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Source: Ardea, 55(1–2) : 299-314

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v82.p299

ARTHROPODS AND SEEDS ARE NOT SUFFICIENT AS CALCIUM SOURCES FOR SHELL FORMATION AND SKELETAL GROWTH IN PASSERINES

JAAP GRAVELAND[1] & TEUN VAN GIJZEN

ABSTRACT We examined to what extent insectivorous and granivorous passerines can obtain the calcium for shell formation and growth of the skeleton from their normal food, and to what extent they depend on additional calcium-rich material, such as snail shells and calcareous grit. We determined the calcium content of forest arthropods and seeds on Ca-rich and Ca-poor soils and the calcium content of females, eggs and nestlings of the Great Tit, *Parus major*, and calculated the calcium budget for females and nestlings. We found that female Great Tits do not store calcium in their skeleton before egg-laying. Thus, all calcium needed for egg-laying must be collected during the laying period. Even on Ca-rich soils the calcium intake from arthropods or seeds covered only 5-10% of the Ca requirements. It is demonstrated that these results also apply to other passerines, with the exception of a few species that include woodlice (Isopoda) and millipedes (Diplopoda) in their diet. These arthropods contain 10-13% (dry matter) calcium; a hundred times more than other arthropods. However, most passerines need Ca-rich material, in addition to their normal food, to meet their calcium demand.

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INTRODUCTION

Many bird species ingest calcium-rich items, such as snail shells and calcareous grit, during the breeding period (Turner 1966, Payne 1972, Jones 1976, Schifferli 1977, Ankney & Scott 1980). This is generally attributed to the fact that birds need calcium for eggshell formation and skeletal growth and that the normal food contains insufficient calcium. However, there are few quantitative data for wild birds to support this (Bilby & Widdowson 1971, MacLean 1974, Turner 1982). Extrapolating the results of work on domestic fowl (Edwards *et al.* 1963, Taylor & Stringer 1965, Simkiss 1975) to wild birds is not appropriate, because of the excessive calcium requirements and the large role of the skeleton in shell formation in the domestic fowl (Urist & Deutsch 1960, Gilbert 1983, K. Simkiss pers. comm.).

In this paper we examine to what extent insectivorous and granivorous passerines can obtain the calcium, necessary for reproduction, from their normal food, and to what extent they depend on additional Ca-rich material. We determined the calcium content of a wide variety of arthropod taxa and of seeds, and the calcium content of adult females, eggs and nestlings of the Great Tit, *Parus major*. Arthropods and seeds were collected in forests on calcium-rich and calcium-poor soils, since Great Tits suffered from calcium deficiency on poor soils, but not on rich soils, and the calcium contents of caterpillars and leaves were related to the calcium content of the soil (Drent & Woldendorp 1989). Females may store Ca for egg-laying in their skeleton (Simkiss 1967, Ankney & Scott 1980, Turner 1982, Pinowska & Krasnicki 1985) and thus reduce the need for Ca-rich items during the laying period. Therefore, we determined the calcium content of Great Tit females before and after the laying period. We used these data to calculate calcium budgets for Great Tit females and nestlings and then proceed to

Accepted 22 June 1994

show that the results apply to other passerines as well.

METHODS

Study areas

The data were collected in Oosterhout forest and two other forests on Ca-rich soil (clay/loam or dune sand, calcium content in top 30 cm of the soil 1.18 g/kg dry matter, *SD* 0.55), and in Buunderkamp and six other forests on Ca-poor, acidic soil (calcium content 0.30, *SD* 0.08, Fig. 1). The forests on rich soil were dominated by Pedunculate Oak, *Quercus robur*, Maple, *Acer pseudoplatanus* and Ash, *Fraxinus excelsior* and (in one case) Corsican Pine, *Pinus nigra*. The forests on poor soil were dominated by Scots Pine, *Pinus sylvestris*, Red Oak, *Q. rubra*, Pedunculate Oak, and Birch, *Betula pendula*.

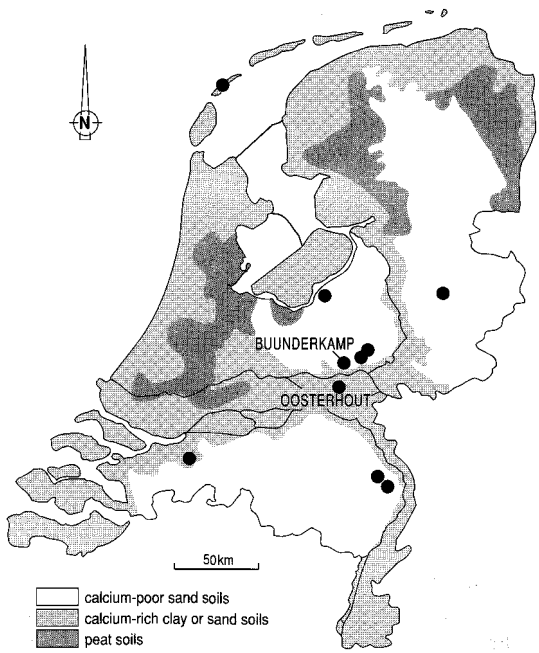


Fig. 1. Study areas on calcium-rich and calcium-poor soil.

Calcium demand: calcium in eggs, nestlings and egg-laying females

Eggs were collected in Buunderkamp (Ca content in top 30 cm of soil 0.33 g/kg dry matter), and in Oosterhout (soil Ca 1.82 g/kg) in 1989. We took one egg per clutch at random, one to two days after clutch completion. Length and width of the eggs were measured to the nearest 0.1 mm with sliding callipers. Egg volume was calculated from the length and width using Ojanen *et al.*'s (1978) formula:

volume = $0.042+0.47 \cdot \text{length} \cdot \text{width}^2$

(volume in mm^3, length and width in mm).

After weighing and measuring, the shell was broken and rinsed with demineralized water. The egg content and the shell were dried for 48 hours at 70 °C and analyzed for their calcium content. We collected 6 females and 15 nestlings for calcium measurements. The nestlings were collected in Buunderkamp forest in 1990, five on the day of hatching, five at one week old and five at two weeks old, each from a different brood. The females were taken from Warnsborn forest, a forest similar to Buunderkamp forest. Three females were taken from the nest at about 21.00 h on the day on which they had produced their first egg, and three other females at about 8.30 h on the first day of incubation. Nestlings and females were killed with ether. Before further processing, we removed the stomach content of the one and two week old nestlings and of the females. The females were dissected and the femora and tarsi were removed to allow separate measurements of their weight and Ca content. The bodies were dried and ground in a grinding mill (Retsch). The calcium content was analyzed with atomic absorption spectrophotometry (Lanyon & Heald 1982).

