Soil Calcium Availability Limits Forest Songbird Productivity and Density

Authors: Pabian, Sarah E., and Brittingham, Margaret C.

Source: The Auk, 128(3) : 441-447

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2011.10283

The Auk

An International Journal of Ornithology

Vol. 128 No. 3 July 2011

The Auk 128(3):441–447, 2011

RAPID COMMUNICATIONS

SOIL CALCIUM AVAILABILITY LIMITS FOREST SONGBIRD PRODUCTIVITY AND DENSITY

Sarah E. Pabian[1] and Margaret C. Brittingham

School of Forest Resources, Pennsylvania State University, 414 Forest Resources Building, University Park, Pennsylvania 16802, USA

Abstract.—Forest soils in many areas of the world are becoming increasingly acidified, in part because of atmospheric deposition of strong acids produced by the burning of fossil fuels. Soil acidification and subsequent calcium depletion of forest soils in eastern North America have the potential to affect forest songbird populations negatively by reducing the availability of calcium-rich food items that are critical for reproduction. Nonetheless, little experimental evidence exists for the purported relationship between soil calcium and avian reproduction. Our objective was to use an experimental and observational study to determine how forest songbird-habitat quality is related to soil calcium availability. We experimentally elevated soil calcium using limestone sand and observed a 1.8-fold increase in Ovenbird (*Seiurus aurocapilla*) territory density, larger clutch sizes and more nests, but no effects on egg characteristics. The observational study of 14 forested sites in central Pennsylvania likewise showed positive relationships between natural soil calcium levels and Ovenbird territory density, clutch size, and nest density. Again, no relationships existed between soil calcium and eggshell characteristics. Snails are a critical calcium source for many breeding birds, and we suspect that snails are the link between soils and birds because snail abundance increased with liming and was positively correlated with soil calcium. We conclude that Ovenbird habitat quality is related to soil calcium, that birds on our sites were calcium-limited, and that reduced soil calcium could play an important role in bird declines in acidified forests. *Received 16 December 2010, accepted 11 April 2011.*

Key words: acidic deposition, clutch size, limestone sand, nutrient limitations, Ovenbird, *Seiurus aurocapilla*, snails.

La Disponibilidad de Calcio en el Suelo Limita la Productividad y Densidad de Aves Canoras

Resumen.—Los suelos de los bosques de muchas áreas del mundo se están haciendo cada vez más ácidos, en parte debido a la deposición atmosférica de ácidos fuertes producidos por la quema de combustibles fósiles. La acidificación y posterior pérdida del calcio en los suelos de bosques del este de Norte América tienen el potencial de afectar a las poblaciones de aves canoras negativamente, reduciendo la disponibilidad de ítems alimenticios ricos en calcio que son críticos para la reproducción. Sin embargo, existe poca evidencia experimental acerca de la supuesta relación entre el calcio del suelo y la reproducción de las aves. Nuestro objetivo fue emplear un estudio experimental y de observaciones para determinar cómo se relaciona la calidad de hábitat de bosque para aves canoras con la disponibilidad de calcio. Elevamos experimentalmente el calcio del suelo usando arena de piedras calizas y observamos un aumento de 1.8 veces en la densidad de territorios de *Seiurus aurocapilla*, nidadas de mayor tamaño y más nidos, pero no encontramos efectos en características de los huevos. De modo similar, el estudio de 14 bosques del centro de Pensilvania basado en observaciones mostró una relación positiva entre los niveles naturales de calcio en el suelo y la densidad de territorios de *S. aurocapilla*, el tamaño de las nidadas y la densidad de nidos. De nuevo, no existió relación entre el calcio del suelo y características de la cáscara de los huevos. Los caracoles representan una fuente crítica de calcio para muchas aves reproductoras, y sospechamos que los caracoles son el vínculo entre suelos y aves porque la abundancia de caracoles aumentó con la adición de calcio y se correlacionó positivamente con el calcio presente en los suelos. Concluimos que la calidad del hábitat de *S. aurocapilla* está relacionada con el calcio del suelo, que las aves de nuestro sitio de estudio estaban limitadas por calcio y que los niveles reducidos de calcio en el suelo podrían jugar un papel importante en la disminución de poblaciones de aves en bosques acidificados.

