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# Effects of acidification on the breeding ecology of a stream-dependent songbird, the Louisiana waterthrush (*Seiurus motacilla*)

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## SUMMARY

1. We compared breeding ecology of the Louisiana waterthrush (*Seiurus motacilla*) on acidified and circumneutral streams in the Appalachian Highlands of Southwestern Pennsylvania from 1996 to 2005.
2. Headwater streams impacted by acid mine drainage and/or acidic precipitation showed reduced pH (range 4.5–5.5) compared to four circumneutral streams (pH *c.* 7). Acid-sensitive taxa, including most mayflies (Ephemeroptera), were almost completely absent from acidified streams, whereas several acid-tolerant taxa, especially stonefly (Plecoptera) genera *Leuctra* and *Amphinemura*, were abundant.
3. Louisiana waterthrush breeding density (*c.* 1 territory $km^{-1}$) was significantly reduced on acidified streams compared to circumneutral streams (>2 territories $km^{-1}$). Territories on acidified streams were almost twice as long as on circumneutral streams. Territories usually were contiguous on circumneutral streams, but they were often disjunct on acidified streams. Breeding density declined on one acidified stream that we studied over a 10-year period.
4. Clutch initiation was significantly delayed on acidified streams, on average by 9 days in comparison to circumneutral streams, and first-egg dates were inversely related to breeding density. Birds nesting along acidified streams laid smaller clutches, and nestlings had shorter age-adjusted wing lengths. Stream acidity had no effect on nest success or annual fecundity (fledglings/female). However, the number of young fledged $km^{-1}$ was nearly twice as high on circumneutral streams as on acidified streams.
5. Acidified streams were characterized by a younger, less site-faithful breeding population. Individuals were less likely to return multiple years to breed, allowing inexperienced breeders to settle on acidified streams. Pairing success was lower on acidified streams, and we observed four cases of waterthrushes emigrating from territories on acidified streams to nearby circumneutral streams in the following year.
6. We conclude that acidified headwaters constitute lower quality habitat for breeding Louisiana waterthrush. However, breeding birds can apparently compensate for reduced prey resources to fledge young on acidified streams by increasing territory size, foraging in peripheral non-acidified areas, and by provisioning young with novel prey.

*Keywords*: habitat quality, productivity, riparian, *Seiurus motacilla*, stream acidification

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## Introduction

Acidification of freshwater ecosystems from anthropogenic causes is a major ecological problem worldwide. Reduced pH in streams occurs from several causes, including abandoned mine drainage (Herlihy *et al.*, 1990; Earle & Callaghan, 1998), and acidic precipitation (Schindler, 1988; Herlihy *et al.*, 1993). Drainage from mines is a direct and localized contaminant; in contrast, acid precipitation from rain and snowfall impacts entire regions. But the acidity of a stream may be affected by local differences in soils and bedrock which can neutralize some acid inputs. In addition, streams can be impacted by past acid precipitation events because continued leeching of acidic compounds from the soil can and do affect forest and stream ecosystems for many years (Likens, Driscoll & Buso, 1996; Hames *et al.*, 2002; Kowalik *et al.*, 2007). Estimates suggest that about one-fifth of streams in the northern Appalachian region of the U.S.A. are acidic, with about half of these due to abandoned mine drainage and half from acid precipitation (Herlihy *et al.*, 1990, 1993).

Headwater streams comprise two-thirds of the linear reach of major catchments and, therefore, are critically important to their ecological integrity (Freeman, Pringle & Jackson, 2007). Effects of acidification on wildlife have been found to occur through shifts in trophic relationships (Schreiber & Newman, 1988). Many benthic macroinvertebrate species are acid-intolerant, and changes in species composition with acidification are well documented. Increased acidity shifts the macroinvertebrate community to a comparatively few acid-tolerant taxa with concomitant loss of a large number of acid-sensitive taxa, including most mayfly (Ephemeroptera) species (e.g. Rutt, Weatherley & Ormerod, 1990; Courtney & Clements, 1998; Guerold *et al.*, 2000). Insectivorous birds, which feed at higher trophic levels, can be negatively affected by changes in prey quality and quantity arising from effects of acid waters on macroinvertebrates (Graveland, 1998). Not only prey abundance, but the availability of key, calcium-rich prey, required for egg formation, also is affected (Ormerod *et al.*, 1991).

For example, the distribution and breeding density of the white-throated dipper (*Cinclus cinclus* Linnaeus) in Great Britain is inversely related to stream pH (Ormerod *et al.*, 1986; Vickery, 1991; Buckton *et al.*, 1998), and acidification has also been found to affect various aspects of dipper breeding ecology, including laying dates, clutch size, territory size and reproductive success (Ormerod *et al.*, 1988, 1991; O'Halloran *et al.*, 1990; Ormerod & Tyler, 1991a; Vickery, 1992). However, some other riparian birds are less affected by stream acidification, presumably because of a lower dependence on aquatic prey (Ormerod & Tyler, 1991b; Vickery, 1991).

