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Landscape acidification has trophic-mediated effects on Ovenbirds (*Seiurus aurocapilla*)

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ABSTRACT—Acid deposition from fossil fuel combustion caused calcium depletion in eastern North America during the 20th century, and calcium is a critical resource for birds during both the egg laying and nesting periods. The effects of acid deposition on animals have largely acted through trophic relationships, with reduced calcium availability in prey possibly being a limiting factor for forest songbirds. Following 21 years of experimental whole-watershed acidification at the Bear Brook Watershed in Maine, we investigated Ovenbird (*Seiurus aurocapilla*) territory size and potential prey (leaf litter arthropod) abundance, assemblage, and calcium concentration during one breeding season. We delineated and estimated the area of 8 Ovenbird territories in an acidified and a control watershed, but found that territory size did not differ between watersheds. However, while calcium concentrations of potential prey also did not differ between watersheds, territory size decreased as calcium concentrations of potential prey increased, regardless of watershed. Our results suggest that calcium limitation can be a determinant of territory size in some landscapes, and this provides further support to importance of the role of calcium in the lives of passerines. *Received 17 June 2020. Accepted 1 October 2021.*

Key words: acid deposition, breeding ecology, calcium, nutrient limitation, trophic interactions.

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La acidificación del paisaje tiene efectos tróficamente mediados en el chipe *Seiurus aurocapilla*

RESUMEN (Spanish)—La deposición de ácido producto de la quema de combustibles fósiles causó pérdidas de calcio en el este de Norteamérica durante el siglo veinte y el calcio es un recurso crítico para las aves durante los periodos de puesta de huevos y anidación. En su mayoría, los efectos de la deposición de ácido en animales han operado por medio de relaciones tróficas, donde una reducción en la disponibilidad de calcio en sus presas es posiblemente un factor limitante para aves canoras de bosque. Siguiendo 21 años de acidificación experimental de toda la cuenca en la Bear Brook Watershed en Maine, investigamos el tamaño del territorio y la abundancia, ensamble y concentración de calcio de las presas potenciales (artrópodos de la hojarasca) del chipe *Seiurus aurocapilla* durante una temporada reproductiva. Delineamos y estimamos el área de 8 territorios de este chipe en una cuenca acidificada y una cuenca control, pero encontramos que el tamaño del territorio no difiere entre éstas. Sin embargo, aunque las concentraciones de calcio de sus presas potenciales tampoco difieren entre cuencas, el tamaño de territorio decreció mientras que la concentración de calcio de presas potenciales se incrementó independientemente de la cuenca. Nuestros resultados sugieren que la limitación de calcio puede ser una determinante de tamaño de territorio en algunos paisajes y esto provee mayor soporte a la importancia del calcio en la vida de las paserinas.

Palabras clave: calcio, deposición de ácido, ecología de la reproducción, interacciones tróficas, limitación de nutrientes.

Effects of acid deposition from fossil fuel combustion on ecosystems came to the forefront of society's ecological consciousness in the latter half of the twentieth century (Lynch et al. 2000). Although anthropogenic acid deposition has since declined, its effects may persist for years into the future. The leaching of base cations from soils led to calcium deficiency and impaired physiological processes (Fernandez et al. 2003). Habitat changes and trophic relationships have also been altered, resulting in impaired organismal development and changes to populations and communities (Graveland and van der Wal 1996).