[3]E-mail: sep195@psu.edu

The Auk, Vol. 128, Number 3, pages 441–447. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2011.10283

Several studies in Europe and North America have suggested links among soil acidification, soil calcium depletion, and reduced avian population sizes or impaired avian reproduction.[1,2,3] Birds may be particularly sensitive to soil calcium depletion because they require large amounts of calcium to successfully produce eggshells and raise young.[4,5] For example, to produce a single clutch of eggs, some small bird species require more calcium than is in their entire skeleton.[6] Small songbirds, which do not store much calcium for reproduction and do not have enough calcium in their normal diets to produce eggs, must rely on calcium-rich food supplements (particularly snails) at the time of reproduction.[5,7] The availability of snails is typically related to the availability of calcium in the soil, because snails require high levels of calcium to produce highly calcified exoskeletons and to reproduce.[3,8] In areas of Europe where acidic deposition has driven down snail abundance, songbirds have laid eggs with thin or even no eggshells.[3] Calcium has also been observed to limit clutch size, reproductive success, and skeletal development of chicks.[9,10]

Understanding the relationships between forest songbirds and soil calcium availability is of great importance in the northeastern United States, where decades of acidic deposition and forest harvesting and aging have resulted in chronically acidified forest soils with depleted calcium availability.[11,12,13] The majority of forested lands in the northeastern United States have naturally acidic soils that are sensitive to acid inputs and receive high levels of acidic atmospheric deposition.[14] Approximately 17% of U.S. forest soils exceed critical acidic deposition loads, with the greatest concentration of acidified forests in the Northeast.[15] In a previous study,[1] we reported preliminary results of a large-scale soil-liming experiment conducted, in part, to determine whether songbird abundance and breeding performance were related to soil calcium availability. We observed a positive response in bird abundance (all species) to liming 3 years after calcium addition, but we did not observe effects of liming on territory size, density, or breeding performance of the focal species, the Ovenbird (*Seiurus aurocapilla*). We hypothesized that, given more time, we would observe positive responses by Ovenbirds to liming and the increased availability of calcium-rich food, and thus we returned 2 years later to test our hypothesis. We also tested the hypothesis that Ovenbird abundance and breeding performance would be related to soil calcium availability across a natural soil-calcium gradient.

Although forest soils in the northeastern United States have low and declining levels of calcium availability and experience high levels of acid deposition, the severe reproductive anomalies that have been observed in acidified areas of Europe[3] have not been seen in North American birds.[16] Nonetheless, some evidence suggests that habitat quality of forest songbirds—and, consequently, their abundance—may be restricted by soil calcium availability.[2,17] However, we lack knowledge of the mechanism(s) by which low and declining soil calcium is related to declines in bird abundances. Potential mechanisms include either reduction of calcium needs by reducing reproductive output or enlargement of territory size (and consequent drop in population density) to provide a sufficient supply of calcium-rich foods for eggshell production and for feeding nestlings.

In the present study, we quantified the relationship between soil calcium and Ovenbird population parameters and breeding performance on experimental and observational plots. Ovenbirds are Nearctic–Neotropical migrants that breed throughout northeastern forests.[18] They forage on forest-floor invertebrates, the abundance and distribution of which are typically linked to soil condition. Ovenbird nests are also accessible because they are located on the ground.[18,19] We hypothesized that birds in acidified forests are calcium-limited and that bottom-up processes of nutrient availability influence Ovenbird populations. Consequently, forests with higher soil calcium availability should provide better habitat for Ovenbirds via greater availability of calcium-rich food to support egg production. Thus, we predicted increases in reproductive output and eggshell thickness, and decreases in territory size, in response to observed increases of soil calcium and snail abundance that followed our liming treatment. In addition, in areas that varied naturally in soil calcium availability, we predicted higher reproductive output, thicker eggshells, and smaller territories in areas with higher soil calcium. Although many factors can influence bird territory size,[20] we predicted—on the basis of our hypothesis of calcium limitation and relationships between habitat quality and calcium availability—that calcium availability would be a strong driver of both bird density and territory size.

Calcium Manipulation

We conducted a liming experiment at four 100-ha forest sites in central Pennsylvania. We measured Ovenbird territory size and quantified breeding performance in 2008 and compared the data with our observations made before (2003) and for 3 years after (2004–2006) dolomitic limestone sand was applied to two of the four sites.[1] Lime was applied at 4,500 kg ha^{-1} using a modified log skidder.[1] We evaluated the effect of liming using the confidence intervals around a time × treatment interaction parameter in a before–after control–impact analysis.[21] Liming successfully increased soil calcium and snail abundance.[1] For details on methods, see our earlier study.[1] Results are presented as means ± SE.

We observed a positive effect of liming on territory density, but no effect on territory size (Fig. 1). Territory density increased by 0.15 ± 0.02 territories ha^{-1} on limed sites from before liming to 5 years after, whereas no change occurred on control sites (0.04 ± 0.04 change in territories ha^{-1}). New territories were formed within areas on limed sites that were previously unoccupied, resulting in an increase in territory density without a decrease in territory size (Fig. 2).