Calcium content of the food

Samples were collected of caterpillars (Lepidoptera, separate samples of 10 species), aphids (Aphidea, 4 spp.) spiders (Araneae, 4 spp.), flies and other Diptera (4 spp.), beetles (Coleoptera, 8 spp.), sawfly larvae (Diprionidae, suborder Symphyta, 3 spp.), bugs (Hemiptera, mixed samples

of many species), Oak Bush Crickets (*Meconema thalassimum*, Tettigoniidae), imagines of Microlepidoptera (Incurvariidae), seeds of Scots Pine and Corsican Pine, *Pinus nigra*, and oak buds (all food types of the canopy), and of soil arthropods: wolf spiders (Lycosidae), earwigs, *Forficula* sp., cockroaches, *Ectobius sylvestris*, millipedes (*Iulus* sp., Diplopoda) and woodlice (*Oniscus asellus* and *Porcellio scaber*, Isopoda). The samples were collected in 1989 and 1990, from mid-April until mid-June, in three forests on Ca-rich soil and in seven forests on Ca-poor soil. For all samples, specimens were collected from at least five trees. The samples were dried for 48 hours at 70° C and analyzed for their Ca-content with atomic absorption spectrophotometry.

Caterpillars, aphids and spiders are common food sources of tits, Firecrests and other insectivorous birds that feed in the canopy in spring (Betts 1955, Gibb & Betts 1963, Van Balen 1973, Thaler 1979, Cramp & Perrins 1993). Pine seeds are eaten by granivorous species such as Chaffinches, *Fringilla coelebs*, and crossbills (*Loxia* spp.), and by some insectivores like Great Tits (Van Balen 1973, own observations). Oak buds are consumed by Blue Tits, *Parus caeruleus*, Chaffinches and other species (Betts 1955, Berthold 1976). Soil arthropods are present in small numbers in the diet of birds that forage partly on the ground, such as flycatchers, *Ficedula* spp., European Robins, *Erithacus rubecula* and Wrens, *Troglodytes troglodytes* (Berndt & Rapsch 1958, Inosemcev 1963, Kristin 1992).

Table 1. Characteristics of eggs (mean+*SD*) collected in 1989 in a forest on Ca-rich soil (Oosterhout) and a forest on Ca-poor soil (Buunderkamp). *T*-tests (percentages arcsine transformed): ** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$.

	Ca-rich	Ca-poor	
N	17	11	
Volume (mm^3)	1442±108	1307±110	**
Fresh weight (mg)	1580±146	1412±148	**
Dry matter (%)	22.6±1.3	22.8±1.5	**
Ca (% of dry matter)	10.1±0.9	9.8±1.0	ns
Ca (mg)	35.9±4.1	31.3±2.8	**
Ca in shell (as % of Ca in egg)	98.5±0.2	98.2±0.5	*

RESULTS

Ca content of eggs, nestlings and egg-laying females

The eggs from Buunderkamp forest were smaller, and had a lower calcium content than eggs from Oosterhout forest (31.3 versus 35.9 mg, Table 1). The Ca content of hatchlings was 4 mg and of two week old nestlings 83 mg (Table 2). The largest increase in Ca content took place in the second week (60 mg). The females that were collected after they had laid one egg had several large follicles in their ovary in various stages of development, and one nearly completed, partly shelled egg in the uterus that would be laid the following morning. The ovary and oviduct, including the egg in the uterus, contained 12 mg of Ca, about 40% of the Ca content of a finished egg (Table 3). The females collected on the first day of incubation had no follicles in the ovary or

Table 2. Weight and calcium content of Great Tit nestlings (mean+*SD*, $n = 5$ for each age group).

Age (d)	Fresh weight (g)	Dry weight (g)	Calcium content	
			% of dry matter	g
0	1.28±0.32	0.214±0.055	2.09±0.37	0.004±0.000
7	8.09±0.41	1.511±0.081a	1.51±0.26	0.023±0.004
14	17.28±1.03	4.632±0.312a	1.79±0.19	0.083±0.012

a. Without stomach contents.

Table 3. Weight and calcium content of female Great Tits at the start (n = 3) and at the end (n = 3) of the egg-laying period (mean+*SD*). Oviduct includes uterus with developing egg (eggs only present in females collected at start of laying). * Denotes significant differences between the start and the end of laying (*t*-tests, percentages arcsine transformed).

	Fresh weight (g)	Dry weight (g)	Calcium % in dry matterm	content g
Whole body[1]				
Start of laying	21.35±0.42**	6.62±0.20**	3.10±0.11	205.5±10.1
End of laying	18.27±0.56	5.59±0.23	3.34±0.17	186.7±16.8
Femora and humeri				
Start of laying		0.120±0.004	22.7±0.5	27.0±1.00
End of laying		0.110±0.012	22.3±1.0	25.0±4.00
Ovary and oviduct				
Start of laying		0.650±0.031***	1.87±0.06***	12.0±0.0***
End of laying		0.083±0.023	0.14±0.03	0.0±0.0

1 including femora and humeri

ovulated eggs, which shows that they had finished laying (clutch sizes 10, 11 and 7 eggs). Their calcium content was 187 mg, only 19 mg lower than of the females collected at the start of the laying period, a difference mainly caused by the 12 mg difference in the amount of Ca in the ovary and oviduct. This implies that the difference in Ca content in the skeleton was only 7 mg, or 20% of the Ca content in one egg. The weight of the pooled femora and humeri of females at the start of the laying period was not significantly higher than in females that had finished laying. We conclude that female Great Tits do not store calcium before egg-laying and collect the calcium that they need for shell formation only during the laying period.

