LOUISIANA WATERTHRUSH ECOLOGY AND CONSERVATION IN THE GEORGIA PIEDMONT

by

BRADY JAMES MATTSSON

(Under the Direction of ROBERT J. COOPER)

ABSTRACT

Louisiana Waterthrushes (waterthrushes; *Seiurus motacilla*) are infrequently studied Neotropical migratory songbirds that breed throughout much of the southeastern U.S, which is undergoing rapid urbanization. They may serve as effective indicators of stream biotic integrity because of their dependence on riparian systems for food and nesting. Furthermore, waterthrushes are easier to survey than complex assemblages of fish and macroinvertebrates. While the relationships between anthropogenic disturbances in watersheds and the biotic integrity of streams is relatively well understood, little is known about birds as indicators of stream ecosystem health. In this study, I address two broad questions regarding linkages among land use, climate, macroinvertebrates, and waterthrush reproductive ecology: 1) How might waterthrushes serve as cost-effective indicators of stream biotic integrity? 2) What factors drive reproduction for individual waterthrushes?

Of the indicators considered, waterthrush occupancy and EPA Visual Habitat Assessment (VHA) together best predicted relative abundances of macrobenthic taxa, while the EPA VHA alone best predicted Ephemeroptera-Plecoptera-Trichoptera (EPT) richness. Using stream-dependent birds as warning signals for degradation of stream biotic integrity could improve the efficiency of watershed monitoring programs in detecting and identifying perturbations within the watershed.

Contrary to arguments that renesting determines reproductive success in passerines, our individual-based model indicated that waterthrush productivity increased only with increasing fledgling survival, daily nest survival, followed by nestling survival. Nest survival was greatest at intermediate levels of rainfall during the nesting period. Nestling survival increased in a linear fashion with increasing rainfall and with decreasing territory size. Fledgling site tenacity increased with decreasing understory cover. Relationships between waterthrush reproduction and other factors, including land use surrounding drainages, edge proximity, aquatic food availability, annual variation in climate, and timing of nesting were relatively weak.

To ensure suitable habitat for multiple, contiguous breeding waterthrush territories within headwater drainages, managers should maintain wide (>40 m) buffers of closed-canopy forest along a contiguous network of streams (>1.5 km). Agricultural land uses beyond such buffers might reduce waterthrush nesting success. In addition, moderate rainfall during spring months (3-8 mm day^{-1}) will likely lead to improved nesting success. Management practices that promote extensive networks of riparian buffers at landscape scales and that minimize the release of greenhouse gasses at a global scale may help ensure persistence of Louisiana Waterthrushes in the Georgia Piedmont.

INDEX WORDS: benthic macroinvertebrate, conservation, fecundity, forest, indicator, individual-based model, information-theoretic approach, Louisiana Waterthrush, mark-recapture, Neotropical migrant songbird, nest survival, nestling survival, Piedmont, rainfall, riparian, *Seiurus motacilla*, stream

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This project is dedicated to my parents

James and Laura Mattsson

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PREFACE

This dissertation includes four manuscripts at various stages ranging from in preparation to in print, and these are book-ended by an introduction and conclusion. The introduction is a revised version of my prospectus and provides the background, literature review, justification, and objectives for this research project. The first manuscript, "Detrimental impacts of radiotransmitters on juvenile Louisiana Waterthrushes," documents video evidence of adults removing transmitters from nestlings and is in press at the Journal of Field Ornithology. The second, "Louisiana Waterthrushes and habitat assessments as cost-effective indicators of instream biotic integrity," compares waterthrushes and visual habitat assessments as indicators of the stream benthic community and has been accepted with minor revisions by Freshwater Biology. The third, "Which life history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush," describes an individual-based model for estimating the variability in seasonal fecundity and is currently in review for publication in The Auk. The fourth, "Territory characteristics and climatic variability influence reproduction by a riparian obligate songbird, the Louisiana Waterthrush (Seiurus motacilla)," evaluates how habitat and temporal variables affect the crucial components of waterthrush reproduction, and I plan to submit this to Oecologia after incorporating comments from my committee. The final chapter provides a summary of my research findings, management recommendations, and potential for future research on Louisiana Waterthrushes.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Forested areas along rivers and streams (riparian ecosystems) harbor high biodiversity and serve many ecosystem functions such as mitigating flow of pollutants into the water and providing organic input to downstream ecosystems (Malanson 1993). Land use changes and water diversions within or near riparian areas alter natural flow regimes, leading to degradation of many aquatic ecosystems (Poff et al. 1997). While maintaining a vegetated zone along rivers may provide some protection to aquatic ecosystems (for review see Wenger 1999), modifications upstream within the drainage area may overwhelm the usefulness of these riparian buffer zones (Roth et al. 1996, Booth et al. 2002). Therefore, monitoring the health of stream ecosystems following modifications to the riparian zone and the surrounding drainage is critical for ensuring high water quality and persistence of stream and riparian biota.

Traditional Bioasessment

Biological assessment has been used extensively to evaluate water quality of streams and to detect aquatic degradation due to non-point source pollution (Yoder 1995). Indicators of ecological integrity in streams were originally developed for fish by Karr (1991). Invertebrates are now the most widely used indicators of stream water quality because they are ubiquitous, have sufficiently long life cycles to integrate the effects of disturbance, and respond to a range of environmental stresses (Rosenberg and Resh 1993). Tolerance indices (e.g., Lenat 1993) and multimetric indices (Kerans and Karr 1994) for invertebrates are available that can be used to assess water quality.

The use of aquatic invertebrates for bioassessment has some limitations. Sample processing can be laborious and workers qualified to classify an assortment of invertebrate taxa must be available. The metrics that have been developed are difficult for non-experts to interpret, and the general public does not connect emotionally with invertebrates. For example, a reduction in EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) is a valuable indicator of degraded water quality, but the measure means little to a lay audience. Macroinvertebrates best reflect microsite conditions such as substrate and stream velocity (Lammert and Allan 1999). Land uses within the drainage impact these microsite conditions (Roy et al. 2003), and therefore benthic macroinvertebrates indirectly reflect conditions within larger scales. Modest land uses (e.g., clearcuts, cattle grazing, low density housing) in well-buffered drainages may have little impact on the insect community (Wenger 1999). When impacts to the landscape and watershed are dramatic (e.g., urban sprawl), aquatic invertebrates remain a very useful indicator of system health (see Kennen 1999, Roy et al. 2003).