We used the number of nests found in each 100-ha site over the entire season by S.E.P., the primary individual to locate nests in all years, as a proxy of nest density (nest density index). Using this measure, we observed a positive effect of liming on the nest density index (Fig. 1). The nest density index did not change from before liming to 5 years after liming on control sites (0.05 ± 0.13 change in number of nests) but increased sevenfold on limed sites (0.38 ± 0.09 change in number of nests).

We also observed larger clutch sizes on limed sites. Comparisons were restricted to nests completed before 15 June (to limit the sample to first nests of the season) and were made by comparing nests from limed and unlimed sites because we did not find enough nests at each site in every year to support a year-by-year analysis. Modal clutch size at both limed and control sites was 5 eggs, but 6-egg clutches were observed only on limed sites (Fig. 3), and overall mean clutch size was larger on limed sites (Table 1). We

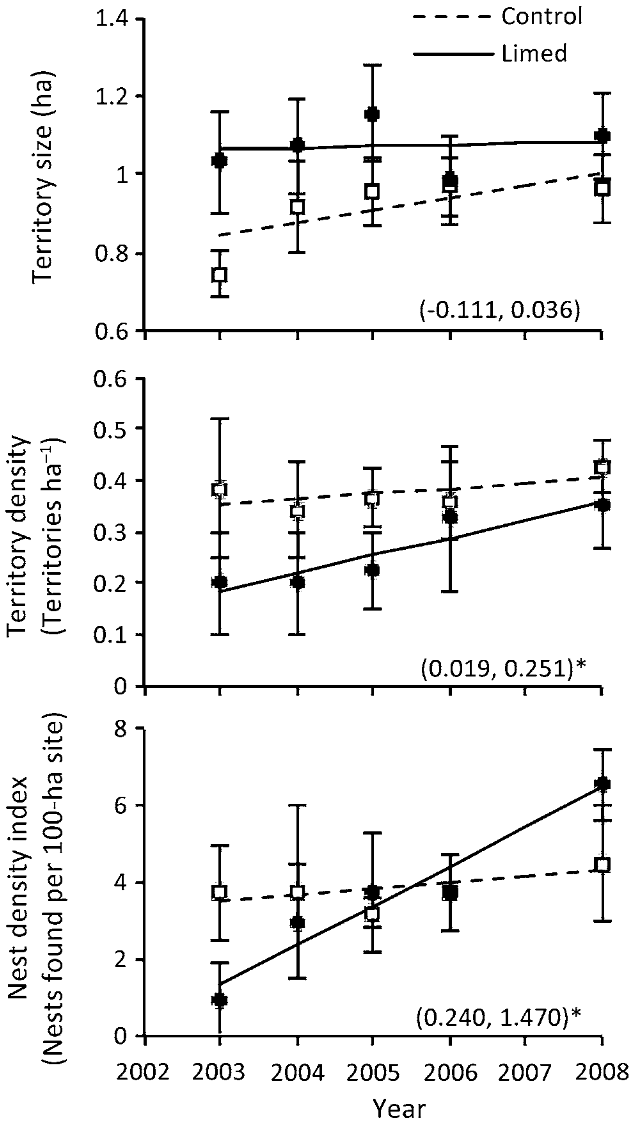

Fig. 1. Ovenbird territory size, territory density, and nest density index (number of nests found by one common observer per 100-ha site, ± SE) for each year on control (open squares) and lime-treated (closed circles) sites with model lines and the confidence intervals for the time × treatment interaction parameter to indicate the fit of the model to the data. Treatment was applied between 2003 and 2004. Differences in the slope of the model lines from 2003 (before liming) to 2008 (after liming) on limed compared with control sites indicate an effect of liming on that variable, as measured using the time × treatment interaction. Asterisk indicates confidence intervals (in parentheses) of the time × treatment interaction that excluded zero and thus indicated a significant effect of liming on that variable.

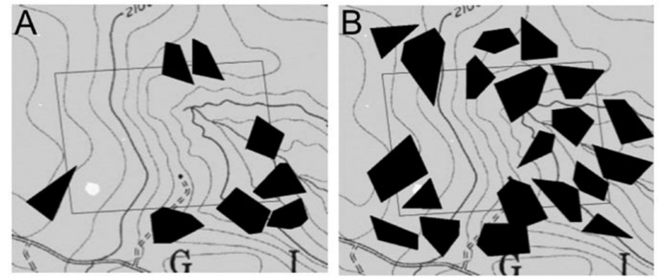

Fig. 2. Ovenbird territories on a lime-treated site in Pennsylvania (A) in 2003, before lime application; and (B) in 2008, 5 years after lime application. Polygons represent individual Ovenbird territories, and the rectangle represents the 30-ha gridded area used for mapping territories.