Ca content of food types found in the canopy, on Ca-rich and Ca-poor soils

Table 4 lists the calcium contents of the food types collected from the canopy. Multiple regression analyses were carried out with the Ca content

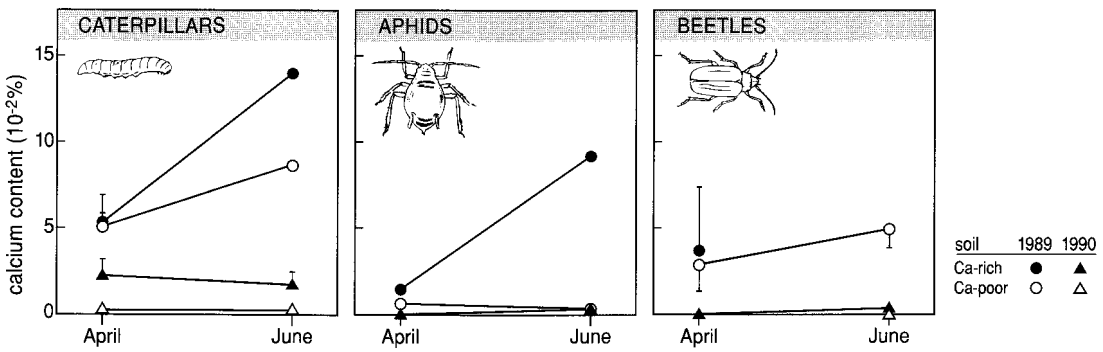


Fig. 2. The calcium content ($\times 10^2$, mean±*SE*) in three groups of insects, showing differences between years (1989 and 1990), between calcium-rich and calcium-poor soils, and between early (mid-March till mid-May) and late spring (mid-May till end of June).

Table 4. The Ca content of food types, sampled in 1989 and 1990, in early and in late spring, in forests on Ca-rich and Ca-poor soils. $\bar{X}$ and *SD* are in 10^2% of dry matter. Early spring: collected between April 1 and May 18 (1989) or May 14 (1990). Late spring: samples collected between May 14 or 18, and June 9. May 18 and May 14 are the median sampling dates for 1989 and 1990.

	Ca-rich soils						Ca-poor soils					
	Early spring			Late spring			Early spring			Late spring		
1989	$\bar{X}$	*SD*	*N*	$\bar{X}$	*SD*	*N*	$\bar{X}$	*SD*	*N*	$\bar{X}$	*SD*	*N*
Caterpillars	5.39	4.84	10	13.87	1.23	7	5.12	3.76	25	8.59	2.65	43
Sawfly larvae	.	.	.	20.44	.	1	25.05	.	1	15.47	7.76	7
Aphids	1.51	1.34	5	9.02	.	1	0.65	1.53	8	0.33	0.37	6
Spiders	.	.	.	.	.	.	14.38	12.44	4	15.83	1.13	2
Beetles	3.61	6.25	3	.	.	.	2.97	3.36	5	4.79	3.79	12
Pine seeds	.	.	.	5.01	0.43	2	0.22	0.20	3	.	.	.
Oak buds	.	.	.	.	.	.	29.36	2.13	2	26.45	.	1
1990												
Caterpillars	2.32	2.01	5	1.80	1.25	3	0.40	0.49	4	0.34	0.58	10
Aphids	0.00	.	1	0.30	0.42	2	0.00	0.00	3	.	.	.
Spiders	6.40	.	1	3.80	0.28	2	3.00	0.86	6	1.34	1.13	7
Diptera	3.16	3.46	5	0.33	0.31	3	1.37	2.52	7	1.30	1.84	2
Beetles	0.06	0.10	7	0.34	0.60	7	0.00	0.00	20	0.07	0.23	24
Hemiptera	.	.	.	1.40	1.22	3	.	.	.	0.40	0.57	5
Bush crickets	.	.	.	1.40	.	1	.	.	.	0.00	.	1

in the dry matter (arcsine transformed) as the dependent variable, and year (1989 = 0, 1990 = 1), soil type (Ca-poor soil = 0, Ca-rich soil = 1) and date as the independent variables. Since no significant differences were found in Ca content between the species within a taxonomic class, the species were pooled per class in the analyses.

Most prey types were collected in only one year or only on Ca-poor soils. Therefore, we did separate analyses for four groups of food types: (a) food types collected on Ca-rich and Ca-poor soils in 1989 and 1990 (caterpillars, aphids, beetles), (b) food types collected on rich and poor soils, only in 1989 (food types as a, plus sawfly larvae and pine seeds), (c) food types collected in 1989, only on poor soils (food types as b, plus oak buds and spiders), and (d) food types collected on rich and poor soils, in 1990 (food types as group b, minus sawfly larvae and pine seeds, plus spiders, Diptera, Hemiptera, imagines of Microlepidoptera and bush crickets). It should be noted that the data sets for the analyses partly overlapped. For instance, the data collected on poor soils in 1989 that conformed to the definition of the food types a, b, and c were used for analyses a, b and c.

The results for group a showed that the Ca contents were higher on Ca-rich than on Ca-poor soils, higher in late than in early spring and higher in 1989 than in 1990 (Table 5a, Fig. 2). The Ca content of caterpillars was higher than that of beetles and aphids, and the Ca content of beetles was higher than that of aphids (Table 5b). The increase of Ca content with date, and the difference in Ca content between years was different for the three groups of arthropods (interactions shown in Table 5a). The results for the food types collected

Table 5a. Calcium content of caterpillars, aphids and beetles in relation to the categorical variables year (1989 = 0, 1990 = 1), julian date, soil type (0 = Ca-poor soils, 1 = Ca-rich soils) and taxonomic group. (a) Results of multiple regression analyses with percentage of Ca in dry matter (arcsine transformation) as dependent variable. A stepwise forward procedure was used to construct the models, retaining only the significant parameters. The significance of the parameters in the full models was tested by dropping the parameters one by one from the model (* $p < 0.025$, ** $p < 0.01$, *** $p < 0.001$).

	I. Model with main effects only.			II. Model with interactions.		
	(Change in) SS[a]	Df	Estimates of coefficients[a]	(Change in) SS[a]	Df	Estimates of coefficients[a]
Null model	33.90	190		33.90	190	
Full model	9.35	185		8.07	181	
Constant			-4.19			17.49
Year	10.57***	1	-17.83			-18.67
Date	1.02***	1	+0.815			+0.0425
Soil type	0.47**	1	+3.84	0.71***	1	+4.56
Insect type	4.02*	2				
Insect × year				0.40*	2	
Insect × date				0.89***	2	

[a] : $\times 10^3$.

