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EGGSHELL CHARACTERISTICS AND CALCIUM DEMANDS OF A MIGRATORY SONGBIRD BREEDING IN TWO NEW ENGLAND FORESTS

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ABSTRACT.—Calcium has been reported to be a limiting nutrient for eggshell production in birds living in areas of northern Europe suffering from heavy acid deposition. To investigate whether calcium might be limiting for birds in northeastern North America, a region also experiencing high and persistent acid precipitation, we analyzed eggshell characteristics and assessed calcium needs for eggshell production of a Neotropical migrant songbird, the Black-throated Blue Warbler (*Dendroica caerulescens*), in two forests in New England that differed in calcium content of their soils. We found no significant differences between the two regions in warbler eggshell mass, thickness, or in the concentration or the amount of calcium in eggshells. Moreover, calculations show that a diet of larval Lepidoptera, a major food source, is not a sufficient source of calcium for this species during egg laying, but that ingestion of eight average-sized (60 mg dry mass) snails during the egg-laying period would supply sufficient calcium for eggshell formation for a 4-egg clutch. Although current densities of snails suggest that they are not a limiting resource for birds at these sites, recent findings of declining calcium availability in New England forest soils suggest that calcium could in the future become a limiting factor for birds in northern temperate forests. *Received 29 August 2000, accepted 15 March 2001.*

Recent concerns about possible declines in bird populations, especially of small songbirds that migrate long distances (Robbins et al. 1989, Askins et al. 1990, Peterjohn et al. 1995), have led to a renewal of interest in the factors limiting avian populations (Rappole and McDonald 1994, Sherry and Holmes 1995, Latta and Baltz 1997). Hypotheses to explain population declines have focused mostly on the effects and ramifications of habitat destruction or fragmentation in both northern breeding grounds and Neotropical wintering areas, as well as along migratory routes (Hagan and Johnston 1992). Recently, however, several studies (mostly from northern Europe) suggested that reduced calcium levels in northern environments, attributed mostly to the effects of acid deposition, have affected eggshell production by birds, leading to increased rates of egg failure and lower reproductive success (Drent and Woldendorp 1989, Graveland 1990, Ormerod et al. 1991, Graveland et al. 1994, Eeva and Lehikoinen 1995, Graveland and Drent 1997, Nybo et al. 1997, Pinxten and Eens 1997, Zang 1998, Tilgar et al. 1999, but see Ramsey and Houston 1999, Mänd et al. 2000). In North America thinner eggshells (Glooschenko et al. 1986) and other reproductive anomalies (Blancher and McNicol 1988, St. Louis and Barlow 1993) were reported in birds breeding in acidified areas, particularly in the vicinity of wetlands. Furthermore, James et al. (1996) noted that bird populations at higher elevations in the eastern United States were declining most severely, and suggested that this could be a result of ecosystem damage due to atmospheric deposition.

The degree to which calcium actually or even potentially limits birds occupying upland forested habitats in areas of eastern North America where acid deposition is prevalent, however, has not been clearly determined (Mahony et al. 1997). In this study, we examined the calcium content and eggshell properties of a migratory bird species that breeds in forests of the northeastern United States, a region where some bird populations have been declining (Holmes et al. 1986; Holmes and Sherry 1988, 2001) and where acid deposition has been well documented and monitored (Likens and Bormann 1974, Likens et al. 1998). Recent studies indicate that the availability of calcium in soils of this region has decreased, with potentially negative effects on forest growth and other ecosystem processes (Likens et al. 1996).

To assess whether calcium might be limit-

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ing eggshell production in forest songbirds, we studied the Black-throated Blue Warbler (*Dendroica caerulescens*), a long distance migratory passerine bird species, in two forested regions in New England that differed in bedrock characteristics and calcium availability. We tested the hypothesis that warblers breeding in a calcium poor site (Hubbard Brook in New Hampshire) would show more signs of calcium stress, as evidenced by thinner eggshells and reduced amounts of calcium in eggshells, than would individuals in a relatively calcium rich site (Downer Forest in Vermont). We also determined the amount of calcium in the most important food items of this species, and assessed the amount of calcium needed for the production of a clutch of eggs and the potential sources of that calcium for this forest-nesting passerine bird.