Birds as Integrative Indicators

Forest songbirds are potentially effective indicators of both stream water quality (Ormerod and Tyler 1993) and riparian buffer conditions (e.g., Kilgo et al. 1998). In addition, forest interior specialists are sensitive to landscape scale perturbations that lead to elevated nest predation and parasitism levels (Faaborg et al. 1995, Robinson et al. 1995). Furthermore, trained amateurs can readily identify focal taxa (e.g., Rosenberg et al. 1999). In a direct comparison of birds and invertebrates, Brown and Batzer (2001) found that birds were in some ways superior to invertebrates as bioindicators in wetlands, especially in terms of cost.

Louisiana Waterthrush as an Indicator of Stream Biotic Integrity

Louisiana Waterthrushes (waterthrushes; *Seiurus motacilla*) are forest-interior, Neotropical migratory songbirds that require streams for food and nesting sites (Robinson 1995). A large portion of their diet includes benthic macroinvertebrates, and their predominant foraging method is picking leaf packs while walking along rocks and other stable substrates in streams and floodplain wetlands (Craig 1987). They are the only breeding bird in the southeastern U.S. that requires forested streams. Waterthrushes possess many of the advantages of fish and invertebrate community bioindicators (Rosenberg and Resh 1993) and few of the disadvantages. Rather than conducting laborious laboratory work, trained amateurs can survey waterthrushes in the field (e.g., Rosenberg et al. 1999). The general public will better identify with a bird than invertebrates, and waterthrushes occupy headwater sections where many fish species are absent. Finally, because of their terrestrial lifestyle and larger home ranges, waterthrushes can serve as indicators of riparian ecosystem health (Brooks et al. 1998).

Before waterthrushes can be recommended as bioindicators, however, they must be shown to provide similar information at less cost or additional information as compared to other rapid assessments of stream health. Thus, I intend to evaluate the use of waterthrushes and visual habitat assessments as indicators of the benthic macroinvertebrate community to determine which of these measures can predict stream biotic integrity. I predict that habitat assessments in conjunction with waterthrush surveys may increase the overall efficacy of bioassessment.

Impacts on Waterthrush Reproduction

Anthropogenic land uses such as urbanization, cattle grazing, and silviculture within headwater drainages can have negative impacts on food, nest site availability, nest survival, dispersal abilities, and ultimately population sizes of Louisiana Waterthrushes in the Georgia Piedmont (Fig. 1.1). The human population in Georgia has grown 26 % between 1990 and 2000 (U. S. Census Bureau 2001). Urban developments are projected to further increase in Georgia as people migrate from outside the state to the Atlanta area, and these developments threaten the integrity of stream ecosystems.

In particular, sediment pollution reduces interstitial spaces for aquatic invertebrates (Wood and Armitage 1997), and may consequently reduce food availability for waterthrushes. Altered flow regimes can cause bank instability (Poff et al. 1997), which can lead to nest losses due to slumping (Stucker 2000) and waterthrush nest site limitation. Increases in edge habitat can lead to increases in avian predators and brood parasites (Donovan et al. 1997), which may reduce waterthrush fledging success. Edges that disconnect riparian corridors may limit waterthrush dispersal, as suggested for other forest songbirds (Machtans et al. 1996). These factors affecting waterthrush biology operate at multiple spatial scales, and therefore explicit treatment of scale is critical for understanding their impacts. The relative effects of habitat characteristics at different spatial scales on macroinvertebrates and Louisiana Waterthrushes has not been investigated.

Presence and abundance of a bird species *per se* may be a poor indicator of reproductive success, and hence habitat quality (e.g., Van Horne 1983). Louisiana waterthrushes may establish territories along streams with narrow riparian buffers in landscapes with high densities of avian predators, and consequently they may experience low reproductive success, low survival rates, and low dispersal abilities. While demographic data such as fecundity and survival are relatively difficult and expensive to obtain, they are necessary to answer questions involving conservation and management of songbird populations (Sherry and Holmes 2000).

For example, Donovan et al. (1995) developed a model using demographic data to predict population dynamics of Ovenbirds (*Seiurus aurocapillus*), a neotropical migratory ground-nesting songbird. The model predicted that Ovenbird populations in fragmented forests of the midwestern U.S. will become extinct within 20 years. In a similar fashion, negative effects of land use on waterthrush reproduction could lead to local extinctions.

To my knowledge, only two studies have investigated population dynamics of Louisiana Waterthrushes in different landscape contexts. Stucker (2000) reported that waterthrush nest predation rates were low but that brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) may create population sinks for waterthrushes in fragmented forests of southeastern Minnesota. Mulvihill (1999) reported some preliminary findings which showed reduced waterthrush breeding success in acidified (from strip mine runoff) compared with nonacidified streams in Pennsylvania. Results from that study have yet to be reported in full, but will provide critical information regarding influences of land use change on Louisiana Waterthrushes. My project differs from that study in that I examined the more widespread effects of rainfall, forest fragmentation, agriculture, and urbanization (non-point sources) on waterthrushes, whereas Mulvihill (1999) focused much effort on examining impacts of extreme water pollution from point sources (strip mines).

Study Region

I sampled headwater streams in or near Athens, Georgia (northern study area) and Piedmont National Wildlife Refuge (southern study area) north of Macon, GA (Fig. 1.2). These areas include three river basins in the southern Piedmont of Georgia and parts of the Oconee National Forest. The Upper Ocmulgee, Upper Oconee and Broad River basins are in the southwestern portion of the southern Piedmont, which extends from east-central Alabama through north-central Georgia, then northeast through western South Carolina and central North Carolina. The Piedmont of Georgia is characterized by rolling hills and predominantly acid crystalline and metamorphic rock. Presettlement vegetation consisted of pine-hardwood forest, and was cleared for agriculture and timber during the 1800's. Topsoil eroded from cleared fields and caused floodplains to fill with sediment and stream beds aggraded (Trimble 1974). Between the 1930's and the 1980's, cotton farms were abandoned following economic failure, and farmers moved to cities. As a result, urban land cover tripled from 1% to 3%, agricultural land cover decreased from 30% to 12%, and the remaining land was planted with loblolly pine or regenerated to pine-hardwood forest (Turner and Ruscher 1988).

