Effects of acid rain on bird populations

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Abstract: In this paper the effects of anthropogenic acidification of soils and waters on bird populations are reviewed. Acidification causes (*i*) declines in the reproductive success and the density of piscivorous birds through declines in the fish populations, (*ii*) shifts in the forest bird community from forest birds to birds of open woodland through large-scale forest dieback, and (*iii*) leads to a lower reproductive success of birds in calcium-poor areas through a decline in the availability of calcium-rich material (needed for eggshell formation and skeletal growth). Acidification may also affect the availability of food and nest sites for insectivorous and hole-nesting birds, but there are no consistent effects on the population sizes of these birds. Effects of declines in populations of invertebrates in aquatic habitats may be mitigated by reduced competition from fish, and acidification in forests in less-advanced stages of dieback can both lead to an increase and a decrease in insect and seed abundance in forests, the outcome depending on species, extent of leaf and needle loss, and other factors. There is some evidence that acidification may strongly affect avian reproduction through an increased exposure to toxic metals such as aluminium. Anthropogenic acidification on a worldwide scale is expected to continue during the next decades. Future research on the effects of acidification on bird populations should focus on remedial action and effects on population sizes in moderately acidified areas, and should more often apply an experimental approach than in the past.

Key words: acid rain, birds, reproduction, calcium, toxic metals, forest dieback.

Résumé : L’auteur présente une revue des effets de l’acidifcation anthropogène de l’eau et des sols sur les populations d’oiseaux. L’acidification cause : (*i*) une diminution du succès de reproduction et de la densité des oiseaux piscivores suite à une diminution des populations de poissons; (*ii*) un déplacement des communautés d’oiseaux forestiers vers celles des oiseaux de forêts ouvertes, suite au dépérissement à grande échelle des forêts; et (*iii*) conduit à une diminution du succès de reproduction des oiseaux dans les régions appauvries en calcium, suite à un déclin de la disponibilité de matériel riche en calcium (nécessaire à la formation de l’écaille de l’oeuf et à la croissance du squelette). L’acidification peut également affecter la disponibilité de la nourriture et des sites de nidification pour les oiseaux insectivores et ceux qui nichent dans des cavités, mais il n’y a pas d’effet congruent sur les dimensions des populations de ces oiseaux. Les effets du déclin des populations des invertébrés dans les habitats aquatiques peuvent être mitigés par une compétition réduite de la part des poissons et l’acidification des forêts à des stades moins avançés de dépérissement pourrait conduire à la fois à une augmentation et à une diminution de l’abondance des insectes et des graines dans les forêts, selon l’espèce, l’importance des pertes en feuilles et en aiguilles et d’autres facteurs. Il y a des preuves que l’acidification peut fortement affecter la reproduction aviaire via une exposition accrue aux métaux toxiques, tels que l’aluminium. Sur une base mondiale, on s’attend à ce que l’acidification antropogène se poursuive au cours des prochaines décades. Les recherches à venir sur les effets de l’acidification sur les populations d’oiseaux devraient porter sur les mesures de remédiations et les effets en relation avec les dimensions des populations, dans les régions modérément acidifiées, et on devraient utiliser beaucoup plus l’approche expérimentale que par le passé.

Mots clés : pluie acide, oiseaux, reproduction, calcium, métaux toxiques, dépérissement des forêts.

Introduction: acidification of soils and water

The acidification of soils and surface waters is a natural process in areas where precipitation exceeds evaporation (Van Breemen et al. 1983). The formation of carbonic (HCO_3^-) and organic acids by degradation of plant material, uptake of cations by the roots, and nitrification lead to a decrease in pH, leaching of cations such as Ca^{2+}, and a decrease in base saturation. However, the rate of soil and water acidification has been greatly accelerated during the last decades owing to the atmospheric deposition of SO_x, NO_x, and NH_x compounds formed by the combustion of fossil fuels, traffic, and intensive animal husbandry (Ulrich 1986; Falkengren-Grerup et al. 1987; Wesselink 1994). The deposition of anthropogenic acidifying compounds is held responsible for 80–90% (De Vries and Breeuwsma 1986) of the soil acidification and is implicated as the chief causal factor in the loss of calcium and other cations from the top soil of poorly buffered soils in Europe (Van Breemen et al. 1983; Heij and Schneider 1991; De Vries 1994; Wesselink 1994).

Acid deposition was recognized as a problem for the first time in the early 1970s, as a result of its effects on commercial fish stocks through acidification of streams and waters (Beamish and Harvey 1972; Likens and Bohrmann 1974). Since then a wealth of information has become available through large-scale national and international research

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programmes. The bulk of the research effort has been directed at the effects of acid deposition on water and soil chemistry, fish, and trees. The effects on fish stocks and forests were often dramatic, and fish and timber represent important commercial assets.

In comparison, studies on the effects of acid deposition on organisms at higher trophic levels of the ecosystem, in particular mammals and birds, have been scarce. This paper presents a review of the available literature on the direct and indirect effects of the acidification of soils and waters on the reproduction and abundance of birds. The reported effects of acidification on birds can be categorized into three groups: changes in the abundance of food, loss of suitable habitat, and toxic effects through chemical changes in the soil or water. The effects of acidification on aquatic birds and on the abundance of insects and other food of insectivorous birds in forests will be treated briefly, since these topics were reviewed in a previous paper (Graveland 1990).

In recent years, the possible effects of changes in the availability of calcium and toxic metals have received most attention in studies dealing with acidification and birds. Therefore, the present paper focuses on effects of changes in calcium availability and toxic metals due to acidification. The cause-and-effect chain with respect to calcium will be treated in some detail since it is relatively well-documented and it may thus serve as an illustration of how air pollution can indirectly affect bird populations through changes in soil and water chemistry.

Effects of acidification on birds

Water and soil acidification have been reported to affect bird populations through (*a*) a decrease in fish abundance; (*b*) changes in the abundance of insects, other invertebrates, and tree seeds; (*c*) an increase in the availability of nest sites by an increase in standing dead timber; (*d*) a change of forest into open woodland; (*e*) a decrease in the availability of calcium; and (*f*) an increase in the biological availability of toxic metals such as aluminium and cadmium.

Decrease in fish abundance

Acidification has caused dramatic declines in fish stocks in lakes and streams in Northern Europe and North America (Almer et al. 1974; Beamish 1974; Haines and Baker 1986). The main cause of the decline is the sensitivity of eggs and fry to a low pH and the increased exposure to toxic metals as a result of a decrease in pH (Schindler 1988). The decline of fish stocks had a large impact on piscivorous birds. The Great Northern Diver or Common Loon (*Gavia immer*) and the Osprey (*Pandion haliaetus*) are among the most-studied species. Research has shown that growth and survival of young chicks in the Great Northern Diver is lower in acidified lakes than in nonacidified lakes and that Great Northern Divers and Common Mergansers (*Mergus merganser*) avoid fishless lakes (Eriksson 1986*b*; McNicol et al. 1987; Alvo et al. 1988). The nesting success of Osprey in Sweden decreased during the last decades, despite a ban on the use of pesticides. Their prey delivery rate was lower and the distance between nests was greater in acidified regions than in nonacidified regions (Eriksson 1986*a*). Most acidified fens in the Netherlands became fishless, which resulted in the local extinction of piscivorous birds such as the Crested Grebe (*Podiceps cristatus*) and the Black Tern (*Chlidonias niger*) (Leuven and Oyen 1987; Schuurkes and Starmans 1987).