The Louisiana waterthrush (*Seiurus motacilla* Viellot) is the only stream-dependent songbird in eastern North America. This forest-interior Nearctic-Neotropical migrant occupies linear territories along headwater streams where it depends primarily on aquatic macroinvertebrates for food (Robinson, 1995). Waterthrushes have been suggested as an important indicator of the ecological integrity of forested riparian ecosystems (O'Connell *et al.*, 2003; Mattsson & Cooper, 2006). They have been found to occupy streams with a prey biomass containing a higher proportion of mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera) (hereafter %EPT; Stucker, 2000; Mattsson & Cooper, 2006). The Louisiana waterthrush is considered a species of conservation concern and is listed as a priority species for several Bird Conservation Regions because of its dependence on a specialized habitat threatened by a number of environmental stressors (Rich *et al.*, 2004).

Our objective in this study was to examine how stream acidification affects Louisiana waterthrush population and breeding biology. We compared the ecology and reproductive success of Louisiana waterthrushes breeding on acidified and circumneutral streams over a 3-year period; and on two streams we studied the effects of acidification over a longer, 10-year period. Because ecology is closely linked to resource availability, and given the known negative impact of acid pollution on aquatic macroinvertebrates, we hypothesized that streams with reduced pH would constitute comparatively low quality habitat for breeding Louisiana waterthrush. We predicted that on acidified streams waterthrushes would: (i) breed at lower densities; (ii) have lower pairing and reproductive success and (iii) be less likely to return to the same stream in subsequent years.

 

## Methods

### *Study sites*

We monitored 2–3 km reaches of first and second order streams in the Ohio River Drainage in the Laurel Highlands of southwestern Pennsylvania. Our study streams were generally in close proximity (2–30 km apart) to one another. Long-term monitoring from 1996 to 2005 was conducted on two streams, Laurel Run (acidic) and Powdermill Run (circumneutral), both located at Powdermill Nature Reserve (PNR), a field station of the Carnegie Museum of Natural History (Westmoreland County). Six additional streams were monitored from 1998 to 2000, including the acidified (pH 4.5–5.5; Table 1) Linn Run (Westmoreland County), Gary's Run (Somerset County) and Jonathan Run (Fayette County), and the circumneutral (pH *c.* 7.0; Table 1) Camp Run (Westmoreland County), Roaring Run (Somerset County) and Blackberry Run (Fayette County). Passive treatment systems to reduce stream acidification, consisting of a Pyrolucite drain and a Successive Alkalinity Producing System (Gangewere, 1998), were installed to treat two point sources of acidic abandoned mine drainage on Laurel Run in autumn 1997. However, additional diffuse, untreated sources of abandoned mine drainage in the catchment, as well as region-wide acid precipitation, have impeded the recovery of Laurel Run, which remains acidic more than 10 years later.

**Table 1** Measures of water quality at spring base flow (mean ± SE) for forested headwater streams in southwestern Pennsylvania

| Stream | pH | Alkalinity (mg $L^{-1}$ $CaCO_3$) | Aluminum (mg $L^{-1}$) |
|---|---|---|---|
| Laurel Run* | 4.7 ± 0.0 | 0.0 ± 0.0 | 7.2 ± 0.0 |
| Linn Run† | 5.4 ± 0.2 | 2.2 ± 0.4 | 0.4 ± 0.0 |
| Gary's Run† | 5.0 ± 0.2 | 1.4 ± 0.3 | 0.4 ± 0.6 |
| Jonathan Run* | 4.5 ± 0.1 | 0.8 ± 0.1 | 2.1 ± 0.4 |
| Powdermill Run | 7.2 ± 0.0 | 18.0 ± 0.0 | <0.1 |
| Camp Run | 7.3 ± 0.1 | 17.1 ± 1.5 | 0.7 ± 0.6 |
| Roaring Run | 7.2 ± 0.1 | 12.9 ± 0.3 | <0.1 |
| Blackberry Run | 7.1 ± 0.2 | 20.6 ± 5.4 | 0.1 ± 0.0 |

Water samples ($n$ = 6) were collected from three points along the length of each stream in 1998–99.

*Acidification due primarily to point source pollution from acid mine drainage.

†Acidification due primarily to acidic precipitation.

All streams were located in contiguous forest (>80% forest cover in a 1 km radius). Mixed deciduous forest surrounding our study streams was characterized by American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.) and yellow poplar (*Liriodendron tulipifera* L.); some sites also had Eastern hemlock (*Tsuga canadensis* L.), black birch (*Betula lenta* L.) and yellow birch (*Betula alleghaniensis* Britton). Typical forest understorey species present at our sites included common spicebush (*Lindera benzoin* L.), witch hazel (*Hamamelis virginiana* L.) and striped maple (*Acer pensylvanicum* L.). The groundcover was largely dominated by fern species and a diversity of vernal woodland wildflowers.

