Oecologia (1996) 105:351–360

ORIGINAL PAPER

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Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines

Received: 27 January 1995 / Accepted: 20 September 1995

Abstract On poor soils in the Netherlands an increasing number of great tits, *Parus major*, and of other forest passerines produce eggs with defective shells and have low reproductive success as a result of calcium deficiency. A similar increase in eggshell defects has been observed in Germany and Sweden. Snail shells are the main calcium source for tits in forests where defective eggshells do not occur, but are very little taken in forests where tits often have eggshell defects. We investigated whether a decrease in snail abundance on poor soils could be responsible for the decline in eggshell quality, and if so, what caused this decrease. Snail density in forests where tits have eggshell defects was much lower than in forests where tits do not have such defects. Snail density correlated with the calcium content and to a lesser extent with pH of the litter layer. Liming of a calcium-poor forest soil with few snails resulted in snail densities comparable to those on calcium-rich soils after 4 years. Snail density has declined on calcium-poor soils over the last two decades, but not on calcium-rich soils. Acid deposition has caused a decline of soil calcium on poor soils. We conclude, therefore, that anthropogenic acidification has caused a decline in snail populations, resulting in an increase in eggshell defects in birds in forests on poor soils.

Key words Snails · Calcium · Eggshell · Avian reproduction · Acidification

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Introduction

An increasing proportion of passerines in forests on poor soils in the Netherlands produce eggs with thin and porous shells and desert their clutch (Drent and Woldendorp 1989). The eggshell defects and the associated low reproductive success are caused by calcium deficiency (Graveland et al. 1994). Laying irregularities similar to those observed in Dutch forests were also reported from other European countries (Schmidt 1990; Smith 1990; Winkel and Hudde 1990; Carlsson et al. 1991).

Insectivorous and granivorous birds need calcium-rich material for eggshell formation, in addition to their normal food (Jones 1976; Turner 1982; Graveland and Van Gijzen 1994). In forests where eggshell defects are not found tits, *Parus* spp., mainly use snail shells as calcium source (Graveland 1995). However, in forests with high rates of eggshell defects, the tits took few snail shells. Instead, they mainly used anthropogenic calcium sources such as chicken eggshells and mortar that they obtained outside the forest at farms and picnic sites.

We examined whether the high rates of eggshell defects were caused by a scarcity of snails and whether the scarcity of snails was caused by the low calcium content of the soil. Laboratory studies have shown that in land snails differences in calcium availability, either in the food or in mineral form, affect reproduction and growth (Schmidt 1955; Voelker 1959; Wäreborn 1970, 1979, 1992; Crowell 1973; Oosterhoff 1977; Gomot et al. 1989; Ireland 1991). Many studies report a positive relationship between snail density, number of snail species and the calcium content of litter and soil (Burch 1955; Mörzer Bruyns et al. 1959; Wäreborn 1969, 1970; Crowell 1973; Dunger 1983; Gärdenfors 1987, 1992).

A causal relationship between the calcium content of the soils and snail density might explain the increase in calcium deficiency in tits observed on poor soils. Acid deposition has caused a decrease in calcium content of soil, vegetation and litter layer on ill-buffered soils (Ulrich 1986; Van Den Burg and Kiewiet 1988; Tamm and

Hallbacken 1988; Hanson et al. 1990; Verstraten et al. 1990). This could have resulted in a decline in snail density. We therefore examined whether the increased calcium deficiency in tits could be caused by a decline of snails on calcium-poor soils.

Methods

Eggshell quality and breeding success

Breeding data for great tits, *Parus major*, were collected in seven forests in 1991 (Fig. 1). Two forests were located on nutrient-rich clay and loam soil, one on dune sand and four on nutrient-poor, podzolic soil. Pedunculate oak, *Quercus robur*, Red oak, *Q. rubra*, Scots pine, *Pinus sylvestris* and Corsican pine, *P. nigra*, were the predominant tree species. Van Balen (1973) and Graveland and Van Gijzen (1994) give more detailed descriptions of the study areas.

Each forest contained 100 or more nestboxes with at least 25 pairs of great tits. Nestboxes were checked once or twice a week to determine breeding parameters such as clutch size and hatching success. In addition, eggshell quality was assessed by visual examination of the eggshell during the egg-laying period. Defective eggshells can easily be recognized at this stage by their rough and dull shell surface and aberrant pigmentation (J. Graveland, unpublished work). Shells of normal eggs have well-defined pigmentation spots that are in most cases evenly distributed over the shell surface. Defective eggshells are characterized by the powdered appearance of the pigmentation and the concentration of pigment around the blunt end of the egg. We have previously shown that the deviant eggshells are thinner (0.077 versus 0.085 mm) and contain less calcium (22.1 versus 30.6 mg) than normal shells (Graveland et al. 1994). Only 3% of the eggs with defective shells hatch, compared to 95% of the eggs with normal shells.