Table 5b. Differences in calcium content between three groups of insects that were sampled in both years. The data were corrected for effects of year, date and soil type by taking the residuals of the regression of Ca content (arcsine transformed) on year, date and soil type (see Table 5a.)

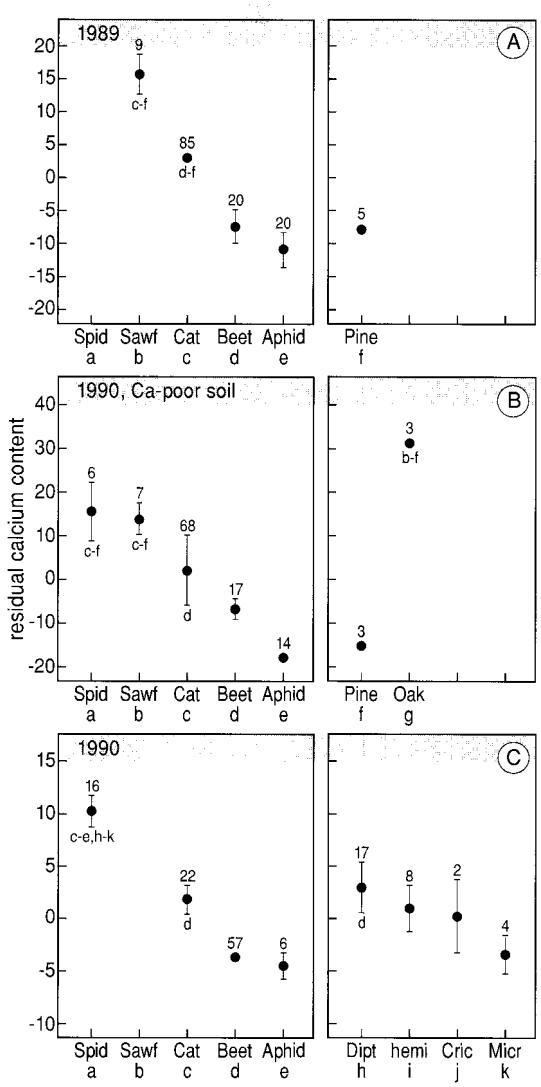
Residuals ($\times 10^3$)	$\bar{X}$	*SD*	*N*	Difference[a]
a. Caterpillars	3.56	7.34	104	bc
b. Beetles	-2.49	6.50	64	ac
c. Aphids	-9.19	8.27	23	ab

[a]Pairwise comparisons, *t*-tests. The letters denote significant differences (in all cases $p < 0.001$).

only in 1989 (group b) were the same as for group a, with respect to effects of date, soil type and the interaction between data and soil type (results of regression analyses not shown). Sawfly larvae had a higher Ca content than the other four food types, and caterpillars a higher Ca content than beetles, aphids and pine seeds (Fig. 3a). Among the food items collected in 1989 on poor soil (-group c) oak buds had a higher Ca content than all the other food types, except spiders. The Ca content of spiders and sawfly larvae was about the same, and higher than the Ca content of caterpillars, beetles, seeds of Scots Pine and aphids. Caterpillars had a higher Ca content than beetles (Fig. 3b). For the data in 1990, the Ca content on rich soils was higher than on poor soils and differed between the food types but we found no effect of date or of the interaction between soil type and food type. Spiders had a higher Ca content than all the other arthropods, except bush crickets, the latter probably due to the small number of samples of bush crickets. Diptera and caterpillars had a higher Ca content than the beetles, the differences with other groups were not significant,

again probably due to the small number of samples (Fig. 3c).

Summarizing, oak buds had a higher Ca content than any of the arthropod groups sampled. Among the arthropods, spiders and sawfly larvae had a higher Ca content than the other groups. Aphids, and to a lesser extent beetles, had a lower Ca content than the other groups. Caterpillars and Diptera were intermediate. The Ca content of pine seeds was quite low and comparable to that of aphids.



The variation in Ca content in the arthropods could partly be caused by differences in Ca content of the leaves that they were feeding on. For four phytophagous insects we calculated whether their Ca content was correlated with the Ca content of the leaves on which they were collected. We found significant correlations for larvae of the Winter Moth, *Opheroptera brumata* (delta SS for adding Ca content of the leaves to model controlling for soil type and date $0.18 \cdot 10^3$, df = 1, F = 8.81, $p < 0.001$) and adult weevils (*Phyllobius sp.*, Curculionidae) (delta SS for a model controlling for year and date $0.023 \cdot 10^3$, df = 1, $F = 4.42$, $p = 0.05$), living on oak, and for an aphid species living on birch leaves ($r_s = 0.69$, $n = 11$, $p = 0.02$), but not for sawfly larvae on oak ($r_s = 0.48$, $n = 9$, $p = 0.19$).

Calcium content of soil arthropods

The calcium content of the cockroaches, earwigs and spiders did not differ from that of the arthropods in the canopy (Table 6). However, the Ca content of millipedes and woodlice was about 100 times as high as any of the other arthropods. They are primitive arthropods, related (milli-

Fig. 3. Differences in Ca content between food types. a) Food types that were collected in 1989, both on Ca-rich and on Ca-poor soils. b) Food types that were collected in 1989, only on Ca-poor soils. c) Food types that were collected in 1990, both on Ca-rich and on Ca-poor soils.
Data presented are the residuals (± 1 *SE*, and $\times 10^3$) of the regression of Ca content (arcsine transformed) on date (b), soil (c) or date and soil (a) (as in Table 5). Sawf refers to sawfly larvae, Cat to caterpillars, Beet to beetles, Pine to seeds of Scots and Corsican Pine, Spid to spiders, Oak to buds of Pedunculate oak, Dipt to Diptera, Hemi to Hemiptera, Cric to bush crickets (Tettigoniidae) and Micr to Microlepidoptera (imagines of incurvariid moths). The right panels show plant material, or insects that were collected in 1990 only. Letters at data points indicate which food types had a lower calcium content than that particular food type (*t*-tests of pairwise comparisons of the food types, as in Table 5b, $p < 0.05$). The numbers refer to the number of samples. Further explanation, see text.

Table 6. The Ca content of soil arthropods collected March-June 1992 (dry matter).

