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Reviews

Effects of acid precipitation on reproduction in birds*

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Summary. Acidification in aquatic habitats reduces the reproductive success of both piscivorous and non piscivorous birds, mainly by reducing the food supply. Piscivorous birds find some compensation in an increased transparency of the water, non piscivorous birds in less competition for invertebrate prey by fish. Acidification in forests often has large impacts on insect populations but how this affects forest birds is unknown. Some woodpeckers and nuthatches temporarily benefit from an increase in standing dead timber. In advanced stages of forest dieback the breeding density of forest birds is very much reduced, but species of open woodland increase. Calcium deficiency reduces the reproductive output of some passerine species, but the extent of this phenomenon is unknown. Increased exposure to toxic metals has reduced the reproductive success of some lake dwelling species. It is difficult to assess the effect of acid precipitation on birds since acidification affects ecosystems in many ways, the evidence is largely correlative and reliable estimates of the population size are often lacking. Future studies should concentrate on carefully selected indicator species suitable for detailed data collection.
Key words. Acid deposition; reproduction; birds; insects; calcium.

1 Introduction

The term 'acid rain' was first used in 1852 to describe the effects of industrial emissions on precipitation in Britain[90]. However, only in the 1950's did it become evident that acid precipitation was a worldwide phenomenon, and it took another 20 years before widespread public concern forced governments to initiate studies on the effects of acidification on ecosystems. Many studies have been carried out since the 1970's and an enormous amount of information has become available on the effects of acid precipitation on the water chemistry and the invertebrate life in aquatic ecosystems[23, 79, 90], on soils[14, 34, 52, 68, 106] and on trees[21, 63, 94, 96]. However, little is known about effects on higher trophic levels, in particular on mammals and birds.

Studies of acidification and birds mostly concern wetland birds, especially in North America[62, 66, 67, 93]. One of the first noticed effects of acidification was the decline of fish populations[2, 6, 7, 42] and this focused the attention on wetlands. Population declines of important game species like the Black Duck *(Anas rubripes)* and public concern for the popular Great Northern Diver *(Gavia immer)* also played a significant role. In Europe, data on the effects of acidification on insects and forest birds have only recently become available[24, 59, 77].

This review aims to bring this information together, to identify the mechanisms by which acidification could affect birds, to identify the problems involved in interpreting the data and to make suggestions for future research. Emphasis will be on the effects of acidification on the reproduction of birds, in particular on the reproductive success of birds initiating a clutch. Other important aspects, such as the proportion of females that initiate a clutch, or the survival of adult birds, are much harder to study and there are virtually no data on the subject.

In sections 2.1 and 3.1 changes in the biotic and abiotic environment due to acidification are reviewed. Sections 2.2 and 3.2 deal with effects of changes in availability of food and vegetation characteristics on various groups of birds. Effects of changes in food quality are treated in sections 4.1 and 4.2.

2 Acidification in aquatic ecosystems

2.1 Effects on water chemistry, availability and quality of food for birds

Numerous studies have been carried out in the last two decades on the effects of acid precipitation on the chemistry of lakes and streams and on the resulting changes in populations of macrofauna [41, 78, 79, 81, 104] and fish [2, 6, 7, 42]. Changes in abiotic factors include a decrease in pH from 6–7 to 4–5 and even lower, a decrease in alkalinity (= acid neutralizing capacity) and an increase in the concentrations of toxic metals such as Al, Hg, Cd and Pb. Acidification may also lead to a decrease in Ca and Mg, especially in streams. The precipitation of humus particles increases at a lower pH, resulting in greater transparency of the water [27, 28].

Acidification has caused fish populations to decline or to disappear completely. Eggs and young fry are very sensitive to low pH levels [90], but a scarcity of invertebrate food and an increase in the accumulation of toxic metals [92] are also implicated. In general, acidification leads to a lower productivity of both plant and animal life. Due to a drop in pH, both macrophytes [96] and zoobenthos and macrofauna communities have decreased [2, 48, 88]. Taxa with a high mineral content, such as snails, clams, crustaceans (crayfish, Amphipods) appeared to be most sensitive and disappeared first [11, 44, 79]. A pH of 6 seems to be a threshold value for these species [44, 80].