### *Water quality and benthic macroinvertebrates*

On each study stream, water samples were collected in June 1998 and 1999 from the lower, middle and upper reaches of the stream during summer base flow for analysis of water chemistry. Results were averaged across years for the length of the study area. Based on water chemistry and known surrounding land use, acidic abandoned mine drainage was the dominant source of chronic acidification for two streams (Laurel Run and Jonathan Run), while the two other acidified steams (Linn Run and Gary Run) showed impacts of episodic acidification from acid deposition. In addition to lower pH levels, aluminum and sulfate levels tended to be elevated at the sites impacted by abandoned mine drainage (Table 1). Circumneutral streams were moderately to well buffered from episodic acidification due to region-wide acid precipitation.

We collected benthic macroinvertebrates from Surber samples in June 1997–99: the two streams at PNR were sampled 1 year; the other study streams were sampled in 2 years. Surber samples were taken from riffles at five stratified random stations along the length of each stream. Individual organisms within each sample were identified to genus, and totals were averaged across stations for each stream (Merritt & Cummins, 1996). Orders represented by >1000 individuals were summed separately, including mayflies, stoneflies, caddisflies and true flies (Diptera). Other macroinvertebrate orders were combined. We calculated the %EPT because the availability of these species has been shown to be correlated with Louisiana waterthrush occupancy (Stucker, 2000; Mattsson & Cooper, 2006).

*Louisiana waterthrush monitoring*

Study areas along each stream were marked with numbered stakes at 50-m intervals, and observations of Louisiana waterthrush were recorded relative to these markers. Waterthrushes on each study area were uniquely marked with a combination of two or three coloured celluloid and one serially numbered U.S. Fish and Wildlife Service ring. Adult waterthrushes were aged as second-year (i.e. <1 year old) or after second-year (>1 year old) based on wing molt limits and rectrix shape (Mulvihill, 1993; Pyle, 1997). Unflattened wing chord and body mass were measured at the time of ringing.

The majority of breeding males (87% across all years) and females (70%) were colour-ringed on our study streams, allowing us to examine population demographics on acidified and circumneutral streams across multiple years. We defined breeding waterthrush each year as either new recruits or returning individuals. By definition, known second-year birds could always be categorized both as new recruits and inexperienced breeders. After the first year of monitoring, we assumed that any other unringed individual arriving on the study stream was also a new recruit, regardless of its age. This included some error since unringed birds could also represent returning individuals that were not successfully ringed the previous year. However, few birds were likely to be erroneously categorized given the high proportion of colour-ringed birds and the observed level of site fidelity of breeding birds. Returning individuals were thus further grouped as either ringed on the same stream the previous year (single return), or ringed even earlier on the same stream (multiple returns). Because of low breeding densities on acidified streams, and because trends appeared to be generally similar between males and females, we pooled the sexes for demographic analysis of populations from acidified and circumneutral study sites.

Waterthrushes were observed on each stream every 1–3 days throughout the nesting period. Territory lengths were determined based on the span of observed upstream and downstream locations of singing and foraging colour-ringed individuals, as well as observed agonistic interactions between males occupying adjacent territories. Males that continued to sing throughout the breeding season, or that were never observed with a female or at a nest, were considered to be unpaired.

We attempted to document all nesting attempts of every waterthrush pair in our study areas through systematic searching of likely nesting sites and observation of adult waterthrush for behavioural cues. In our study reaches, based on the number of paired waterthrushes on territories, an estimated 90% of all nests were found. These were most often found during the nest building or incubation stages. Clutch initiation dates, if not directly known, were backdated from observed hatching or fledging dates, assuming a 13-day incubation period (beginning with the last egg laid) and a 10-day nestling period (Robinson, 1995). Nest contents were subsequently checked every 3–4 days to monitor egg and chick survival. Many nests were under almost daily observation from a blind for a related study of parental provisioning rates and nestling diet. Nestlings were uniquely colour-ringed when they were 7 to 10 days old. If hatching was not directly observed, the ages of nestlings were estimated based on laying dates, by backdating from fledging dates or based on developmental (e.g. feathering) stage (Eaton, 1958). For analysis, individual nestling measurements were standardized for age by subtracting the mean of the age at which the measurement was taken and dividing by the standard deviation for that age. With a mean of zero and standard deviation of one for each age, individual measurements were on the same scale as a relative difference from other individuals of the same age. Measurements could then be compared across ages (McCarty, 2001). Observations of ringed fledglings and/or of adults carrying food were used to confirm nesting success; nests were considered successful if at least one young fledged.

*Statistical analysis*

The software package R for Windows version 2.6.1 (R Development Core Team, 2007) was used to perform statistical tests. Data were tested for normality using Shapiro–Wilk normality tests and data were log-transformed when appropriate. Two-tailed *t*-tests with unequal variance were used to compare between groups. Linear regression was used to examine relationships between variables. Residual plots of the regression analysis were examined. Data presented are means ± SE values unless otherwise stated.

For count data we used a 2 × 4 contingency table with Fisher's exact test to compare between groups. Nest success was calculated according to the Mayfield method (Mayfield, 1975; Johnson, 1979). Differences between stream types were compared using a chi-squared test in the programme CONTRAST (Hines & Sauer, 1989). For all tests, we interpreted a $P \leq 0.05$ as representing a statistically significant difference or change; $0.10 > P > 0.05$ was interpreted as a marginally significant tendency.