	Ca-rich soil		Ca-poor soil	
	$\bar{X}\pm SD$	*N*	$\bar{X}\pm SD$	*N*
Millipedes (Diplopoda)	13.05	1	13.98±0.65	2
Woodlice (Isopoda)	11.36±0.91	2	10.34±0.18	4
Wolf spiders (Lycosidae)	-	-	0.04	1
Cockroaches (*Ectobius sylvestris*)	-	-	0.017±0.024	2
Earwigs (*Forficula sp.*)	-	-	0.006±0.003	2

pedes) or belonging (woodlice) to the crustaceans and unique among forest arthropods in having an calcified exoskeleton (Seifert 1961).

Food intake of females and nestlings

There are no measurements of the food intake of free-living female Great Tits during the egg-laying period. Therefore, we calculated the food intake using data on energy expenditure from the literature, under the assumption that a female consumed as much food as was necessary to cover her energy demands for maintenance and egg formation. Details of the calculations follow below, and the results are listed in Table 9.

The daily energy expenditure for maintenance (including activity and temperature regulation) of a non-growing and non-reproducing passerine (*DEE*) is related to the body weight: (1) $E = 18.59 \cdot W^{0.5224}$ (Kendeigh *et al.* 1977). The *DEE* is temperature dependent. For captive Great Tits of 17 g the relationship between *DEE* and temperature is given by: (2) $DEE = 80.3\text{-}1.28 \cdot T$ (Gavrilov 1974). For a freeliving bird this value has to be multiplied by 1.09 (Kendeigh *et al.* 1977). Combining (1) and (2) for a 19.8 g bird (Table 3) at 12 °C (April temperature) gave an estimate of $DEE = 76.7$ kJ. $(=1.09 \cdot (80.3\text{-}1.28 \cdot 12) \cdot (19.8/17)^{0.5224})$. A second estimate, 79.3 kJ, was obtained from measurements of the basal metabolic rate ($BMR = 30.5$ kJ, the mean of four references in appendix 5.1 in Kendeigh *et al.* 1977) and the relationship between *DEE* and the basal metabolic rate ($DEE = 2.6 \cdot BMR$, Drent & Daan 1980). The two estimates are almost identical and correspond well with measurements of the *DEE* of freeliving Great Tits at other times of the year. Birds spending the night in nestboxes had a *DEE* of 73.6 kJ (winter period, 3 °C) and females tending a brood had a *DEE* of 100 kJ (J. Tinbergen pers. comm.).

The energy content of Great Tit eggs is about 4.4 kJ/g (4.35 in Ojanen 1983; 4.46 J. Mertens pers. comm., cf. Kendeigh *et al.* 1977) and the egg mass is approximately 1.5 g (Table 1). The biosynthesis efficiency for egg formation is 75% (Ricklefs 1974, Kendeigh *et al.* 1977, Walsberg 1983). Therefore, the costs of egg formation are about 9 kJ, resulting in a *DEE* for maintenance and egg formation of about 90 kJ.

To calculate how much food a female needs to ingest to cover the estimated energy demand of 90 kJ we used data on the energy content and the digestion efficiency of various food types, taken from the literature (Table 7 and 8). There is not much variation among the food types and there seems to be no difference in digestion efficiency between nestlings and adult birds. For the calculations we used an energy content of 23 kJ/g and a digestion efficiency of 70%. It follows that the food intake of a female is $(90/23) \cdot (100/70) = 5.6$ g dry matter/day (Table 9).

This value corresponds well with real measurements of the energy or food intake of birds in captivity. Gibb (1957) measured an energy intake of 102.5 kJ (food intake 3.5 g of dry matter) for birds on a seed diet, at 4 °C in winter. Captive Great Tits, fed ad libitum with a mash of ground beef heart, hard boiled eggs and bread crumbs,

Table 7. Energy content of common food types of passerines (in kJ/gram dry matter). 1, Gibb (1957); 2, Kale (1965) cf. Kendeigh *et al.* (1977); 3, Kendeigh & West (1965), mean of 55 species of grass and dicotyledon herbs, *SD* 1.9; 4, Norberg (1978); 5, Schroeder (1977); 6, Turner (1982).

Food type	Energy content (kJ/g)	Authors
Arthropods		
Caterpillars	24.3	5
Weevils (Curculionidae)	22.0	4
Psocids (Psocoptera)	21.7	4
Various insects	24.4	1
Various insects	23.0	2
Aerial insects	22.8	6
Spiders	23.6	4
Mealworms	27.6	1
Seeds		
Scots Pine	25.7	1
Grass and herb seeds	20.6	3

about 75 kJ, assuming a digestion efficiency for energy of 70% (Kendeigh *et al.* 1977), close to the estimates for *DEE* in our study.

For the food intake of the nestlings' measurements were available from studies compiled by Van Balen (1973). Van Balen found a food intake in oak wood of 84.6 g per nestling over the entire nestling period, or 4.45 g per day (average for 20 broods), Kluyver (1950) measured a consumption in a pine forest of 3.4 and 7.5 g per nestling per day, for an early and a late brood, respectively, and Gibb & Betts (1963) measured 4.66 and 7.28 g per nestling per day in two similar broods (fresh weights in all cases). For the calculations we shall use the mean, 5.25 g. To convert this figure to dry weight we used data on the dry matter content in our samples: 20.9% ($SD = 3.0$, $n = 59$) for caterpillars, 22.8% (2.1, 4) for the sawfly larvae, 38.1% (12.5, 10) for aphids, 30.3% (4.5, 4) for spiders and 35.8% (10.6, 14) for beetles. Since the diet of nestlings mainly consists of caterpillars and spiders (Gibb & Betts 1963, Van Balen 1973) we assume a dry matter content of 25%, which results in a dry matter intake of 1.3 g per day (Table 9).

Table 8. Metabolizable energy intake (energy digested as % of energy intake) in passerines. 1, Blem (1978); 2, Bryant & Westerterp (1980); 3, Diehl (1971); 4, Gibb (1957); 5, Kale (1965) cf. Westerterp (1973); 6, Mertens (1977); 7, Turner (1982); 8, Westerterp (1973).

