 25 kg/ha/year K)	effect (-) of grazing on <i>Calluna</i> cover, and interaction (-) with N addition, (no independent effect of N); increase in grass cover in response to N addition, species determined by grazing	improvement of <i>Calluna</i> as forage, and ability of grasses to invade where heather canopy is disturbed	1	Hartley and Mitchell, 2005
	<i>Calluna</i> and grasses	NE Scotland	grazing exclusion and fertiliser addition (75 kg/ha/year N, 12.5 kg/ha/year P, 25 kg/ha/year K)	<i>Nardus stricta</i> acquired nutrients faster than <i>Calluna</i> in pots, but only favoured in grazed plots	ability of <i>Calluna</i> to close canopy in the absence of grazing	1	Hartley, 1997
	seven species, including <i>Calluna</i> , <i>Molinia caerulea</i> and <i>Deschampsia flexuosa</i>	SE Scotland	experimental addition of nitrogen as ammonia (0-128 kg N/ha/year) and ammonium (4-48 kg N/ha/year)	foliar N increased with ammonium for all species, but with ammonia for only two species (including <i>Calluna</i>); <i>Calluna</i> autumn/winter water loss increased with ammonia (compared with ammonium)	biological differences between plant species	1	Leith et al., 2001

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the species composition of moors by suppressing herbs at the expense of tall growing grasses (Schellberg et al., 1999).

Moorland is in a dynamic balance between heather, grass, scrub and woodland, and grazing is vital to maintain this balance (Miles, 1988). However, sheep numbers increased markedly in most upland regions of Britain in the 1970s and 1980s (Fuller and Gough, 1999), and this has coincided with changes in the cover of heather and grass in the uplands. Red deer (*Cervus elephus*) have also increased in the Scottish highlands (Clutton-Brock et al., 2004). The succession of heather moorland to grassland (dominated by species such as *Deschampsia flexuosa*, *Nardus stricta* and *Molinia caerulea*) under conditions of heavy grazing has been well documented and much of the evidence is summarised in Thompson et al. (1995). Increased grazing pressure by sheep is the likely main cause of the long-term loss of heather moorland in the northern Peak District (over one third lost 1913-1976) (Anderson and Yalden, 1981). More widely across the UK, increases in sheep numbers are generally considered as the main cause of the conversion of heather to grass-dominated moorland, although this is often in combination with inappropriate management regimes (Bardgett et al., 1995, Thompson et al. 1995, Mackey et al. 1998). In north-east Scotland, a stocking rate of 2.7 sheep/ha was estimated to cause heather decline given average heather growth of 4.7 cm/year, although the potential effects of cattle grazing were considered more substantial (Welch, 1984). Sheep graze grasses in preference to *Calluna*, and so at low to intermediate grazing levels heather cover increases. However, at high levels of grazing *Calluna* will be grazed, and the disturbance of the heather canopy allows grasses to invade. Increased stocking rates have probably not been driven by increased nitrogen deposition, but rather by agricultural funding mechanisms. Nitrogen deposition may have facilitated increased grazing to some extent, by increasing the nutritive value of vegetation, but the importance of this, while very difficult to determine, is likely to have been small.

In moorland and heathland, *Calluna* is usually a more effective competitor than grasses, even at high nutrient levels (Alonso et al., 2001), although the findings of some studies do not concur with this (van der Eerden et al., 1991). While grazing has independent

effects on heather cover, interactions with fertiliser applications have been observed. In Aberdeenshire, *Nardus stricta* acquired fertiliser nutrients faster than *Calluna* in pots, but fertiliser addition in the field (which included phosphorus and potassium as well as nitrogen) only favoured *Nardus stricta* in unfenced areas. This is possibly because in the absence of grazing *Calluna* was able to close its canopy and exclude the shade-intolerant grass (Hartley, 1997). Exclusion of grazing had a greater (positive) impact on the performance of *Calluna* and grasses (except for the unpalatable *Nardus stricta*) than did the addition of nutrients, although *Deschampsia cespitosa* responded positively to fertiliser addition, and *D. cespitosa* (height) and *Calluna* (growth) both showed positive interactions between fertiliser and exclusion of grazing (Alonso et al., 2001). Excluding grazing significantly benefited *Calluna*, while *Calluna* cover declined on grazed plots, even where they were unfertilised (Hartley and Mitchell, 2005). However, fertiliser application increased the rate of grazing on *Calluna*, which may be influenced by its proximity to grass patches (Palmer et al., 2003). In the absence of grazing, increased nitrogen did not lead to a loss of *Calluna* cover, even after six years of fertiliser addition, but there was a marginally significant ($p=0.05$) fertiliser/fencing interaction; *Calluna* cover declined by over 40% on grazed plots with nitrogen added, but under 20% in grazed plots without nitrogen added (Hartley and Mitchell, 2005). Grass cover increased with nitrogen addition, although which species increased was determined by whether or not the plot was grazed. Invasion by bracken has also caused loss of heather moorland, and some studies have suggested that nitrogen availability mediates competition between bracken and *Calluna* (Anderson and Hetherington, 1999; Werkman and Callaghan, 1996, in Bobbink et al., 2003), possibly through interactions with water availability (Gordon et al., 1999).

Heather beetle outbreaks can also significantly affect heather cover. A survey of the extent of heather beetle damage in Scotland in 1997-2001 found that 5.4-10.4% of heather was affected, and that not all heather recovered (Pakeman et al., 2004). Nevertheless, the evidence suggests that the major threat to *Calluna* moorland in the British uplands is increased grazing intensity, although inappropriate burning regimes exacerbate the problem. Burning has the effect of exporting nutrients from moorland (and

lowland heath) vegetation. Grazing has independent negative effects on heather cover, while *Calluna* is able to out-compete grass species in the absence of grazing, even at high nutrient levels. Nevertheless, significant interactions between nutrient levels and grazing, suggesting that increased nitrogen deposition exacerbates the problem of heather loss due to grazing, even though the major cause of increased stocking densities has been agricultural subsidies. Nitrogen deposition may improve the forage value of *Calluna*, and of moorland grasses, which can lead to incidental grazing of nearby *Calluna* (Palmer et al., 2003).