## Results

We monitored a total of 18 km on eight study streams. We identified 55 territories on acidified streams and 152 territories on circumneutral streams. From 1996 to 2005, Louisiana waterthrush breeding density was significantly lower on acidified Laurel Run than circumneutral Powdermill Run ($t = -13.12$, $n = 20$, $P < 0.01$). Density declined significantly on the acidified stream ($r^2 = 0.56$, $P = 0.01$; Fig. 1), but did not decline on the circumneutral stream ($r^2 = 0.00$, $n = 10$, $P = 0.92$). From 1998 to 2000 breeding density on all acidified streams combined was lower, averaging 1.0 ± 0.1 territory $km^{-1}$ (range: 0.5–1.8), compared to 2.6 ± 0.2 territories $km^{-1}$ (range: 1.5–3.6) on circumneutral streams (1998: $t = -3.08$, $n = 8$, $P = 0.02$, 1999: $t = -3.00$, $n = 8$, $P = 0.03$ 2000: $t = -2.89$, $n = 8$, $P = 0.04$) (Fig. 2). However, density of territories was variable on circumneutral streams, and there was some overlap in breeding density, with two streams (Camp and Blackberry) supporting <2.0 territories $km^{-1}$ at least in some years. Territories for which

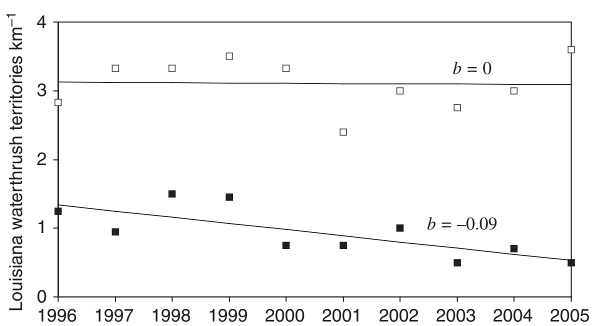


**Fig. 1** During a 10-year period Louisiana waterthrush breeding density remained consistently lower on acidified Laurel Run (solid squares) compared to circumneutral Powdermill Run (open squares). Density of breeding birds declined significantly on the acidified stream during this period.

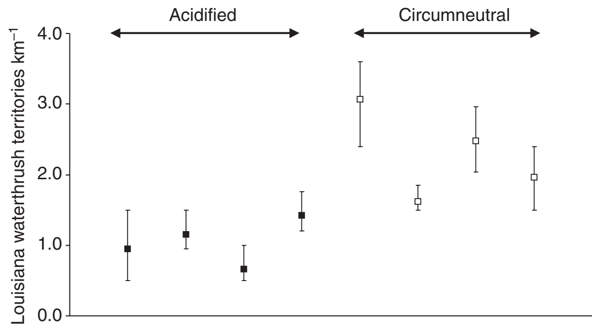


**Fig. 2** Mean (±SE) breeding density of Louisiana waterthrush on acidified (solid squares) and circumneutral streams (open squares) in southwestern Pennsylvania. Laurel Run and Powdermill Run were monitored 1996–2005; other streams were monitored 1998–2000.

approximate length was available averaged 630 ± 50 m ($n = 32$) on acidified streams, and 370 ± 10 m ($n = 88$) on circumneutral streams, and this was significantly different ($t = 4.56$, $n = 128$ $P < 0.01$). Territories were as small as 250 m on both stream types, but were ≥700 m only on acidified streams. Extensive areas were unoccupied on all acidified streams, but such occupancy gaps were rare on circumneutral streams.

Mean abundance of all macroinvertebrates on acidified streams was 184 ± 32 individuals $m^{-2}$ and was not significantly different from 195 ± 29 individuals $m^{-2}$ on circumneutral streams ($t = -1.03$, $n = 70$, $P = 0.30$). Mean biomass on acidified streams (62 ± 13 mg $m^{-2}$) was significantly less than on circumneutral streams (124 ± 21 mg $m^{-2}$; $t = -2.52$, $n = 60$, $P = 0.01$). Mayflies as a component of the macroinvertebrate community almost completely disappeared from acidified streams, whereas two stonefly genera, *Leuctra* and *Amphinemura* were especially abundant (Fig. 3). As a result, the overall %EPT did not change significantly ($t = 0.91$, $n = 15$, $P = 0.37$). Louisiana waterthrush breeding density was not related to overall %EPT ($r^2 = 0.00$, $n = 21$, $P = 0.97$), but there was a significant relationship between waterthrush breeding density and %EPT when *Leuctra* and *Amphinemura* stoneflies were excluded from the analysis ($r^2 = 0.68$, $n = 21$ $P < 0.01$; Fig. 4).