Use of snail shells by great tits

The calcium source was investigated by examining the nest material. Nestlings require calcium-rich material in addition to their normal food for the growth of their skeletons (Graveland and Van Gijzen 1994). Some items that are fed to the nestlings end up in the nest material. The presence of calcium-rich items in the nest material correlates well with the presence of such items in droppings and pellets of nestlings and can thus be used as an index for the consumption (Graveland 1995). Nests were collected from the same forests as where the breeding data were collected at the end of the breeding season in 1990–1992. Only nests with juveniles at least 1 week old were used in the analyses since the consumption of calcium-rich material mainly takes place in the 2nd and 3rd weeks of the nestling period. Females often desert clutches with defective eggshells before the eggs hatch (Graveland et al. 1994). Thus, in forests with high rates of eggshell defects only a small number of nests could be searched and data from several locations had to be lumped.

Snail density

In most studies on snail abundance only the number of live snails is determined. To birds however, empty snail shells may be more important as calcium source than live snails. Empty shells are easier to obtain, have often partly decayed and may therefore be more digestible, and lack the toxic compounds that live snails sometimes contain (B. Baur, personal communication). We therefore did not discriminate between live snails and empty shells and snail densities mentioned in this paper include both categories.

Throughout this paper, snail densities are expressed as the number of snails per unit surface area. Expressing the snail density as number of snails per litter volume would have led to the introduction of the thickness of the litter layer as a confounding factor. On calcium-rich soils the litter layer is thinner than on calcium-poor soils, since the litter decays more rapidly. As will be shown below, using snails/m^2 instead of snails/l of litter did not affect the conclusions.

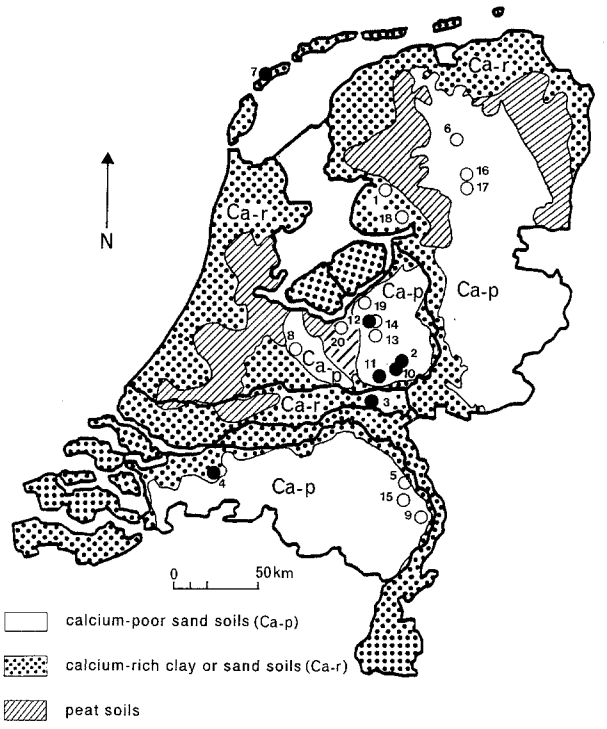

Fig. 1 Study sites. Soil parameters and snail density were determined in all forests (see text), breeding data of tits in seven forests (*closed circles*). See Appendix 1 for soil and snail data

Data on snail shell density, soil pH and soil calcium content were collected in the forests for which breeding data for tits were available. In addition, data on snail density were collected in seven other forests for which data on the soil chemistry were available. To confirm the observational data, experimental data on the relation between soil calcium and density were obtained by investigating the snail density in forest plots that had been limed 4 years previously. All data refer to forests dominated by pedunculate oak.

To allow a comparison of past and present snail density on rich and poor soils, data on snail density were collected in forests that had been investigated in the past.

Snail density and soil calcium: observational data

The snail density was determined by counting the number of snail shells in litter samples collected from late April to early June 1992. Samples were collected at one or two sites per forest, the number of sites depending on the availability of breeding data for tits, on the availability of chemical soil parameters, and on the size of the forest. The sites in a forest were several hundred meters apart. Ten randomly chosen samples of 25×25 cm were collected per site. The samples contained the litter layer plus the top 2 cm of the mineral soil.

To avoid bias, the sample labels were replaced by random numbers before further processing. The samples were dried at 65 °C, fractioned with five sieves with meshes of 0.5–5 mm and searched by eye for snail shells. The searching time per sample was about 55 min. Only snail shells of which at least 50% was left were counted as individuals. After counting, the shells were rinsed to remove the adhering soil. The snail shells were then pooled by site and weighed. The shells were dried at 65 °C for 48 hours and weighed to the nearest mg.

Shell fragments of large *Cepaea* sp. (mainly *C. nemoralis*) and *Arianta arbustorum* snails were an important calcium source for tits (Graveland 1995). These snails are scarce in most forests, but common in verges of roads or in other open areas with a well developed herb layer. These snails occur in low densities, compared to the small litter-dwelling species of the forest floor, but are easily spotted because of their large size. Therefore, the density of these snails was estimated as the number of snails counted in one to three 1×10 m transects in herb-rich road verges adjacent to the forest. Each transect was searched for 0.5 h and the density of the snails was classified into three categories: 0, 1–5, or more than 10 snails found per 10 m^2.

Snail density and soil calcium: experimental data

A liming experiment was performed in two oak stands on poor sandy soil at Sint Anthonis (51° 35′ N, 5° 50′ W, location 15 in Fig. 1). One stand, planted in 1953, consisted of oaks (height c. 20 m) and had a sparse ground cover (5–10%) of wavy hair-grass, *Deschampsia flexuosa*. The other stand was planted in 1980 and consisted of oaks (4 m), and some birch, *Betula pendula*, Scots pine and mountain ash *Sorbus aucuparia*. The forest floor was covered (45–80%) with mosses (mainly *Hypnum cupressiforme*), grasses (mainly *D. flexuosa*) and some herbs (*Corydalis claviculata*, *Urtica dioica*).