The remaining species contain less Ca than previously; e.g. the Ca content of stoneflies (Plecoptera) in streams in Wales was about 0.2 % in streams with $pH < 6.5$, compared to 0.45 % at $pH > 6.5$ [80]. As birds need a great deal of Ca for reproduction (formation of eggshells, development of juvenile skeleton) a decrease in Ca availability could affect them. Concentrations of toxic metals in tissues of invertebrates and fish from acidified lakes are often higher than in non-acidified lakes [9, 57]. In Ontario, Canada, metal levels in Mink (*Mustela vison*) and Otter (*Lutra canadensis*) varied with the levels in crayfish and fish, indicating an accumulation of these metals via the food chain [118]. This could also apply to birds.

Some effects of acidification are beneficial to birds. The reduced predation by fish sometimes leads to an increase in invertebrates, or a move of invertebrates from the sheltered parts of the lake to open water, which makes them accessible to birds [49]. The increase in zooplankton, also a result of reduced predation by fish, can lead to lower phytoplankton levels. This could help piscivorous birds that hunt by sight [27, 28].

2.2 Food availability and the reproduction of aquatic birds

Piscivorous birds. Studies on the Great Northern Diver in North America [66] showed a negative relationship between the acidity of the lake and reproductive success (growth and survival of young chicks). However, studies by Parker [82], and an extensive study on the Black-throated Diver (*Gavia arctica*) in Sweden by Eriksson [30, 31] failed to affirm this relationship, possibly because the pH was not as low as in the other studies and chicks were not wholly dependent on fish but were also fed invertebrate food. Juveniles of fish eating species feed largely on invertebrates, so less fish in the diet is sometimes compensated for by more invertebrates. In the case of the Black-throated Diver a reduced risk of predation by Pike (*Esox lucius*) might also play a role [60]. Populations of the Great Crested Grebe (*Podiceps cristatus*) in the Netherlands, breeding on small acidic lakes on poor sandy soil, have declined due to a drastic decrease in pH [95]. The distribution is now limited to those lakes that still contain fish. An obligate fish-eating species like the Osprey (*Pandion haliaetus*) does not benefit from an increased transparency of the water or a higher number of invertebrates. Despite the ban on the use of persistent pesticides, the breeding success of Ospreys in Sweden has declined in recent years, especially on acidified lakes. In the more acidified areas the distance over which the Osprey delivered fish to their young was greater and the nests were more widely spaced [29, 32].

In summary, acidification has deleterious effects on the reproductive success of piscivorous birds. Unfortunately, there are no census data for most species, which makes it very difficult to determine whether the above-described mechanisms led to a decrease in aquatic bird populations. An exception are the 'dead lakes' in Scandinavia.

Non-piscivorous birds. Studies have indicated that birds in acidified lakes may sometimes benefit from a decrease in fish populations. In Europe, Eriksson [25] showed that the food choice of fish and adult Goldeneye (*Bucephala clangula*) overlapped considerably. He removed fish from one lake and found that Goldeneyes started to feed in this lake more frequently than before, and more than in an adjacent control lake with fish. Similar results were obtained for the Canadian prairie Black Duck. Ducklings raised on lakes with fish had a lower foraging efficiency and growth rate than ducklings raised on a control lake without fish, as a result of competition for invertebrate prey [55]. However, in other studies the growth rate of Black Duck ducklings was lower on acidified as compared to non-acidified wetlands [20, 86]. Similar results were obtained with ducklings of the Ring-necked Duck (*Aythya collaris*). Competition from fish did not play a role here as there were none [64].

The decline of the Dipper (*Cinclus cinclus*) population in Scotland and Wales may also be caused by acidification. Population density, clutch size, and foraging efficiency were all positively correlated with the pH of the streams [80]. Acidification caused a decrease in the abundance of caddisfly (Trichoptera) and mayfly (Ephemeroptera) nymphs and the complete disappearance of *Gammarus* species, all important food items of Dippers. Summarizing, similarly to piscivorous birds, non-piscivorous species often have a lower reproductive success due to lack of food. In less extreme cases the birds may find some compensation in, or even temporarily benefit from, the reduced competition by fish.