Birds require large amounts of calcium during reproduction and development for eggshells and chick growth, respectively (Barclay 1994). Unsurprisingly therefore, calcium deficiency has been linked to a suite of negative effects on bird reproduction and their populations. Decreased calcium in adult diets results in thinner eggshells (Graveland and Berends 1997, Reynolds 2001), while in chicks calcium deficiency reduces skeletal growth (Johnson and Barclay 1996, Dawson and Bidwell 2005). Clutch size, recruitment, and fledgling mass have all been positively correlated with soil calcium content (Wilkin et al. 2009). Over 90% of the calcium needed for eggshell formation is consumed within breeding territories during the egg-laying period in some passerines (Graveland and Berends 1997), and nestlings that receive calcium supplements grow faster, although this faster growth may be a result of a trade-off in parental foraging for calcium-rich versus calorically dense items (Dawson and Bidwell 2005). The reported effects of modern acidification on clutch sizes, however, have been mixed, with studies reporting delayed clutch initiation, smaller clutch sizes, and no effect (e.g., Johnson and Barclay 1996, Reynolds 2001, Dawson and Bidwell 2005, Mulvihill et al. 2008). Arthropods common in temperate passerine diets contain inadequate calcium to meet physiological demands during breeding, while calcium-rich but rarer dietary arthropods (woodlice and millipedes), as well as snail shells, may represent the majority of calcium consumed by some passerines (Dawson and Bidwell 2005, Pabian and Brittingham 2007).

The majority of the impressive body of work linking songbird reproduction to soil calcium, however, has relied on correlations between calcium and bird characteristics within large regions affected by industrial pollution. There has been little experimentation at the landscape level, and what has been done has involved calcium addition (liming), not acidification (Pabian and Brittingham 2007, 2011). Further, the studies by Pabian and Brittingham (2007, 2011) on Ovenbirds (*Seiurus aurocapilla*) reported effects of calcium availability on reproduction weaker than other studies, which suggests that other mechanisms might be in play for at least some of the strong correlational evidence reported by others. Here, we take advantage of a watershed-scale acidification experiment to compare the breeding behavior and prey base of a migratory songbird in 2 watersheds that were initially selected for their ecological similarity. One of these landscapes was treated bimonthly with ammonium sulfate for over 2 decades prior to this study. To our knowledge, this represents the first study of calcium effects on songbird reproduction in an acidification experiment with 2 carefully matched and adjacent landscapes.

Like Pabian and Brittingham (2007), we measured the breeding behavior and foraging base of Ovenbirds, which are territorial, forest-dwelling, ground-nesting, and ground-feeding Neotropical migrants that are common breeding birds in eastern North America and feed on a variety of leaf litter insects, including Coleoptera, Lepidoptera, and Diptera (Stenger 1958, Holmes and Robinson 1988). Male Ovenbirds establish territories upon arrival at breeding sites for feeding, mating, and nesting (Stenger and Falls 1959). Social cues, predation risk, habitat structure, and past reproductive performance all may play roles in territory selection (Smith and Shugart 1987).

Territory size can also be an index of foraging success, and as such may be sensitive to calcium availability if it is important for reproduction (Pérot and Villard 2009). We predicted that territories in the acidified landscape would be larger if acidification limited the ability of Ovenbirds to provide their offspring with adequate calcium. Territories of Louisiana Waterthrush (*Parkesia motacilla*) along acidified streams were almost twice as long, often disjunct, and more likely to be occupied by younger males than territories along circumneutral streams (Mulvihill et al. 2008). In contrast, the liming experiment of Pabian and Brittingham (2007, 2011) did not report any effects on Ovenbird territory size, but described higher territory densities in landscapes with supplemental calcium.

Here, we investigate the effects of acid deposition on Ovenbirds in a landscape with 2 paired watersheds, one a control and the other experimentally acidified. First, we mapped Ovenbird territories and tested for differences in territory size between acidified and control watersheds. Second, we determined the abundance, assemblage structure, and calcium concentration of leaf litter arthropods that could be prey for territorial Ovenbirds. Together this represents the first landscape-scale experimental test of acidification on songbird reproduction with controls selected for ecological similarity prior to acidification.