4.3.2. Lowland heath

Lowland heath has been declining in northwest Europe since at least the late 1970s (de Smidt, 1995). Invasion by grasses (*Deschampsia flexuosa* in dry heaths and *Molinia caerulea* in wet heaths) able to out-compete *Calluna* at heightened nitrogen levels has been blamed for the changes; critical nitrogen loads to cause a shift from lowland heath to grassland have been determined to be in the range of 15-22 kg/ha/y (Heil and Bobbink, 1993). Cryptogams disappeared from Dutch lowland heath in experimentally fertilised plots prior to an increase in grasses, indicating a direct effect of fertilisers on these taxa (de Smidt, 1995). However, there have been some contradictory results from experiments designed to test the effects of nutrient additions. In the Netherlands, addition of nitrogen over 11 years saw a dramatic replacement of *Calluna* by *Festuca ovina*, which was facilitated in fertilised plots of mature *Calluna* by a heather beetle attack (Heil and Diemont, 1983). Conversely, while *Calluna* yield was reduced when grown with *D. flexuosa* in experimental pots, addition of nitrogen did not additionally affect competition between the species (Britton et al., 2003). *Calluna* was found to be competitively superior to *Molinia caerulea* at a range of levels of nutrient application, due to its light interception capacity, suggesting that the starting situation played an important role in allowing *Molinia* to displace *Calluna* (Aerts et al., 1990). In wet heaths grasses are competitively favoured over *Erica tetralix* at heightened levels of nitrogen application (Aerts, 1993).

Increased nitrogen availability stimulates both *Calluna* and grasses (Heil and Bruggink, 1987); the latter are only competitively superior in the early stages of heath development before a dense heather canopy has developed (Berdowski and Zeilinga, 1987; Aerts et al., 1990; Aerts, 1993). Thus other processes that open the canopy, including heather beetle attacks, drought or frost, increase the invasion of heath by grasses (Barker et al., 2004). However, these processes can be facilitated by increased nutrient availability, as heather beetle grazing is affected by the nutritional value of *Calluna*, its sole food plant (Crawley, 1983, in Bobbink et al., 1998), which in turn is increased by additions of nitrogen (as described above), which can increase the frequency, and severity of outbreaks (Bobbink et al., 1998). Outbreaks of heather beetles can cause large gaps to open up, allowing invasion of other species (Berdowski and Zeilinga, 1987). Heather beetles also increase nutrient availability, by reducing competition from *Calluna* for resources, and by the addition of nutrients from heather beetle larval faeces and *Calluna* decomposition.

In contrast to the concerns about increased grazing intensity on heather moorland, reduced management intensity in the forms of grazing and burning may be more of a threat to lowland heath (Barker et al., 2004). In the Breckland of East Anglia, a selection of heathlands showed a variety of changes over the period 1983-1991, from continued *Calluna* dominance, to almost complete replacement by grasses (Marrs, 1993). Heightened nitrogen inputs were suggested as a possible cause of the shifts, via such mechanisms as susceptibility to frost, increased herbivory, and changes in competitive balance, but it was noted that the sites had largely been unmanaged over much of the period, and there was no evidence for nitrogen deposition as the major causal factor. In the Netherlands free ranging cattle grazing restricted grass invasion, and led to a recovery of *Calluna* in grass-dominated heaths, although not on all soil types (Bokdam and Gleichman, 2000).

Transition to scrub and woodland has received less attention in the literature, but these habitats also displace lowland heath (Mitchell et al., 1997, 1999). In Dorset, the area of heathland declined, and fragmentation increased, between 1987 and 1996, which was

attributed largely to succession to scrub and woody vegetation (Rose et al., 1999). Experimental addition of phosphorus in Dorset heathland was positively related to *Betula* spp. seedling densities, although *Betula* seed availability was the single greatest limiting factor on seedling density (Manning et al., 2004). Phosphorus is limiting in these soils, and atmospheric nitrogen deposition may have played less of a role in the loss of heathland than changes to management, specifically reductions in grazing and burning (Rose et al., 1999).

4.3.3. Summary

The major effect of increased nitrogen levels in both moorland and lowland heath is a shift from *Calluna*-dominated vegetation to vegetation dominated by graminoids, although this is unlikely to happen on upland moorlands in the absence of at least moderate grazing pressure. Management regime and nitrogen inputs are critical in determining the magnitude of the changes. The changes in vegetation composition occur because of the shift in the competitive balance between *Calluna* and other species, in which nitrogen levels play an important role, although this is in conjunction with other factors that cause the heather canopy to break up. Application of nitrogen in the absence of other disturbance does not lead to the replacement of *Calluna* by grasses, but foliar nitrogen content helps to determine the frequency and severity of heather beetle attacks, while heather dieback, apparently due to drought sensitivity, is also heightened by atmospheric nitrogen deposition. Both of these mechanisms for the break up of heather canopy can be directly related to nitrogen deposition; an incontrovertible relationship with the third, and potentially most important, mechanism cannot be established. This is increased grazing pressure, which has been cited as the major cause for the loss of *Calluna* cover. Grazing has effects on heath and moorland vegetation independent of the effects of fertiliser, and stocking rates are likely to have increased in these habitats regardless of the nutrient status of soils, as funding mechanisms have been the major driver of increased grazing intensity. The increased primary productivity and nutritive value of vegetation resulting from atmospheric nitrogen deposition may have enabled

higher stocking rates than would otherwise have been possible, and the break up of heather canopy as a result of heavy grazing could have allowed for further increases in stocking rates. However, its contribution is practically impossible to determine, and is likely to have been small.

The mechanisms described above are likely to be major contributors to loss or change of upland moorland habitat in the United Kingdom. In lowland heath, despite a considerable body of work from lowland heath, particularly in the Netherlands (Aerts and Heil, 1993), atmospheric deposition of nitrogen appears to be less important in driving the loss of habitat, at least in the UK. This is not to say that nitrogen deposition is not a threat to lowland heath; rather that there are other processes that currently threaten to a greater extent, such as succession to scrub and woodland, and land clearance, notably for urban uses. One of the major problems presented by increased soil nutrient content has been its role as an obstacle to the recreation or restoration of lowland heath habitats (Smith et al., 1991; Pywell et al., 1994).

4.4 Effects of nutrient increases on invertebrate prey items

Studies of invertebrates in *Calluna*-dominated habitats have tended to examine the invertebrate community for its own intrinsic and conservation value, rather than as food items for birds, although this has been addressed in a recent review (Buchanan et al., in press). Although moorland birds take a wide range of invertebrate taxa, relatively few appear to be taken widely, with Diptera (particularly Tipulidae) and Coleoptera (particularly Carabidae, Curculionidae and Elateridae) being the most important. I present some background information on invertebrate communities in heath and moorland, both heather- and grass-dominated, but there is insufficient information available to systematically pursue connections between nutrient levels, these communities and bird populations.