Data on the effects of acidification on strictly herbivorous birds (geese, swans) are lacking. In lakes in Ontario the diversity of Bryophytes was positively correlated with the pH, and Charophytes did not occur below pH = 5.2[96]. However, acid tolerant plant species may increase[95]. Macrophytes are affected because there are less nutrients in acidified lakes, but they may benefit from the increased water transparency. Therefore, it is still not clear how acidification affects herbivorous waterfowl.

3 Acidification in forest ecosystems

3.1 Effects on soils, trees and the availability of food for forest birds

There is no longer any doubt that acid precipitation is the most important cause of the forest decline in Europe and North America[40,91,94]. The direct effects of acid precipitation on soils and trees are acidification of the soil, i.e. leaching of cations (Ca, Mg, K) from the root zone and increased mobility of Al and other toxic metals, and leaching of cations from leaves and needles[43,94,109,111]. These processes disturb the uptake of nutrients by the roots, affect the vitality of the trees and make them more susceptible to infections by insects and fungi. In the heavily polluted areas of Silezia (Poland) and Bohemia (Czechoslovakia), and mountainous areas of Germany and Switzerland, whole forests have died and been replaced by open woodland. Coniferous forests at higher altitudes are most affected, probably because of the combined effects of acid deposition, poorly buffered soils and a harsh climate. Effects of acidification on birds can be classified as follows: a) changes in the availability of invertebrates and seeds, b) increase in standing dead timber, c) forest dieback and replacement by open woodland, d) decrease in Ca availability and e) increased exposure to toxic metals.

Recently a great deal of information about the effects of acidification on insects has become available. When trees are affected by environmental stress the frequency of outbreaks of phytophagous insects increases[3,40,59]. This pattern can have several causes. Irrespective of the exact way acid deposition affects the trees, the ultimate effect is often an increase in soluble nitrogen, resulting in a higher nutritional value for insects[115]. This process may also explain the increase in seed production in response to acidification: instead of using the nitrogen for vegetative growth it is used to form seeds. Changes in the formation of secondary compounds are more diverse and seem to depend more on the specific type of stress[59]. However, plants exposed to acidic air pollution are usually less resistant to insect attacks than non-exposed plants. It has also been suggested that outbreaks of insect pests increase because acid stress affects parasites more than their hosts, or makes parasites less effective[3,45]. Various groups of invertebrates respond differently to the new situation. Aphids seem to benefit most from acidification[12,13,22,70], followed by chewing insects like caterpillars[74]. However, gall-forming insects perform less well on trees exposed to acid rain[59]. Larsson[59] suggested that differences in feeding habits were responsible for this variation. Even species from the same genus may respond differently[46].

A positive effect of acid deposition can turn into a negative effect at high levels of exposure[47,54,115] and different acidic compounds (SO_2, NO_x) may elicit quite different reactions[22].

Larsson noted a discrepancy between the increase in outbreaks of insect pests due to acidification and experiments showing a growth reduction of larvae exposed to air pollution[59]. A difference in response between parasites and hosts may explain this paradox.

3.2 Food availability, forest dieback and forest birds

Food availability. Compared to aquatic habitats, there are very few studies on the effects of changes in the number of insects caused by acidification on the reproduction and population size of birds in forests. In Spruce *(Picea abies)* forests in Sweden needle loss by acid deposition resulted in a decrease in the number of large, but not of small spiders[38]. Gunnarsson suggested that needle loss made the spiders more visible and thus liable to increased predation by birds. Spiders are a major food source in winter and early spring for passerines in spruce forests[39,50,56]. A higher predation rate in winter could result in a reduced abundance of spiders in spring, with possible repercussions for egg laying. The decrease during the last decade of the residential Goldcrest *(Regulus regulus)*, Crested Tit *(Parus cristatus)* and Coal Tit *(P. ater)* in Denmark[72] might be caused by a decrease in the number of spiders[38]. On the other hand, laying females might benefit from an increase of aphids in spring. Aphids are especially numerous in spring, before other insects are available, and species such as tits may rely to a large extent on aphids for the formation of eggs.