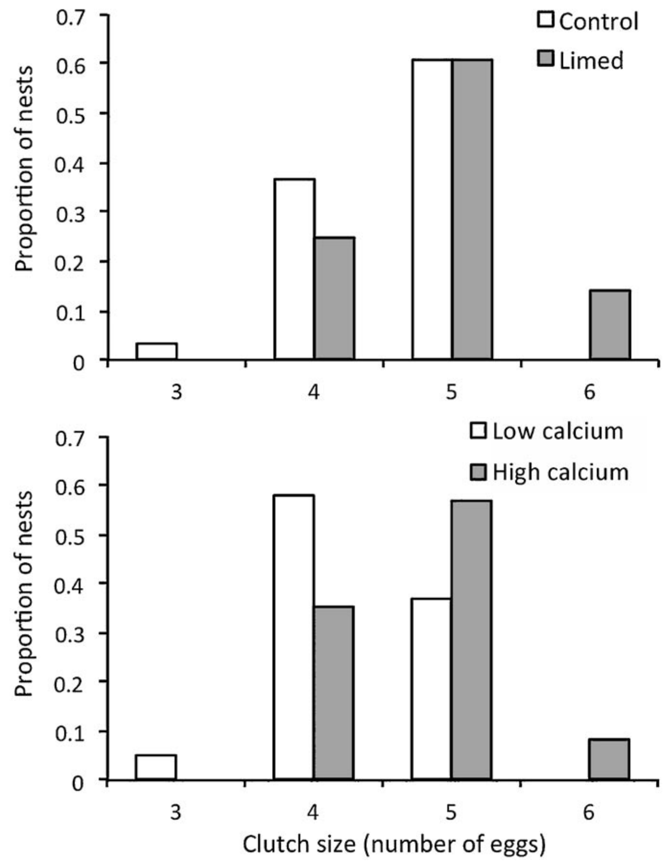

Fig. 3. Proportion of Ovenbird nests found in the early breeding season (before 15 June) with each clutch size on control (n = 33) and lime-treated (n = 28) sites during the years after liming (2004, 2005, 2006, and 2008), and on seven low-soil-calcium (<7.0 meq Ca per 100 g; n = 19) and seven high-soil-calcium (>8.9 meq Ca per 100 g; n = 37) sites in 2006, 2007, and 2008, in Pennsylvania.

observed no differences in egg size, shell thickness, or shell mass between limed and control sites in the years after liming (Table 1). Nest success (survival of eggs and nestlings to fledging) did not differ substantially between limed (Mayfield nest success = 0.44; 95% confidence interval [CI]: 0.31–0.63) and unlimed (0.31; 95% CI: 0.19–0.51) sites.

Observational Study

We conducted an observational study at fourteen 100-ha forest sites throughout central Pennsylvania. We chose seven sites located on bedrock with a limestone component as "high-calcium"

Table 1. Differences in Ovenbird clutch size and egg measurements from nests found early in the season (before 15 June) between control and lime-treated sites in all years after liming (2004, 2005, 2006, and 2008) and between seven low-soil-calcium (<7.0 meq Ca per 100 g) and seven high-soil-calcium (>8.9 meq Ca per 100 g) sites in 2006, 2007, and 2008 in Pennsylvania. Ninety-five percent confidence intervals [CIs] are in parentheses; asterisks denote CIs that exclude zero, indicating a difference between the two groups.

(A) Experimental study

	Control		Limed		
	Mean ± SE	*n*	Mean ± SE	*n*	Difference
Clutch size	4.58 ± 0.10	33	4.89 ± 0.12	28	–0.32 (–0.63 to –0.01)*
Egg length (mm)	20.26 ± 0.22	23	20.20 ± 0.21	20	0.06 (–0.56 to 0.68)
Egg width (mm)	15.56 ± 0.10	23	15.72 ± 0.18	20	–0.16 (–0.58 to 0.25)
Shell thickness (μm)	71.10 ± 1.10	23	68.81 ± 1.66	20	2.29 (–2.24 to 6.81)
Shell mass (g)	0.131 ± 0.003	23	0.128 ± 0.003	20	0.003 (–0.005 to 0.012)