The effect of water acidification on piscivorous birds is sometimes mitigated, at least temporarily, by an increase in the transparency of the water, and thus an increase in the hunting efficiency of birds, with decreasing pH (Eriksson 1985). However, the impact of water acidification on populations of piscivorous birds represents one of the major effects of acidification on birds.

Changes in abundance of invertebrates

Aquatic habitats

Acidification of surface waters generally leads to a decrease in zoobenthos and macrofauna communities (Almer et al. 1974; Hendrey et al. 1976; Roff and Kwiatkowski 1977). Among insects, mayflies (Ephemeroptera), caddisflies (Trichoptera), and dragonflies and damselflies (Odonata) are affected most (Glooschenko et al. 1986; Blancher and McNicol 1991; Ormerod et al. 1991). These insects are important food sources for insectivorous birds. The decline in the abundance and reproductive success of the Dipper (*Cinclus cinclus*) along acidifying streams in Great Britain was caused by a decrease in the abundance of their main prey: mayflies, caddisflies, and amphipods (*Gammarus* spp.) (Ormerod and Tyler 1986, 1987; Ormerod et al. 1988, 1991). Dippers nesting along acidified streams spent more time foraging, nested later, produced smaller and fewer eggs, and fledged fewer young than birds along nonacidified streams (Ormerod et al. 1988, 1991). Tree Swallows (*Tachycineta bicolor*) had smaller clutches and their nestlings had lower growth rates in acidified than in nonacidified wetlands, presumably owing to a decrease in the abundance of mayflies, their main prey (Blancher and McNicol 1988). The growth rate of Black Duck (*Anas rubripes*) and Ring-necked Duck (*Aythya collaris*) ducklings was lower in acidified than in circumneutral wetlands (DesGranges and Rodrigue 1986; Rattner et al. 1987; McAuley and Longcore 1988).

Results are not always so clear-cut. Blancher and McNicol (1988, 1991) reported 10-fold differences in mayfly abundance in response to variations in pH but no effect on Tree Swallow reproduction, even though mayflies were their main prey. The effects of a decrease in the abundance of arthropods as a result of acidification are often mitigated by reduced food competition from fish and the movement of some insect taxa from vegetated areas to open water in response to the reduction in predation by fish (Eriksson 1979; Hendrikson and Oscarson 1981; Hunter et al. 1986). The proportion of Odonata in the diet of Tree Swallows was negatively correlated with the abundance of fish, independent of pH (Blancher and McNicol 1991) and Tree Swallows nested later in lakes with fish than in lakes without fish (Blancher and McNicol 1988). These examples show that water acidification can have substantial effects on the reproduction of insectivorous birds, but the type of effect depends to a large extent on local conditions, in particular the presence of fish.

Forests

Some studies indicate that soil acidification affects the vitality of trees and thus makes them more susceptible to infections by phytophagous insects (Alstad et al. 1982; Hain 1987). Other

Table 1. Abundance, yearly survival, and reproduction of Coal Tit and Crested Tit in the Ore Mountains in southern Germany (after Möckel 1992).

	Coal Tit		Crested Tit	
	1972–1980	1981–1987	1972–1980	1981–1987
Density[a]	14.6	9.2	4.3	2.4
Density 1974–1977 and 1984–1987[a]	15.6	7.4	4.8	2.4
Recruitment (%)[b]	3.7	0.5	2.4	0.4
Survival adults (%)[a]	39	26	62	48
Fledglings per initiated clutch	5.6	5.1	4.0	4.1
Spruce seed index	1.6	1.0	1.6	1.0

[a]Breeding pairs per 100 nest boxes.
[b]Proportion of fledglings nesting in the area in their 2nd year.

studies suggest that there is no clear link between acidification and the infestation rate. There are large differences between taxa of phytophagous insects in the response to acid stress (Larsson 1989); high concentrations of acidifying compounds may have negative instead of positive effects on insect abundance (Hughes et al. 1982; Heliövaara et al. 1989) and a reduction in tree vigour does not always lead to an increase in the number of insects. For instance, the insect abundance per 100 leaves in affected sugar maple (*Acer saccharum*) stands in Canada was 32% lower than that in healthy stands (DesGranges et al. 1987). The affected stands also had less foliage, so that overall the affected stands had 57% fewer insects than the healthy stands. Gunnarsson (1988) reported a 50% reduction in the abundance of spiders larger than 2.5 mm living on spruce (*Picea abies*) as a result of needle loss in acidified forest.

To my knowledge, only one study has examined the nesting success of insectivorous birds in relation to insect availability in acidified and nonacidified forests. Darveau et al. (1993) measured insect abundance and food delivery rates in the Least Flycatcher (*Empidonax minimus*) in unaffected and affected sugar maple stands (20–30% foliage loss). They found that insect abundance was lower, but nestlings received more food in affected than nonaffected stands. There was no difference in the number of fledglings between affected and nonaffected stands. However, parents spent more time brooding their young in the affected stands. Darveau et al. suggested that the absence of cover in the affected forests created a cooler microclimate. That might explain the higher food intake and brooding rate in the affected stands. Acidification might thus affect the population of these birds indirectly, by causing a decline in the survival of adults as a consequence of increased parental effort.

Mahony et al. (1997) investigated the foraging behaviour and prey delivery rate of the Black-capped Chikadee (*Parus atricapillus*) and the Chestnut-sided Warbler (*Dendroica pensylvanica*) in a healthy and declining sugar maple forest. They found that the number of dead trees was twice as high, and the number of dead branches and the crown transparency of life trees was 20% higher, at the declining site than at the healthy site. The data indicated that the declining site was moderately affected. The chikadees foraged lower in the canopy at the declining site than at the healthy site, apparently in response to the loss of foliage in the crown. However, there were no differences in the two species in the rate at which prey (caterpillars) was delivered to the nestlings or in the breeding success.

Möckel (1992) carried the studies on the effects of acidification on populations of forest birds one step further by examining recruitment (proportion of juveniles settling into the local breeding population) and adult survival, in addition to nesting success. Between the middle 1970s and middle 1980s the number of breeding pairs of the Crested Tit (*Parus cristatus*) and the Coal Tit (*Parus ater*) in coniferous forest in the Ore Mountains was reduced by 50% (Table 1). The nesting success per nesting attempt did not decline in that period. Instead, the recruitment rate of fledged juveniles into next year's breeding population dropped by 85% and the survival of adults dropped by 22–33%. The low survival of juveniles and adults was probably caused by a decrease in the availability of food during the winter; a survey of the yearly seed production in a large number of forests revealed that the production of spruce seeds decreased by some 40% during the study period (Table 1). Needle loss of up to 40% in some places probably also had a great effect on the abundance of invertebrates. Most studies on the effects of acidification on bird populations concentrate on nesting success, since nesting success is much easier to determine than recruitment and survival. The important implication of Möckel's work is that acidification may greatly affect population size, without affecting the nesting success.

The study by Möckel implies that acidification may not only affect birds through changes in invertebrate abundance but also through changes in seed production by trees. As in the case of invertebrates, the effects of acidification on seed production varies. Contrary to Möckel, Hölzinger and Kroymann (1984) reported an increase in spruce seed production in acidified forests, at least temporarily, and an increase in Crossbills (*Loxia recurvirostra*) as a result.