Laying commenced as early as 18 April during our study, and the date of laying in the first nest on each stream was significantly related to annual breeding density ($r^2 = 0.47$, $n = 37$, $P < 0.01$; Fig. 5). On circumneutral streams, laying in the earliest nest each year

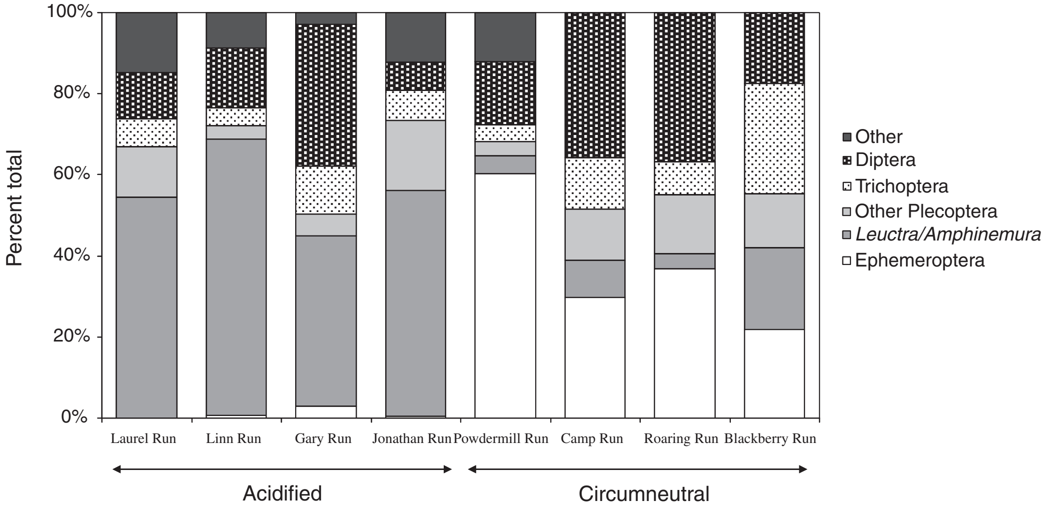


**Fig. 3** With moderate levels of stream acidification (4.5–5.5) acid-intolerant mayflies were replaced by two acid-tolerant stonefly genera, *Leuctra* and *Amphinemura*.

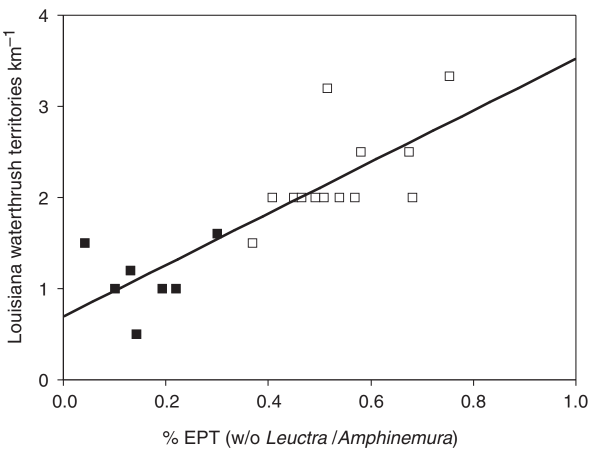


**Fig. 4** Breeding density of Louisiana waterthrush on acidified (solid squares) and circumneutral (open squares) streams was strongly related to %EPT in macoinvertebrate samples when two acid-tolerant stonefly genera were excluded.

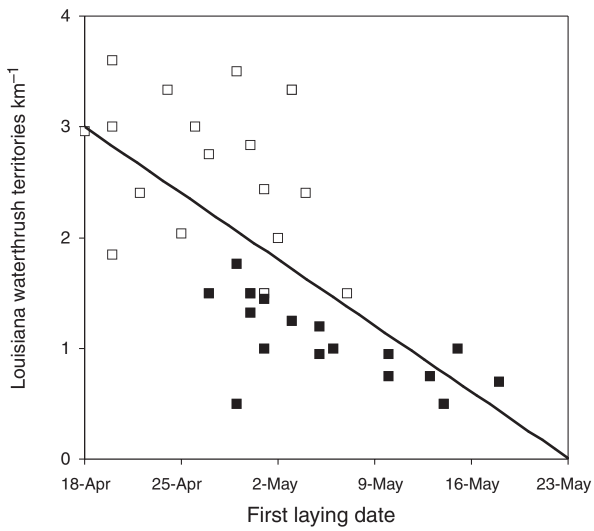


**Fig. 5** Louisiana waterthrush breeding density was significantly related to first laying dates on each stream in southwestern Pennsylvania, 1996–2005. The first nests on acidified streams (solid squares) averaged 9 days later than on circumneutral streams (open squares).

was initiated on average 26 April ± 1 day, 9 days earlier than on acidified streams, which averaged 5 May ± 2 days ($t = 3.99$, $n = 37$, $P < 0.01$). Laying dates for known first nesting attempts tended to be earlier on circumneutral streams (3 May ± 1 day) compared to acidified streams (5 May ± 1 day; $t = 1.83$, $n = 153$, $P = 0.07$).