Site Selection

In 2002, I identified stream networks that were forested >15 m on both sides from the headwaters throughout a >2.5 km reach as determined from 1993 digital orthophoto quadrangles (DOQQs; USGS 1995), which were the most recent DOQQs available at the time. A 1999 Landsat TM image was classified into forested and non-forested cover types in the study area using an unsupervised classification method in ERDAS IMAGINE (1997). This reclassified image was used to estimate percent forest within 500 m of potential stream networks. I then randomly selected stream networks stratified by percent forest to ensure an equal number of streams in landscapes ranging from fragmented to contiguous forest. Of the original chosen sites, nine were discarded by insistence of the land managers for reasons such as conflicts with spring turkey hunting. Several sites were also discarded because of recent disturbances to the drainage network such as road crossings and dams. Of the surveyed sites, 29 were chosen regardless of land ownership in the northern study area and 20 were on public lands in the southern study area. Of the 29 northern sites, timber companies managed seven, independent individuals managed 16, the U.S. Forest Service (USFS) managed five, and a timber company and the USFS co-managed one of the surveyed drainages. These sites had varying amounts of forest, pasture and recent clearcuts within the surrounding landscape. Field assistants surveyed each drainage once between sunrise and 4 hr after sunrise from 24 March through 9 April 2002. These observers conducted a 5 min point count every 250 m along the channel, recording locations and behaviors of waterthrushes both during and between point counts. I used results from these surveys to obtain an index of waterthrush abundance.

In 2002, I selected ten streams in ten different drainages for intensive study on waterthrush reproductive ecology (Fig. 1.2). To ensure sufficient sample sizes, only drainages with ≥ 1.5 waterthrush males km^{-1} of stream length were considered that year (Fig. 1.3, Fig. 1.4). These drainages were chosen to represent some of the human developments occurring in the region that can impact stream health and waterthrush ecology. A 30-m resolution, 1998 Georgia land cover database was used to determine the dominant land use type (e.g., pasture, forest, silviculture) within 500 m of streams within each drainage (NARSAL 2002). I selected two drainages in each of the following categories: 1) a single, unmaintained culverted road crossing with forested uplands, 2) forested uplands where clearcuts will be applied during fall and winter of 2002-2003, 3) agricultural uplands with cattle access to the stream, 4) forested uplands with no road crossings, and 5) uplands clearcut during 2001. We monitored these ten drainages intensively from 2002-2005. For 2004 and 2005, we added two additional drainages that were dominated by urban land uses beyond the 15 m buffer and contained some road crossings.

Research Questions

There are established relationships between anthropogenic disturbances in watersheds and the biotic integrity of streams (Allan et al. 1997). However, the linkages among land uses, macroinvertebrates, and the reproductive ecology of Louisiana Waterthrushes are unclear (Fig. 1.1). To fill these gaps in knowledge, I addressed the following questions regarding Louisiana Waterthrushes and riparian systems in the Georgia Piedmont:

1) How well can waterthrushes serve as cost-effective indicators of stream biotic integrity?
2) Which life history components determine reproduction for individual waterthruhses?
3) What environmental factors drive these crucial components of reproduction?

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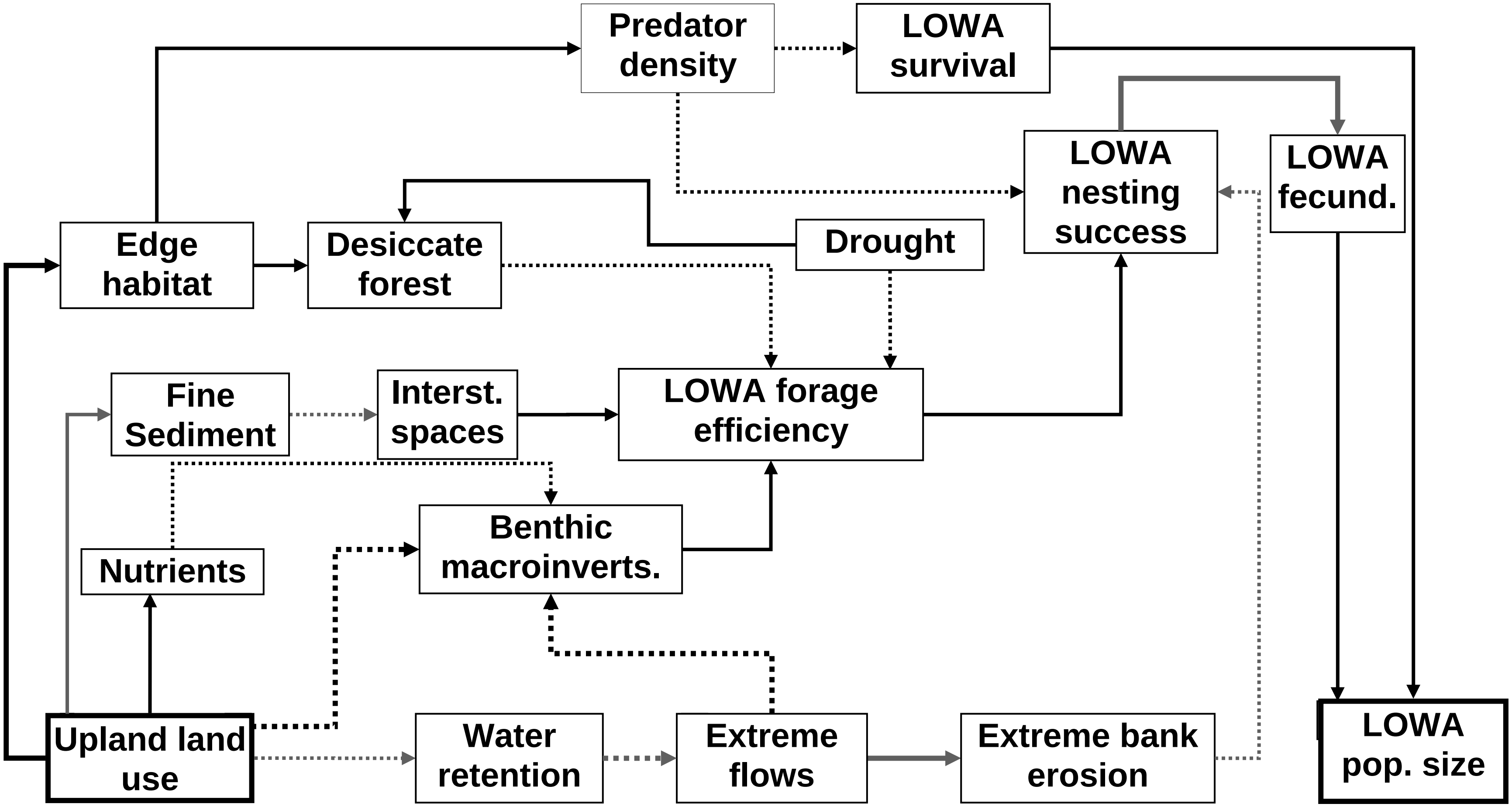