Both stands had been limed with dolomite ($CaMgCO_3$) in the spring of 1988. Plots of 20×20 m (young stand) or 30×30 m (old stand) had been limed doses of 0, 0.3, 0.6 and 0.9 kg per m^2, respectively, in two series of four plots per stand. Litter samples were collected as described above in May 1992. The number of litter samples collected in the unlimed plots was higher (10 versus 5 per plot) than in the limed plots since the snail density was expected to be lower and more variable in the unlimed plots.

Soil chemistry

Litter and soil samples were collected for chemical analyses in the seven forests from which tit breeding data and data on snail density were obtained. Litter samples consisted of all litter from a 25×25 cm^2 plot excluding intact leaves. The soil samples were core samples (diameter 3 cm) of the top 30 cm of the soil excluding leaves. Ten litter samples and ten soil samples were collected at each location where snails were sampled in autumn 1992. The samples were pooled by site, dried and the snails were removed. Total calcium content was determined after destruction with H_2SO_4 and H_2O_2, the exchangable calcium fraction after extraction with 1 M ammonium acetate at pH 7. The pH(KCl) and pH(H_2O) were determined in a soil:water suspension 1:7.5 for the litter samples and 1:2.5 for the soil samples.

Comparison of past and present snail density

Historical data were tracked by interviewing malacologists and examining excursion reports. The number of locations suitable for resampling was restricted because of inadequate descriptions of historical sampling locations, procedures or results and manmade changes in the vegetation. Suitable data sets were found of three ash, *Fraxinus excelsior*, forests on clay (one forest) or loam soils (Reinink 1979; K. Reinink unpublished work; locations 18–20 in Fig. 1), and of two forests on poor sandy soil, with oak, birch and Scots pine (Zoer 1971; locations 16 and 17 in Fig. 1). Reinink collected ten 25×25 cm^2 litter samples per forest in September 1973 and we repeated this in September 1992. The two forests on poor soil were sampled in November 1970. Zoer took five (Zuurlander Esch) or four (De Nul) 0.5 m^2 samples several hundred meters apart. He presented the numbers per species per site in five density classes (0, 1–5, 6–15, 16–25, 26–55 or 56–125 individuals per m^2); the original counts are no longer available. New samples of 0.5 m^2 were collected in November 1992. The sample was thoroughly mixed, and one half of each sample was searched for snails. The presentation of snail density by classes did not allow the data for separate species in 1970 to be lumped for statistical analyses. Therefore, we used the median of each class as representing the number of individuals in 1970.

Results

Relation between eggshell quality and snail density

The incidence of eggshell defects was inversely related to the use of snail shells as estimated by the presence of snail shells in the nest material (Fig. 2a). There were also significant inverse relationship between the proportion of clutches with defective eggshells and the density of small litter-dwelling snails in the forest (r_s=0.67, Fig. 2b) or large *Cepaea* spp. and *A. arbustorum* snails in the vegetation of road verges outside the forest (Mann-Whitney *U*-test, locations with >10 snails/m^2 versus 0–5

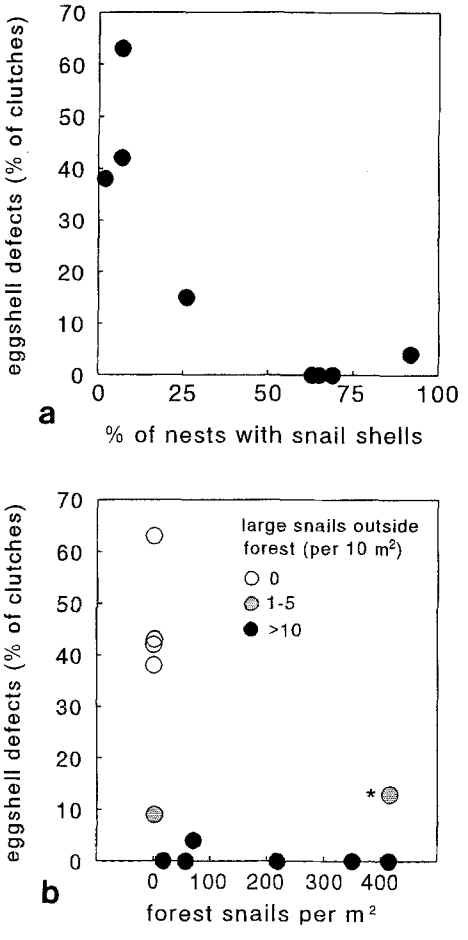

Fig. 2 Relation between eggshell quality in great tits and **a** the utilization (r_s=–0.75, n=8, P=0.03) and **b** the density of shells of litter-dwelling snails (r_s=–0.67, n=12, P=0.02) in oak forests. Number of great tit nests per forest of which the nest material was searched varied between 19 and 104. The data in **b** are divided into three categories, according to the number of larger snail species found along roads just outside the forest. The *outlier* marked * refers to a sampling location in a calcium-poor forest where the soil had been limed locally and the data on eggshell quality was collected from a much larger area