The maintenance of high invertebrate species diversity on moorland has been shown to benefit from a mosaic of *Calluna* ages (Gimingham, 1985; McFerran et al., 1995; Haysom and Coulson, 1998; Dennis, 2003), and of heather-grass proximity (Coulson and Butterfield, 1985). Carabid beetle communities reflect vegetation development (Gardner, 1991), and carabid abundance is greatest in the pioneer and degenerate stages of *Calluna* development (Gimingham, 1985). In four invertebrate communities associated with moorland in northern England, worms comprised 24-92% of the standing crop, while Lepidoptera and Diptera formed important proportions of the standing crop in the various communities (Coulson and Butterfield, 1985; Coulson, 1988). At a site in the Pennines, spider abundance was lower in *Calluna/Eriophorum*-dominated moorland than in either *Festuca/Nardus* rough grassland or *Juncus squarrosus* sedgeland, although it was higher than in heavily grazed calcareous grassland (Cherrett, 1964). Across eight habitats spider abundance was significantly correlated with the abundance of other arthropods. An increase in grass cover in areas otherwise dominated by continuous heather cover is likely to increase invertebrate food supplies for birds (Buchanan et al., in press), although wet areas within moorland, which provide grouse, waders and insectivorous passerines with abundant invertebrate food in spring (Fuller and Gough, 1999). Invertebrate abundance and diversity are strongly affected by soil type and moisture content (Buchanan et al., in press), and these elements may be more important than the overlying vegetation (which may itself be partly determined by soil characteristics).

Increased nitrogen content is likely to increase abundance of phytophagous invertebrates in heather, and this was observed in Hemiptera following experimental fertiliser addition to plots on Scottish moorlands (Hartley et al., 2003), and Hemiptera species richness was higher in grass moor than heather moor in British uplands (Littlewood et al., 2006). Several groups of phytophagous insect have their greatest abundance in the pioneer or building stages, and management such as grazing and/or burning that promotes regeneration should maintain higher invertebrate density within heather (Gimingham, 1985). By contrast, some groups are more abundant in mature heather; in northern Britain, Lepidoptera larval abundance and diversity were positively related to *Calluna* height, due to the presence of uncommon moth species on taller *Calluna*, and a change in

the contribution of common species to the community in different height zones (Haysom and Coulson, 1998).

Grazing has indirect effects on the arthropod fauna of the uplands by modifying the vegetation structure (Dennis, 2003). High intensity grazing removes more above ground foliage, and reduced grazing intensity is likely to increase phytophagous invertebrates and spiders (Coulson, 1988). For example, invertebrate abundance was lower in heavily grazed rather than lightly grazed moorland in Scotland and northern England (Baines, 1996). In the Grazing and Upland Bird (GRUB) project in Scotland, foliar spiders, hemipterans and beetles all increased in abundance under reduced stocking densities, but tipulid larvae decreased (Dennis et al., 2005). Additionally, sheep dung supports some invertebrates, notably Diptera and some beetles, that would not be present in its absence, and which can be locally very abundant (Coulson, 1988). However, these studies were conducted in areas of graminoid-dominated moorland, where the effects of grazing, particularly in relation to the rate of increase in height and density of vegetation, are likely to be very different from those observed on heather moorland. Here was no shift from grass to heather moorland on any of the grazing treatments in the GRUB project (Dennis et al., 2005).

One invertebrate species for which there is strong evidence for the effects of nitrogen deposition, growth rates and population density is the heather beetle (Berdowski, 1993). While research has largely concentrated on the effects of outbreaks on *Calluna*, these beetles may be an important food source for birds, the availability of which is mediated by nutrient levels.

4.5. Effects of nutrient increases on birds

From the review of studies of the effects of nitrogen deposition on upland moorland and lowland heath vegetation presented above, it appears that the major threat to birds is likely to be habitat change arising from shifts in vegetation cover. The likelihood of birds

being negatively affected by such changes will therefore be determined by how reliant they are on the heather component of moorland or heath. However, due to the nature of both vegetation types, forming spatial and temporal mosaics, the effects on birds may be complex and subtle, as most bird species do not favour complete *Calluna* cover, but prefer mosaics of varying composition. Therefore, the effects of a shift from heather to grass cover on breeding birds will vary between different sites according to the initial vegetation composition on the site. One of the difficulties in discerning habitat preferences is that studies have frequently examined these at larger scales and at relatively coarse resolution, so that relationships may be found between bird abundances and heather moorland, where a finer-scale analysis may find that the birds are using other vegetation components within the moorland. A recent study of bird-habitat relationships in northern Britain has examined the vegetation effects in fine detail and also attempted to disentangle these effects from other site and management effects that may be confounded with the vegetation condition (Pearce-Higgins and Grant, 2006). I review the evidence for reliance on moorland and heath vegetation and suggest ways in which species have been, or could possibly be in the future, affected by habitat loss/change.

4.5.1. Upland moorland

Changes to bird populations and communities in the uplands may be driven by several processes, including afforestation and seral succession to scrub (Gillings et al., 1998), climate change, and changes in moorland management (e.g. game shooting and grazing regimes). As already indicated (see 4.2) some of these at least are likely to be more important than the effects arising from increased nutrient inputs. This is for a number of reasons but foremost amongst them is the fact that they may: (i) cause an actual loss of the moorland area (e.g. afforestation); (ii) affect predation rates, and hence productivity and survival of moorland birds (e.g. game management); and (iii) are likely to be responsible for greater changes in the composition and structure of the moorland vegetation (e.g. grazing regimes). The greatest potential threat to moorland birds from increased atmospheric deposition of nitrogen (when combined with relatively intense

grazing) is likely to be the change in habitat as *Calluna*-dominated moor shifts to grass moor. Bird species that rely on *Calluna*-dominated moor will be negatively affected by such changes, whereas species that prefer grass moor, or that have no strong preference, should be unaffected. Many species require a mosaic of *Calluna* and graminoid vegetation; the effects of habitat loss on these species will depend on the initial quantities and spatial distribution of the different vegetation-types they require. In the current review, I concentrate on the potential effects of *Calluna* loss and changes to the configuration of *Calluna* and graminoid vegetation. The evidence for the effects of loss of *Calluna*-moorland on birds is summarised in Table 4.3. Below I deal with some of the main bird species that breed on UK moorlands and assess the extent to which they may be affected by the conversion of heather to grass cover.