Louisiana waterthrush typically lay five eggs (range 3–6). Average clutch size was smaller on acidified streams compared to circumneutral streams ($t = -2.03$, $n = 189$, $P = 0.04$; Table 2). On acidified streams no females laid clutches of six eggs compared to 6% of females on circumneutral streams. However, due to some combination of hatching failure and partial predation of clutches, there was no difference in mean brood size between nests on acidified and circumneutral streams ($t = -0.61$, $n = 130$, $P = 0.53$). Overall nest success varied among years (range 23–80%), but low breeding density on acidified streams did not allow us to compare success by year. When combined across years, nesting success did not

**Table 2** Louisiana waterthrush breeding on acidified streams in southwestern Pennsylvania 1996–2005 showed no change in nest success or annual fecundity

| | Acidified | Circumneutral |
|---|---|---|
| Daily survival estimate ± SE | 0.980 ± 0.005 | 0.973 ± 0.003 |
| Mayfield success (nests) | 57% (46) | 49% (146) |
| Exposure days | 738 | 2189 |
| Clutch size ± SE (nests) | 4.5 ± 0.1 (40) | 4.8 ± 0.1 (140)* |
| Brood size ± SE (nests) | 4.2 ± 0.1 (33) | 4.2 ± 0.1 (102) |
| Fecundity ± SE (territories) | 3.2 ± 0.3 (43) | 3.4 ± 0.2 (132) |
| Fledglings $km^{-1}$ ± SE | 2.6 ± 0.4 | 5.0 ± 0.4** |

However, females laid smaller clutches and fewer young were fledged on acidified streams (*$P$ < 0.05; **$P$ < 0.01).

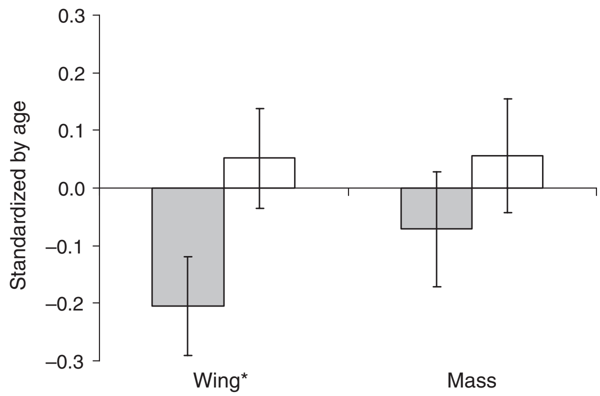


**Fig. 6** Mean (± SE) standardized wing chord and body mass for 7- to 10-day old nestling Louisiana waterthrush on acidified ($n$ = 112, gray bars) and circumneutral streams ($n$ = 359, white bars) in southwestern Pennsylvania, 1996–2005. Standardized wing chords were significantly shorter on acidified streams than on circumneutral streams (*$P$ < 0.05).

differ between acidified and circumneutral streams ($\chi^2$ = 1.44, d.f. = 1, $P$ = 0.23; Table 2), and fecundity was also not significantly different ($t$ = −0.603, $n$ = 176, $P$ = 0.54; Table 2). However, because of significantly lower breeding density, the number of young fledged $km^{-1}$ was significantly lower on acidified streams than on circumneutral streams ($t$ = −4.36, $n$ = 37, $P$ < 0.01; Table 2).

We found no evidence that Louisiana waterthrush adults breeding on acidified streams were smaller or in poorer condition than on circumneutral streams. There was no difference in wing chord or body mass for either males ($n$ = 153) or females ($n$ = 99) nesting on acidified streams compared to circumneutral streams (all $t$-tests: $P$ > 0.05). Standardized wing chord lengths of nestlings were significantly shorter on acidified streams than on circumneutral streams ($t$ = −2.52, n = 458, $P$ = 0.01), however, there was no difference in standardized body mass ($t$ = −1.12, $n$ = 471, $P$ = 0.26; Fig. 6).

The proportion of colour-ringed birds known to be site-faithful and/or experienced breeders was marginally different between acidified and circumneutral streams (Fisher's exact: $P$ = 0.07; Table 3). Acidified streams had a higher proportion of inexperienced recruits (second-year birds), and many fewer birds nesting on acidified streams returned to breed in multiple years. In contrast, circumneutral streams had fewer recruits overall, a smaller proportion of inexperienced recruits, and a higher proportion of birds returning to breed multiple years (Table 3). Thus, acidified streams were characterized by a younger, less site-faithful population compared to circumneutral streams. Several individuals were observed to disperse between study streams. Four colour-ringed birds emigrated from territories on acidified streams to territories on a circumneutral stream between years. A single bird dispersed from one circumneutral stream to another between years, and one bird moved from a circumneutral stream to an acidified stream in the same year, after losing its original territory following a territorial dispute early in the season.