snails/m^2, P=0.005). On four forest locations without snail shells in or outside the forest, 38–63% of the great tit females produced eggs with defective shells (Fig. 2b). On a location without snails in the forest, but with 1–5 large snails/10 m^2 outside the forest, 10% of the females produced eggs with defective shells. In one location, we found 1–5 large snails/m^2 outside the forest and more than 400 litter-dwelling snails/m^2 in the forest, but the forest snails only occured under a few beech, *Fagus sylvatica*, trees where the soil had been limed in the 3 years before sampling. Among the great tit females nesting in an area of 250 m radius around these trees, 13% produced eggs with defective shells. In six locations where the density of forest snails varied between 17 and 416 snails/m^2, and the density of large snails outside the forest was higher than 10 snails/10 m^2, none of the females produced eggs with defective shells.

It was not possible to separate the effect of the presence of small litter snails in the forest from the effect of the presence of large *Cepaea* and *A. arbustorum* snails outside the forest, since the densities of these snails were highly correlated.

Snail species used as calcium sources by great tits

Fragments of *Cepaea* and *A. arbustorum* shells, obtained outside the forest, were the main calcium source of great tits in forests where they produced few eggs with defective shells (Graveland 1995). However, in forests with a high proportion of defective eggshells complete shells of small litter-dwelling species were more often taken than fragments of large snail shells.

The snail shells in 29 nests of great tit and blue tit, *P. caeruleus*, collected from two forests with high rates of eggshell defects in 1991 (sites no. 11-1, 11-2, 2-2 and 2-3 in Appendix 1) were identified to species (Table 1). Seven small snail species were identified, with *Nesovitrea hammonis* and *Trichia hispida* both representing about 30% of the shells. *N. hammonis* was the most abundant species in the litter samples (Appendix 1). *T. hispida*, *Oxychilus* sp. and *Discus rotundatus* were present in the nests but were not detected in the litter samples collected in these forests. These species, in particular *T. hispida*, are species of more calcium-rich soils (A.J. de Winter, personal communication). *D. rotundatus* was accidentally found on a nutrient-rich site beside an arable field in one forest and all three species were presumably present along road verges and in gardens outside the forest, together with *Cepaea*.

Snail density and correlations with chemical soil parameters

There was a strong correlation between the number of snail shells and the total calcium content of the litter (Fig. 3). The snail shell density in the 14 oak forests (21 sites) varied between 0 and 1580 individuals/m^2. Snails did not occur in forests with a litter Ca content under 1.9 mg/g. Snail were always present at litter calcium contents higher than 2.8 mg/g. The highest density, 1580 individuals/m^2, was found in a young mixed deciduous forest on clay soil containing sub-fossil sea shells. *N. hammonis*, and to a lesser extent *Euconulus fulvus* were often virtually the only species on calcium-poor soils, but they were less dominant in samples collected in forests on calcium-rich soils (Appendix 1). Ca-rich soils had up to five species per plot (25×25 cm^2).

The snail density correlated more strongly with the chemical characteristics of the litter layer than with characteristics of the mineral soil (0–30 cm, Table 2, data are listed in Appendix 1). Snail density showed a much higher correlation with total calcium or exchangable calcium than with pH-H_2O or pH-KCl, in particular in the mineral soil. A multiple regression analysis with both

Table 1 Remains of snail shells in the nest material of 46 nests (identified shells from 29 nests) of great tit and blue tit in two forests on calcium-poor soils (locations 11-1, 11-2, 2-2 and 2-3 in Appendix 1); n and % refer to number of shell fragments and complete shells (see text)

Snail species	n	%
Cepaea/Arianta fragments	33	38
Complete shells of small species	55	62
Complete shells (identified)		
Total	48	100
Nesovitrea hammonis	15	31
Trichia hispida	13	27
Discus rotundatus	7	15
Oxychilus sp.	5	10
Euconulus fulvus	4	8
Cochlicopa lubrica/lubricella	2	4
Vitrina sp.	2	4

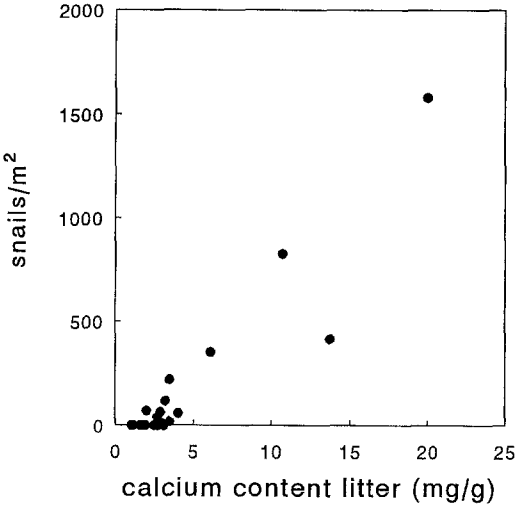

Fig. 3 Relation between the total calcium content of the litter and the snail density (r_s=0.80, n=21, P<0.001). Snail density is expressed as the number of snails in the litter layer and the top 2 cm of the soil. The number of sampling plots per location varied between 5 and 20