Fig. 1.1. Flow diagram showing hypothesized interactions among anthropogenic land use, flow regime, water pollution, macroinvertebrates and population ecology of Louisiana Waterthrushes. Bold boxes indicate start and end points. Solid arrows represent positive, while dashed arrows represent negative effects.

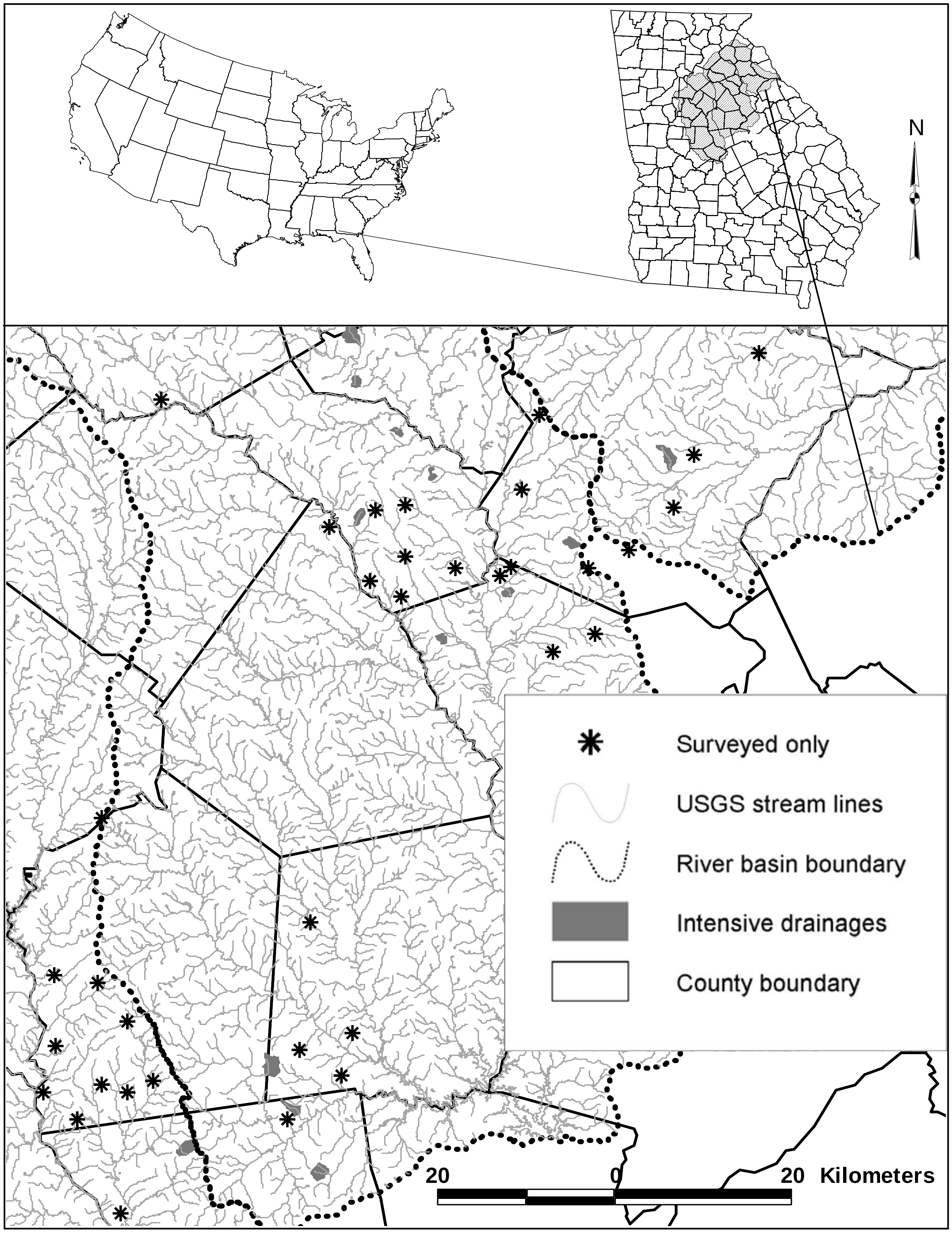

Fig. 1.2. Study drainages for studying Louisiana Waterthrush ecology in headwater streams of the Georgia Piedmont. Asterices represent drainages visited only twice during initial surveys in 2002, and drainages were sampled intensively for waterthrush breeding biology 2002-2005.