4.5.1.1. Red grouse

Only one species is considered to be confined to heather moorland: red grouse (Thompson et al., 1995). Red grouse feed extensively on *Calluna* shoots and this forms the main staple of the diet for birds that are more than a week or two old, so that the requirement for heather is clear. Nitrogenous fertiliser may improve the nutritive value of heather and benefit red grouse (Cadbury, 1992). Young heather shoots are preferred and disturbance (particularly fire) that stimulates heather regrowth without replacing it with graminoids will also be beneficial. There is some evidence that the species does benefit from some heterogeneity in the sward, but although *Calluna* monocultures may not be optimal, high cover values (e.g. 50 – 70 %) clearly are (Pearce-Higgins and Grant, 2006). However, where loss of heather cover occurs, habitat will become less suitable. In the northern Peak District, long-term loss of heather moorland attributed to increased grazing pressure was concurrent with the reduction in red grouse stocks in the area (based on game bags) (Anderson and Yalden, 1981). In Scotland, long-term declines in red grouse (as measured by grouse bags) over the period 1913-1990 were attributed largely to the loss of heather cover, which declined by 48% between 1948 and 1988 (Thirgood et al., 2000). Red grouse is the species most likely to suffer negative effects from loss of heather cover.

4.5.1.2. Black grouse

The red-listed black grouse is a bird of woodland and moorland fringes for which there is evidence of detrimental effects of high grazing pressure (Baines, 1996, Calladine et al., 2002). Two mechanisms suggested for the negative effects of grazing were the reduced vegetation height and cover to protect nesting birds from predation, and reduced invertebrate abundance on heavily grazed moors. Additionally, adult black grouse rely on *Calluna* as a staple food, particularly from autumn to late winter (Picozzi and Hepburn 1986, Beeston et al., 2005), whilst tall heather may provide suitable nesting sites (Cayford et al., 1989). However, despite the importance of the availability of *Calluna* to black grouse, they require access to other vegetation-types of open ground habitats, and both *Vaccinium myrtillus* dominated areas and wet, grassy, habitats may be critical for broods (Grant and Dawson, 2005). Overall, on open ground habitats, mosaics of dwarf shrub and graminoid dominated vegetation may provide the most suitable conditions (Pearce-Higgins et al., 2005). On grass-dominated moorland in northern England, reductions in grazing pressure resulted in initial increases in grouse densities, but these were not sustained and densities began to decline five to seven years after the grazing reduction (Calladine et al., 2002, Warren et al., 2003). Nitrogen inputs *per se* are unlikely to have a major effect on black grouse populations.

4.5.1.3. Golden plover

Moorland is the major breeding habitat of golden plover (Thompson et al., 1995), and in northern British moorland, golden plover abundance was positively associated with the cover of short (0–15 cm) dwarf shrubs (including heather, crowberry and bilberry), but not with taller height categories of this vegetation-type (Pearce-Higgins and Grant, 2006). Therefore, this probably reflects a stronger dependence on an appropriate vegetation structure rather than on dwarf shrubs themselves, whilst crowberry and bilberry can replace heather under intermediate grazing regimes. Golden plover were also found to be more abundant on grouse moors than non-grouse moors in

Table 4.3. Some effects of spatial or temporal variation in upland moorland vegetation on birds

Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
nine moorland bird species	northern Britain	relationships between bird abundance and vegetation variables (accounting for confounding site and management effects)	relationships detected for eight species, notably positive relationships with heather for red grouse and stonechat	various preferences for vegetation and structural features	2	Pearce-Higgins and Grant, 2006
upland breeding birds	south Pennines	relationships between breeding abundances and habitat variables	relationships with altitude and/or slope for several wader species; merlin, short-eared owl and red grouse associated with heather moorland, whinchat with bracken, dunlin and golden plover with blanket bog, merlin and curlew with tall heather	habitat preferences	2	Stillman and Brown, 1994
meadow pipit and red grouse	northern Britain	relationship between habitat variables and abundances of meadow pipit and red grouse on grouse moors	meadow pipit abundance negatively related to <i>Calluna</i> cover and muirburn, positively related to grass cover; red grouse abundance influenced by regional location and altitude	habitat preferences of meadow pipits within grouse moors; moors were managed for red grouse	2	Smith et al., 2001
eight bird species	south Pennines	relationship between habitat variables and breeding abundances of golden plover, dunlin, redshank, curlew, ring ouzel, twite, short-eared owl and merlin	various relationships, including: positive for <i>Calluna</i> cover and twite, ring ouzel and merlin; negative for <i>Calluna</i> cover and dunlin and curlew; positive for <i>Eriophorum</i> cover and dunlin, redshank and golden plover; positive for <i>Pteridium</i> cover and merlin and twite	various preferences for vegetation and topographical features	2	Haworth and Thompson, 1990
eight bird species	eastern Scotland	relationships between topography and vegetation variables and bird abundance	five species related to site topography; six species related to habitat composition	various preferences for vegetation and structural features	2	Brown and Stillman, 1993

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study

Table 4.3. (cont.) Some effects of spatial or temporal variation in upland moorland vegetation on birds

Group	Location	Process	Effects	Possible cause	Strength of evidence ¹	Reference
red grouse	Peak District	historical changes in game bags (1930s-1970s), sheep numbers (1930-1976) and heather moorland cover (1913-1976)	grouse numbers more than halved; one third loss of heather; trebling of sheep numbers	loss of red grouse habitat	3	Anderson and Yalden, 1981
hen harrier	Orkney	hunting patterns in a declining population	male hunting positively related to amount of unmanaged grass; female hunting negatively related to prevalence of both managed grass heather cover and to vegetation height	population decline driven by loss of rough grass habitat due to increased grazing intensity	2	Amar and Redpath, 2005
meadow pipit	British uplands	relationship between breeding abundance and vegetation variables	non-linear relationships with heather cover and with grass cover	requirement for habitat mosaic	2	Vanhinsbergh and Chamberlain, 2001
red grouse	south Scotland	historical changes in abundance (measured by game bags), raptor abundance and heather cover	grouse bags declined with heather loss while raptor numbers were low, but declined further as raptor numbers increased	long-term declines related to habitat loss, but subsequently high predation kept grouse numbers low	2	Thirgood et al., 2000
ring ouzel	Tayside	breeding biology	nests were placed in tall heather on steep slopes, but home ranges contained more grass moor than heather	requires grass-heather mosaic for nesting and foraging	2	Burfield, 2002
ring ouzel	south-east Scotland	changes in site occupancy between 1952-85 and 1998-2000, related to changes topographical and habitat variables	sites more likely to have remained occupied at higher altitudes and with greater heather cover	heather loss may prevent otherwise suitable breeding sites from being occupied	2	Sim et al., in prep.