(B) Observational study

	Low calcium		High calcium		
	Mean ± SE	*n*	Mean ± SE	*n*	Difference
Clutch size	4.32 ± 0.13	19	4.73 ± 0.10	37	–0.41 (–0.75 to –0.08)*
Egg length (mm)	20.23 ± 0.16	19	20.43 ± 0.22	36	–0.20 (–0.75 to 0.34)
Egg width (mm)	15.65 ± 0.11	19	15.68 ± 0.09	36	–0.03 (–0.32 to 0.25)
Shell thickness (μm)	68.74 ± 1.21	18	67.34 ± 0.97	37	1.40 (–1.74 to 4.54)
Shell mass (g)	0.135 ± 0.004	18	0.134 ± 0.002	36	0.001 (–0.008 to 0.010)

sites (mean = 14.6 ± 2.0 meq Ca per 100 g; range: 8.9–23.4) and seven sites located on bedrock without a limestone component as "low-calcium" sites (mean = 6.2 ± 0.3 meq Ca per 100 g; range: 5.3–7.0). We visited sites for an equivalent number of days to collect data on Ovenbird territory size and breeding performance. We also calculated the proportion of territories with nests, the date of clutch initiation for the earliest nest, and the mean number of nests found in territories with nesting Ovenbirds. Because Ovenbirds raise a single brood each year and nest success did not differ between low- and high-calcium sites (below), the number of nests per territory represents the propensity of females to renest following nest failure. Snail abundance was positively correlated with soil calcium ($r = 0.78$, $P < 0.001$). Four of the 14 sites were defoliated by Gypsy Moth (*Lymantria dispar*) larvae during the study. Gypsy Moth defoliation can affect the abundance of breeding birds, so we added a Gypsy Moth term to the statistical models.[22]

We observed positive relationships between soil exchangeable calcium and Ovenbird territory density, nest density index, proportion of territories with nests, and number of nests found in each territory with nesting birds (Fig. 4). We observed negative relationships between soil calcium and territory size and the date of clutch initiation for the earliest nest (Fig. 4). We found between 1 and 23 nests at each site. Because we found few nests at most of our low-calcium sites, we compared sites on the basis of bedrock geology for nest and egg analyses. We observed larger clutch sizes at the high-calcium sites than at the low-calcium sites for nests completed before 15 June (Table 1 and Fig. 3). As in the liming experiment, we observed no relationships between soil calcium and egg size, shell thickness, and shell mass (Table 1). Nest success did not differ between high-calcium (Mayfield nest success = 0.22; 95% CI: 0.14–0.34) and low-calcium (0.25; 95% CI: 0.13–0.47) sites.

Discussion

The increase in territory density and clutch size in response to our addition of calcium to soils demonstrates causality and establishes that soil calcium is an important determinant of Ovenbird habitat quality. Our experimental results are supported by the relationships between calcium availability and both territory density and clutch size under natural conditions in the observational study. We used territory density and size, as well as reproduction, as indicators of habitat quality because density alone can be a misleading indicator of habitat quality and reproductive potential.[23] Because Ovenbird habitat quality was positively related to soil calcium, depletion of soil calcium by acid deposition could potentially negatively affect Ovenbird abundance and productivity. This conclusion, which is likely applicable to other Nearctic–Neotropical migratory songbirds breeding in eastern forests, provides strong support for the conclusions of the indirect, correlative studies that identified a link between high levels of acid deposition and declining forest songbird abundances in North America.[2,17]

Our results and those of other studies suggest that snail availability was an important link between soil calcium and Ovenbird territory density and breeding performance.[1,3] Increases in snail availability could directly affect clutch size and the probability that females produced clutches by increasing the calcium in bird diets. Indirectly, increased snail availability could make the tradeoff between acquiring calcium-rich and energy-rich food