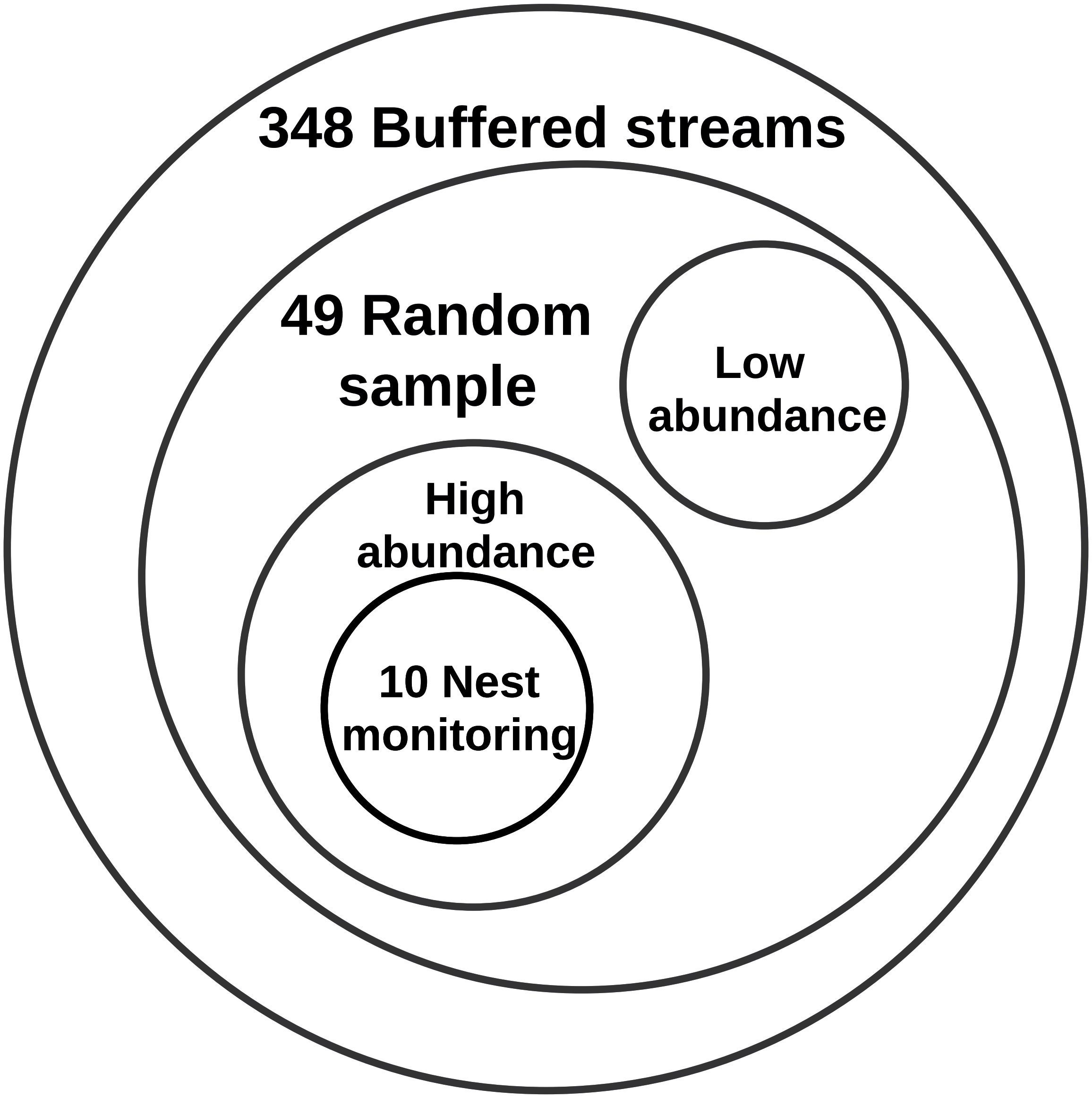

Fig. 1.3. Venn diagram illustrating site selection procedure. Drainages were randomly selected from a pool of stream networks with >15 m forest buffers. Intensive study sites were hand-picked from drainages with $\geq$1.5 waterthrush males km^{-1} of stream length.

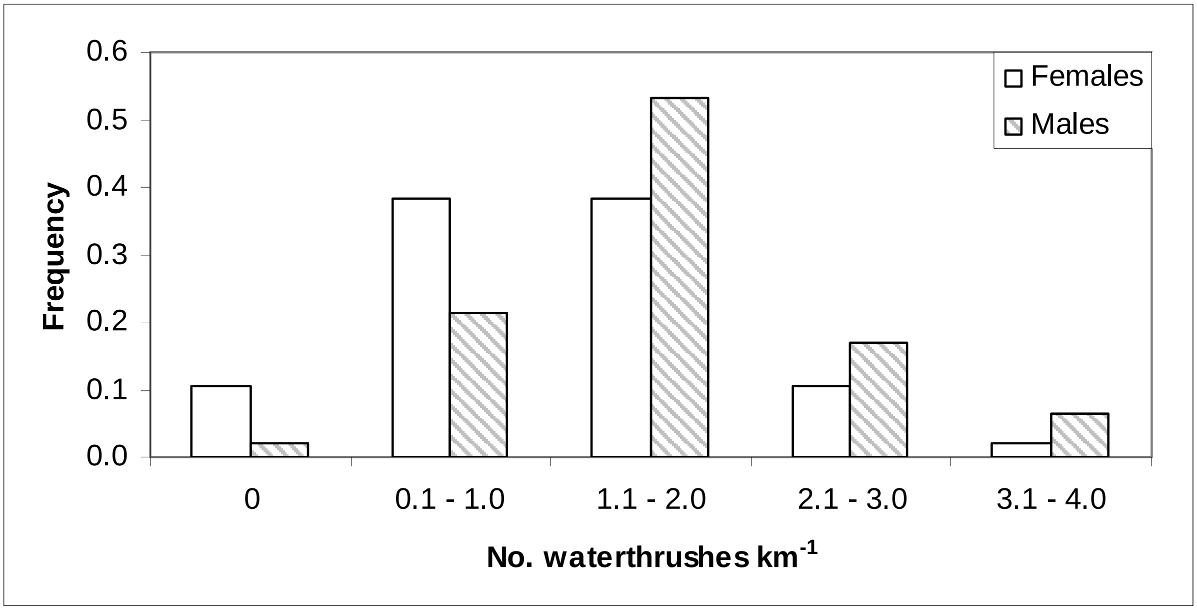

Fig. 1.4. Frequency distribution for apparent densities of Louisiana Waterthrushes during initial surveys (n = 49) along headwater streams of the Georgia Piedmont in spring of 2002.

CHAPTER 2

DETRIMENTAL IMPACTS OF RADIO TRANSMITTERS ON JUVENILE LOUISIANA WATERTHRUSHES[1]

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[1] Mattsson, B.J., J. M. Meyers, and R. J. Cooper. 2006. *Journal of Field Ornithology* 77:1-5. Reprinted here with permission of publisher.