STUDY SITES AND METHODS

We conducted this study in the Hubbard Brook Experimental Forest in West Thornton and Woodstock, New Hampshire (43° 56′ N, 71° 45′ W) and in the Charles Downer State Forest in Sharon, Vermont (43° 45′ N, 72° 24′ W). These sites, located about 53 km apart, differ in bedrock geology. Hubbard Brook is underlain by calcium poor, crystalline, silicate rocks of the Upper Rangeley Formation (Lyons et al. 1997), whereas Downer Forest is situated on calcium rich carbonate and silicate rocks of the Waits River Formation (Doll et al. 1961). The Downer Forest soil parent material contains free calcite, which not only supplies relatively large amounts of calcium, but also buffers soil pH, preventing acidification from acid deposition. This is evidenced by the calcium levels in the soil cation exchange pool that are five times greater at Downer Forest than at Hubbard Brook (Blum et al. 2000).

Despite differences in bedrock geology, the forests at the two localities were similar. Both were dominated by northern hardwoods, mainly sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with scattered softwoods such as red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). Similarly, the understories in both forests consisted of saplings of the dominant tree species, plus low-growing shrubs (e.g. hobblebush, *Viburnum alnifolium*) and small trees (e.g., striped maple, *A. pensylvanicum*).

Black-throated Blue Warblers arrive at these breeding sites in mid- to late May after migration from the Caribbean region. Clutches are initiated within two weeks of arrival, and one egg is laid per day (Holmes 1994). During June 1996, we located warbler nests at widely separated localities within each of these forested areas by following females during nest building. At each site, nests were situated in different watershed drainages and at distances of >500 m and some at >1000 m from each other. We thus considered nests (clutches) within a site as independent, randomly selected replicates.

When clutches were complete, we collected the eggs (under permits from federal and state agencies and with procedures approved by the Institutional Animal Care and Use Committee of Dartmouth College). Caterpillars (Geometridae and Notodontidae) and snails also were collected near nest locations. Eggs were stored frozen and then broken open, allowing easy separation of egg contents from shells. Eggshells were weighed in the fresh frozen state, dried overnight at 105° C, and then reweighed to determine dry mass. Caterpillars were ashed overnight in acid-washed silica crucibles at 500° C, and then they, as well as snail shells, were digested in ultra-pure 10 M nitric and hydrochloric acids, evaporated to dryness, and redissolved in ultra-pure 1 M nitric acid for analysis. Solutions were diluted to appropriate concentration ranges, spiked with an yttrium internal standard, and analyzed for the concentration of calcium using a Finnigan magnetic sector inductively coupled plasma mass spectrometer with an accuracy of ± 5%.

Eggshell thickness was determined from sections examined with a scanning electron microscope. Eggshells were mounted in epoxy and cross sections of the shells were polished and carbon coated. Secondary electron photomicrographs were obtained for each sample. To reduce variation due to location within different parts of the shell, measurements were taken from the photomicrographs at three sites along the equator of each eggshell. Two measurements were taken: (1) the full thickness, measured from the shell surface to the inner shell membrane, and (2) the thickness of the palisade and cone layers (Board and Scott 1980), which were heavily calcified and appeared as bright white layers in the photomicrographs.

A nested analysis of variance (ANOVA) was used to test for statistical differences in eggshell thickness measures between the two forests, among clutches within the same forest, and among eggs within each clutch. Analyses of covariance (ANCOVA) were used to test for differences in total calcium mass of eggshells among clutches within and between forest sites, with egg size as measured by total egg mass being the covariate. For all analyses, clutches were considered a random effect, and we verified that our data met all model assumptions. Statistical analyses were performed using JMP, version 3.2.6 (SAS Institute 1997).