Table 2 Spearman rank correlations between snail density and soil parameters in litter layer and in top 30 cm of soil (including titter). The data are listed in Appendix 1

	Number of snails	Snail mass	N
Litter			
Ca total	0.80***	0.80***	21
Ca exchangable	0.75***	0.78***	19
pH-H_2O	0.62**	0.61**	21
pH-KCl	0.65**	0.64**	21
Litter+mineral soil			
Ca total	0.71**	0.70**	14
Ca exchangable	0.80***	0.78***	14
pH-H_2O	0.39 ns	0.38 ns	14
pH-KCl	0.13 ns	0.11 ns	14

*** $P<0.001$, ** $P<0.01$, * $P<0.05$, ns $P>0.05$

the calcium content and the pH als dependent variables showed a significant effect of the calcium content ($F_{[1,18]}=26.0$, $P<0.001$) but not of the pH ($F_{[1,18]}=2.40$, $P=0.14$) on the snail density.

The number of snail species counted on calcium-poor soils was lower than on calcium-rich soils (Appendix 1). However, this might be caused by a reduced sampling effort, since fewer snail shells were counted on poor than on rich soils.

Effect of liming on snail density

The liming of the soil caused an increase in exchangable calcium (Table 3). pH(KCl) had hardly increased by the liming. Total calcium content and pH-H_2O were not measured since the results are misleading, because of the presence of lime concretions in the top soil and the sensitivity of pH-H_2O to evaporation. The number of snails on the limed plots 4 years after liming was much higher than on the unlimed plots (Fig. 4). The number of snails in the young stand (planted in 1980) was about 20 times higher than in the old stand. The snail density in limed plots of the young stand was similar to the snail density in forests on calcium-rich soils (Fig. 3).

N. hammonis and *E. fulvus* accounted for more than 99% of all individuals and were the only species present in the unlimed plots. One *Oxychilus* sp., one *Cochlicopa lubrica* and four *Vitrina pellucida* individuals were found

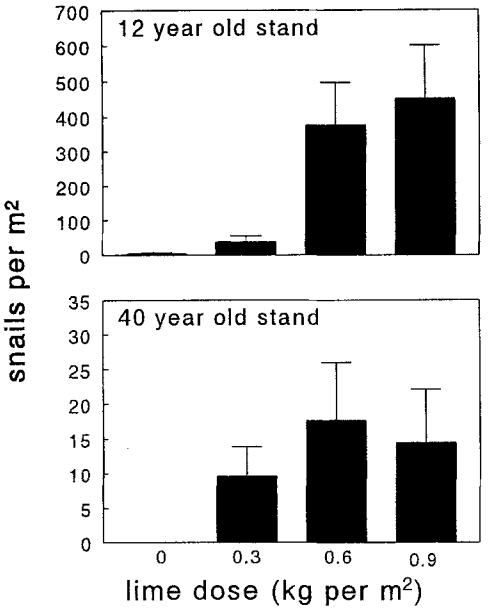

Fig. 4 Effect of a single dose of dolomitic lime on the snail density in two oak forests on calcium-poor soil 4 years after liming. Young stand: $F_{[3,46]}=17.03$, $P<0.001$; old stand $F_{[3,46]}=5.29$, $P<0.01$. Snail numbers log(x+1) transformed to obtain equal variances. Mean values ±1 SD are given, with $n=10$ per treatment (unlimed plots $n=20$)

in the 30 samples in the limed plots in the young stand, corresponding with 0.5, 0.5 and 2.1 individuals/m², respectively. Limed plots tended to have a higher proportion of young individuals of *N. hammonis* and *E. fulvus* than unlimed plots. This is best illustrated by the size of the snails, but it was not feasible to measure all the snails. Instead, individuals were weighed and a subsample was also measured. Size differences explained 85% of the variance in mass in *N. hammonis* (correlation between mass (log-transformed) and size $r=0.92$, $n=35$, $P<0.001$). The presence of juvenile snails was apparent by the slightly bimodal distribution in shell mass in both species at the higher lime doses. *N. hammonis* individuals in the 0.6–0.9 kg/m² plots were on average lighter than individuals in the 0–0.3 kg plots (2.0±1.5 versus 3.0±1.2 mg, Mann-Whitney U-test, $n=180$, $P=0.02$), and *E. fulvus* individuals in the 0.9 kg plots were lighter than in 0–0.6 kg plots (1.0±0.5 versus 1.3±0.6 mg, Mann-Whitney U-test, $n=156$, $P=0.007$).

Table 3 Effect of liming with dolomitic lime in June 1988 on soil parameters in March 1991 and number of snails (x±SD) in June 1992

Lime dose (kg per m²)	0	0.3	0.6	0.9
Young stand				
pH-KCL litter	3.3	3.4	3.3	3.5
Exchangable calcium litter (mg/kg)	0.10	0.90	1.01	0.59
Nesovitrea hammonis[a]	1.6±7.2	12.8±23.6	169.6±257.7	214.4±268.7
Euconulus fulvus[a]	2.4±7.8	24.0±33.9	198.4±128.9	227.2±248.2
Old stand				
pH-KCL litter	3.7	3.7	3.5	3.7
Exchangable calcium litter (mg/kg)	0.16	0.75	1.02	1.30
Nesovitrea hammonis	0	0	0	0
Euconulus fulvus	0	9.6±3.5	17.6±26.6	14.4±24.4