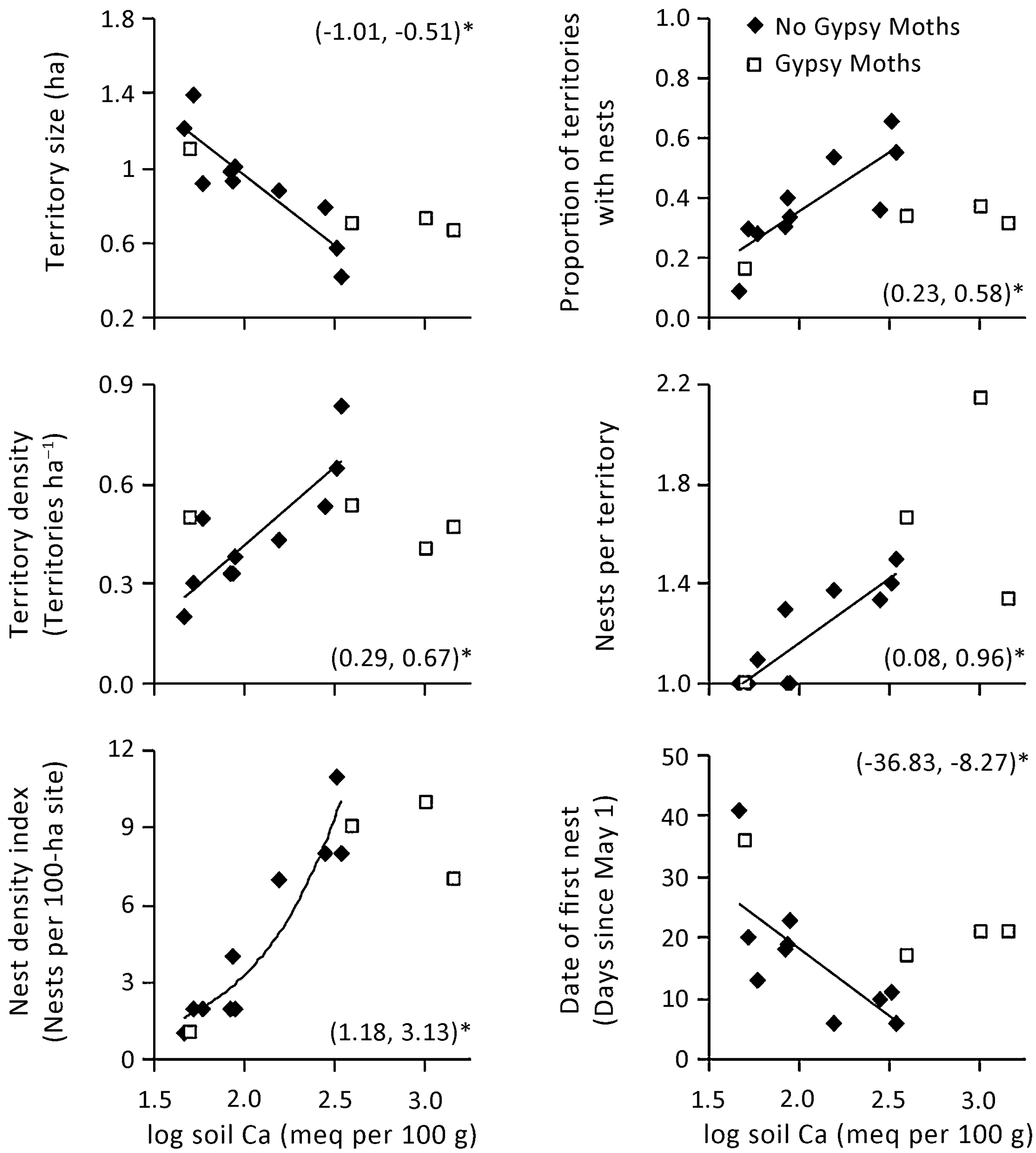

FIG. 4. Relationships between soil calcium and Ovenbird territory size, territory density, nest density index (number of nests found by one common observer per 100-ha site), proportion of territories with at least one nest, mean number of nests found within territories with nesting Ovenbirds, and the date that we observed the first nest with one egg at 14 sites across central Pennsylvania (2006–2008). Model lines were calculated using the 10 sites not defoliated by Gypsy Moths. The 95% confidence intervals (CIs; in parentheses) for the slope parameter estimates are included in each graph for model evaluation. Asterisk indicates that the CI excluded zero and therefore indicated a significant relationship of a variable with soil calcium (or snail abundance).

more manageable, giving females the opportunity to acquire more energy, or other resources, for reproduction. We also observed increases in bird densities with increased soil calcium, which indicates a likely indirect effect of calcium availability. Potentially, the increase in population and individual productivity could result in greater recruitment in future years. Also, if birds are using habitat variables related to soil calcium to evaluate habitat quality, these indicators would result in more bird territories. In the observational study, many habitat features changed with soil calcium, including snail abundance and vegetative characteristics that Ovenbirds could use to evaluate habitat quality. In the liming study, however, we observed very little change in vegetation (S. E. Pabian unpubl. data), which suggests that, of the variables that we measured, snails were the most likely mechanism for changes in Ovenbird abundance and reproduction.

More fertile soils usually have higher productivity, as measured by the yield in crops or timber that a soil can support. Similarly, for forest songbirds, fertile soils with more calcium were more productive. The addition of limestone sand increased soil calcium availability by approximately 2.3-fold,[1] which resulted in a 1.8-fold increase in Ovenbird territory density and 1.1× larger clutch sizes. If we assume similar nesting success (as we documented) and renesting rates, the increase in territory density and clutch size yielded twice as many young from experimentally limed plots as from control sites. Extrapolating from the observational study produced a similar conclusion. Given the 0.05 territories ha^{-1} increase in territory density for every 10% increase in natural soil calcium, and 9.5% larger clutch sizes on high-calcium sites, we would expect a 2.82-fold difference in productivity between our lowest (5.3 meq Ca per 100 g) and our highest-calcium site (without Gypsy Moths; 12.6 meq Ca per 100 g). Further, renesting rate is higher in areas with higher soil calcium, potentially making the difference even greater. The predicted increases in productivity are also based on the assumption that survival of young is equal once they have fledged, but other research has shown that birds supplemented with calcium often produce larger fledglings[24] and that larger fledglings often exhibit higher first-year survival.[25] Higher potential recruitment of young fledged from sites with more calcium available would magnify the difference in productivity between low- and high-calcium sites.