In The Netherlands needle loss, soil acidification and excess nitrogen led to an explosive increase of the Wavy Hairgrass *(Deschampsia flexuosa)* in Scots Pine *(Pinus sylvestris)* forests. Red Ants *(Formica rufa)* are a major food item for Green Woodpeckers *(Picus viridis)* in these forests but they need bare soil to build their mounds. Today the number of mounds is only a fraction of the number in 1972 and that is probably the reason for the population decline of the Green Woodpecker since then (Post, unpubl.).

In Germany, the Crossbill *(Loxia curvirostra)* and the Citril Finch *(Carduelis citrinella)* are increasing, due to a stress-induced increase in seed production of Spruce, their staple food[51].

Several wood-boring species have at least temporarily benefited from the increase in standing dead timber. The Three-toed Woodpecker *(Picoides tridactylus)*, who prefers forests with a great deal of dead wood[17], has increased in Germany[51]. DesGranges[19] recorded an increase of the White-breasted Nuthatch *(Sitta carolinensis)* in Sugar Maple *(Acer saccharum)* forests in Canada. Eighty-five percent of the forests showed advanced signs of dieback.

Forest dieback. The last step in the degradation of forests caused by acidification is a large-scale dieback of trees, now apparent in the coniferous forests of central Europe[94] and the Sugar Maple forests in North America[19]. Especially forests at higher elevations are suffering. The degradation takes place in steps, starting with an opening in the canopy due to loss of leaves and needles, followed by the dying off of branches and individual trees, and an increase in shrubs and herbs in the undercover, and finally the replacement of the forest by open woodland dominated by shrubs[77]. Taking this change into consideration, a shift would be expected in the bird community from forest species to species of open woodland. This is confirmed by bird surveys in the Harz[77], Bohemia[102] and Canada[19]. In Europe, populations of forest species like the Robin *(Erithacus rubecula)* and the Chaffinch *(Fringilla coelebs)* were decimated in areas of forest dieback; and Firecrests (*Regulus* spp.) and ground-gleaning birds like the Blackbird *(Turdus merula)* and the Song Trush *(T. philomela)* decreased, as did forest-gleaning birds like the Red-eyed Vireo *(Vireo olivaceus)*, Wood Thrush *(Hylocichla mustelina)* and Ovenbird *(Seiurus aurocapillus)* in the Sugar Maple forests in Canada. Species characteristic of the shrub layer (Wren, *Troglodytes troglodytes*, Dunnock, *Prunella modularis*) showed a much smaller decrease. Some species increased: i.e. the Willow Warbler *(Phylloscopus trochilus)* and Redstarts (*Phoenicurus* spp.) in the Harz and the Eastern Wood Peewee *(Contopus virens)* in Canada. The European Tree Pipit *(Anthus trivialis)*, a species of open woodland, increased the most, especially in the most advanced stages of forest dieback. Nevertheless, in spite of an increase of some species, the breeding density of all birds combined decreased: 75 % in Bohemia, 40 % in the Harz. The shift from forest to open woodland due to acidification is often accelerated by changing forestry practices. In response to acid rain foresters will fell trees at an earlier stage to use the timber before decay makes it worthless, and reforestation is stalled because foresters consider it pointless[51]. This may have consequences for species limited to old stands of coniferous forest like the Black Woodpecker *(Dryocopus martius)*[17]. Some very rare species benefit from the forest dieback, creating bizarre problems for the conservationist: e.g. the Rock Bunting *(Emberiza cia)* in the Black Forest, or the Ring Ouzel *(Turdus torquatus)* that colonized the denuded parts of the Harz in 1986[51].