In conclusion, acidification can both lead to an increase and a decrease in the abundance of specific prey items in forests. Also, a decline in insects due to acidification may not result in a lower nesting success but affect bird populations more indirectly, through an effect on the survival of fledglings and adult birds. Thus, the effect of acidification on particular bird species depends on their prey choice during the breeding season and, in residential species, on their prey choice during winter.

Increase in standing dead timber

Soil acidification affects the vitality of trees and increases the amount of standing dead timber. In more advanced cases of forest dieback, closed forest is replaced by open woodland. The

Table 2. Changes in abundance of bird species in acidified forests in the Harz Mountains in eastern Germany (pairs/10 ha).

(*a*) Density of Coal Tits (*Parus ater*) in three forest plots (mean ± SD for three 6-year periods, calculated from data in Zang 1990).

	1969–1975	1976–1982	1983–1989
Norway spruce (*Picea abies*), 820–900 m altitude	1.6±0.7	0.9±0.3	0.1±0.3
Norway spruce (*Picea abies*), 670 m altitude	2.0±0.7	1.1±1.0	2.0±1.4
Beech (*Fagus sylvatica*), 450 m altitude	3.2±1.9	3.3±2.4	1.6±1.9

(*b*) Bird densities (mean ± SE) in six forests between 400 and 1000 m elevation in the West Harz (after Oelke 1989).

	1972	1987
Species of deciduous or mixed forest		
Chaffinch (*Fringilla coelebs*)	11.2±3.0	8.7±2.8
European Robin (*Erithacus rubecula*)	4.2±1.4	0
Dunnock (*Prunella modularis*)	1.7±0.6	1.1±0.6
Blackbird (*Turdus merula*)	0.9±0.4	0.2±0.2
Songthrush (*Turdus philomelos*)	1.0±0.6	0.4±0.2
Species of coniferous forest		
Goldcrest (*Regulus regulus*)	3.9±0.9	0.7±0.2
Firecrest (*Regulus ignicapillus*)	0.5±0.2	0.1±0.1
Coal Tit (*Parus ater*)	1.1±0.4	1.2±0.7
Crested Tit (*Parus cristatus*)	0.7±0.1	0
Great Tit (*Parus major*)	0.7±0.4	0.8±0.5
Species of woodland		
Tree Pipit (*Anthus trivialis*)	3.1±1.6	4.0±1.7
Willow Warbler (*Phylloscopus trochilus*)	0.6±0.3	2.2±0.9
Chiffchaff (*Phylloscopus collybita*)	0.4±0.3	0.8±0.7
Common Redstart (*Phoenicurus phoenicurus*)	0.3±0.2	2.7±1.5
Black Redstart (*Phoenicurus ochruros*)	0.5±0.5	0.6±0.3
Total	29.0±4.6	19.1±5.1

increase in standing dead timber might benefit wood-boring bird species that nest in tree holes and extract their food from the bark. There are a few examples showing that such birds do indeed benefit from the adverse effects of acidification on trees, at least temporarily. The Three-toed Woodpecker (*Picoides tridactylus*) is a species of old-growth forest with much dead wood in central Europe that has greatly increased during the last decades (Hölzinger and Kroymann 1984). The White-headed Nuthatch (*Sitta carolinensis*) increased in Canadian sugar maple forests affected by acidification (DesGranges 1987). Other studies failed to show such a positive effect of an increase in the amount of dead wood. There was no increase in the number of wood-boring or hole-nesting bird species in affected forests in the Harz or Ore mountains in eastern and southern Germany (Stastny and Bejcek 1985; Oelke 1989). On the contrary, Oelke (1989) found that the Treecreeper (*Certhia familiaris*) was present in three study plots in the Harz Mountains in 1972 but had disappeared in 1987. Thus, there is no clear-cut effect of an increase in dead wood in forests on acidifying soils on the abundance of wood-boring, hole-nesting bird species.

Change of forest into open woodland

Perhaps the most dramatic effect of soil acidification on terrestrial ecosystems is the large-scale dieback of forest, in particular coniferous forests at higher elevations. However, there are very little data on the possible effects on bird communities. For instance, there are no data from the Netherlands, a country where the majority of forests are strongly affected by acidification and extensive research programmes have been carried out (Heij and Schneider 1991; Schneider 1992). The results listed below are to my knowledge the only quantitative data on this subject.

In Europe, the most affected areas are located in central and eastern Europe, such as in the Harz and Ore mountains. One would expect a shift in the bird community from forest-dwelling species to species of open woodland in these areas. A comparison of census data from the 1960s, early 1970s, and the late 1980s showed that such a shift did indeed take place (Table 2). Populations of forest species such as the European Robin (*Erithacus rubecula*), the Goldcrest (*Regulus regulus*), and the Firecrest (*Regulus atricapillus*) were decimated, and populations of species that also inhabit open woodland or small forest plots such as the Chaffinch (*Fringilla coelebs*) and the Great Tit were less severely affected, whereas species characteristic of open areas such as the Tree Pipit (*Anthus trivialis*) and Meadow Pipit (*Anthus pratensis*), Redstarts (*Phoenicurus* spp.), and Willow Warbler (*Phylloscopus trochilus*) increased (Tables 2*b* and 3). As expected the species that were most closely linked to coniferous trees suffered the most: Crested Tit, Coal Tit, Goldcrest, and Firecrest. The decline in Coal Tit, Crested Tit, and Firecrest in Denmark during the last decades may also be attributed to acid deposition (Nohr et al. 1986).

DesGranges et al. (1987) investigated the abundance of bird species in 25 healthy and 30 dieback-affected stands of sugar maple (Table 4). In affected stands they found higher numbers of trunk species such as the White-breasted Nuthatch (*Sitta carolinensis*), lower numbers of canopy species such as the

Table 3. Bird densities (pairs/10 ha) in three Norway spruce (*Picea abies*) stands in various stages of dieback in an area heavily affected by soil acidification in the Ore Mountains in the Czech Republic (after Stastny and Bejcek 1985).

	Proportion of dead trees		
	0	75	100
Age of stand (year)	40–80	40	40
Elevation (m)	680–750	800–810	840–870
Bird density			
Forest species			
European Robin (*Erithacus rubecula*)	6.0	0.7	0
Chaffinch (*Fringilla coelebs*)	14.5	5.3	2.0
Coal Tit (*Parus ater*)	5.0	0.7	0
Goldcrest (*Regulus regulus*)	6.0	2.7	0
Dunnock (*Prunella modularis*)	3.0	1.3	0
Species of open woodland			
Tree Pipit (*Anthus trivialis*)	2.0	2.0	4.0
Meadow Pipit (*Anthus pratensis*)	0	0	1.5
Total	47.0	15.4	7.5

Table 4. Bird densities (mean ± SD, pairs/10 ha) in 25 plots of healthy (less than 15% loss of crown foliage) sugar maple (*Acer saccharum*) forest and 30 plots of affected (50% loss) sugar maple forest in Quebec, Canada (after DesGranges et al. 1987).