RESULTS

Eggshells did not differ significantly in total thickness ($F_{1,6} = 0.10$, $P = 0.77$) or in depth of the palisade/cone layer ($F_{1,6} = 0.017$, $P = 0.90$) between the two sites (Table 1). Variation among clutches within forests was marginally significant for the palisade/cone layer ($F_{6,25} = 2.35$, $P = 0.06$) and insignificant for total eggshell thickness ($F_{6,25} = 1.13$, $P =$

TABLE 1. Physical characteristics of Black-throated Blue Warbler eggshells at Hubbard Brook, New Hampshine, and Downer Forest, Vermont, 1996. Values are means ± 1 SE; n = 4 clutches at each site (4–5 eggs/clutch).

	Hubbard Brook (Calcium poor site)	Downer Forest (Calcium rich site)
Eggshell mickness (μm)		
Shell surface to inner membrane	95.66 ± 4.51	93.93 ± 3.30
Palisade/cone layer only	59.38 ± 3.81	58.80 ± 2.46
Eggshell mass (mg dry mass)	89.91 ± 2.90	78.72 ± 2.90
Eggshell calcium concentration (mg/mg dry mass)	0.22 ± 0.02	0.25 ± 0.01
Eggshell calcium (mg/egg)	19.43 ± 1.27	19.55 ± 1.34

0.37). There were, however, highly significant differences in shell thickness among eggs within individual clutches for both the palisades/cone layer ($F_{25,66}$ = 7.84, $P < 0.0001$) and total eggshell thickness ($F_{25,66}$ = 22.25, $P < 0.0001$), indicating that variance among clutches was less than the variance among eggs within a clutch.

Mean eggshell mass was slightly higher at Hubbard Brook than at Downer Forest (Table 1), although the difference was not statistically significant and there was no significant interaction of site with egg size (Table 2). The mean concentration of calcium in eggshells was similar at both forest sites (Table 1, $F_{1,6.02}$ = 1.80, P = 0.23), but there was some variation among clutches within sites ($F_{6,25}$ = 2.57, P = 0.04). Total calcium mass per eggshell, which was a function of the concentration of calcium in each eggshell and the total mass of that eggshell, did not differ significantly between the two sites or among clutches within sites (Table 2). We performed a retrospective power analysis to determine if our data were sufficient to detect a biologically relevant difference in eggshell calcium between sites. The only information available on the latter was Graveland's (1995) finding that deficient Great Tit (*Parus major*) eggshells in calcium poor sites had 84.9% of the calcium by mass compared to that in normal eggshells. If such a difference existed between sites in our study, the true mean calcium content would have been 2.94 mg/egg more at Downer Forest than at Hubbard Brook (compared to actual difference of 0.12 mg/egg; Table 1). The power analysis indicated that our measurements would have detected this difference between Downer Forest and Hubbard Brook (i.e., an effect size of 2.94) with a probability of >0.99. Even if the true difference were only half that reported by Graveland (1995), our test would probably still have detected it ($1 - \beta > 0.82$). These results, therefore, indicate that any difference in calcium levels of Black-throated Blue Warbler eggshells between the calcium rich and the calcium poor sites was probably not biologically relevant, at least when compared to levels reported for Great Tits in the Netherlands (Graveland 1995).

TABLE 2. Results of analyses of covariance (ANCOVA) on mass and calcium content of eggshells of Black-throated Blue Warblers at two New England forest sites, 1996, with egg mass as covariate.

Source of variation	MS	df	F	P
Eggshell mass (mg)				
Site[a]	0.00021	1	1.475	0.24
Clutch [site][b]	0.00020	6	1.416	0.25
Egg mass	<0.00001	1	0.092	0.76
Site × Egg mass	0.00016	1	1.139	0.30
Error	0.00014	23		
Eggshell calcium (mg)				
Site[c]	0.0052	1	0.001	0.98
Clutch [site][b]	21.3344	6	2.915	0.03
Egg mass	0.2348	1	0.032	0.86
Site × Egg mass	0.0052	1	0.001	0.98
Error	7.3193	23		

[a] Error term for site = 0.004 × clutch[site] + 0.996 × residual; df Error = 23.26.
[b] Random effect in model.
[c] Error term for site = 0.004 × clutch[site] + 0.996 × residual; df Error = 23.54.