ABSTRACT. The Louisiana Waterthrush (waterthrush; Seiurus motacilla) is a forest-dwelling, Nearctic-Neotropical migratory passerine that nests along streams. We attached radiotransmitters (0.6–0.8 g) to 12 nestling waterthrushes using snug, elastic loops. At three nests, adult waterthrushes were videotaped removing radio-tagged young from the nest. In addition, we recovered nine radio-backpacks (with two still attached to nestling carcasses) near nests within a few days after attaching transmitters. Only one of 12 radio-tagged young was relocated more than 24 h after attaching the transmitter. Thus, the method of transmitter attachment we used was not effective. Using snug, non-elastic loops (e.g., nylon) for the harness may reduce the loss of transmitters, but may injure the skin as fledglings grow. Other possible alternatives include 1) gluing the transmitter to skin on the back of nestling, 2) capturing fledglings in mist nets and attaching transmitters a week or more after fledging by which time contour feathers have grown and the likelihood of a parent removing the transmitter may be reduced, or 3) attempting to monitor fledglings without attaching transmitters. The success of the latter two alternatives would likely be enhanced by attaching transmitters to adults and then tracking them to locate their still-dependent fledglings.

INTRODUCTION

Estimating juvenile songbird survival is critical for improving models of population dynamics for migratory species (Donovan and Thompson 2001). However, juvenile songbirds are often inconspicuous during the post-fledging stage, and until recently this has limited our ability to study their survival and habitat use. The increasing miniaturization of transmitters has enabled the use of radio telemetry to overcome this limitation by providing unbiased locations of fledged young (e.g., Anders et al. 1998). The efficacy of affixing radio transmitters to small-bodied birds, and particularly young individuals of these species, has received relatively little attention. Studies of radio transmitter attachment techniques have generally focused on larger species such as raptors, waterbirds, and gallinaceous birds (see Mech and Barber 2002), while impacts of radio attachments on small (< 25 g) songbirds have received less attention. Nearly all of those studies report limited or no negative effects (Brigham 1989, Sykes et al. 1990, Neudorf and Pitcher 1997, Naef-Daenzer et al. 2001, Wells et al. 2003) Johnson et al. (1991), however, found that all of the surviving Northern Cardinals (Cardinalis cardinalis) in their study dropped their transmitters within 21 days after attaching the radios with glue. Cardinals may be disturbed by the radio attachment and can use their strong bills to remove it. Rappole and Tipton (1991) developed a method for attaching radio transmitters to small songbirds (< 50 g). Investigators have used this method in several studies of juvenile songbirds, and they reported no noticeable negative impacts of the transmitters on juvenile behavior or survival (Anders et al. 1998, Naef-Daenzer et al. 2001, Lang et al. 2002, Wells et al. 2003).

The Louisiana Waterthrush (waterthrush; Seiurus motacilla) is a small (20 g), forest-dwelling, Nearctic-Neotropical migratory passerine that nests in stream banks and among roots of fallen trees near streams (Robinson 1995). Nestlings, therefore, are easily accessible for capture and attachment of radiotransmitters. Furthermore, fledgling waterthrushes are usually within 30 m of streams (personal obs.), reducing the probability that they would escape the range of telemetry receivers (100-500 m) stationed along the stream. For these reasons, waterthrushes have great potential as a model species for estimating survival of small fledgling songbirds. We provide evidence here, however, that there are negative effects of radios on juvenile waterthrushes, which stem in part from adults attempting to remove radios from their offspring. Furthermore, because negative effects were documented in three broods distributed throughout two distinct river basins, we believe that this may be a general problem in the population. Our best evidence is in the form of several videotape sequences of parent birds tugging at the transmitter harness; this is the first time to our knowledge that such behavior has been videotaped. We make recommendations for future radio telemetry studies of juvenile songbirds that include videotaping parental response to transmitter attachment.

METHODS

Our observations took place in two forested, headwater drainages of the southern Piedmont in north-central Georgia. One of the drainages is in the Upper Oconee River basin near Watkinsville, Georgia (33°51' N, 83°24' W), and the other is in the Upper Ocmulgee River basin in Piedmont National Wildlife Refuge, Georgia (33°07' N, 83°45' W). The study sites and nests described here are a subset of those monitored as part of a concurrent study. Following the suggestions by Rappole and Tipton (1991) and advice from researchers using this method on juveniles of similar size (K. Suedkamp Wells and J. D. Lang personal communications), we applied radio transmitters to 12 9-day old waterthrushes from four different nests. By this time, primary feathers usually began to emerge, and most nestlings could hop and vocalize (Eaton 1958, B. Mattsson personal observation). We used 0.6-0.8 g transmitters manufactured by Holohil Systems Ltd.©, which were 3.8-5.6% of nestling body weight (range: 14.3-16.0 g). We attached each transmitter with 1 mm diameter elastic string to accommodate growth of the fledglings. Naef-Daenzer et al. (2001) reported that transmitters weighing less than 5% of body weight had minimal impacts on juvenile tit (Family Paridae) behavior and survival. We captured most adults and all nestlings from each nest and attached unique combinations of colored leg bands and a USGS aluminum band, which enabled us to identify most adults during videotaped observations using a Sony Handycam ©. All bird handling procedures were approved by the required permits from University of Georgia Animal Care and Use, U.S. Bird Banding Laboratory, and Georgia Department of Natural Resources.

We visited territories to observe adults and their fledglings 1-7 days per week to document juvenile survival and movements about the territory during their first four weeks after fledging. We videotaped as many nests as possible to document nestling provisioning using a Sony Handycam ©. As part of this effort, we videotaped three nests with young soon after we fitted them with transmitters and returned them to their nests. We placed the camera on a tripod 3-5 m away from each nest and set the zoom so that an area of 400-1,600 cm^2 centered on each nest filled the view. Each video session lasted at least 1 hr or until the battery died (approx. 90 min). When reviewing the tapes, we distinguished the male and female parents based on their unique color band combinations.

RESULTS AND DISCUSSION

We tracked 12 radiomarked fledglings and 18 non-radiomarked fledged broods during our study. We recovered two intact radio backpacks attached to nestling carcasses and 7 backpacks without carcasses near these nests within a few days after attaching the radios. Only 1 of the 12 radio-tagged young was resighted beyond 24 hours of attaching the radio. The strongest evidence that adults removed radios came from videotaped observations of nestlings after attaching radios and returning them to their nests.