	Healthy	Affected
Number of species (per census plot of 0.5 ha)	10.6±0.4	12.5±0.6
Number of breeding pairs	322±12	330±18
Number of trunk species	0.5±0.1	1.0±0.2
Number of pairs of trunk species	12±2	22±4
Least Flycatcher (*Empidonax minimus*)	46±4	20±4
Red-eyed Vireo (*Vireo olivaceus*; canopy species)	24±4	28±2
Blue-throated Blue Warbler (*Dendroica caerulescens*; shrub species)	10±2	18±2

Red-eyed Vireo (*Vireo olivaceus*), and higher numbers of shrub species such as the Black-throated Blue Warbler (*Dendroica caerulescens*), than in healthy stands.

Besides causing changes in species composition, forest dieback also resulted in a lower total number of breeding birds in some cases. In the Harz and Ore mountains, the total number of breeding birds decreased by 40–75% in the affected areas (Stastny and Bejcek 1985; Oelke 1989). On the other hand, there were no differences in the total number of breeding pairs or the number of species between the healthy and affected stands of sugar maple in Canada (DesGranges et al. 1987). It is not clear whether the decline in density of insectivorous birds is caused by a decline in the abundance of insects, a decline in cover providing protection against predators, a decline in standing biomass, or other factors.

In conclusion, forest dieback has resulted in a shift from forest species to woodland species and, in some cases, to substantial decreases in the overall abundance of insectivorous birds.

Decrease in availability of calcium

Calcium uptake and metabolism in birds

Avian eggshells contain about 35% calcium and are usually formed in less than a day (Romanoff and Romanoff 1949; Simkiss 1967; Pinowska and Krasnicki 1985; Graveland and Van Gijzen 1994). The amount of calcium that can be stored prior to egg laying is limited so that most of the required calcium has to be ingested during the egg-laying period (Schifferli 1979; Ankney and Scott 1980; Graveland and Van Gijzen 1994; Graveland and Berends 1997; Pahl et al. 1997). As a result, the calcium demand of egg-laying females is quite high. They need 10–15 times as much calcium per hour as similar-sized reptiles or mammals with developing eggs or embryos (Fig. 1).

The normal food of most birds, in particular insectivorous and granivorous species, contains insufficient calcium for eggshell formation (MacLean 1974; Turner 1982; Graveland and Van Gijzen 1994). Therefore, proper eggshell formation mainly depends on the intake of additional calcium-rich material such as snail shells and calcareous grit (Ormerod et al. 1988; Blancher and McNicol 1991; Graveland 1996; Graveland and Van Der Wal 1996).

Nestlings require large amounts of calcium for the development of their skeletons. Calculations of the calcium budget of nestlings, observations of parents feeding their nestlings, and examination of the stomach contents of nestlings showed that nestlings require and ingest calcium-rich material, in addition to their normal food (Bilby and Widdowson 1971; Blancher and McNicol 1991; Graveland and Van Gijzen 1994; Graveland 1996).

Effect of acidification on calcium availability

Soil acidification causes leaching of calcium and other cations from the top soil, a decrease in pH, and an increase in the soil solution of toxic metals such as aluminium and cadmium (Ulrich 1986; Tamm and Hallbacken 1988; Hanson et al. 1982; Heij and Schneider 1991; Schneider 1992). The decreased calcium concentration (Fig. 2*a*) and the increased aluminium concentration in forest soils lead to in a reduced calcium intake by the roots and thus a lower calcium content of the leaves (Fig. 2*b*). As a result, soil and litter in acidified forests have a lower calcium content than that in nonacidified forests (Graveland and Van Der Wal 1996). Similarly, acidification of surface waters leads to a decrease in pH and calcium concentration and an increase in toxic metals in these waters.

The calcium content and, to a lesser extent, the pH are important factors determining the abundance of calcium-rich invertebrates such as snails, millipedes, and crustaceans in terrestrial and aquatic habitats (Seifert 1961; Gärdenfors 1987; Wäreborn 1992; Graveland and Van Der Wal 1996). As a result of soil acidification, snail populations in forests on poorly buffered soils have drastically declined during the last two decades (Wäreborn 1992; Gärdenfors et al. 1995; Graveland and Van Der Wal 1996). In acidifying aquatic ecosystems, populations of invertebrate taxa with a high calcium content, such as snails and crustaceans, were among the first to disappear (Okland and Okland 1986; Harvey and McArdle 1986).

The decrease in the availability of calcium-rich material is reflected in the intake of these items by birds (Table 5). The nests and stomachs of Tree Swallows nesting along acidified

Fig. 1. The calcium requirements of vertebrates during reproduction. (Graveland 1995; and after Simkiss 1967). ●, egg-laying females (birds) or females with developing embryos (mammals and reptiles); ▲, lactating females.

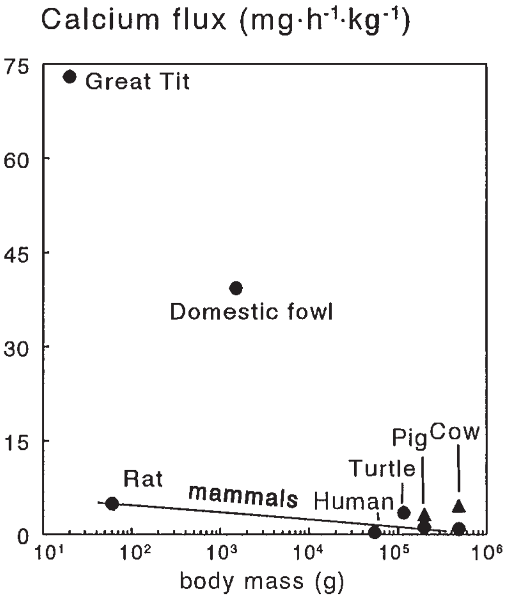
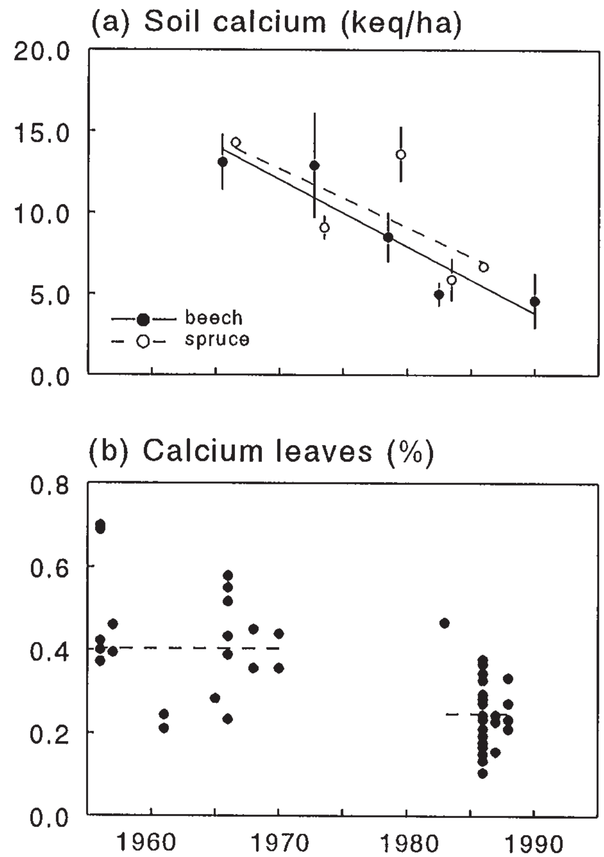


Fig. 2. Changes in the concentration of calcium in the soil solution and in leaves by soil acidification. (*a*) Decrease in exchangeable calcium in top 50 cm of the mineral soil in forests at Solling, Germany (drawn from data in Wesselink 1994). (*b*) Decrease in the calcium content of 0.5-year-old Scots pine (*Pinus sylvestris*) needles in De Peel region, Netherlands (drawn from data in Van Der Burg and Kiewiet 1989).



lakes in Canada contained fewer calcium-rich items than those along circumneutral lakes. The proportion of nests of Great Tits containing snail shell fragments was much lower in acidified forests on poor soils than in unaffected forests on calcium-rich soils.