4 Acidification, food quality and reproduction of birds

4.1 Reduced availability of calcium

Usually invertebrate food does not contain sufficient Ca to meet the Ca requirements of a laying bird (Arctic Sandpipers, *Calidris* spp.[65]; Swallow, *Hirundo rustica*, and Sand Martin, *Riparia riparia*[108]). Therefore, the birds store Ca in their skeleton before laying or select items rich in Ca, varying from snail shells (Blue Tits, *Parus caeruleus*[84]) and Lemming teeth (*Calidris* spp. on tundra[65]), to cement (Crossbill, *Loxia curvirostra*[105]) and calcareous grit (Red Quelea, *Quelea quelea*[58]). Laying hens show a specific appetite for food rich in Ca if fed a diet deficient in Ca, and can even distinguish Ca-rich solutions from others[53]. There are no studies of wild birds showing that they need to be able to select items rich in Ca. This habit is, however, widespread and without the extra Ca the amount of Ca that would need to be stored in the skeleton would be extremely high, so it seems very likely that birds need this additional Ca supply. The same may apply to growing juveniles. Parents often feed their young with items rich in Ca (Tree Swallow[11]; Lapland Longspur, *Calcarius lapponicus*[97]; *Calidris* spp.[65]). Nestlings of the Song Thrush and the Blackbird only received enough Ca because the soil in earthworms, their main food, was rich in Ca[8].

The Ca content of the soil may even determine the distribution of the Pheasant, *Phasianus colchicus*[18] and the Partridge, *Perdix perdix*[116] in North America. In The Netherlands[100] (Van Balen unpubl.) and in England[84] nestlings of tits breeding in coniferous forests on poor podzolic soil sometimes have weak legs due to Ca deficiency.

Many examples of selection of items rich in Ca are found in areas with low nutrient levels: selection of ash rich in Ca by Boreal Chickadees *(Parus hudsonicus)* in Alaska[35]; Lemming bones and teeth by Sandpipers on the tundra[65]; bones, putty or cement by Crossbills in coniferous forests[83, 69, 105].

Leaching of Ca and the increased mobility of Al in acidified soils disturb the Ca uptake by the roots[91, 94]. The Ca content of leaves and needles decreases due to this process and by direct leaching of Ca from the leaves and needles (see Boxman and Van Dijk[14]). It is not clear to what extent this also causes a decrease in the Ca levels of invertebrates, or a decrease of species that need large amounts of Ca (e.g. snails). Contrary to aquatic ecosystems, this aspect has received little attention in terrestrial systems. There are some scattered reports but much of the information is anecdotal. A German report mentions that there were holes in the shells of live snails in acidified forests (Van Noordwijk, pers. comm.). On lime soils the species richness and abundance of snails is much greater than on poor, sandy soil[113] and relationships such as those between shell thickness, fecundity and the Ca content of the soil are well documented[114] (Bauer, pers. comm.). However, there is no quantitative data over a range of years.

The first indication of a Ca shortage would be a deterioration of the quality of the egg shell, not only because the Ca requirements of birds peak shortly before or during egg-laying, but also because the Ca content of invertebrates is often low in spring[87]. In Canada, female Eastern Kingbirds *(Tyrannus tyrannus)* breeding in acidic wetlands laid eggs with thinner and more permeable shells than females in less acidic wetlands[36]. Tree Swallows *(Tachycineta bicolor)* breeding near acidified wetlands had smaller clutches and fed their nestlings fewer snail or clam shells and parts of crustaceans than their fellows who were breeding close to circumneutral wetlands[10]. In Wales, female Dippers breeding near streams with a low pH laid eggs with thinner shells than those near streams with a high pH[80]. The Ca content of the food had decreased, largely because *Gammarus* species with their calcified exoskeletons had disappeared. However, the variation in shell thickness explained by stream acidity was low compared to the variation explained by other factors that were not related to stream acidity and the hatchability of the eggs was not impaired.

A recently published study on the Great Tit *(Parus major)* indicates that forest birds may also be affected by Ca deficiency[24]. In forests on poor sandy soil, where trees showed clear signs of damage by acid precipitation, an increasing number of females produced eggs with defective shells, laid fewer eggs or no eggs at all. The affected shells were thin and porous and most of the eggs dried out. This increase did not occur in forests less affected by acidification. Other residential species (Blue Tit, Coal Tit, Nuthatch, *Sitta europaeas,* Great Spotted Woodpecker, *Dendrocopus major*) also produced eggs with defective shells, but the migrant Pied Flycatcher *(Ficedula hypoleuca)* did not. The Ca content of leaves and caterpillars in forests with defective shells was much lower than in forests where eggs were normal, but lack of Ca-rich items like snail shells might also play a role (Graveland, unpubl.). There is as yet no conclusive evidence that the lower reproductive success observed in these studies was caused exclusively by Ca deficiency. Other factors such as a general food shortage or higher susceptibility to diseases might also be involved. Studies are currently being carried out, both in Europe and North America, to clarify the role of Ca deficiency in the decrease in reproductive success due to acidification.