We videotaped radiomarked nestlings from two of the nests (nest 1 and nest 2) in the Upper Oconee drainage. We attached radio transmitters and leg bands to all five nestlings from nest 1 on 5 May 2003. After placing them back in their nest, we videotaped the nest from 08:55 until 10:07. The female and male each fed the nestlings twice, and then during the fifth visit at 09:26, a nestling at the front of the nest fluttered its right wing. Immediately, the female tugged beneath the wing with her beak (presumably on the radio harness looped around the leg) for 22 s before departing. We did not observe this tugging behavior during 78 h of videotape observations on nests containing non-radiomarked waterthrush nestlings in 2002 and 2003. Within 2 min after the female departed, the probed nestling and two other nestlings climbed out of the nest and fell out of view. The second fledged 53 s after the first, and the third fledged 83 s after the first. Several adult waterthrush chips were audible on the videotape only after the first young fledged, suggesting that the first young departed on its own volition. The female returned with food at 09:30, but appeared to swallow the food without feeding either of the remaining nestlings. Instead, she poked at one of the nestlings and departed 51 s after arriving. Finally, at 09:40 the female fed one young. Immediately after, she grasped the harness in her bill and flew below the view of the camera with the young hanging from her bill. The fifth nestling was fed for the last time at 09:47 and climbed from the nest 26 s after the female departed.

We recovered three of the five radio transmitters with their respective harnesses attached (hereafter, referred to as backpacks) from nest 1. We found one of the three backpacks 5 m from the nest discarded on dry ground the day after fledging, 6 May 2003. On the same day, we found another backpack attached to a chewed carcass on the bank edge, directly across from the nest. We excavated a backpack from the stream beneath the bank across from the nest on 11 May 2003. High amounts of rainfall during the morning of 6 May 2003 could have forced the radio into the bank. We excavated a radio with a broken harness from a submerged root wad 100 m downstream of the nest on 13 May 2003. We never recovered the fifth radio, but we last detected its signal in this root wad. The pair began a new nest on 11 May 2003, five days after their first brood fledged, and we never observed them tending juveniles from their first nest during 17 subsequent visits to their territory. This behavior indicates that none of their radiomarked juveniles survived.

At nest 2, we radiomarked, banded, and videotaped a lone nestling on 23 May 2003. The video view was much closer to the nest, allowing us to document more detailed observations than for the first nest. The female brought a mayfly larva to the nest 10 min after videotaping began at 08:55. For the first 24 s, she poked at the nestling without feeding. Instead of feeding, she turned toward the stream, ate the larva, turned back toward the nestling, and made four attempts at tugging off the harness. Finally, she grasped the harness in her bill, and flew below the view of the camera while carrying the young at 08:56. Between 08:56 and 09:55, adult chip notes were audible on the videotape. Quiet periods lasted no more than 10 min, and these could have coincided with foraging trips by the adult (the male was not observed in the territory after 5 May 2003). Waterthrush contact calls and juvenile begging calls were audible on the videotape between 09:46 and 09:55, indicating that the juvenile survived for at least 1 h after fledging.

We retrieved the intact backpack from nest 2 in the stream below the nest the following day, 24 May 2003, at 11:55. While searching for the radio, the female chipped persistently within a 10 m radius around the nest. We did not observe the female or juvenile during 5 subsequent visits to the territory.

We banded, radiomarked and videotaped two of the three nestlings at nest 3 on 5 June 2003. An unbanded adult carried food to the nest at 20:35, 11 min after videotaping began. After 9 s, one of the radiomarked young moved to the rim of the nest, lifted its right wing, and the adult probed near the harness with its bill. Then, the adult flushed, presumably causing the young to tumble and fall below the view of the camera. According to the audio recording on the videotape, the juvenile landed on dry land, chirped and splashed into the water at 20:36.

Waterthrush fledglings swim well in calm water for at least 2 m (B. Mattsson personal observation), and this nest was above a 1 m wide pool and across from a 1 m wide sandbar. Adults did not visit the nest again before dark at 20:52.

On the next day, we read colorbands on the one non-radiomarked nestling on the sandbar across from nest 3, and one radiomarked nestling was still in the nest at 07:57 on 6 June 2003. Thirteen min later, we recovered an intact backpack in a pool 5 m upstream of the nest. Later that day at 16:32, the radiomarked fledgling was on the sandbar next to the stream, directly across from the nest. On 7 June 2003, we recovered the second, intact backpack and observed several feather sheaths next to the backpack in a pool 10 m upstream of the nest.

We banded and radiomarked all five nestlings from nest 4 on 6 May 2003, but they were not videotaped because of logistical constraints. Two of the radio signals were never detected despite thorough searches in the territory on three subsequent days. On 10 May 2003, we excavated one of the intact backpacks attached to a carcass beneath the bank 70 m downstream of the nest. We excavated a second intact backpack beneath the bank 150 m downstream of the nest on 23 May 2003 after many attempts to excavate it starting on 10 May 2003. We observed the third radiomarked fledgling for 10 consecutive days after fledging. The male and female tended the juvenile each day, and the adults never seemed disturbed by the backpack. On the second and third day after fledging (8-9 May 2003), the juvenile hid beneath leaf litter and hollow stumps. Juveniles are difficult to observe during the first few days after fledging (Anders et al. 1998), so we cannot compare this behavior with that of other waterthrush fledglings without radios. This fledgling flew 5-25 m during each of the last six days of observation, and its behavior was similar to non-radiomarked fledglings of similar age (B. Mattsson personal observation). After 10 d of tracking, the signal remained 5-7 m up in a large tree until we recovered the unoccupied backpack at the base of the tree on 20 May 2003. We never resighted this juvenile during many subsequent visits to the territory. We did, however, observe the adult female with 2 other elusive waterthrushes near her second, active nest on 8 June 2003. Though we were unable to resight color bands on two of the waterthrushes, we suspect that one of them was probably the adult male and the other might have been the juvenile that dropped its backpack on 20 May 2003. At this age, waterthrush juveniles still depend on adults for food (Eaton 1958), but they are usually easy to resight after repeated visits to their territory (B. Mattsson, personal observation).

Three possible explanations exist for how each intact backpack was removed: (1) a predator removed the radio and consumed the nestling without leaving tooth marks on the radio, breaking the harness, or kinking the antenna, (2) the juvenile removed the radio on its own by stepping out from the loops around its legs, and (3) an adult waterthrush removed the radio.