The concentration of calcium in larval Lepidoptera averaged 1.16 ± 0.07 SE and 2.05 ± 0.28 (n = 9 in each case) mg/g dry mass at Hubbard Brook and Downer Forest, respectively, a difference that was statistically significant ($F_{1,16}$ = 5.46, P = 0.03). The mean calcium concentration (mg/g dry mass) of snail shells was 220.6 ± 32.0 SE (n = 6) at Hubbard Brook. Only one snail was sampled at Downer Forest, and the calcium concentration of its shell was 350.0 mg/g dry mass.

DISCUSSION

If calcium were limiting egg production by birds in these two forests in New England, we expected to see differences in eggshell properties and calcium contents between Hubbard Brook (which is situated on a low calcium substrate and where calcium has declined in the last decade; Likens et al. 1996, 1998) and Downer Forest (where calcium is relatively more available; Blum et al. 2000). In fact, we found no significant differences in warbler eggshell mass, thickness, or calcium content between the two sites. The highly significant variability in shell thickness within eggs of a clutch suggests the possibility that calcium becomes progressively more limited as additional eggs are laid, but unfortunately we did not determine the order in which eggs were laid in our study. Furthermore, it is unlikely that this within-clutch variability relates to depletion of calcium stores, given the radiographic evidence of Pahl et al. (1997) that passerine birds do not remobilize calcium from their skeleton during egg laying, and the isotopic evidence of Blum et al. (2001) that no outlier strontium isotopic values were evident among Black-throated Blue Warbler eggs within a clutch.

Thus, there is little evidence from this study for calcium limitation of birds in these two forests in New England, even for one site which has naturally low levels of calcium availability and has been impacted by acid deposition for several decades (Likens et al. 1996). This conclusion is further supported by results of intensive studies of the population ecology of Black-throated Blue Warblers at Hubbard Brook. From 1986–2000, more than 100 nests of this species were observed each breeding season, and the fates of all eggs determined. During this time, no gross abnormalities in eggshells or other evidence of egg failure were recorded (Holmes et al. 1992, 1996; RTH, unpubl. data). Similarly, Mahony et al. (1997) found no differences in clutch sizes or hatching success of two bird species, one resident and one migrant, in acidified maple forests in Ontario, Canada.

Nevertheless, if acid precipitation continues to leach calcium and other cations from these forests (Likens et al. 1996), it is possible that calcium could become limiting. This raises the question of how much of a calcium buffer exists, which in turn requires considerations of where these warblers and other forest birds obtain their calcium and how much calcium is needed for the production of a clutch of eggs. Some types of birds are known to store calcium in medullary bone, from which it can then be transferred to the oviduct when an eggshell is being formed (Scheuhammer 1991). However, evidence from mass balance calculations (e.g., Graveland and van Gijzen 1994) and from high resolution radiography (Pahl et al. 1997) indicates that passerine birds do not store large quantities of calcium, indicating that calcium for egg production must be derived mostly from food sources in the local breeding area. Recent studies of the eggs and tissues of Black-throated Blue Warblers at Hubbard Brook and Downer Forest confirm this. Using natural variations in the stable strontium isotope ratios ($^{87}Sr/^{86}Sr$) as a surrogate for calcium, Blum et al. (2001) showed that eggshell calcium for this species is derived from the local breeding area and not transported from tropical winter grounds. Thus, this long distance migrant, and probably most other bird species in these temperate forests, appear to obtain their calcium for eggshell formation from local sources within the breeding areas.