Eggshell defects

Glooschenko et al. (1986) were the first to propose that acidification might affect bird populations through a reduction in the availability of calcium. Since then an increasing number of studies have reported that a low calcium availability leads to (*i*) the formation of thin and porous eggshells that break easily or result in desiccation of the egg content; (*ii*) a high desertion rate of the clutch; (*iii*) the incidence of empty nests, sometimes with females incubating them; (*iv*) increased mortality of females on the nest; and (*v*) bone malformations and high mortality rates in nestlings (Table 6).

Eggshells of Dippers (*Cinclus cinclus*) in Great Britain and Norway were 5–6% thinner along acidified streams than along nonacidified streams (Ormerod et al. 1988, 1991; Nybo et al. 1997) and eggshells of Eastern Kingbirds were 27% thinner in acid than in circumneutral marshland (Glooschenko et al. 1986). In the case of the Dippers in Wales, the amount of variation in eggshell quality in relation to pH was small in comparison with differences between clutches, and there was no relation between hatching success and pH (Table 6). Great Tits (*Parus major*) nesting in forests on calcium-poor, acidified, and sandy soils in the Netherlands produced eggs with 7% thinner shells than in forests on well-buffered clay soils (Graveland et al. 1994; Graveland 1996). This difference was caused by the fact that 41% of the eggs in the calcium-poor forests had thin and porous shells, compared with less than 4% in calcium-rich forests (Graveland 1995). Almost 40% of the females produced eggs with defective shells, compared with only 2% in nonacidified forests (Table 6). More than 90% of the eggs with defective shells failed to hatch, compared with only 10% for eggs with normal shells. Defective shells of Great Tits were 77 μm thick, compared with 86 μm for normal shells.

Desiccation was the main cause of hatching failure in the case of the Great Tit and was four times as common as eggshell breakage (Graveland et al. 1994). The water content of Great Tit eggs at the start of incubation was 57% for eggs with defective shells and 77% for eggs with normal shells (Graveland 1995). The eggshell permeability of Dipper eggs from the acidified area in Norway was 13% higher than that in the non-acidified area (Table 6). The difference was not significant but may be attributed to the small sample size. There was no difference in hatching success of Dipper eggs between acidified and nonacidified areas. Surprisingly, Glooschenko et al. (1986) did not find any difference in the desiccation rate in eggs of Kingbirds from acidified and circumneutral areas, in spite of a difference in the eggshell thickness of 25% (Table 6). To my knowledge, there are no other studies in which the eggshell permeability was compared between birds from acidified and nonacidified areas. However, Weimer (1994) determined the desiccation rate of eggs taken from forests on calcium-poor bedrock (bundsandstein) and calcium-rich lime

Table 5. Occurrence of calcium-rich items in the food and in nests of birds in acidified and circumneutral lakes and forests.

	Acidified	Control	Ref.
Tree Swallow			
Items/stomach	0.3	1.1	St. Louis and Breebaart 1991[a]
Proportion in food(%of items)	0.2	1.1	Blancher and McNicol 1991[b]
Great Tit			
Proportion of nests withsnail shell fragments	16	75	Graveland 1996

[a]Comparison between birds nesting near wetlands with pH < 5 and pH > 6.
[b]Study of 56 lakes with natural variation in pH.

Table 6. Characteristics of reproduction of birds in acidified and nonacidified areas. Studies are listed where the authors attributed the low breeding success in the acidified areas to calcium deficiency.

	Acidified	Control	Ref.
Dipper (*Cinclus cinclus*)			
Eggshell thickness	94	99	Ormerod et al. 1988
Eggshell thickness (μm)	116.1	124.1	Nybo et al. 1997
Vapour permeability (μg $H_2O \cdot day^{-1} \cdot torr^{-1} \cdot mm^{-2}$)	0.96	0.85	Nybo et al. 1997
Hatching success (%)[a]	88	90	Ormerod et al. 1991
Laying date (January days)[b]	115	92	Ormerod et al. 1991
Eastern Kingbird (*Tyrannus tyrannus*)			
Eggshell thickness (μm)	36	49	Glooschenko et al. 1986
Desiccation rate ($mg \cdot day^{-1} \cdot cm^{-2}$)[c]	3.5	3.4	Glooschenko et al. 1986
Great Tit (*Parus major*)			
Eggshell thickness (μm)	82.3	88.0	Personal observation
Hatching success	80	91	Graveland 1996
Desertion rate (%, before hatching)	28	17	Graveland 1996
Clutches with defective shells (%)	39	2	Graveland 1996
Tree Swallow (*Tachycineta bicolor*)			
Hatching success	73	86	St. Louis and Barlow 1993

[a]Calculated from mean clutch size and brood size.
[b]Six to eight days of difference in date is explained by differences in altitude.
[c]Acidified: comparison of birds nesting at lakes with pH 4.3–5.0 and 5.1–6.0.

stone in Germany. He found that the desiccation rate was 50% lower in the latter. The hatching success did not differ between the soil types (88.5 ± 13.4% on limestone, 87.6 ± 15.8% on bundsandstein).

Eggshell defects, at rates similar to those observed in the Great Tit, were also observed in the Blue Tit (*Parus caeruleus*) and Coal Tit (Graveland 1995). The Marsh Tit (*Parus palustris*), Crested Tit, Nuthatch (*Sitta europaea*), and Great Spotted Woodpecker also produced eggs with defective shells (personal observation), but there were too few nests to determine which proportion of the eggs was defective.

One study provided experimental evidence for the fact that the high rates of eggshell defects in acidified forests may be caused by calcium deficiency. A feeding experiment using limited amounts of snail shell and chicken eggshell resulted in a drastic decline in the proportion of eggs with defective shells and an increase in hatching success among Great Tits in the Netherlands (Graveland et al. 1994; Graveland and Drent 1997). The calcium supplements also reduced the high rates of clutch desertion and complete but empty nests that were associated with the incidence of eggshell defects (see below).

Clutch desertion and empty nests

Among Great Tits and other species of tits in acidified forests on calcium-poor soils in the Netherlands, the rate of clutch desertion was 30–50%, as compared with 10–20% among birds nesting in forests on nonacidified soils (Graveland 1995, 1996). There was a close association between clutch desertion and eggshell quality: 43% of the females that produced eggs with defective shells deserted the clutch before the eggs could hatch (usually during egg-laying) compared with 16% for females with normal eggshells (Graveland 1996). Nybo et al. (1997) reported that the clutch desertion rate among Dippers in Norway was much higher in acidified areas than in nonacidified areas, although no data were provided.