¹ I classified the studies into three tiers: 1. Strong evidence, usually based on experimental proof; 2. Intermediate evidence, generally an observed relationship in space and time; 3. Weak evidence, a suggested cause based on observed patterns. These levels are not intended as a judgement on the quality of the research, and I judge the strength of evidence for effects of nutrient inputs and associated mechanisms, which may not have been the purpose of the study.

northern Britain, but grouse moors had less tall heather (and no greater cover of heath) (Tharme et al., 2001). This reflects the benefits on *Calluna*-dominated moorland of muirburn management or the control of predators, or a combination of both, to golden plovers. Other studies have not found associations between golden plover abundance and heather cover, and blanket-bog may be preferred to either heather or grass moorland (Brown, 1993). An examination of environmental features associated with the breeding distribution of this species in the south Pennines identified crowberry (*Empetrum*) as a strong predictor, with *Vaccinium-Calluna* and *Calluna-Eriophorum* cover as less important predictors, and no significant predictive value of *Calluna* moorland (Haworth and Thompson, 1990). Elsewhere, no relationship between golden plover abundance and heather moor cover was found in the south Pennines (Stillman and Brown, 1994), although a negative association with grass cover was found in the Grampians (where altitude appeared to be the best predictor) (Brown and Stillman, 1993). In the south Pennines, golden plover chicks occupied home ranges containing more cotton grass and bare peat, but less heather and grassland, than was available generally (Pearce-Higgins and Yalden, 2004). Tipulid adults and larvae form a major part of the diet of golden plover chicks, and exploitation of this food resource was positively correlated with the use of cotton grass and peat areas. Breeding adults may use different habitats for feeding chicks and for nest placement, with concealment being important when nesting, and food availability when chicks have hatched (Whittingham, 1996, in Fuller and Gough, 1999). Overall, on moorland vegetation, structure is probably the key determinant of golden plover distribution. Golden plover may require a mosaic of blanket-bog, graminoids and heath cover, but *Calluna*-dominated heath is not preferred to other dwarf shrubs (Pearce-Higgins and Grant, 2006). At least in the absence of muirburn management, golden plover appear most likely to benefit from the conversion of continuous heather cover to such habitat mosaics. This suggests that increased nitrogen deposition would have detrimental effects on the species only if it were causing wholesale conversion of heather to graminoid cover.

4.5.1.4. Other waders

Resurveys of upland areas in the early 2000s found that breeding wader populations (especially those of dunlin, curlew and lapwing) had shown widespread, although not ubiquitous, declines (Sim et al., 2005). Possible reasons suggested for these declines were afforestation, increased grazing pressure from sheep and red deer, and declines in grouse moor management. Curlew breeding on moorland may use grass habitats on marginal farmland adjacent to moors due to increased invertebrate prey (earthworms and tipulid larvae) for adult birds (Robson et al., 2002). Topography (particularly the presence of high plateaus) was a strong predictor of the presence of breeding dunlin, redshank and curlew (and golden plover) in the south Pennines; *Eriophorum* cover was also a strong predictor for the first two (Haworth and Thompson, 1990). Also in the south Pennines, dunlin abundance was negatively related to heather cover, while curlew and snipe abundance in this area and in the Grampians showed no relationship with heather cover (Stillman and Brown, 1994). Another study in the Grampians found no significant relationships for snipe, while curlew abundance was negatively associated with bog cover (and with high altitude) (Brown and Stillman, 1993). Heterogeneous vegetation structure appears to favour many wader species, and this was found to be the case for curlew and snipe in northern Britain (Pearce-Higgins and Grant, 2006). There appears to be little evidence for strong dependence on heather cover for waders in upland Britain. The loss of heterogeneous swards, which could occur as a result of changes in grazing pressure or on some moors through declines in muirburn, is likely to be more important than loss of heather cover for these species.

4.5.1.5. Merlin

Merlin, hen harrier and short-eared owl all breed predominantly on heather moorland (Thompson et al., 1995). The wide-ranging nature of these species can cause difficulties in quantifying their associations with different moorland vegetation-types. However, in Wales, the south Pennines and Northumberland, *Calluna* cover (also *Pteridium* cover in the south Pennines) was a strong predictor of merlin breeding abundance (Bibby, 1986; Newton et al., 1986; Haworth and Thompson, 1990). Conversion of heather moorland to grass moorland due to sheep grazing was suggested as a possible contributing factor to

the decline of merlin in the Peak District, but not a crucial one, as organochlorine pesticides were considered to be the most important factor (Newton et al., 1981). Merlin populations may be artificially low in suitable habitat due to persecution (Rebecca et al., 1992). Given the strong association of this species with heather moorland for breeding, it seems likely that a loss of heather cover could be detrimental, and indeed this has been asserted (Cadbury, 1992). However, many of the studies have been broad-scale, and the main prey of merlin on moorlands is likely to be passerine birds, species of which tend to either prefer non-heather components or show no preference (see below). Thus it is likely that a mixture of tall heather (for nesting) and grass-heather mosaic (for foraging) will be most suitable for merlin. Once again, the initial composition of moorland vegetation will determine the effect of heather loss on merlin populations.

4.5.1.6. Hen harrier

Persecution by humans, in an attempt to reduce harrier predation on grouse, is a major determinant of the distribution of hen harrier (Etheridge et al., 1997). Nevertheless, heather moorland is strongly preferred as nesting habitat; while young conifer plantations are used for nesting, as they mature they become unsuitable for both nesting and hunting (Madders, 2003). However, harrier populations and breeding productivity declined in Orkney between the 1970s and 1990s in the absence of persecution (Meek et al., 1998). The loss of rough grassland at the moorland edge, due to agricultural improvement and increased grazing pressure, leading to a reduced food supply, is suggested as the most likely cause for the decline (Amar and Redpath, 2005). Hen harrier are likely to be affected by loss of heather cover as tall heather is selected for nesting (Redpath et al., 1998). It may also be affected if prey abundance (including meadow pipit, red grouse chicks and small mammals) is reduced due to changes in habitat, although meadow pipit and vole abundance are likely to increase in grass-dominated habitats. Hen harrier are most abundant in areas and years where meadow pipit and small mammal abundance are greatest (Redpath and Thirgood, 1999). As with merlin, initial heather cover will determine the effects of heather loss; it is likely to have a negative effect if it removes suitable nesting habitat and habitat mosaics where prey is most abundant, but an increase in grass moorland will be beneficial if it occurs where heather cover predominates.

4.5.1.7. Other raptors

Golden eagle are strongly associated with moorland, as are short-eared owl, and several other raptors such as goshawk, buzzard, red kite, peregrine and kestrel also make use of it as feeding habitat. However, it is difficult to establish whether they have any particular preference for heather- rather than grass-dominated moorland, and as such there is no evidence that loss of heather cover will have negative effects on these raptors.