Results from other studies suggest that birds obtain calcium from calcareous grit, animal bones, or food items rich in calcium just prior to egg laying (Graveland and van Gijzen 1994, Graveland 1996, Graveland and Drent 1997, Reynolds 1997). However, the availability of grit, animal bones, or even access to exposed mineral soil in our two study sites and probably in most New England forests is extremely limited (RTH, unpubl. data), leaving invertebrate food items as the most likely source of calcium for Black-throated Blue Warblers and probably most other birds in these forest interiors.

The major food of Black-throated Blue Warblers and many other species at Hubbard

Brook are larval and adult Lepidoptera, along with adult Diptera and Coleoptera (Robinson and Holmes 1982, Goodbred and Holmes 1996). Graveland and van Gijzen (1994) argued that arthropods, in general, provide insufficient calcium for eggshell production by passerine birds. Calculations from our data support that conclusion. With approximately 20 mg of calcium per eggshell (Table 1), a clutch of four eggs would require a female to mobilize 80 mg of calcium, just for the four eggshells. We found that caterpillars contained approximately 1–2 mg Ca/g dry mass at Hubbard Brook and Downer Forest, respectively. From these values, we calculate that females would need to ingest at least 61 g dry weight of caterpillars at Hubbard Brook and 38 g dry weight of caterpillars at Downer Forest per day for four days to obtain the calcium necessary to produce a clutch of eggs. This assumes further that all calcium in these prey items is assimilated by the female and is used in egg production, which is undoubtedly an overestimate (Graveland and van Gijzen 1994). The calculated amount of 40–60 g dry weight of caterpillars to be consumed per day represents approximately 4–6 times the live mass of the bird itself, and is clearly an unrealistic amount for a small insectivorous bird to consume (see Graveland and van Gijzen 1994).

Land snails have been identified in other temperate systems as a major source of calcium (Graveland and van Gijzen 1994). These occur at Hubbard Brook and in other New England forests, but are small (usually <1 mm in length) and inconspicuous. They are found mainly in the forest litter, often under logs and decaying dead wood, places that make them relatively inaccessible to a foraging warbler and most other arboreal species. Although female Black-throated Blue Warblers are rarely seen foraging in this layer, when they do it is early in the summer, coincident with the early nesting period, i.e., during egg-laying (RTH, pers. obs.). Thus, although the evidence is circumstantial and inferential, snails seem the most likely major source of calcium for birds in these forests.

Assuming snails are the main source of calcium for these birds, we can calculate how many would be needed to provide calcium for a clutch of eggs. Based on the average calcium content of 20 mg per eggshell (Table 1) and the calcium concentration in snail shells (220 mg Ca per g dry mass at Hubbard Brook), we calculate that a female Black-throated Blue Warbler would need to ingest about 91 mg of snail shell each day during the egg laying period to obtain the calcium needed for each egg. With whole snail shells at Hubbard Brook averaging 60 ± 1.0 SE mg dry mass ($n = 8$; EHT, unpubl. data), this would require the consumption of less than two average-sized snails per day (or per eggshell), assuming complete transfer of calcium from snail to egg. Thus, a clutch of four eggs would require the consumption of eight average-sized snails during the egg-laying period. With snail densities at Hubbard Brook averaging about $2/m^2$ (M. E. Smith and S. P. Hamburg, pers. comm.) and a territory of a Black-throated Blue Warbler averaging 1.5 ha or 15,000 m^2 in area (Holmes 1994), snails would not appear to be a limiting resource at the present time.

Our results and calculations suggest that calcium is not currently a limiting resource for eggshell production by Black-throated Blue Warblers at Hubbard Brook or Downer Forest. We point out, however, that these results are from only one species and from only two localities within its breeding range. Differences may occur among localities, as well as among species. Moreover, because most forest birds are dependent upon calcium rich foods for their calcium needs, we caution that if continued soil acidification in the region begins to have an adverse effect on snails or on other calcium rich food items, the reproductive success of forest birds could be affected.

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