4.2 Increased exposure to toxic metals

Al and other toxic metals (Cd, Pb, Hg) are normally bound to soil particles or are present in insoluble form. Many studies have demonstrated that acidification leads to mobilization of these metals, resulting in higher concentrations in food items of birds (sections 2.1, 3.1). The determination of the exact mechanism by which acidification affects the reproduction of birds is complicated by the fact that the toxicity of metals, especially Al and Pb, depends to a very large extent on the Ca and P content of the food. If the amounts of Ca and P in the food are high, the metals are much less toxic than if the Ca and P supplies are low[15,89,99,117] (Scheuhammer, unpubl.). Feeding experiments with growing chickens[61,103], Mallard *(Anas plathyrhynchos)* and Black Duck ducklings[101] as well as with laying females of the Ring Dove *(Streptopelia risoria)*[16] demonstrated that Al concentrations in the food of up to 0.1 % affected growth and survival only if the P content of the food was low (but sufficient in the absence of Al). Usually the efficiency of the Al absorption is low and virtually all Al is excreted. However, in the intestine Al binds phosphate from the food to form insoluble aluminiumphosphate ($AlPO_4$), resulting in a lower uptake of phosphate. If the P/Al-ratio in the food is lower than 2, the uptake of phosphate is so low that it disturbs the Ca-P metabolism (review by Scheuhammer, in prep.). Low Ca levels, as well as low P levels in the food may also lead to disturbance of the Ca-P metabolism in the presence of Al. The Ca necessary for the formation of egg shells is largely stored in the skeleton, in the form of medullary bone: a porous bone tissue formed in the marrow of the most vascularized bones[98,107]. Prior to egg-laying, hormonal changes induce the birds to increase the secretion of Ca-binding protein in the intestine. This makes a higher absorption efficiency possible so that the birds can build up medullary bone. However, if the food has a low Ca content, other metals (Al and Pb in particular) may bind with it and become incorporated in the skeleton[99]. Recent experiments with Starlings *(Sturnus vulgaris)* showed effects of low Ca and high Al levels in the food on mortality and egg-laying, but they appeared to be more related to a Ca content than to a high Al content of the food (Blancher, pers. comm.). A deficiency of Ca in diets may also facilitate the uptake and thereby the toxicity of Cd[110].

There are relatively few studies on the effects of this additional exposure to toxic metals on reproduction of birds. Eriksson[26] measured higher Pb levels in eggs of Goldeneye in acidified wetlands in Sweden, but he did not report any effects on reproductive success. In a more recent study Eriksson et al.[33] analyzed the metal contents of livers of juvenile Goldeneyes just before fledging, from acid, circumneutral and limed lakes. They found no significant differences between the three groups but a few individuals from the acidified lakes had such high levels of Hg in their livers that "effects on behaviour were not unlikely". In Eastern Kingbirds in Ontario, the Hg content of livers and feathers of females breeding in acidic wetlands were higher than those in birds from less acidic wetlands[36]. The porosity of the eggs was also greater in the more acidic areas, but it was not clear whether this could be attributed to lead poisoning, to Ca deficiency or both. The hatchability and the clutch size appeared not to be affected, so the overall effect on reproduction was probably small. Great Northern Divers breeding in acidified lakes in Canada had higher methyl-Hg-contents in their tissues than birds breeding in less acidified waters, which was probably the reason for the lower reproductive success on acidified lakes[5]. Ahlgren et al.[1,31] demonstrated that the Hg content of eggs of the Black-throated Diver in southern Sweden was higher than in Barr's study. However, the sample size was too small for a comparison between acidified and non-acidified lakes. The most serious effects of acidification on the reproductive success to date were reported from Sweden. Female Pied Flycatchers breeding along the shore of acidified lakes laid fewer eggs and abandoned their clutch more often than birds breeding further inland. They also laid a large number of eggs with defective shells[76]. The shells had a rough surface and were very porous. Bluethroat *(Luscinia svecica)*, Reed Bunting *(Emberiza schoeniclus)* and Willow Warbler also suffered in this way. The medullary bone of female Pied Flycatchers laying eggs with affected shells contained more Al than of those producing sound eggs. Stoneflies, the main food of birds breeding close to shore, contained large amounts of Al (up to 0.9 %), a result of mining activities in the catchment area of the lake combined with acidification. Nyholm[75] therefore suggested that the affected birds suffered from Al poisoning. Ca deficiency was also suggested as a possibility[89] (Scheuhammer, unpubl.) but this does not explain why only birds breeding close to the shore had problems.