Surprisingly, we observed evidence of calcium limitation without observing thin eggshells. Although thin eggshells were one of the most extreme warning signs of the negative effects of acid deposition on forest birds in Europe,[3] researchers have failed to find evidence of severe reproductive anomalies in the acidified forests of North America[16,26] and in other studies across northeastern forests.[27,28,29] Like other North American studies, our study found no evidence of thin eggshells, even in low-calcium forests with some of the highest levels of acid deposition in the country and soil calcium levels comparable to those in Europe, where thin eggshells were observed.[1,3,25] We found no relationships between any eggshell measurements and calcium availability and actually observed some of the thickest eggshells from sites with the lowest soil calcium levels.

A potential mechanism that explains low bird abundance without thin eggshells in areas with extremely low soil calcium is that bird species studied in North America simply forgo reproduction when they cannot find enough calcium. We found nests in a lower proportion of territories at sites with low soil calcium, possibly because some pairs did not reproduce or because some males did not attract mates. Birds may compensate for thin eggshells by using protoporphyrin pigmentation to strengthen thin eggshells.[30] However, a preliminary examination of Ovenbird eggshell pigmentation yielded no evidence for relationships between the density or size of pigmented patches and soil calcium or eggshell thickness (S. E. Pabian unpubl. data).

Although we observed no relationships between soil calcium availability and eggshell thickness, we found a strong trend toward thinner eggshells at our sites with high soil calcium. Similarly, Taliaferro et al.[16] observed a trend toward thinner eggshells in Black-throated Blue Warblers (*Dendroica caerulescens*) nesting in a northeastern U.S. forest with higher natural availability of soil calcium. Although counterintuitive, it is important to note that the extremely low frequency of hatching failure that we detected (<1% of eggs) suggests that even the thinnest eggshells in our study were thick enough to avoid reproductive problems. Ovenbirds on sites with low calcium started laying eggs later in the season and rarely laid a replacement clutch if the initial attempt failed. Potentially, females at low-calcium sites responded to the low availability of dietary calcium by delaying initial egg laying in order to find enough resources to reproduce and invest more in their eggs because it was their only attempt for the season. By contrast, at sites with higher soil calcium, we observed earlier dates of first nesting and up to three renesting attempts by females whose previous nests failed. Potentially, females at these sites responded to the high availability of dietary calcium by investing slightly less calcium in their eggs because they had the opportunity and nutritional resources to renest.

In conclusion, Ovenbird habitat quality was linked to soil calcium availability and there is now experimental evidence that calcium limitation exists in forest songbirds in North America. The positive responses of territory density and clutch size to liming provided evidence of strong bottom-up control of avian population processes in a nutrient-depleted forest. Our finding that birds can be calcium-limited without displaying obvious reproductive problems, in contrast to what has been observed in Europe,[10] suggests the possibility that effects of calcium limitation on other avian species of eastern forests may be widespread but go undetected because of their subtle effects. Our results provide strong, experimental evidence to support the correlations observed by James et al.[17] and Hames et al.[2] of low or declining populations of forest songbirds in acidified forests in North America. We therefore posit that reductions in soil calcium, in addition to habitat loss and fragmentation, are contributing to declines in the abundance of songbirds in acidified forests.

Acknowledgments

We thank W. Sharpe and W. Tzilkowski for advice and support. We thank the many field assistants involved in this project. Funding was provided by the Pennsylvania (PA) Wild Resource Conservation Program and the PA State University Agricultural Experiment Station. Liming was funded by the PA Department of Environmental Protection through an Environmental Stewardship and Watershed Protection grant to PA State University. Use of field sites was permitted by the PA Department of Conservation and Natural Resources and the PA Game Commission. Please see the Supplementary Online Material for details about field and analytical methods (dx.doi.org/10.1525/auk.2011.10283).

Literature Cited

1. Pabian, S. E., and M. C. Brittingham. 2007. Terrestrial liming benefits birds in an acidified forest in the Northeast. Ecological Applications 17:2184–2194.
2. Hames, R. S., K. V. Rosenberg, J. D. Lowe, S. E. Barker, and A. A. Dhondt. 2002. Adverse effects of acid rain on the distribution of the Wood Thrush *Hylocichla mustelina* in North America. Proceedings of the National Academy of Sciences USA 99:11235–11240.
3. Graveland, J., R. van der Wal, J. H. van Balen, and A. J. van Noordwijk. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. Nature 368:446–448.