Species	food type	% digested	authors
Nestlings/fledglings			
House Martin, *Delichon urbica*	insects	70	2
Swallow, *Hirundo rustica*	insects	73	7
Red-backed Shrike, *Lanius collurio*	insects	70	3
Great Tit, *Parus major*	caterpillars	69	6
House Sparrow, *Passer domesticus*	seeds/insects	69	1
Sand Martin, *Riparia riparia*	insects	73	7
Starling, *Sturnus vulgaris*	insects	70	8
Adults			
Coal Tit, *Parus ater*	insects	67	4
Coal Tit	seeds	81	4
Blue Tit, *P. caerulescens*	seeds	76	4
Great Tit	seeds	80	4
Marsh Wren, *Telmatodytes palustris*	insects	76	5

consumed approximately 4 g dry matter per day during the laying period (Graveland, own observations). These values correspond with a *DEE* of

Table 9. Values of physiological parameters used to calculate the calcium intake of egg-laying females and nestlings of Great Tits. 1, Drent & Daan 1980; 2, Gavrilov 1974; 3, Hurwitz & Griminger 1961; 4, Kendeigh *et al.* 1977; 5, Ojanen 1983; 6, Mertens pers. comm., cf. Kendeigh *et al.* 1977; 7, Ricklefs 1974; 8, Simkiss 1967; 9, Simkiss 1975; 10, Sturkie 1965; 11, Taylor 1962; 12, Van Balen 1973; 13, Walsberg 1983.

Parameter	Value	Source
Body weight of egg-laying female (g)	19.8 g	table 3
Daily energy expenditure for maintenance, activity and temperature regulation[a]	ca. 80 kJ	1, 2, 4; see text
Egg mass	1.5 g	table 1
Energy content of egg	4.4 kJ/g	5, 6
Biosynthesis efficiency for egg formation	75%	4, 7, 13
Costs of making an egg	9 kJ	
Total daily energy expenditure of egg-laying female	90 kJ	see text
Energy content of the food	23 kJ/g	table 7
Digestion efficiency of energy	70%	table 8
Daily food intake of egg-laying female, covering her energy expenditure	5.6 g	see text
Daily food intake of nestling (fresh weight)	5.3 g	12
Dry matter content of food	25%	this study, see text
Daily dry matter intake of nestling	1.3 g	see text
Retention rate for calcium	60%	3,8,9-11, see text

a. For non-growing, non-eproducing bird

Ca intake of egg-laying females and nestlings, compared to the calcium demand

The Ca intake was calculated from the daily food intake, the calcium content of the food and the calcium retention rate (retention rate defined as (intake-excretion)/intake x 100%). Data on retention rate for Ca are scarce and are mainly based on work with domestic fowl. Estimates range from 50% (Taylor 1962), 60.4% (Hurwitz & Griminger 1961) to 67-70% (Sturkie 1965, Simkiss 1967, 1975). Great Tits deposited about 55-60% of the Ca (fed ad libitum) into eggs, so the retention rate was probably higher than 60% (Graveland & Berendse, own obs.). In the calculations we used a retention rate of 60% (Table 9).

For each food type in the canopy, we calculated the daily calcium intake, if a bird ate this food type only, and we expressed this calcium intake as a percentage of the calcium demand. We performed separate computations for the samples collected on Ca-poor and Ca-rich soils, for 1989 and 1990. The Ca intake of a female with a food intake rate of 5.6 g dry matter/day and a 60% retention rate for Ca is:

I. Ca intake (mg/day) = 5.6·0.6·(% Ca-content/100)·1000 = 33.5·% Ca content of the food.

The Ca intake for a nestling (with a dry matter intake of 1.3 g/day) is:

II. Ca intake (mg/day) = 1.3·0.6·(% Ca content/100)·1000

= 7.8·% Ca content of the food.

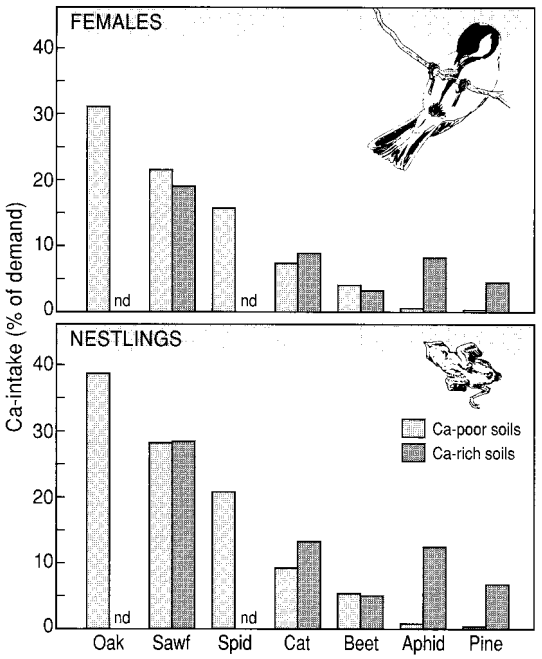


Fig. 4. The daily Ca intake of egg-laying females and of nestling Great Tits, as a percentage of their Ca requirements. The Ca intake for each food type is the calculated intake if a bird ate only that particular food type. The Ca contents used were from 1989 (in 1990 they were much lower, see Table 4) and are the mean of the samples collected in late and early spring. nd: no data. For abbreviations of names of food types, see Fig. 3. Further explanation in text.

We assumed that the daily Ca demand of an egg-laying female was equal to the amount of Ca in one egg (31.3 mg on poor soils, 35.9 mg on rich soils, Table 1), as females produce one egg per day. We assumed that the average daily Ca demand of a nestling was 1/14 of the difference in Ca content between 0 and 14 days old nestlings, 5.6 mg per day (the peak demand is higher since the growth of the skeleton mainly takes place in the second week).

The results clearly demonstrate that, irrespective of the type of arthropod or the Ca content of the soil, arthropods can only be a minor Ca source for Great Tits (Fig. 4). Even in 1989, the year in which the Ca contents were much higher than in 1990 and if Great Tits fed exclusively on spiders and sawfly larvae, the arthropods with the highest Ca content, they would still not be able to cover more than 20-25% of their Ca demand. With oak buds they would be able to cover 30-40% of the Ca demand but oak buds are not a major part of the diet. Most arthropods had a lower calcium content than caterpillars (Table 4) and would not cover more than 5% of the Ca demand. The percentages for the females are somewhat lower than for the nestlings (Fig. 4). The daily food intake of females is four times as high as for nestlings, but their calcium demand is five times as high.