Methods

Our field study was conducted at the Bear Brook Watershed in Maine (hereafter BBWM; 44.86°N, 68.11°W), which consists of 2 adjacent watersheds that were originally similar in biotic and abiotic characteristics (Norton et al. 1999). From November 1989 through the summer of this study (2010), one watershed (West Bear) was treated with ammonium sulfate bimonthly while the East Bear watershed remained as a control. Total ammonium sulfate additions to West Bear were 25.2 kg N ha^{-1} yr^{-1} and 28.8 kg S ha^{-1} yr^{-1} (Fernandez et al. 2003), mimicking areas that had received high levels of acid deposition. Ammonium sulfate additions resulted in the loss of calcium and other base cations from the soils of West Bear and less base cation uptake and retention by vegetation (Fernandez et al. 2003). Ammonium sulfate additions at BBWM ended in August 2016.

From 14 May to 17 July 2010 we conducted spot mapping (International Bird Census Committee 1970) of Ovenbird territories at BBWM from ~0500 to 1000 h. A total of 389 song posts were mapped. Territories that were completely within East Bear or completely off of both watersheds were considered non-acidified, control territories ($N = 4$), while those on West Bear were acidified territories ($N = 3$). One territory was situated on the border of both watersheds and was considered a mixed territory and excluded from the categorical (acidified vs. control) territory analyses. We produced 2 minimum convex polygon (MCP) estimates: one that excludes song posts disconnected from the core of a territory (MCP1) and a second, less conservative method, that includes those points (MCP2). We tested for differences in mean territory area between watersheds using mixed effects models with watershed as a fixed effect and visits (number of days males were recorded at each territory) as a random effect fit by maximum likelihood with the Satterthwaite method. Further details on territory mapping methods are provided in the Supplement. We also tried to monitor nestling growth but did not find sufficient nests to assess differences statistically (see Supplement).

We investigated the abundance, community composition, and calcium concentration of available prey (arthropods, with a focus on Coleoptera) from within known territories during July, after the observed start of chick provisioning (mid-June, see Supplement). Full arthropod methods are described in the Supplement. We tested for differences in calcium concentrations of adult Coleoptera between watersheds using a *t*-test. We also tested for a relationship between territory area (using both estimate methods) and calcium availability using mixed effects models and the calcium concentration of Coleoptera adults (the most commonly captured arthropod >0.5 cm in length) from the territory in which they were collected, with the number of territory mapping visits included as a random effect fit by maximum likelihood with the Satterthwaite method. We initially included adult Coleoptera abundance as a covariate in this analysis, but it was not significant and was dropped from the model.

Table 1. (a) Means and standard errors of raw territory areas (square meters) of Ovenbirds nesting in Bear Brook Watershed, Maine, in 2010, controlling for number of visits (LS means) in the control and acidified watersheds for both MCP methods employed (see text). *F* and *P* values are for mixed effects analyses on log-transformed territory area with mapping effort (number of observer visits) as a random effect. Degrees of freedom = 1,6. (b) Means and standard errors of calcium concentrations (mg Ca per kg of dry body mass) of adult Coleoptera and calcium concentrations for aggregate groups of Coleoptera larvae, Diptera larvae, and Geophilomorpha in control and acidified watersheds, with *F* and *P* values for the mixed effects analysis on calcium concentrations in adult Coleoptera. Degrees of freedom = 1,3.

	Control		Acidified			
Area method	Mean	SE	Mean	SE	*F*	*P*
(a) Area						
Raw (m^2)						
MCP1	3,255.9	914.2	4,947.1	1,114.1		
MCP2	5,343.7	1,750.7	5,475.2	1,260.6		
LS means						
MCP1	8.18	0.30	8.34	0.36	0.86	0.39
MCP2	8.75	0.27	8.40	0.27	<0.01	0.96
(b) Calcium (mg/kg)						
Coleoptera adults	580	67	560	92	0.04	0.86
Coleoptera larvae	3,753		2,778			
Diptera larvae	3,252		2,625			
Geophilomorpha	12,872		5,046			

Results

Eight territories were found and monitored: 4 control, 3 acidified, and 1 on both watersheds (Supplemental Fig. S1). Raw (unadjusted) territory areas are in Table 1a. Controlling for the number of days males were observed, territory area did not differ between watersheds (Table 1a). Further, we found no differences in arthropod abundance, community structure (Supplemental Table S1), or mean calcium concentrations of Coleoptera adults between watersheds (Table 1b). When controlling for territory mapping effort, Ovenbird territory area was significantly inversely related to calcium concentration in adult Coleoptera for both MCP methods (Fig. 1; MCP1: $F_{1,6} = 97.6$, $P < 0.0001$; MCP2: $F_{1,6} = 7.5$, $P = 0.03$). Associated data have been deposited online in Figshare (Pintar and Olsen 2021).