4. Reynolds, S. J., and C. M. Perrins. 2010. Dietary calcium availability and reproduction in birds. Pages 31–74 *in* Current Ornithology, vol. 17 (C. F. Thompson, Ed.). Plenum Press, New York.
5. Graveland, J., and T. van Gijzen. 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. Ardea 82:299–314.
6. Graveland, J. 1995. The quest for calcium: Calcium limitations in the reproduction of forest passerines in relation to snail abundance and soil acidification. Ph.D. dissertation, Netherlands Institute of Ecology, Centre for Terrestrial Ecology, The Netherlands.
7. Pahl, R., D. W. Winkler, J. Graveland, and B. W. Batterman. 1997. Songbirds do not create long-term stores of calcium in their legs prior to laying: Results from high-resolution radiography. Proceedings of the Royal Society of London, Series B 264:239–244.
8. Hotopp, K. P. 2002. Land snails and soil calcium in central Appalachian mountain forests. Southeastern Naturalist 1:27–44.
9. Tilgar, V., R. Mand, and M. Magi. 2002. Calcium shortage as a constraint on reproduction in Great Tits *Parus major*: A field experiment. Journal of Avian Biology 33:407–413.
10. Tilgar, V., R. Mänd, I. Ots, M. Mägi, P. Kilgas, and S. J. Reynolds. 2004. Calcium availability affects bone growth in nestlings of free-living Great Tits (*Parus major*), as detected by plasma alkaline phosphatase. Journal of Zoology (London) 263:269–274.
11. Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. BioScience 51:180–198.
12. Adams, M. B., J. A. Burger, A. B. Jenkins, and L. Zelazny. 2000. Impact of harvesting and atmospheric pollution on nutrient depletion of eastern US hardwood forests. Forest Ecology and Management 138:301–319.
13. Hamburg, S. P., R. D. Yanai, M. A. Arthur, J. D. Blum, and T. G. Siccama. 2003. Biotic control of calcium cycling in northern hardwood forests: Acid rain and aging forests. Ecosystems 6:399–406.
14. National Atmospheric Deposition Program. 2010. NADP Program Office, Illinois State Water Survey, Champaign. [Online.] Available at nadp.sws.uiuc.edu.
15. McNulty, S. G., E. C. Cohen, J. A. Moore Myers, T. J. Sullivan, and H. Li. 2007. Estimates of critical acid loads and exceedances for forest soils across the conterminous United States. Environmental Pollution 149:281–292.
16. Taliaferro, E. H., R. T. Holmes, and J. D. Blum. 2001. Eggshell characteristics and calcium demands of a migratory songbird breeding in two New England forests. Wilson Bulletin 113:94–100.
17. James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. Ecology 77:13–27.
18. Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). *In* The Birds of North America, no. 110 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
19. van Straalen, N. M., and H. A. Verhoef. 1997. The development of a bioindicator system for soil acidity based on arthropod pH preferences. Journal of Applied Ecology 34:217–232.
20. Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: The role of habitat structure. Ecology 68:695–704.
21. McDonald, T. L., W. P. Erickson, and L. L. McDonald. 2000. Analysis of count data from before–after control–impact studies. Journal of Agricultural, Biological, and Environmental Statistics 5:262–279.
22. Gale, G. A., J. A. DeCecco, M. R. Marshall, W. R. McClain, and R. J. Cooper. 2001. Effects of gypsy moth defoliation on forest birds: An assessment using breeding bird census data. Journal of Field Ornithology 72:291–304.
23. Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
24. Dawson, R. D., and M. T. Bidwell. 2005. Dietary calcium limits size and growth of nestling Tree Swallows *Tachycineta bicolor* in a non-acidified landscape. Journal of Avian Biology 36:127–134.
25. Garnett, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. Ibis 123:31–41.
26. Mahony, W., E. Nol, and T. Hutchinson. 1997. Food-chain chemistry, reproductive success and foraging behavior of songbirds in acidified maple forests of central Ontario. Canadian Journal of Zoology 75:509–517.
27. Duguay, J. P., P. Bohall Wood, and J. V. Nichols. 2001. Songbird abundance and avian nest survival rates in forests fragmented by different silvicultural treatments. Conservation Biology 15:1405–1415.
28. Martin, T. E. 2004. BBIRD: Breeding Biology Research and Monitoring Database. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.
29. Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source–sink dynamics. Ecological Applications 15:1504–1514.
30. Gosler, A. G., J. P. Higham, and S. J. Reynolds. 2005. Why are birds' eggs speckled? Ecology Letters 8:1105–1113.

Associate Editor: M. T. Murphy