For woodlice and millipedes the picture is quite different. We calculated that females on a diet of woodlice or millipedes would ingest 10-15 times their daily calcium demand, and nestlings 15-20 times. Females would be able to cover their Ca requirements if they included about 5-6% (of dry matter) woodlice or millipedes in their diet. For nestlings 3-4% would be sufficient.

DISCUSSION

The contribution of the skeleton to shell formation in passerines

We will demonstrate that the results of the calculations of the calcium budget of Great Tit females and nestlings are valid for most other passerines. This applies to the role of the skeleton in shell formation, to the calcium requirements, and to the calcium intake from normal food.

The skeleton contains about 98% of the amount of Ca in the avian body (Simkiss 1967). Many bird species store calcium in the skeleton as medullary bone prior to egg-laying (Pfeiffer *et al.* 1940, Bloom *et al.* 1941, March & Sadleir 1975, Jones 1976, Schifferli 1977, Turner 1982, Pinowska & Krasnicki 1985). However, as in the Great Tit, in all species studied the amount of Ca stored was quite small compared to the amount of Ca needed. Schifferli (1979) reported that the dry weight of the skeleton of female House Sparrows, *Passer domesticus*, before laying was only 0.21 g higher than that of females that had produced 4

eggs, whereas a single egg contains 0.17 g of Ca. Pinowska & Krasnicki (1985) found a difference in skeletal Ca between females before and after laying, equal to 85% of the amount of Ca in one egg. Houston *et al.* 1995 found no decrease in skeletal Ca in captive Zebra Finches, *Poephila guttata*, over the laying period. The skeleton of most small passerines contains only three to five times the amount of calcium in a single egg (Graveland & Sandee own obs.). The ratio of the amount of calcium in a clutch to the calcium in the skeleton is 0.5 for the Dipper, *Cinclus cinclus* (Ormerod *et al.* 1988), 0.7 for the Red-billed Quelea (Jones 1976), 0.6 for the Great Tit (this study) and 1.1 for the Blue Tit (Perrins 1979).

The capacity of birds to use skeletal calcium for shell formation, with or without prior storage, is therefore quite limited. Medullary bone is a labile type of bone from which calcium can be mobilized much faster than from structural bone (Simkiss 1967, Hurwitz 1987). Birds on a calcium deficient diet keep the amount of medullary bone constant, by converting structural bone. The calcium in the medulla therefore probably does not serve as a calcium store per se, but mainly acts as a buffer against the peaks in calcium demand during the short periods of shell formation (Ankney & Scott 1980, Etches 1987, Hurwitz 1987). We conclude that females of passerines store little or no calcium in their skeleton before egg-laying and must collect all the calcium needed for shell formation during the laying period.

Estimates of energy demand and food intake

In the calculation of food intake we assumed that females did not eat more than needed to balance their energy requirements of maintenance and egg production. One might argue that females eat more in cases where a nutrient such as calcium is limiting. Therefore, we calculated the calcium intake of a female with a maximum metabolizable energy intake (*MME*), since this intake is close to what a bird can maximally ingest (Kirkwood 1983). *MME* scales with body mass as: $MME = 1713\ kJ/kg^{0.72}$. For 10-50 g birds, *MME* is 1.2-1.4 times the normal energy expenditure ($DEE = 18.59W^{0.5224}$, Kendeigh *et al.* 1977) and the corresponding calcium intake would therefore be 1.2-1.4 times the intake used in the calculations of the calcium budget. This would still be much too low to cover the calcium requirements (Fig. 4). Moreover, data on captive birds suggest that calcium deficient birds do not increase their food consumption (Gilbert 1983, Graveland & Berendse own obs.) and data on wild birds suggest that reproduction is limited by food availability in spring, which makes it unlikely that the energy intake can be much higher than what is needed for egg-laying and maintenance (Perrins 1970, Davies & Lundberg 1985, Daan *et al.* 1989, Nager & Van Noordwijk 1992).

Our estimates of the food intake of Great Tit females were derived from general relationships between body size, temperature and energy expenditure in passerines. Studies with doubly-labelled water have shown that these relationships are robust and generally valid (Nagy 1987). This was confirmed by the close agreement between our estimates and real measurements of energy expenditure and food intake in the case of the Great Tit. Our estimates of energy demand and food intake provide a reliable base for the calcalation of the calcium intake not just of Great Tits, but of other passerines as well.

The calcium content and the retention rate for calcium from arthropods and seeds

Table 10 lists data of the Ca content of arthropods and seeds, taken from the literature. Although the values are often somewhat higher than our own data (Table 4), most of them are much too low to fulfil the Ca demands of small passerines like the Great Tit.

It was assumed that the birds could metabolize 60% of the calcium present in their normal food. This figure was based on studies in which calcium in the food was present as calcium-carbonate, such as in oyster shell, limestone or snail shells. However, the metabolizable calcium intake from insects and seeds is probably much lower than 60%. The correlation between the calcium content of herbivorous insects (caterpillars,

Table 10. The Ca content of arthropods and seeds (% of dry matter). Data compiled from the literature. 1, Bilby & Widdowson (1971); 2, MacLean (1974); 3, Ormerod *et al.* (1988); 4, NethersoleThompson 1975; 5, Reichle *et al.* (1969); 6, Turner (1982); 7, this study.