Even if concentrations of metals are higher in acidified habitats, this does not necessarily mean that the levels in the tissues of birds are also higher. Ormerod et al.[80] measured higher Al concentrations in acidified streams in Wales, but not in the eggs of the Dipper. The evaluation of the effects of increased metal exposure of birds due to acidification is complicated by the fact that emissions of acidifying compounds and toxic metals often occur simultaneously. Moreover, the toxicity of several metals depends on the amount of Ca and P in the food (section 4.2), and the Ca content of the food is especially affected by acidification. The additional effect of increased exposure to toxic metals by acidification is probably small compared to the general problem of metal poisoning in aquatic habitats (Scheuhammer, unpubl.). However, in spite of these reservations, the studies mentioned above show that at least some aquatic birds suffer from an increased exposure to toxic metals as a result of acidification. To my knowledge, there are no examples of acidification-induced metal poisoning of terrestrial birds. Unfortunately, the numerous reports from Eastern Europe about effects of air pollution on birds do not discriminate between the separate effects of acidifying compounds and toxic metals. More data need to be collected on the Ca, P and metal content of the food to elucidate the respective roles of Ca deficiency and metal poisoning in reducing the reproductive success of birds in acidified habitats.

5 Discussion

5.1 Problems with respect to the study of acidification and birds

The problems involved in studies on effects of acid deposition on birds are manifold. Most conclusions are based on correlative evidence as experimental results are often lacking. An increase in acid deposition is but one of many changes in the environment with which the birds are confronted. The decline of some migrant passerines might as well be caused by acidification in the breeding areas as by desertification, or the use of pesticides in their wintering areas. Even though acidification is considered the most important reason for the present forest dieback, in Europe there is still much discussion about the role of drought and insect pests. The increase of the Black Woodpecker in The Netherlands is more likely a result of the maturing of the forests (most forests were planted in the 1920's) than by an increase in standing dead timber due to acidification. Acidification may be accompanied by eutrophication, as in Sweden[71], and often emissions of acidic compounds occur simultaneously and from the same source as emissions of toxic metals and dust.

Similar problems occur regarding the question of how acidification affects a bird species. Acidification may lead to reduced productivity of plants and trees, lower density of the canopy, changes in the vegetation structure as a whole, changes in insect abundance, Ca availability and exposure to toxic metals, all of which may affect reproductive success. Hole nesting species can benefit from an increase in standing dead timber, not only because it provides them with more food but also because it provides them with more nesting opportunities.

Another problem is that effects of acidification may escape notice because of compensatory effects: a reduced reproductive output can be compensated for by a lower mortality or a higher immigration rate[24]. Birds may find compensation in reduced competition from fish[27], or from other bird species that are more sensitive to acidification (suggested by Hölzinger and Kroymann[51] to explain the increase of the Firecrest in parts of Germany). Reduced abundance of prey can be compensated for by a better detectability: spiders in coniferous trees showing needle loss[38], fish in acid water with a high transparency[27]. Harmful effects of acidification on insects may be counteracted by even more harmful effects on their parasites[45,85]. Birds may also shift their feeding habits, or move to less acidified areas, as some waterfowl do[67].

Effects of acidification can also be very subtle. The laying of eggs with defective shells by Great Tits[24] would have gone unnoticed, but for the fact that this species is intensively monitored for other purposes. Similarly, lichens of the genus *Usnea* ('beard moss') are very sensitive to SO_2 concentrations in the air and are the first to disappear from the woods. This is probably the reason for the decline of the Northern Parula Warbler *(Parula ameri-*

cana) in North America, that uses these lichens as nesting material[4].