Discussion

Responses by animals to acidification are largely an indirect effect through habitat changes and trophic relationships (Graveland and van der Wal 1996). We experimentally investigated the potential for landscape acidification to have trophic-mediated effects on insectivorous Ovenbirds. We found no differences in arthropod abundances, community structure, or Ovenbird territory size (a potential index of foraging quality) between the acidified and control watersheds. However, territory size was inversely correlated with the calcium content of the most abundant invertebrate potential prey species within them (Fig. 1): larger territories contained prey with lower calcium concentrations.

Although leaf litter arthropod abundances and assemblages did not differ between watersheds,

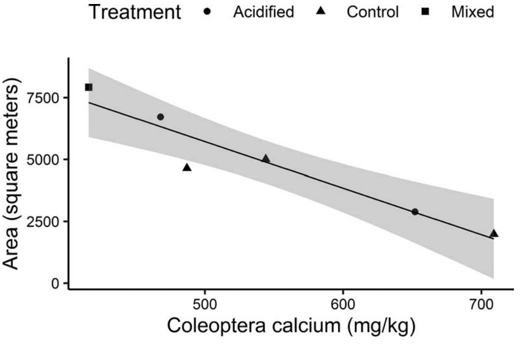

Figure 1. Estimated Ovenbird territory area vs. calcium concentration in adult Coleoptera from Bear Brook Watershed, Maine, in 2010. Territory area determined using the minimum convex polygon of the core territory (MCP1). Points indicate whether territories were on the experimentally acidified watershed, the control watershed, or on both watersheds (mixed).

our leaf litter samples were not representative of Ovenbird diets reported in the literature (Stenger 1958, Holmes and Robinson 1988); notably missing from our samples were Lepidoptera, because they are not leaf litter insects. Pitfall samples of the forest floor invertebrate community at BBWM from the previous summer (2009) did show trophic shifts in abundance of some of the same orders we report here (J. Wharff, unpubl. data). Coleopterans were also the most common larger taxa (>2 mm length) for that study. Wharff's samples were taken randomly across each watershed, irrespective of bird territories, whereas our samples only represent the subset of the landscapes occupied by Ovenbirds. Certainly, the precise placement of territories is one way birds can ameliorate larger-scale habitat variability, although we did not test that explicitly here.

Arthropod calcium concentrations did not statistically differ between watersheds (Table 1b), but the calcium concentration of coleopteran adults was inversely related to Ovenbird territory size (Fig. 1). Coleoptera typically account for only small portions of Ovenbird diets (~4%: Stenger 1958, Holmes and Robinson 1988). We hypothesize that Coleoptera calcium load is an index of calcium availability across the food web within the territory, and their relationship with Ovenbird territory size is most likely due to the net calcium availability across more commonly eaten items. The calcium needs of breeding birds, for example, would much more easily be met by Geophilomorpha, which gram-for-gram in our measurements contained ~7–31 times more calcium than adult Coleoptera (although we did not sample them frequently enough to estimate their concentrations by bird territory). Birds often rely on calcium-rich items to meet their requirements, and Geophilomorpha have been reported as occasional prey items of Ovenbirds (Stenger 1958). If coleopteran calcium concentrations are an index of calcium in these or other prey items, we suggest that males increased the defended area of their territories to meet the base cation needs of themselves, their mates, and their offspring.