Calcium deficiency apparently leads to some females not laying eggs at all. A nationwide survey in 40 forests in the Netherlands revealed a close association between the incidence of empty nests and eggshell defects (Graveland 1993). In forests with high rates of eggshell defects approximately 10% of the nests remained empty (Graveland and Drent 1997). Some of these nests were incubated for periods of up to 4 weeks (Graveland 1995). Möckel (1992) reported a high incidence of empty nests among nests of Coal Tits and Crested Tits in the Harz Mountains in Germany.

Some studies reported an increase in the incidence of empty nests of Great Tits in forests on calcium-poor, acidified soils in Sweden, Germany, and Netherlands (Schmidt 1990;

Carlsson et al. 1991; Graveland 1993; Winkel 1993; Fig. 3). In some areas the incidence of empty nests dropped at the end of the eighties while the incidence of eggshell defects remained about the same (Fig. 3). This difference in trends for eggshell effects and empty nests is hard to explain since a feeding experiment had shown that the high incidence of eggshell defects and empty nests is caused by a shortage of calcium (Graveland and Drent 1997). There is no reason to assume that the calcium availability has increased in recent years. A failure to lay may reflect the inability of a bird to find any calcium, while laying eggs with defective shells implies that the birds could at least find some calcium. Perhaps the decrease in the incidence of empty nests is due to the fact that some birds have started to exploit alternative calcium sources such as plaster and chicken grit that can be found at human settlements (Graveland and Van Der Wal 1996).

In conclusion, the decrease in the availability of calcium-rich material due to soil and water acidification affects avian reproduction through a decrease in eggshell quality, an increase in clutch desertion, and an increase in the proportion of females that do not produce eggs.

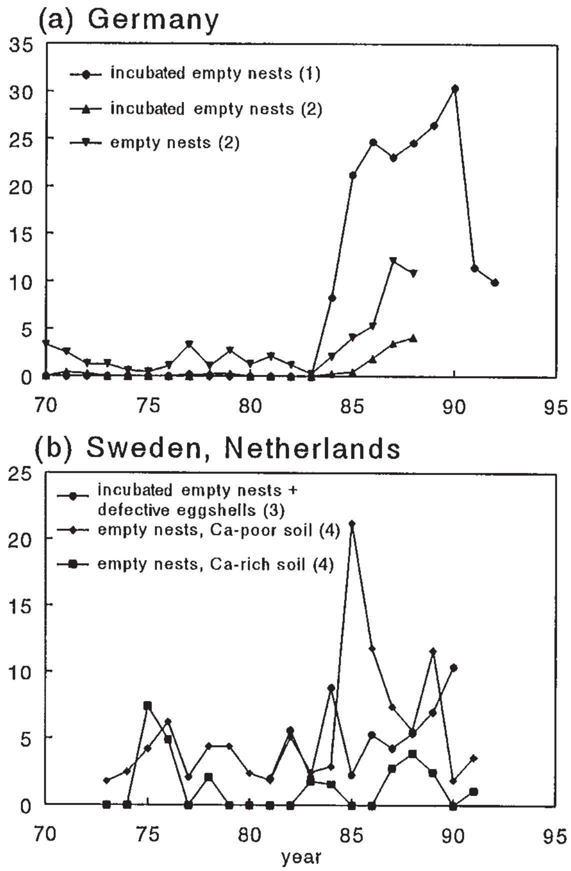
Impaired skeletal growth

Soil acidification might lead to an increase in the frequency of rickets among nestlings, since the formation of their skeletons often requires the intake of Ca-rich shells of molluscs and crustaceans, and these arthropods are affected by acidification.

Bone malformations in nestlings were observed in Great Tits in Scotland (MacKenzie 1950); Great Tits and Chiffchaffs (*Phyllosopus collybita*) in the Netherlands (G. Van Tol, personal communication; J. Graveland, unpublished observations); Coal Tits and Crested Tits in Germany (Möckel 1992); and Tree Pipits (*Anthus trivialis*) in the Czech Republic (S. Bures, personal communication). All the observations were done in forests on calcium-poor soils. Since there are no data on the incidence of bone malformations in the course of time, it remains unclear whether bone malformations have become more common as a result of soil acidification. However, a recent study by Beintema et al. (1997) provides some indirect evidence for such an increase. Black Terns used to be a common breeding bird of raised bogs in the Netherlands, but nowadays they hardly nest there at all. They have also disappeared from small oligotrophic ponds, probably owing to a decline in fish stocks because of acidification (Leuven and Oyen 1987). Small fish are an important prey of Black Terns. In 1995 Black Terns started to nest in Bargerveen, a restored raised bog on the border with Germany. Observations at the nests indicated that there was more than enough food for the nestlings (mainly dragonflies) and the chicks had a high growth rate during the 1st week after hatching. However, both in 1995 and 1996 none of the approximately 10 pairs raised any chicks. All chicks developed bone and leg deformations a week after hatching and died. Postmortem analysis showed advanced symptoms of rachitis (rickets), such as an ill-developed skeleton and multiple fractures in wing and leg bones.

Beintema also carried out a feeding experiment to determine whether the bone malformations among the tern chicks were really caused by calcium deficiency. He fed a number of chicks with calcium pills, which resulted in the normal development and fledging of these chicks. The results of this study suggest that the terns could successfully nest in such bogs in the past, because there were fish and dragonflies available, but are unsuccessful today owing to a lack of fish (dragonflies contain very little calcium). Another important aspect of this study was that it revealed that the incidence of calcium deficiency is not limited to passerine birds or to forests.

Fig. 3. Trends in the proportion of empty Great Tit nests in forests on calcium-poor soils in Europe. Sources of data: *1*, Winkel 1993; *2*, Schmidt 1990; *3*, Carlsson et al. 1991; *4*, personal observation.



Increased biological availability of toxic metals

Acidification of soils and water bodies increases the biological availability of toxic metals such as aluminium, cadmium, and lead (Hanson et al. 1982; Lodenius 1987; Eriksson et al. 1989; Van Straalen and Bergema 1995). In addition, the toxicity of ingested metals greatly increases when calcium intake is low, since the metals start to occupy sites on transport proteins in the gut normally occupied by calcium, and thus enter the blood stream (Six and Goyer 1970; Carlson and Nielson 1985; Van Barneveld and Van Den Hamer 1985). Experiments with captive birds showed that ingestion of metals that did not have a toxic effect when combined with a high calcium intake and had serious effects when combined with a low (but sufficient for maintenance and reproduction) calcium intake (Steinborn et al. 1957; Scheuhammer 1987, 1996; Sparling 1990). Internal symptoms of metal toxicity include damage to the intestinal wall, kidney, and testes and bone degeneration as a result of a disturbance of the absorption of calcium from the intestine (Scheuhammer 1987, 1991). Outward symptoms are the formation of defective eggshells, incomplete clutches, clutch desertion, and aberrant incubation behaviour (Sell 1975; Ando et al. 1978; Hamilton and Smith 1978; Leach et al. 1979; Frank 1986; Myklebust et al. 1993; H.C. Pedersen, personal communication).