4.5.1.8. Meadow pipit

Meadow pipit is the most abundant breeding bird on upland moorland, and is an important prey item for many predatory bird species of the uplands (Vanhinsbergh and Chamberlain, 2001). A series of studies has found that it generally shows a preference for mixed grass and heather moorland. On heather-dominated grouse moors in northern Britain, meadow pipit abundance was positively related to grass cover, and negatively related to muirburn and *Calluna* cover (Smith et al., 2001), while in the Grampians, its strongest relationship was with altitude (negative), and it showed no significant preference for broad vegetation categories (Brown and Stillman, 1993). A more detailed study, incorporating finer resolution vegetation data, found that meadow pipit was most abundant in graminoid-heather mixes, but where graminoids were more abundant than heather (Pearce-Higgins and Grant, 2006). In one study in the south Pennines it was positively associated with heather moor cover (Stillman and Brown, 1994). Examination of habitat preferences using BBS data concluded that meadow pipit showed non-linear relationships with both heather and grass cover, suggesting that dominance of either habitat is likely to be detrimental (Vanhinsbergh and Chamberlain, 2001). Meadow pipit should benefit from grazing that is sufficient to fragment heather without removing it entirely (Pearce-Higgins and Grant, 2002; Dennis et al., 2005). The level of grazing that will achieve this will vary from site to site, depending on the initial vegetation cover. In the northern Pennines, meadow pipit nests were positioned on the interface between blanket bog and alluvial grassland, allowing them to exploit crane-fly emergence for their first broods and grassland invertebrates for the second brood (Coulson and Whittaker 1978, in Hudson, 1988), and selection of grassland for food resources (tipulids,

Coleoptera and Diptera) has been noted elsewhere (Smith et al., 2001). The meadow pipit, therefore, would initially benefit from the loss of heather cover and its replacement with grass, in areas where heather cover is currently dominant. However, beyond a certain proportion of grass cover (40-60% by one estimate (Vanhinsbergh and Chamberlain, 2001) and 60-70% by another (Pearce-Higgins and Grant, 2002), loss of heather would be detrimental.

4.5.1.9. Skylark

Moorland is a major breeding habitat for the red-listed skylark (Thompson et al., 1995; Chamberlain, 2001), but this species shows positive associations with grass cover and grazing intensity in the British uplands (Brown and Stillman, 1993; Pearce-Higgins and Grant, 2002; Dennis et al., 2005; Pearce-Higgins and Grant, 2006). Resurveys of upland areas found declines in some areas, but not the very large declines seen on lowland farmland (Sim et al., 2005), and it appears that grazing and loss of heather cover would be beneficial to skylarks.

4.5.1.10. Ring ouzel

Ring ouzel have declined markedly in the UK and are now a species of high conservation concern (Gibbons et al., 1993, Gregory et al., 2002). Moorland provides their major breeding habitat (Thompson et al., 1995). At a broad scale, ring ouzel breeding abundance was positively related to *Calluna* cover, *Pteridium* cover and *Molinia* cover in the south Pennines (Haworth and Thompson, 1990), while in Scotland, ring ouzel abundance was positively related to heather/smooth grass mosaic, and negatively with improved pasture (Buchanan et al., 2003). However, as with many wader species, ring ouzel forage to a large extent on the invertebrates of adjacent grassland (Burfield, 2002). Studies in Tayside found that although ouzels selected tall heather on steep slopes for nesting, they selected short grass areas (usually within 500 m of their nests) for foraging, and during the nestling period their home ranges contained greater amounts of grass moor and grazed pasture than heather moor, relative to the availability of these habitats within the study area (Burfield, 2002). Similarly, an association of ring ouzel with pasture in the south Pennines may have reflected the availability of abundant soil invertebrates close to

nest sites located in heather or bracken cover (Haworth and Thompson, 1990). However, there are some indications that heather loss may be linked to declines. Across Scotland greatest declines occurred where the extent of smooth grass-heather mosaics was initially highest, such habitats being particularly vulnerable to heather loss from grazing (Buchanan et al., 2002, Clarke et al., 1995). Furthermore, historical breeding sites in the Moorfoot Hills, southern Scotland, were more likely to have remained occupied in 1998-2000 where current heather cover was greatest, implying a possible association between heather loss and declines (Sim et al., in press). Therefore, heather-grass mixes appear to provide suitable breeding habitat for ring ouzels, but extensive heather loss may be detrimental, and so in some situations N deposition could be a contributory factor in causing declines.

4.5.1.11. Other passerines

Resurveys of upland areas found significant declines in twite in some study areas, general increases in stonechat and raven, and inconsistent changes in other passerines (Sim et al., 2005). Heather moorland was considered a major breeding habitat for whinchat and stonechat, and locally important breeding habitat for twite (Thompson et al., 1995). Although twite nest and roost predominantly in heather moor, they require seed rich hay meadows and pastures nearby (Orford, 1973). In the South Pennines, *Calluna* cover and *Pteridium* cover were strong predictors of twite breeding abundance (Haworth and Thompson, 1990). In the same area, breeding twite were associated with moorland edge at relatively low altitude; breeding performance was better for birds nesting in heather-dominated moorland, compared with grass-dominated or other moorland (Brown et al., 1995). It appears that twite require tall heather at the moorland edge, rather than using a grass-heather mosaic within moorland. Whinchat, which have declined from much of lowland Britain due to agricultural improvement, are positively associated with bracken in the uplands (Brown and Stillman, 1993; Stillman and Brown, 1994; Allen, 1995; Pearce-Higgins and Grant, 2006). In British upland moorland, stonechat abundance showed a strong positive association with heather cover, although relationships with other vegetation variables indicate that abundance was greatest where there was some heterogeneity within a heather-dominated sward (Pearce-Higgins and Grant, 2006).

Another passerine typical of the uplands, wheatear, showed no association with vegetation in two studies (Stillman and Brown, 1994; Pearce-Higgins and Grant, 2006), and was positively associated with grass/bracken cover in a third (Brown and Stillman, 1993). Of the species considered here, stonechat and twite are most likely to be sensitive to the loss of heather moorland.

4.5.2. Lowland heath

Loss of lowland heath is likely to be detrimental to bird species that rely on this habitat (Liley and Clarke, 2003). However, while increased soil fertility may make restoration or creation of heathland more difficult (Pywell et al., 1994; Barker et al., 2004; Allison and Ausden, 2006), and has the potential to contribute to heathland loss there are many other threats to this habitat in the UK. These include changed management regimes, habitat destruction and ecological succession (Bunce, 1989). In addition, I consider that birds are not the best indicator of the overall health of lowland heath. All of the bird species that are traditionally thought of as typical of lowland heath are increasing, largely due to factors outside of heathland habitat itself, and/or because of targeted and intensive management programs. Stone-curlew are intensively managed in two small areas; woodlark and nightjar populations have increased markedly, which is related to the presence of early-stage plantations and associated bare ground, although intensive restoration of heath habitat also contributes (Scott et al., 1998; Wotton and Gillings, 2000; Eaton et al., 2005); milder winters have favoured Dartford's warbler in recent years (Gibbons and Wotton, 1996).