Interpretation is further hampered by lack of knowledge. We do not know for example how much Ca wild birds can store in their skeleton when Ca is scarce and how dependent birds are on items rich in Ca (like snail shells) for shell formation. The answers to these questions are crucial if we want to know to what extent acidification affects the birds in an early stage of forest damage. Another question that needs to be answered is why in England the Dipper population has declined as result of acidification, whereas other riverine species like the Grey Wagtail *(Motacilla cinerea)* and the Common Sandpiper *(Tringa hypoleucos)* have not[112].

There are also problems of a more practical nature. In most cases reliable estimates of the present population size are lacking, let alone estimates from the pre-acidification era. Birds are often hard to count, especially in northern latitudes with widely dispersed populations in often very remote areas. Species that have become rare are by definition hard to study but need to be studied most urgently. Another problem is that effects may only become apparent after a number of years, for instance in the case of metal accumulation. Also, effects of acidification do not always follow a gradual, predictable course. The work of Ormerod et al.[80] showed that the availability of Ca first decreased gradually with the pH, but dropped very rapidly when the pH became lower than 6.5.

5.2 Suggestions for future studies

The problems summarized in section 5 were the reasons why studies on the effects of acidification on birds were started much later than studies on other aspects of acid rain and that most results have only been published recently. The conclusion of an international survey by the International Council for the Protection of Birds (ICPB) in 23 countries was that we suspect a great deal but know very little[37]. However, another conclusion, namely that birds have proved poor indicators of acid precipitation and were not so much affected as for instance trees and fish, may have been premature. The point is that many experimental studies have shown that acidification does affect some reproductive parameters of individual birds, but that comparative data on the reproductive success of free-living birds, or population estimates over a range of years, are lacking. It is therefore very difficult to apply results of controlled experiments to the field.

Studies are called for, in which experiments are combined with data collection on the reproductive success of wild birds as well as accurate yearly counts, in both acidified and in non-acidified habitats. These studies should concentrate on species that are numerous, widespread, easy to study and representative for a general group of birds. In aquatic habitats, the piscivorous Common Merganser *(Mergus merganser)* and the non-piscivorous Common Goldeneye are suitable subjects. Both readily accept nestboxes, making it easy to collect data on reproductive success, and both occur in North America and Eurasia. The situation is more complicated in forests as much less is known about the effects of acidification on forests birds than on aquatic birds. Studies should focus on the changes in abundance of prey species that are known to respond to acidification and that are an important food in the reproductive stage: spiders, aphids and caterpillars. Such studies should always be combined with the collection of data on reproductive success of birds. In Europe, the Great Tit and the Blue Tit are suitable candidates for the reasons mentioned above and because they are already being intensively studied, often in long-term studies on population dynamics. Ca deficiency is another aspect of acidification, of which little is known but that may affect forest birds. The questions here are: how do birds get the Ca for shell formation, does acidification reduce Ca availability to such extent that birds get insufficient Ca, and what are the consequences for their reproductive success and the size and composition of the population? Here data on tits can be compared with data for the Pied Flycatcher. Similarly to the tits, this species is quite numerous, well studied and nests in nestboxes.

The species mentioned are good candidates for use as indicators of the effects of progressive acidification on birds, and for measuring the effectiveness of measures to be taken to improve the situation. Shell thickness or relative shell weight (weight/surface) appear to be good indicators of Ca deficiency.

Studies in the past mainly dealt with the effects of acidification on the reproduction of birds, or more precisely, with effects on the reproductive output of birds that produced a clutch. Future research should also include effects on adult birds. In acidified areas females may not be capable of getting enough protein-rich food for egg-laying and may therefore avoid breeding altogether. Acidification could also affect their survival, e.g. by causing a lower availability of food or high concentrations of toxic metals. These aspects can have great repercussions on the size of the population.

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* Interested readers may also wish to refer to EXPERIENTIA's April and May 1986 issues featuring the 2-part Multi-author Review 'The Ecological Effects of Acid Deposition' coordinated by O. Ravera.– Ed.

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