Several studies have demonstrated that birds in acidified environments do indeed absorb more metals than birds in nonacidified areas (see review in Scheuhammer 1991). Feathers of Eastern Kingbirds in acidified marshes contained more mercury than birds from less acidic marshes (Glooschenko et al. 1986). Lead levels in the livers of Goldeneye (*Bucephala clangula*) in Sweden were higher in acid than in circumneutral wetlands (Eriksson et al. 1989). The same applied to aluminium levels in the tissues of Dippers in Norway (Nybo 1997). Ptarmigan (*Lagopus* spp.) in Norwegian heathlands contained high levels of cadmium in their kidneys and liver (Pedersen and Myklebust 1993).

Acidification leads to a decrease in the availability of calcium and an increase in the mobility of toxic metals. Also, metals become more toxic for birds when their calcium intake is reduced. Calcium deficiency and metal toxicity have partly similar effects on tissues and reproductive performance. It is, therefore, difficult to determine the relative contributions of calcium deficiency or metal toxicity to the high incidence of eggshell defects and laying irregularities in acidified calcium-poor areas. A high metal concentration in tissues and low reproduction suggest a causal relationship between the two. However, both a high metal concentration and a low reproductive output could be caused by a low calcium availability. For instance, Nybo (1997) found that Dippers in Norway had higher aluminium levels in acidified areas than in nonacidified areas, but there were no differences in the aluminium content of the food.

To show that soil acidification can affect avian reproduction both through calcium deficiency and through metal toxicity, and to point out possible differences between calcium deficiency and metal toxicity in effects on reproduction, I will compare two studies that have reported the most extreme effects of acidification on avian reproduction to date. One study attributes the observed effects to calcium deficiency, the other to metal poisoning. Both studies dealt with small insectivorous passerines that often share the same habitat, and in both studies 30% or more of the females produced eggs with defective shells and more than 40% of the clutches were deserted. The first study was carried out by Nyholm and co-workers on Pied Flycatchers (*Ficedula hypoleuca*) and other small passerines in the Ammarnäs region in northern Sweden (Nyholm and Myhrberg 1977; Nyholm 1981), and the second study was carried out on tits (*Parus* spp.) and Pied Flycatchers in forests in the Netherlands (Graveland 1996; Graveland et al. 1994; Graveland and Drent 1997).

Calcium shortage or aluminium toxicity: a comparison of two case studies

Large numbers of female Pied Flycatchers, Bluethroats (*Luscinia svecica*), Reed Buntings (*Emberiza schoeniclus*), and Willow Warblers (*Phylloscopus trochilus*) nesting along the shores of acidified lakes in Sweden produced eggs with defective shells, laid small clutches, abandoned their clutch, or were found dead on the nest (Table 7). Birds nesting only 100 m from the shore had a normal reproductive output. Nyholm suggested that the laying irregularities were caused by aluminium poisoning. The birds nesting close to the lakes fed on stoneflies (Plecoptera) that occurred in huge numbers along the shores. The stoneflies contained up to 0.1% aluminium owing to a combination of soil acidification and mining activities in the catchment area of the lake. Nyholm (1981) found elevated aluminium levels in the medullary bone of females that had died on the nest.

Table 7. Characteristics of the reproduction of Pied Flycatchers nesting along acidified, aluminium-polluted lakes in Sweden. Shore refers to birds nesting along the lakes and inland refers to control birds nesting 100 m from the lakes (after Nyholm and Myhrberg 1977).

	Inland	Shore	% of inland
Hatching success[a]	91	75	82
Desertion rate (%)[b]	14	58	414
Clutches with defect. shells (%)	0	36	—
Clutch size[c]	5.6	4.3	77

[a]Cases of predation and desertion excluded.

[b]Before hatching, 50% in clutches without eggshell defects and 83% in clutches with eggshell defects.

[c]Size of clutches that were not deserted before hatching.

An argument against a primary causal role of aluminium toxicity is that aluminium is usually not toxic, even at concentrations of up to 1%, unless the calcium availability in the food is low (Storer and Nelson 1968; Sparling 1990; Scheuhammer 1991; Nybo 1997). However, there are several arguments in favour of a causal role of aluminium poisoning, and against calcium shortage as an alternative explanation.

(1) Birds nesting only 100 m from the shore of the lakes did not show an impaired reproduction. There is no reason to believe that the calcium availability (presence of snail shells, calcareous grit) varied much over such a small distance. Even if it did, observations of Great Tits and other species indicate that egg-laying females collect calcium-rich material 100s of metres from their nests (Graveland 1995; Graveland and Van Der Wal 1996). However, the shore and inland zone did differ in the availability of aluminium-rich Plecoptera.

(2) In Ammarnäs, Pied Flycatchers showed a much higher rate of eggshell defects and clutch desertion than Great Tits (E. Nyholm, personal communication), while data from the Netherlands showed that Pied Flycatchers are much less likely to suffer from calcium deficiency than Great Tits. In forests in the Netherlands, where 30–50% of Great Tit females produced eggs with defective shells and had a high desertion rate, Pied Flycatchers hardly produced eggs with defective shells and had a normal desertion rate (Graveland 1995). The soils in these forests mainly consist of mineral sand (quartz) and contain very little aluminium (contrary to Ammarnäs, where the bedrock largely consist of aluminium-rich gneiss and granite). Calcium-feeding experiments showed that the eggshell defects were caused by calcium deficiency. Observations of parents feeding nestlings and examination of the nest material and stomachs revealed that Pied Flycatchers suffered much less from calcium deficiency than Great Tits, because they included millipedes and wood lice in their diet and ground-living arthropods with calcified exoskeletons, while Great Tits did not (Graveland 1995; Graveland and Van Gijzen 1994).

(3) Contrary to Great Tits, Pied Flycatchers gather a large proportion of their food from the ground. Soil arthropods

contain higher levels of toxic metals than insects and spiders in the canopy (Bengtsson and Rundgren 1984; Sawicka-Kapusta 1987), and Pied Flycatchers are therefore much more likely to absorb toxic metals than Great Tits. Pied Flycatchers nesting near copper smelters that emitted large amounts of copper, lead, and nickel had a much lower hatching success than Great Tits (Nyholm 1993; Eeva and Lehikoinen 1995).

(4) The type of damage to the eggshells differed between the two cases. The defective eggshells of the Pied Flycatchers were characterized by a mosaic of parts where the shell appeared normal and parts with a thin shell or no shell. The shells in the affected parts looked compact and had a shiny surface, indicating that the cuticle (a waxlike substance deposited after deposition of the calcite crystals is finished) was present. The defective shells of Great Tits had a rough appearance over the entire surface, reflecting the incomplete deposition of calcite crystals and lack of a cuticle, and there were no visible differences in the degree of damage between parts of the shell (Graveland 1995). Although it is not clear how aluminium toxicity and calcium deficiency can lead to such different eggshell defects, the differences seem too great to have the same cause.

Because of these arguments, I conclude aluminium toxicity is a more likely explanation for the high rate of eggshell defects observed in Nyholm's study than calcium deficiency. The available evidence thus suggests that acidification can affect avian reproduction through both metal poisoning and calcium deficiency. The relative importance of metal toxicity and calcium deficiency depends on soil characteristics and feeding habits of the birds.