4.5.2.1. Woodlark

In the UK woodlark are found predominantly in young conifer plantations and in heathland (Sitters et al., 1996). Numbers have fluctuated over the past century, rising from a low of approximately 250 pairs in 1986 to over 1400 pairs in 1997 (Wotton and Gillings, 2000). Reduced grazing pressure due to less intensive management (but also following the introduction of myxomatosis) probably affected woodlark (and stone-

curlew) populations, as they prefer short swards for feeding (Fuller and Gough, 1999). Recent milder winters are likely to have favoured woodlark, although succession of heathland to scrub, and reductions in grazing pressure from rabbits and stock are suggested as major causes of the long-term decline of the species (Sitters et al., 1996). Loss of lowland heath to grassland is likely to be detrimental to this species, but plantation programs may have more of an effect on this species than changes to habitat resulting from nitrogen deposition.

4.5.3. Summary

Loss of habitat, through a shift towards grass-dominated landscapes is likely to be the major indirect effect of increased nitrogen deposition on the birds of upland moorland. I have identified some major mechanisms by which nitrogen deposition could be the cause of such habitat loss, although a causal link between nitrogen deposition and grazing intensity has not been definitively established. In addition, most birds typical of upland moorland benefit from some degree of grass cover within heather moorland, or show no particular preferences for heather cover *per se*. Table 4.4 summarises the likely effects of heather cover on upland birds for those species where I consider there was sufficient evidence to make an informed estimate. Two species (red grouse and stonechat) are identified as having high sensitivity to heather loss, because they are heavily reliant on this habitat. Six species (curlew, snipe, golden plover, skylark, wheatear and whinchat) are listed as having low sensitivity. The remaining seven species (black grouse, golden eagle, hen harrier, merlin, meadow pipit, ring ouzel and twite) are listed as intermediate. These are species for which a mosaic of heather and grass moorland has been identified as the most suitable habitat in at least one study of upland areas. These species may or may not benefit from the loss of heather cover, depending on the habitat configuration present, and their long-term responses to shifts in moorland habitat are likely to be complicated. It is important to stress that sensitivity to heather loss does not mean that this will necessarily be a limiting factor for bird populations; other factors such as winter severity and persecution may well more strongly drive population changes. In lowland

heath, I consider that while nitrogen deposition may negatively affect the habitat, it is difficult to establish links between nitrogen deposition and bird populations in the United Kingdom.

Table 4.4. Predicted effects of loss of heather cover to moorland birds

Species	Category ¹	Sensitivity	Likely reaction to loss of heather cover
red grouse	confined to heather moorland	high	loss of heather food resource; loss of nesting habitat
black grouse	major breeding habitat	moderate	increased predation and loss of food resource
hen harrier	breed mainly on moorland	moderate	loss of nesting habitat and prey items
golden eagle	feeding habitat	moderate	loss of nesting habitat and prey items
merlin	breed mainly on moorland	moderate	loss of nesting habitat and prey items
golden plover	breed mainly on moorland	low	strong effects unlikely
snipe	locally important breeding habitat	low	strong effects unlikely
curlew	major breeding habitat	low	strong effects unlikely
skylark	major breeding habitat	low	probable benefit from increase in grass cover
meadow pipit	major breeding habitat	moderate	loss of appropriate mosaic of habitats
whinchat	major breeding habitat	low	probable benefit from increase in bracken cover
stonechat	major breeding habitat	high	loss of nesting sites and appropriate mosaic of habitats
wheatear	locally important breeding habitat	low	probable benefit from increase in bracken or grass cover
ring ouzel	habitat	low	loss of appropriate mosaic of habitats;
twite	major breeding habitat	moderate	loss of nesting habitat
	locally important breeding habitat		loss of appropriate mosaic of habitats;
	habitat	moderate	loss of nesting habitat

¹ Use of heather moorland as described by Thompson et al. (1995).

5. References

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Appendix 1. Scientific names of birds named in the text.

Anatidae	<i>Cygnus olor</i>	mute swan
	<i>Cygnus cygnus</i>	whooper swan
	<i>Cygnus columbianus</i>	Bewick's swan
	<i>Anser brachyrhynchus</i>	bean goose
	<i>Anser albifrons</i>	white-fronted goose
	<i>Anser anser</i>	greylag goose
	<i>Branta bernicla</i>	brent goose
	<i>Tadorna tadorna</i>	shelduck
	<i>Anas penelope</i>	wigeon
	<i>Anas strepera</i>	gadwall
	<i>Anas crecca</i>	teal
	<i>Anas platyrhynchos</i>	mallard
	<i>Anas acuta</i>	pintail
	<i>Anas querquedula</i>	garganey
	<i>Anas clypeata</i>	shoveler
	<i>Netta rufina</i>	red-crested pochard
	<i>Aythya ferina</i>	pochard
	<i>Aythya fuligula</i>	tufted duck
	<i>Aythya marila</i>	scaup
	<i>Aythya affinis</i>	lesser scaup
	<i>Somateria mollissima</i>	eider
	<i>Clangula hyemalis</i>	long-tailed duck
	<i>Melanitta nigra</i>	common scoter
	<i>Melanitta fusca</i>	velvet scoter
	<i>Bucephala clangula</i>	goldeneye
	<i>Mergus serrator</i>	red-breasted merganser
	<i>Mergus merganser</i>	goosander
Tetraonidae	<i>Lagopus lagopus</i>	red grouse
	<i>Tetrao tetrix</i>	black grouse