[a] Other snail species occurred only sporadically

Table 4 Comparison of snail density and number of snail species between 1970/1973 and 1992 for **a** two forests on calcium-poor soil, **b** three forests on calcium-rich soil. Snail density on poor soils is given as density classes (– 0, *1* 1–5, *2* 6–15, *3* 16–25, *4* 26-55, *5* 56–125, *6* 126–375 snails per m²)

a Poor soil

	De Nul			Zuurlanderesch			Total
Species	1970	1992		1970	1992		
Nesovitrea hammonis	4 3 3 2 2	3 2 1 – –		5 4 2 1	5 4 2 –		
Euconulus fulvus	1 2 1 1 1	– – – – –		4 3 4 –	– – 2 –		
Columella aspera	1 – 2 1 1	– – – – –		4 2 2 –	– – – –		
Cochlicopa lubrica	– – – – –	– – – – –		1 – 2 1	– – – –		
Vitrina pellucida	3 – – – –	– – – – –		– – – –	– – – –		
Punctum pygmeum	1 – – – –	– – – – –		– – – –	– – – –		
Vallonia sp.	– 1 – – –	– – – – –		– – – –	– – – –		
Individuals/m²	34±22	7±9	*	81±70	39±45	ns	0.08
Species per sample	3.4±0.9	0.6±0.5	**	3.3±1.0	1.0±1.0	*	***
Without *N. hammonis*							
Individuals/m²	14±10	0	**	45±35	3±5	0.06	***
Species per sample	2.4±0.9	0	**	2.1±1.0	0.5±0.6	0.06	***

b Rich soil

	Hierden			Oldenaller			Voorst			Total
	1973	1992		1973	1992		1973	1992		
Individuals/m²	112±88	120±76	ns	35±22	72±57	ns	304±178	206±101	ns	ns
Species per sample	3.3±1.2	3.4±1.6	ns	1.1±0.3	2.5±1.8	ns	3.4±1.6	4.8±1.8	0.05	0.06

*** $P<0.001$, ** $P<0.01$, * $P<0.05$, ns $P>0.05$

Comparison of past and present snail density

Snails declined in the two forests on calcium-poor soils, both in density and in number of species (Table 4a). The number of individuals per square meter declined from 34 in De Nul and 81 in Zuurlanderesch in 1970 to 7 and 39 in 1992. *N. hammonis* and *E. fulvus* were the most abundant species. *N. hammonis* was most numerous (60% and 45% of snails in the two forests in 1970) and declined much less than the other six species present in 1970. *N. hammonis* tended to decline from 21 to 7 in De Nul (Mann-Whitney *U*-test, $P=0.09$), but remained constant in Zuurlander Esch (36±40 versus 35±41, $P=0.44$). Of the six other species present in 1970, five were not found again in 1992. *E. fulvus* remained present in only one out of nine sites, compared to eight out of nine sites in 1970. In none of the three forests on nutrient-rich soils did the snail density decline between 1973 and 1992 (Table 4b, Appendix 2). The number of species tended to be higher in 1992 than in 1973. In contrast to the two forests on poor soils, *N. hammonis* and *E. fulvus* composed only a small fraction of the total number of individuals (approximately 25% for *N. hammonis* and 2% for *E. fulvus*).

Discussion

Snail density and soil calcium

This study showed that scarcity of snails was responsible for the limited use of snail shells by tits and thus for the calcium deficiency and eggshell defects in tits on calcium-poor soils. Snail density correlated better with calcium content than with the pH in the observational data (Table 2). Applying 0.3 kg/m² dolomitic lime of the soil greatly increased the exchangable calcium content and the number of snails but hardly affected the pH (Table 3). Higher doses of lime did not lead to higher numbers of snails. This is probably due to the fact that the higher doses did not lead to a further increase in exchangable calcium (Table 3). Moreover, the presence of lime concretions in the limed plots may have outweighed the effects of differences in the size of the original lime doses. The low correlation, in comparison with calcium, between pH and snail density is in line with findings elsewhere (Gärdenfors 1987, 1992; Wäreborn 1992). In Wäreborn's data set from 20 forests in southern Sweden snail density correlated better with the litter calcium content (1965, $r_s=0.86$ and 1987, $r_s=0.80$) than with the pH ($r_s=0.62$ and $r_s=0.70$; in all cases $P<0.01$). Thus, litter calcium seems more important than pH in explaining variation in snail density among sites.

The normal food of snails, live or decaying plant material, often does not contain sufficient calcium for egg-laying and shell growth, and snails obtain additional calcium by scraping from rock, ingesting soil and possibly by absorption through their foot (Schmidt 1955; Voelker 1959; Crowell 1973; Fournié and Chétail 1982; Gärdenfors 1987; Gomot et al. 1989). Feeding experiments with snails showed that the calcium content of the food, and the availability of additional calcium, affect the egg production, hatching success and the growth and thickness

of the shell (Voelker 1955; Crowell 1973; Hunter 1988, 1990; Ireland 1991). A low pH may have a specific effect independent of that of a low soil calcium content, by the direct effect of acid on the skin (Wäreborn 1970). However, snail density seems mainly to be determined by the calcium content of the soil.