Discussion

Effects of acidification on bird populations

This compilation of the effects of acidification on birds shows that the relation between acidification and birds is complex. Acidification may affect bird populations in various ways and studies in which a specific effect of acidification on birds was examined often gave different results, e.g., with respect to changes in the availability of invertebrates. Three effects of acidification on birds are consistent and clear: declines of fish stocks (effect *a*), advanced stages of forest dieback (effect *d*), and large declines in calcium availability (effect *e*) have great impacts on the reproduction and population size of piscivorous birds, forest birds, and insectivorous or granivorous birds, respectively. With respect to calcium deficiency, there are many areas with soils with a low content of readily available exchangeable calcium where calcium-rich items such as snail shells and calcareous grit are scarce (Graveland 1996). Such areas are particularly sensitive to acidification owing to the low buffering capacity of the soil (Van Breemen et al. 1983; Heij and Scheider 1991; De Vries 1994). Calcium limitation as a result of acidification is therefore probably widespread.

The results of studies on the effects of acidification on bird populations through changes in the abundance of invertebrates or seeds (effect *b*) and through an increase in the amount of standing dead timber (effect *c*) were much less consistent (see also Graveland 1990). There were at least three reasons for the apparent inconsistency in the results with respect to effects of changes in the abundance of invertebrates and seeds. (*i*) The availability of invertebrates and seeds may increase or decrease, depending on the taxon and on the extent of acidification. (*ii*) Effects of a decline in invertebrate abundance might be mitigated by compensatory mechanisms such as reduced competition of fish and increased foraging efficiency due to lack of cover for invertebrates, for instance by leaf or needle loss. (*iii*) Acidification may affect the population size without affecting the breeding success, which is usually the object of study (Möckel 1992; Darveau et al. 1993). It is not clear why populations of hole-nesting species increased in some cases and declined in others. The effects of a loss of cover or lower insect abundance due to loss of leaves or needles may have counterbalanced the effect of an increase in nest site availability in some cases, but the small number of studies precludes making any firm conclusions. Summarizing, acidification can affect the size of populations of insectivorous and hole-nesting birds in forests and wetlands through changes in the abundance of invertebrates, seeds, and nest sites. However, owing to the wide range in effects that were found and the limited amount of data, it is at present difficult to predict how acidification will affect the availability of food and nest sites, and thus the population size, of insectivorous and granivorous birds in forests and aquatic habitats in specific cases.

I gave examples of studies that showed that acidification of soils and waters can lead to higher intakes of toxic metals by birds (effect *f*). However, Scheuhammer (1991) and Nybo (1997) concluded that the levels reported in birds are too low to have an effect on the birds' reproductive rate and thus on the size of the population. Scheuhammer attributed the eggshell defects and laying disorders in Pied Flycatchers that Nyholm and Myhrberg (1977) reported to calcium deficiency. However, in my opinion, for the reasons listed above, Nyholm's study provides a good example and, to my knowledge, the only one of how acidification can seriously affect avian reproduction through an increase in the exposure to toxic metals in areas with soils with a high content of toxic metals, in this case aluminium in gneiss and granite.

Acidification in the future

Many countries in the western world have implemented measures to reduce emissions of acidic compounds. However, these measures do not seem to be sufficient. For instance, the average critical acid load for coniferous and deciduous forest on non-calcareous sandy soils in the Netherlands is ca. 1400 mol H^+/(ha·year) (De Vries 1994). At this level the most adverse effects of acidification on trees and soils are prevented. Once this deposition level is reached, the ratio of dissolved Al to Ca is expected to decrease below the critical level, and the base saturation and pH of strongly acidified soils are expected to recover quickly (De Vries 1993; De Vries et al. 1994*a*). If the emission reductions occur according to schedule, this level will be reached around 2030. The target deposition level for 2010 is 2400 kmol/(ha·year). The present deposition rate is 4000 kmol/(ha·year) (Schneider 1992; Rijksinstituut voor Volksgezondheid en Milieu 1997). If the current rate of decline is any indication for the future, the target levels will not be reached, and even if they are reached, soil acidification will continue in the coming decades and effects on birds are likely to become greater. Contrary to the Netherlands, elsewhere in Europe even the planned reductions in acid deposition are insufficient to decrease anthropogenic soil acidification (De Vries 1994; De Vries et al. 1994*b*). In North America deposition levels are expected to rise to a peak around 2005 and to decline rapidly thereafter, in particular by a reduction of SO_2 emissions as a result of the planned retirement of coal-fired electric utility plants (Streets 1991). However, these future projections are subject to a high degree of uncertainty. In developing countries with booming economies, in particular in southeast Asia, the amount of acid rain is increasing instead of decreasing (e.g., see Rohde et al. 1988). Ironically, deposition of calcium emitted by smoke stacks (calcium is used to remove sulphur from the emittant) was an important calcium source in the past, but the deposition has greatly decreased in recent years in response to the overall reduction in industrial emissions. In eastern Germany this reduction has caused serious acidification in some areas (Hüttl et al. 1996).

It is, therefore, to be expected that the breeding success and population sizes of birds on poorly buffered soils in large parts of the world will, to an increasing extent, become affected by the acidification of soils and waters.

What kind of studies are needed?

Our understanding of the effects of acid deposition on the reproduction and population size of birds has greatly increased during the last 20 years. The emphasis in the funding by governments has shifted from research on effects of acidification to remedial action, such as liming of forests and streams (e.g., see Hildrew and Ormerod 1995). At the same time, anthropogenic acidification is expected to continue during the next decades. Therefore the feasibility and effectiveness of remedial action should be an important research topic.

Areas under moderate levels of acid stress are larger than strongly affected areas such as parts of central and western Europe. However, at present there is no clear picture of the effects of acidification on the population sizes of insectivorous or hole-nesting forest birds in such areas, owing to the differences in outcome of previous studies and the small number of studies that have been carried out. To my knowledge, Tables 1–4 present the results of the only bird censuses that have been published. The results of Möckel (1992) and Darveau et al. (1993) showed that acidification may affect the size of bird populations without affecting the reproduction. There is thus a great need for bird census data. Census data are relatively easy to collect and they provide good insight in the extent of the effects of acidification at the population level. Where possible, studies aiming to provide insight into the mechanism of the effect of acid deposition on the population level should not only examine the breeding success but also recruitment and survival.

Comparisons of characteristics of eggshells in museum collections and freshly collected eggs might reveal trends in eggshell quality and might thus provide insight in effects of acidification on avian reproduction over a longer period than is possible with data sets on reproductive success in free-living birds, which usually span a period of less than 2 decades.

There is a need for studies that provide insight in the relative importance of calcium deficiency and metal toxicity in causing eggshell defects and laying disorders in acidified areas. The common opinion seems to be that metal toxicity is not a serious problem (e.g., see Scheuhammer 1991), since the levels in birds are too low to be harmful, but in my opinion the results of Nyholm's study (Nyholm and Myhrberg 1977; Nyholm 1981) imply that metal poisoning can greatly affect avian reproduction, at least at a local scale. The differences in the type of eggshell defects between Nyholm's study and the study on Great Tits in the Netherlands suggest that these differences might be used to discriminate between calcium deficiency and aluminium poisoning.

Finally, almost all the evidence presented in this paper on the effects of acidification on birds consists of correlative data. There is a great need for experimental work, such as calcium feeding experiments and the manipulation of the availability of nest sites and food. Experimental data provide stronger evidence than correlative data alone, which is both important from a scientific and a conservation point of view.

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