Taxa	Ca content	Authors
Arthropods		
Earthworms (without gut content)[a]	0.23	1
Crane flies (Tipulidae), larvae	0.35	2
Crane flies, adults	0.08	2
Aerial insects	0.35	6
Stonefly nymphs (Plecoptera)	0.29	3
Caddisfly larvae (Trichoptera)	0.18	3
Mayfly nymphs (Ephemeroptera)	0.24	3
Diptera	0.27	3
Gammarus (Isopoda)	13.64	3
Millipedes	16.36	5
Chilopoda	0.06	5
Spiders	0.20	5
Harvestmen (Phalangida)	0.76	5
Beetles	0.09	5
Diptera	0.14	5
Seeds		
Spruce, *Picea abies*	0.10	4
Scots Pine, *Pinus sylvestris*	0.07	4
Sunflower seeds	0.04	7

[a]Possibly with traces of soil adhering to the skin.

sawfly larvae) and leaves, and the low calcium content of insects compared to leaves (Drent & Woldendorp 1989, own obs.), suggest that most calcium in insects is present in the leaf material in the gut. Calcium in plants is often bound to oxalate (in green matter) or phytate (in seeds), salts that are much harder to dissolve than calcium-carbonate (Simkiss 1967, Simons 1986). Litter dwelling snails are less abundant in oak and coniferous forest than in maple or lime forest, because in the former calcium is mainly bound to oxalate, and in the latter to readily dissolvable citrate or malate (Wäreborn 1969, 1970). We used a retention rate of 60%, since we could not find figures for the retention of calcium from plants or insects. However, one study is interesting in this context. Houston (1978) reported that juvenile *Gyps* vultures metabolized only 14% of the calcium present in meat, compared to 78% of the calcium in bones (a tri-calcium phosphate complex). We conclude that the amount of calcium that birds can obtain from insects and seeds is probably even less than was calculated in this study.

Insectivorous and granivorous birds ingest calcium-rich items for shell formation and skeletal growth

This study showed that the female skeleton and the normal food of insectivorous and granivorous birds contribute little calcium to shell formation. Females therefore have to ingest specific calcium-rich material such as snail shells and calcareous grit during the egg-laying period. Nestlings also require calcium-rich material for the growth of their skeletons. A review of the literature shows that almost all birds of which the diet was studied in detail (examination of stomach contents, neck-collar studies) do indeed ingest calcium-rich items during egg-laying and during the nestling period (Graveland own obs.). Egg-laying females consume more calcium-rich items than nonlaying birds (Sadler 1961, MacLean 1974, Jones 1976, Schifferli 1977) and nestlings ingest most calcium-rich items at a time of maximum skeletal growth (Bilby & Widdowson 1972, Thaler 1979). The main calcium sources are snail shells and calcareous grit (Creutz 1953, Schifferli 1977, Graveland own obs.). If these are scarce, as is the case on calcium-poor soils, birds use alternatives such as bones and 'anthropogenic' calcium sources (Susic 1981, Payne 1972). Work with domestic fowl and captive Great Tits revealed that most consumption of calcium-rich items takes place in the late afternoon and evening, during the first hours of shell formation (Mongin & Sauveur 1974, Graveland & Berendse own obs.). This is probably the reason why calcium consumption is rarely observed in wild birds. That in turn might explain why the calcium demand of birds has received little attention in

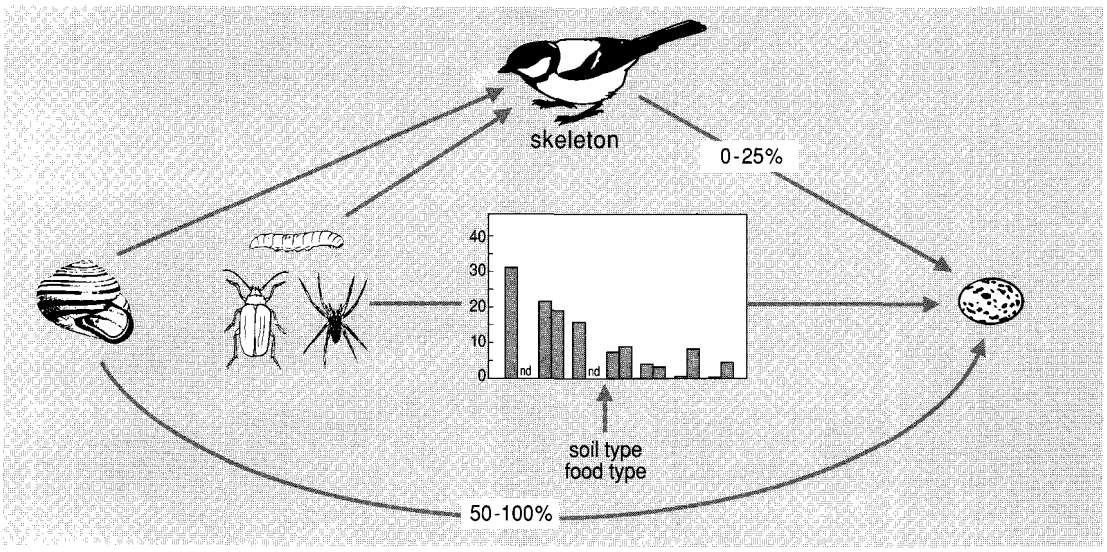


Fig. 5. Flow diagram showing the relative amounts of shell calcium coming from the food, additional calcium-rich material and the skeleton in an average passerine.

studies of birds' food requirements, compared to the demand for protein or energy.

ACKNOWLEDGEMENTS

We thank A.J. Cavé, R.H. Drent, A.G. Gosler, C.M. Lessells, R. Nager, J.H. Van Balen, S. Verhulst and J.W. Woldendorp for their comments on earlier versions of the manuscript, and W. Smant, R. Wagenaar and S.R. Troelstra for carrying out the chemical analyses.

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SAMENVATTING

Wij gingen na in welke mate kleine zangvogels de calcium die ze nodig hebben voor de vorming van de eischaal en voor de groei van het skelet kunnen betrekken uit hun normale voedsel, geleedpotigen (meest insecten) en zaden. We bepaalden het calciumgehalte van geleedpotigen en zaden uit bossen op kalkarme en kalkrijke grond, het calciumgehalte van vrouwtjes, eieren en nestjongen van de Koolmees en berekenden daarmee een calciumbudget voor vrouwtjes en nestjongen. Vrouwtjes bleken voor de eileg geen calcium op te slaan in het skelet en dus alle benodigde calcium te verzamelen tijdens de legperiode. Zelfs op kalkrijke bodem bleek de calciumopname via geleedpotigen en zaden slechts 5-10% van de calciumbehoefte te kunnen dekken. We laten zien dat deze resultaten ook van toepassing zijn op de meeste andere zangvogels. Een uitzondering vormen een aantal soorten die miljoenpoten en pissebedden in hun menu hebben. Die bevatten 10-13% calcium (droge stof), honderd keer zoveel als andere geleedpotigen. De meeste zangvogels zijn echter afhankelijk van calciumrijk materiaal zoals slakkehuizen en kalkhoudend gesteente om in hun calciumbehoefte te voorzien.