Acid deposition, decline of snail populations and avian reproduction

At low calcium levels only *N. hammonis* and, in smaller numbers, *E. fulvus*, were present (Appendix 1). *N. hammonis* declined less than other snail species (Table 4a) and laboratory experiments showed that *N. hammonis* tolerated lower pH values and calcium levels than *D. rotundatus* or *T. hispida* (Wäreborn 1970). *D. rotundatus* and *T. hispida* were limited to soils with a high calcium content in this study (Appendix 1) and were restricted to limed plots in both Swedish (Gärdenfors 1992) and our own liming experiments. However, even *N. hammonis*, the species that appeared most tolerant to low soil calcium, declined on calcium-poor soils and showed a considerable increase in response to liming.

Decline in snail populations seems to be a general phenomenon on ill-buffered soils in Europe. Mörzer Bruyns et al. (1959) reported a snail density of 70 live individuals/m^2 as characteristic of oak-birch forests on poor sandy soil in the Netherlands in the 1950s, a density of 100–400 for richer soils and more than 1000 for Ca-rich soils. Their figures for calcium-poor soils are in close agreement with the densities of live snails reported by Zoer (1971) in three forests on poor soils (Table 4). We measured a density of less than 10 live snails/m^2 in the same forest types in 1992 (Appendix 1). Wäreborn (1992) in Sweden collected the most extensive set of data in this respect. He measured snail density and soil parameters in 20 oak and spruce forests on poor soils in 1965 and 1987 (Wäreborn 1969, 1992). The snail density decreased in almost all forests and most on soils with the lowest calcium content (Fig. 5a). The relation between snail decline and the original soil calcium content, and the relation between the soil calcium content and the reproduction, growth and density of snails, suggest that the decline in snail density is mainly caused by a decline in soil calcium.

Leaching of calcium from the top soil is a natural process in soils in temperate and boreal areas where the precipitation exceeds the evaporation (Ulrich 1986; van Breemen et al. 1983). However, in large parts of Europe and North America atmospheric deposition of acidifying compounds (SO_2, NO_x and NH_3) has greatly accelerated this process (Ulrich 1986; Tamm and Hallbacken 1988; Hanson et al. 1990; Heij and Schneider 1991). Another common air pollutant, ozone (O_3) may have an additional effect since it damages the leaves, thus causing direct leaching of cations from the leaves (Heij and Schneider 1991). However, acid deposition is now considered the chief causal factor for a decrease in calcium content of ill-buffered soils in the Netherlands, Northern Europe and elsewhere (Verstraten et al. 1990; Heij and Schneider 1991; de Vries 1994).

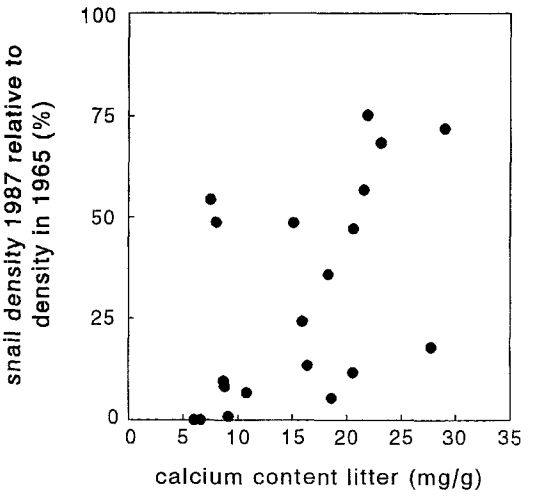

Fig. 5 Decline in snail density in 20 forests on poor soils in southern Sweden between 1965 and 1987 (after Wäreborn 1992). The percentage of snails left in the plots in 1987, relative to 1965, was positively correlated with the litter calcium content in 1965 (r_s=0.57, P=0.009; calcium content in mg Ca/g ash free dry mass)

Snail shells are the main calcium source for eggshell formation in many species of birds (Creutz 1953; Schiffer-li 1977; Graveland 1995). Scarcity of snail shells causes eggshell defects in tits in forests in the Netherlands. Many tits managed to compensate for the lack of snail shells by using anthropogenic calcium sources, such as chicken eggshells and mortar (Graveland 1995). However, we think that the lack of snails and the associated low reproductive success among passerines are common features of less densely populated and more natural acidified areas elsewhere in Europe and North America. The relation between soil calcium and snail density applies in particular to soils with a low calcium content (Wäreborn 1992) and small differences in calcium content can result in large differences in snail density (Fig. 3). An increase in eggshell defects in forest birds is therefore to be expected for the near future.

Acknowledgements We thank E. Gittenberger and A.J. de Winter for their advice, for help in the identification of snail species and for critically reading the manuscript. The comments of B. Baur, R.H. Drent, J.H. Van Balen, J.W. Woldendorp and two anonymous referees further improved the manuscript. We are grateful to T. Van Gijzen and S. Ens for their help in collecting and processing the snail samples, to W. Smant, S.R. Troelstra and R.Wagenaar for carrying out the soil analyses and to H. Van Der Voet for statistical advice. W. de Vries of Staring Centre DLO and J. Van Den Burg of the Institute for Forestry and Nature Research kindly provided their data on chemical soil parameters. K. Reinink and J.A. Zoer provided an important contribution by giving us access to their unpublished data on snail density in the past. The study was supported by grants from the Department of Agriculture, Nature Management and Fisheries and the Department of Housing, Physical Planning and the Environment.