Overall, Ovenbird territory sizes did not differ between watersheds, and territory size was tightly correlated with coleopteran calcium concentration (Fig. 1)—i.e., the most commonly sampled prey item in both watersheds for both this study and an unpublished sampling effort (J. Wharff). This suggests that calcium limitation may be a determinant of Ovenbird territory size in some landscapes, particularly those that may be of marginal quality. These results add further experimental support to the wider body of research that calcium availability plays an important role in the lives of passerines. Anthropogenic acid deposition has had a clear effect on base cation concentrations in soils, waters, and plants in forests of the northeastern United States, and we expect that the loss of nutrients like calcium has affected, and may continue to affect, breeding birds and other animals in these forests through complex trophic interactions.

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Literature cited

Barclay RMR. 1994. Constraints on reproduction by flying vertebrates: Energy and calcium. American Naturalist. 144:1021–1031.

Dawson RD, Bidwell MT. 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.

Fernandez IJ, Rustad LE, Norton SA, Kahl JS, Cosby BJ. 2003. Experimental acidification causes soil base-cation depletion at the Bear Brook Watershed in Maine. Soil Society of America Journal. 67:1909–1919.

Graveland J, Berends AE. 1997. Timing of the calcium intake and effect of calcium deficiency on behaviour and egg laying in captive Great Tits, *Parus major*. Physiological Zoology. 70:74–84.

Graveland J, van der Wal R. 1996. Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. Oecologia. 105:351–360.

Holmes RT, Robinson SK. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin. 100:377–394.

International Bird Census Committee. 1970. Recommendations for an international standard for a mapping method in bird census work. Bird Study. 16:249–255.

Johnson LS, Barclay RMR. 1996. Effects of supplemental calcium on the reproductive output of a small passerine bird, the House Wren (*Troglodytes aedon*). Canadian Journal of Zoology. 74:278–282.

Lynch JA, Bowersox VC, Grimm JW. 2000. Acid rain reduced in eastern United States. Environmental Science & Technology. 34:940–949.

Mulvihill RS, Newell FL, Latta SC. 2008. Effects of acidification on the breeding ecology of a stream-dependent songbird, the Louisiana Waterthrush (*Seiurus motacilla*). Freshwater Biology. 53:2158–2169.

Norton SA, Kahl JS, Fernandez IJ, Haines T, Rustad LE, et al. 1999. The Bear Brook Watershed, Maine (BBWM), USA. In: Norton SA, Fernandez IJ, editors. The Bear Brook Watershed in Maine: A paired watershed experiment. Dordrecht (Netherlands): Springer; p. 7–51.

Pabian SE, Brittingham MC. 2007. Terrestrial liming benefits birds in an acidified forest in the Northeast. Ecological Applications. 17:2184–2194.

Pabian SE, Brittingham MC. 2011. Soil calcium availability limits forest songbird productivity and density. Auk. 128:441–447.

Pérot A, Villard MA. 2009. Putting density back into the habitat-quality equation: Case study of an open-nesting forest bird. Conservation Biology. 23:1550–1557.

Pintar MR, Olsen BJ. 2021. Data from: Landscape acidification has trophic-mediated effects on Ovenbirds (*Seiurus aurocapilla*). Figshare. https://doi.org/10.6084/m9.figshare.16646092

Reynolds SJ. 2001. The effects of low dietary calcium during egg-laying on eggshell formation and skeletal calcium reserves in the Zebra Finch *Taeniopygia guttata*. Ibis. 143:205–215.

Smith TM, Shugart HH. 1987. Territory size variation in the Ovenbird: The role of habitat structure. Ecology. 68:695–704.

Stenger J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk. 75:335–346.

Stenger J, Falls JB. 1959. The utilized territory of the Ovenbird. Wilson Bulletin. 71:125–140.

Wilkin TA, Gosler AG, Garant D, Reynolds SJ, Sheldon BC. 2009. Calcium effects on life-history traits in a wild population of the Great Tit (*Parus major*): Analysis of long-term data at several spatial scales. Oecologia. 159:463–472.