Phasianidae	<i>Perdix perdix</i>	grey partridge
	<i>Coturnix coturnix</i>	quail
Gaviidae	<i>Gavia stellata</i>	red-throated diver
	<i>Gavia arctica</i>	black-throated diver
	<i>Gavia immer</i>	great northern diver
Podicipedidae	<i>Podilymbus podiceps</i>	pie-billed grebe
	<i>Tachybaptus ruficollis</i>	little grebe
	<i>Podiceps cristatus</i>	great-crested grebe
	<i>Podiceps auritus</i>	Slavonian grebe
	<i>Podiceps nigricollis</i>	black-necked grebe
Phalacrocoracidae	<i>Phalacrocorax carbo</i>	cormorant
Ardeidae	<i>Botaurus stellaris</i>	bittern
	<i>Ardea alba</i>	great egret
	<i>Ardea cinerea</i>	grey heron
	<i>Ardea herodias</i>	great blue heron
Ciconiidae	<i>Mycteria americana</i>	wood stork
Acciptridae	<i>Milvus milvus</i>	red kite
	<i>Circus aeruginosus</i>	marsh harrier
	<i>Circus cyaneus</i>	hen harrier
	<i>Accipiter gentilis</i>	goshawk
	<i>Buteo buteo</i>	buzzard
	<i>Aquila chrysaetos</i>	golden eagle
Falconidae	<i>Falco tinnunculus</i>	kestrel
	<i>Falco columbarius</i>	merlin
	<i>Falco peregrinus</i>	peregrine falcon
Rallidae	<i>Rallus aquaticus</i>	water rail
	<i>Porzana porzana</i>	spotted crake
	<i>Gallinula chloropus</i>	moorhen
	<i>Crex crex</i>	corncrake
	<i>Fulica atra</i>	coot
Haematopodidae	<i>Haematopus ostralegus</i>	oystercatcher

Recurvirostridae	<i>Himantopus mexicanus</i>	black-necked stilt	
	<i>Recurvirostra avosetta</i>	avocet	
Burhinidae	<i>Burhinus oedicephalus</i>	stone curlew	
Charadriidae	<i>Charadrius hiaticula</i>	ringed plover	
	<i>Charadrius ociferus</i>	killdeer	
	<i>Charadrius alexandrinus</i>	Kentish plover	
	<i>Pluvialis apricaria</i>	golden plover	
	<i>Pluvialis squatarola</i>	grey plover	
	<i>Vanellus vanellus</i>	lapwing	
	Scolopacidae	<i>Calidris canutus</i>	knot
<i>Calidris alba</i>		sanderling	
<i>Calidris maritima</i>		purple sandpiper	
<i>Calidris alpina</i>		dunlin	
<i>Gallinago gallinago</i>		snipe	
<i>Limosa limosa</i>		black-tailed godwit	
<i>Limosa lapponica</i>		bar-tailed godwit	
<i>Numenius phaeopus</i>		whimbrel	
<i>Numenius arquata</i>		curlew	
<i>Tringa erythropus</i>		spotted redshank	
<i>Tringa totanus</i>		redshank	
<i>Tringa nebularia</i>		greenshank	
<i>Tringa ochropus</i>		green sandpiper	
<i>Actitis hypoleucos</i>		common sandpiper	
<i>Arenaria interpres</i>		turnstone	
Stercorariidae		<i>Stercorarius parasiticus</i>	Arctic skua
		<i>Stercorarius skua</i>	great skua
Laridae	<i>Larus melanocephalus</i>	Mediterranean gull	
	<i>Larus ridibundus</i>	black-headed gull	
	<i>Larus canus</i>	common gull	
	<i>Larus fuscus</i>	lesser black-backed gull	
	<i>Larus argentatus</i>	herring gull	

	<i>Larus marinus</i>	great black-backed gull
	<i>Rissa tridactyla</i>	kittiwake
Sternidae	<i>Sternula albifrons</i>	little tern
	<i>Chlidonias niger</i>	black tern
	<i>Sterna sandvicencis</i>	sandwich tern
	<i>Sterna hirundo</i>	common tern
Columbidae	<i>Columba palumbus</i>	woodpigeon
	<i>Streptotelia decaocto</i>	collared dove
	<i>Streptotelia turtur</i>	turtle dove
Cuculidae	<i>Cuculus canorus</i>	cuckoo
Tytonidae	<i>Asio flammeus</i>	short-eared owl
Caprimulgidae	<i>Caprimulgus europaeus</i>	nightjar
Alcedinidae	<i>Alcedo atthis</i>	kingfisher
Picidae	<i>Picus viridus</i>	green woodpecker
Alaudidae	<i>Lullula arborea</i>	woodlark
	<i>Alauda arvensis</i>	skylark
Hirundinidae	<i>Tachycineta bicolor</i>	tree swallow
	<i>Hirundo rustica</i>	barn swallow
Motacillidae	<i>Anthus trivialis</i>	tree pipit
	<i>Anthus pratensis</i>	meadow pipit
	<i>Motacilla flava</i>	yellow wagtail
	<i>Motacilla alba</i>	pie wagtail
Cinclidae	<i>Cinclus cinclus</i>	dipper
Troglodytidae	<i>Troglodytes troglodytes</i>	wren
Turdidae	<i>Saxicola rubetra</i>	whinchat
	<i>Saxicola torquatus</i>	stonechat
	<i>Oenanthe oenanthe</i>	wheatear
	<i>Turdus torquatus</i>	ring ouzel
	<i>Turdus merula</i>	blackbird
	<i>Turdus pilaris</i>	fieldfare
	<i>Turdus philomelos</i>	song thrush

	<i>Turdus iliacus</i>	redwing
	<i>Turdus viscivorus</i>	mistle thrush
Sylviidae	<i>Cettia cetti</i>	Cetti's warbler
	<i>Locustella naevia</i>	grasshopper warbler
	<i>Acrocephalus paludicola</i>	aquatic warbler
	<i>Acrocephalus schoenobaenus</i>	sedge warbler
	<i>Acrocephalus scirpaceus</i>	reed warbler
	<i>Sylvia communis</i>	whitethroat
	<i>Sylvia undata</i>	Dartford warbler
	<i>Phylloscopus trochilus</i>	willow warbler
Timaliidae	<i>Panurus biarmicus</i>	bearded tit
Laniidae	<i>Lanius collurio</i>	red-backed shrike
Corvidae	<i>Pica pica</i>	magpie
	<i>Pyrhocorax pyrrhocorax</i>	chough
	<i>Corvus monedula</i>	jackdaw
	<i>Corvus frugilegus</i>	rook
	<i>Corvus corone</i>	carrion crow
	<i>Corvus corax</i>	raven
Sturnidae	<i>Sturnus vulgaris</i>	starling
Passeridae	<i>Passer domesticus</i>	house sparrow
	<i>Passer montanus</i>	tree sparrow
Fringillidae	<i>Fringilla coelebs</i>	chaffinch
	<i>Fringilla montifringilla</i>	brambling
	<i>Carduelis chloris</i>	greenfinch
	<i>Carduelis carduelis</i>	goldfinch
	<i>Carduelis cannabina</i>	linnet
	<i>Carduelis flavirostris</i>	twite
Emberizidae	<i>Emberiza citrinella</i>	yellowhammer
	<i>Emberiza cirrus</i>	cirl bunting
	<i>Emberiza schoeniclus</i>	reed bunting
	<i>Emberiza calandra</i>	corn bunting