**Table 3** Percentages of color-ringed Louisiana waterthrush on acidified ($n$ = 53) and circumneutral ($n$ = 148) streams in southwestern Pennsylvania, 1996–2005

| | Acidified (%) | | Circumneutral (%) | |
|---|---|---|---|---|
| | Males | Females | Males | Females |
| Inexperienced Recruits | 15 | 18 | 10 | 11 |
| Experienced Recruits | 18 | 4 | 12 | 11 |
| Returned Once | 18 | 18 | 18 | 14 |
| Returned Again | 6 | 3 | 16 | 8 |

On acidified streams more inexperienced breeders (known age < 1 year old) were recruited into the population compared to experienced birds (known age > 1 year old), and fewer birds returned to breed over multiple years.

There were marginally significant differences in pairing success between acidified and circumneutral streams (Fisher's exact test: $P$ = 0.07). Across all acidified streams and all years, 84% of males

($n$ = 55) were paired, while on circumneutral streams 92% ($n$ = 152) of males were paired. Unpaired males may contribute to a 'floating' or non-territorial population. Evidence for a population of 'floater' males comes from the bird-ringing programme at PNR where, from 1996 to 2005, 65% ($n$ = 29) of waterthrushes captured in the ringing station's suboptimal, non-forested habitat in May were male, and 65% ($n$ = 17) of these were young (second-year) birds (R.S. Mulvihill, unpubl. data).

## Discussion

Multiple measures, including lower breeding density, later first laying dates, lower site fidelity, an increased proportion of inexperienced breeders, and opportunistic movements from acidified to circumneutral streams all indicate that stream acidification negatively affects Louisiana waterthrush during the breeding season. Birds appear to occupy acidified streams only as secondary or suboptimal habitat when higher quality habitat is not available. Our results suggest that older or more experienced individuals may be excluding birds from circumneutral streams, consistent with the 'ideal-despotic' model of habitat selection (Fretwell, 1972).

Unexpectedly, we found no difference in reproductive success, daily nest survival estimates, or fecundity between pairs nesting on acidified and circumneutral streams. These observations tend to fit the 'ideal-free' model of habitat selection in which distribution occurs according to resource availability (Fretwell & Lucas, 1970). By decreasing breeding density, pairs appeared to be able to successfully raise young on acidified streams. Other studies have found similar increases in the number of inexperienced young birds in poor quality habitat where the breeding density may be lower and territories larger (Holmes, Marra & Sherry, 1996; Petit & Petit, 1996). In contrast, reduced productivity has been found in dippers breeding on acidified streams (Vickery, 1992). However, in our study, there could be additional costs to adults or young, such as reduced post-breeding survival, which we were unable to detect.

The fact that Louisiana waterthrushes can achieve reproductive success on acidic streams indicates that they are able to compensate for the reduced pH and its associated effects on food availability. One way they are able to compensate is by increasing territory size. The length of linear territories of several other riparian bird species has also been related to food availability (Davis, 1982; Vickery, 1991; Feck & Hall, 2004). Presumably with reduced food resources, a larger territory is needed to provide sufficient resources for maintenance and reproduction.

However, waterthrush pairs defending longer territories on acidified streams may incur additional costs. We did not test whether adults had to fly farther to obtain food, although given the size of their territories this would seem likely. Birds are likely to forage farther away from the nest when food is less available (Tremblay *et al.*, 2005), and dippers have been shown to spend more time foraging on acidified streams than on circumneutral streams (O'Halloran *et al.*, 1990). Formal and informal surveys of the conspicuous droppings of waterthrush, easily visible on exposed rocks and debris within the wetted stream channel, found much greater concentrations of droppings on circumneutral peripheral tributaries within the territories of birds nesting on acidified streams (Mulvihill, 1999). In addition, during protracted nest watches, we observed adults feeding young novel prey items (e.g. terrestrial salamanders) much more frequently at nests on acidified streams than on circumneutral streams (Mulvihill, 1999). Thus, waterthrushes nesting on acidified streams likely compensated for food shortages associated with lower quality habitat by foraging farther from their nests and by feeding their young larger prey items (see also Tremblay *et al.*, 2005).

Our finding that fecundity (i.e. number of fledglings per pair) did not vary significantly between Louisiana waterthrush pairs on acidified and circumneutral streams was somewhat surprising and may be due primarily to higher rates of nest predation on circumneutral streams. Along with waterthrushes, a variety of potential nest predators co-inhabit headwater streams and associated hardwood forests. These include species like raccoons (*Procyon lotor* L.) and mink (*Neovison vison* Schreber) that, like waterthrushes, also rely to some degree on aquatic prey, as well as corvids, raptors, squirrels and other rodents. Although we did not survey for them, such predators may be less abundant along acidified streams due to reduced prey availability. Lower rates of nest loss in acidified streams compared to circumneutral streams may also be due in part to the greater dispersion of waterthrush nests in these sites (Martin, 1993). If typical nest predators like corvids and rodents learn to search for nesting birds in systems where nests are more abundant, Louisiana waterthrush pairs nesting at higher densities along circumneutral streams may suffer an increased cost in terms of predation. This density-dependent pattern has been shown in numerous other studies (Stephens & Krebs, 1986; Kamil, Krebs & Pulliam, 1987).