Appendix 1 The density of small litter-dwelling snail species in 14 oak forests (21 sites) on calcium-rich and calcium-poor soils. Total snail density (number of shells per m^2) decreases from left to right. The numbers of the locations are the same as in Fig. 1

Location	1	2-1	3-1	4-1	4-2	5	6	3-2	7-1	8	7-2	9	2-2	10	11-1	11-2	2-3	12-1	12-2	13	14
Nesovitrea hammonis	288.0	457.6	28.0	121.6	90.2	80.0	35.2	67.2	3.2	27.2	9.6	8.0	3.6	1.6	–	–	–	–	–	–	–
Euconulus fulvus	–	92.8	–	59.2	–	33.6	28.8	3.2	8.0	1.6	3.2	–	–	–	–	–	–	–	–	–	–
Oxychilus sp.	44.8	–	–	115.2	62.5	3.2	–	–	4.8	4.8	3.2	–	–	–	–	–	–	–	–	–	–
Cochlicopa lubrica	99.2	73.6	27.0	–	40.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trichia hispida	1027.2	–	304.0	–	17.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aegopinella nitidula	–	0	28.0	6.4	2.9	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–
Punctum pygmeum	3.2	179.2	–	–	–	–	–	–	17.6	–	–	–	–	–	–	–	–	–	–	–	–
Discus rotundatus	–	–	–	38.4	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Columella aspera	–	–	–	–	–	–	–	–	22.4	–	1.6	–	–	–	–	–	–	–	–	–	–
Vitrina pellucida	–	6.4	–	–	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–
Carichium tridentatum	38.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Succinea putris	3.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxyloma sp.	16.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vitrea sp.	–	16.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unknown	60.8	–	–	9.6	2.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	1580.8	825.6	415.0	350.4	218.2	116.8	64.0	70.4	57.6	35.2	17.6	8.0	3.6	1.6	–	–	–	–	–	–	–
Snail mass (mg)	10155	925.2	2562	793.9	365.2	111.7	90.5	89.6	56.0	55.1	38.7	16.8	10.9	8.0	–	–	–	–	–	–	–
Species/sample[a]	5.4	4.0	4.0	4.0	2.1	1.7	1.8	1.3	2.0	1.5	1.6	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Number of samples	5	5	10	10	11	10	5	5	5	10	10	10	4	10	8	4	9	20	10	10	10
Ca-total in litter (mg/kg)	20.00	10.71	13.72	6.10	3.48	3.21	2.91	2.01	4.06	2.69	3.46	3.06	2.61	2.56	1.02	1.59	2.71	1.89	1.11	2.4	73.10
Ca-exchang. litter (mg/kg)	–	6.52	–	4.03	2.10	2.06	2.66	0.98	2.13	2.16	2.60	2.30	1.98	1.31	0.82	0.90	1.69	1.06	0.68	1.70	0.96
pH-H_2O litter	6.2	4.8	5.5	4.4	3.7	3.7	3.6	3.7	4.1	3.8	4.0	4.5	3.7	3.5	3.5	3.6	3.6	3.7	3.4	4.1	3.9
pH-KCl litter	6.0	4.2	5.1	3.9	2.9	2.9	2.6	2.9	3.3	2.9	4.0	3.8	2.8	2.7	2.7	2.7	2.7	2.7	2.5	3.0	2.9

[a] In samples containing snails

Appendix 2 Number of live snails (per m^2, ±SD) in three forests on nutrient-rich soil in 1973 and 1992. Based on ten samples per year and per forest

	Hierden		Oldenaller		Voorst	
	1973	1992	1973	1992	1973	1992
Arianta arbustorum	8.0±11.3	0	0	0	0	1.6±5.1
Carychium tridentatum	0	25.6±43.5	0	0	0	20.8±18.6
Cochlicopa lubrica	1.6±5.1	17.6±25.5	0	0	96.0±43.3	27.2±22.7
Discus rotundatus	8.0±17.3	3.2±5.7	0	28.8±21.1	105.6±139.5	43.2±37.8
Euconulus fulvus	4.8±10.8	0	0	1.6±5.1	0	0
Nesovitrea hammonis	11.2±20.0	49.6±24.2	25.6±22.9	20.8±26.2	0	6.4±11.2
Oxychilus sp.	6.4±15.5	1.6±5.1	0	0	67.2±48.8	24.0±15.5
Punctum pygmeum	0	3.2±6.7	0	6.4±11.2	0	0
Succinea sp.	0	1.6±5.1	0	0	0	0
Trichia hispida	41.6±76.6	6.4±8.3	3.2±6.7	0	20.8±31.1	72.0±64.1
Vallonia excentrica	0	0	0	0	0	3.2±6.7
Vitrea crystallina	9.6±13.5	0	0	0	0	0
Vitrina pellucida	0	1.6±5.1	6.4±20.2	6.4±11.2	4.8±10.8	0
Zonitiodes nitidus	20.8±32.9	8.0±17.3	3.2±10.1	0	11.2±26.2	8.0±17.3
Unidentified	0	1.6±5.1	0	1.6±5.1	0	0

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