Louisiana waterthrush depend predominantly on aquatic macroinvertebrates for food, both on their breeding and wintering grounds (Robinson, 1995). Our results suggest that reduced stream pH affects Louisiana waterthrush breeding ecology by altering the aquatic macroinvertebrate community. Although overall macroinvertebrate abundance and biomass were lower on some acidified streams, the most consistent difference was that acid-sensitive taxa, such as mayflies, almost completely disappeared from acidified streams and were replaced by two acid-tolerant genera of stoneflies, *Leuctra and Amphinemura*. This shift in the macroinvertebrate community has been previously documented to occur at similar pH-levels in the region (Kimmel *et al.*, 1985; Sharpe *et al.*, 1987; Griffith, Perry & Perry, 1995). In our study, density of breeding waterthrush was highly correlated with %EPT but only when these two acid-tolerant stoneflies were excluded from the analyses. Other studies have found that the presence of Louisiana waterthrush is correlated with %EPT (Stucker, 2000; Mattsson & Cooper, 2006), but our results further suggest that mayflies, in particular, may be especially important in the diet of breeding Louisiana waterthrush. Several dipper species (*Cinclus* spp.) that occupy a similar niche world-wide have also been found to consume a high percentage of mayflies when they are available (Ormerod & Tyler, 1991a), and density of breeding dippers has been correlated with favoured mayfly species (Feck & Hall, 2004).

Our results suggest that the effects of stream acidification on Louisiana waterthrush could be most directly linked to food shortages, especially of preferred prey. Results such as the smaller clutch size, as well as smaller nestlings, may be related to abundance of preferred, perhaps higher quality food resources (e.g. Arcese & Smith, 1988; Ormerod & Tyler, 1991a). However, similar effects can occur through calcium shortages (Tilgar, Mänd & Mägi, 2002). Acid precipitation has been associated with reduced calcium availability in soils and decreased abundance and lower nutritional value of many invertebrate prey species at pH levels below *c.* 6.5 (Scheuhammer, 1991). Crustaceans, mollusks or fish fry are likely the only source of calcium for egg-forming passerines along rivers, since they are unable to gain sufficient calcium when laying daily and feeding on insects (Ormerod & Rundle, 1998). For example, grey wagtail (*Motacilla cinerea* Tunstall) uses mollusks gleaned in the riparian zone, and this may be one of the key differences in flexible foraging that distinguishes its acid-tolerance from *Cinclus*. In another study, calcium supplementation resulted in swallow nestlings with longer feathers prior to fledging (Dawson & Bidwell, 2005).

Environmental changes associated with acid precipitation may reduce calcium in the environment, but can also affect breeding waterthrush through a potential increase in other toxic chemicals (Scheuhammer, 1991; Graveland, 1998; Hames *et al.*, 2002). In dippers, thinner egg shells and decreased levels of calcium in blood serum have been found in acidified areas (Ormerod *et al.*, 1988, 1991). Although we did not examine egg shell thickness or blood serum in Louisiana waterthrush, we found no evidence that adults were in poorer condition on acidified streams. Recent research suggests that waterthrush may be at risk from the effects of elevated levels of mercury (Evers *et al.*, 2005), but moderately elevated levels of mercury do not appear to affect reproduction in dippers (Henny *et al.*, 2005). In addition, some streams in this study, such as Camp Run, recorded slightly elevated levels of aluminum (Table 1). Whether aluminum levels have some responsibility for the consistently lower density of breeding waterthrush on this stream is unknown, but should be studied.

Our results show that Louisiana waterthrush breeding density tends to be lower on acidified streams, and reproductive output per unit area is very different between the two stream categories. In our study area it takes almost double the length of an acidified stream to produce the same number of fledglings as a circumneutral stream. The average density of 2.6 territories $km^{-1}$ observed for circumneutral streams in our study is similar to that found elsewhere in the northeastern U.S. (Robinson, 1995). Because of differences in breeding density related to stream pH, Louisiana waterthrush may provide an important indicator of stream acidification, similar to the white-throated dipper (Ormerod *et al.*, 1986; Vickery, 1991;

Buckton *et al.*, 1998). Our results support continued monitoring of this species as an indicator of water quality and biotic integrity of forested headwater streams (O'Connell *et al.*, 2003; Mattsson & Cooper, 2006). Louisiana waterthrush also occupy headwater streams in the Caribbean, Mexico, and Central America during the non-breeding season, where preliminary studies indicate that winter densities also may be influenced by habitat quality (Master *et al.*, 2003). Further work should examine the effects of stream habitat quality on the Louisiana waterthrush throughout its annual cycle.

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CONTENTS



FRONT COVER: A Louisiana waterthrush poised on a rock at the water's edge. Like dippers and wagtails, the waterthrush feeds extensively on the adult and immature stages of aquatic insects. Like other species that forage at the interface of land and moving water, the waterthrush 'bobs' its tail up and down continually as it forages. Its specific scientific name, *motacilla,* comes from the Greek and means moving or wagging tail – a scientific name that it shares with the true wagtails (Motacillidae). From Robert S. Mulvihill *et al.*, p.2158. The painting is an original watercolour by world renowned bird sculptor, Larry Barth.

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