The first explanation is unlikely, as radios removed by predators usually show noticeable damage (Johnson et al. 1991, J. D. Lang personal communication). Removing its own harness would require the juvenile to pull away at one of the elastic strings while stepping out, perhaps with the aid of a branch or its own beak. The third explanation is more likely, because adult waterthrushes have bills that are coordinated for pulling items while foraging and nest building. An adult waterthrush could tug at the elastic and allow the juvenile to step out of the loop. During at least 5 subsequent visits to their territories, we never resighted the juveniles that lost their radios. In contrast, we were able to regularly resight fledglings from non-radiotagged broods. Therefore, we believe that the juveniles died after losing their radios.

Whatever the causes, it appears that the radio attachment method we used is ineffective for studying survival and habitat use of juvenile waterthrushes during the dependent stage.

Alternative methods include: (1) replace elastic string with non-elastic string to prevent adults from removing the backpack, (2) glue the radio to the skin on the back of the nestling (Sykes et al. 1990), (3) capture juveniles with mist nets and apply transmitters after they have spent one or more weeks out of the nest when they have more complete contour feathers to reduce the likelihood of a parent removing the transmitter, and (4) track fledglings without radio telemetry. Juvenile Wood Thrushes (Hylocichla mustelina) in the wild retained their transmitters attached with non-elastic string until predators remove them (J. D. Lang personal communication). Captive Common Yellowthroats (Geothlypis trichas) retained transmitters attached with adhesive for a median of 24 days, which is near the life span of these radios (Sykes et al. 1990). Although the first two alternatives may increase the probability that the radio stays on the fledgling, some adults may repeatedly tug at the radios and cause physiological stress to juveniles. The third alternative would result in lower sample sizes and the estimates of fledgling survival would ignore the crucial first week out of the nest when young are probably most vulnerable to predation (Anders et al. 1998). The final alternative of tracking juveniles without telemetry lacks the rigor of obtaining many unbiased locations, but it is a non-invasive alternative that can provide much useful information on juvenile songbirds.

In addition to probable increased mortality of fledglings, the radio attachments led to much time spent recovering lost radios (~30 min per lost radio every 2-3 days until found) which ultimately reduced our time for tracking juvenile waterthrushes without radio transmitters. We often resighted color-banded juveniles after spending less than 30 min searching the territory.

We have three recommendations for research studies that plan to employ radio-telemetry with small juvenile songbirds, especially when the effects for a particular species are unknown. First, videotaping the nest for at least 30 min after returning the nestlings to their nest can provide crucial information on how adults respond to the radio attachments on their young. Second, placing radios on half of the nestlings enables direct comparisons of the disturbance endured by radiomarked and nonradiomarked young. Third, attaching radios to adults, in addition to their nestlings, ensures that observers can track fledged broods in the event that the adults remove radios from their nestlings. Finally, if the goals of the study are to describe habitat use or dispersal of juveniles, then attaching radio transmitters to >1 week old fledglings would be a wise practice.

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CHAPTER 3

LOUISIANA WATERTHRUSHES (*SEIURUS MOTACILLA*) AND HABITAT ASSESSMENTS AS COST-EFFECTIVE INDICATORS OF INSTREAM BIOTIC INTEGRITY[1]

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[1] Mattsson, B.J., and R. J. Cooper. Accepted by *Freshwater Biology*.
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ABSTRACT.-Benthic stream animals (henceforth, macrobenthos) are good indicators of water quality, but sampling requires much time and expertise to obtain accurate indices of biotic integrity. Thus, tools for bioassessment that include measurements other than macroinvertebrates would be valuable additions to volunteer monitoring protocols. We evaluated the usefulness of a stream-dependent songbird, the Louisiana waterthrush (waterthrush, *Seiurus motacilla*), and the EPA Visual Habitat Assessment (EPA VHA) as indicators of the macrobenthos community in headwater streams of the Georgia Piedmont, U.S.A. We sampled macrobenthos, surveyed waterthrushes, and measured habitat characteristics along 39 headwater reaches across 17 drainages ranging from forested to heavily urbanized or grazed by cattle. Of the indicators considered, waterthrush occupancy was best for predicting relative abundances of macrobenthic taxa, while the EPA VHA was best for predicting Ephemeroptera-Plecoptera-Trichoptera (EPT) richness. Individual components of EPA VHA scores were much less useful as indicators of EPT richness and % EPT when compared to the total score. Waterthrushes were found along streams with higher % EPT, a lower Family Biotic Index (FBI) values, and greater macrobenthos biomass. While macrobenthos remain one of the most direct indicators of stream water quality, stream bird surveys and reach-scale habitat assessments can serve as cost-effective indicators of macrobenthos. Using stream-dependent birds as an early warning signal for degradation of stream biotic integrity could improve the efficiency of watershed monitoring programs in detecting and identifying perturbations within the watershed.

INTRODUCTION

Land use changes and water diversions within or near riparian areas alter natural flow regimes, leading to degradation of many aquatic ecosystems (Poff et al. 1997, Paul and Meyer

2001, Roy et al. 2003, King et al. 2005). While maintaining a vegetated zone along rivers may provide some protection to aquatic ecosystems (for review see Wenger 1999), modifications upstream within the drainage area (catchment) may overwhelm the usefulness of these riparian buffer zones (Roth et al. 1996, Booth et al. 2002, Walsh 2004). Therefore, monitoring the health of stream ecosystems following modifications to the riparian zone or catchment is critical for detecting problems with water quality and stream biota.

Biological assessment has been used extensively to evaluate water quality of streams and to detect aquatic degradation due to non-point source pollution (Yoder 1995). Benthic macroinvertebrates are now the most widely used indicators of stream water quality because they are ubiquitous, have sufficiently long life cycles to integrate the effects of disturbance (Rosenberg and Resh 1993), and respond to changes at different spatial scales ranging from the stream reach to the entire catchment (Lammert and Allan 1999, Roy et al. 2003, King et al. 2005). In this paper, stream biotic integrity is used synonymously with the condition of the benthic macroinvertebrates and larval salamanders (henceforth, macrobenthos) living in the stream.

Many volunteer groups have used bioassessments to monitor stream water quality in their local communities (Kerr et al. 1994, Lathrop and Markowitz 1995, Danielsen et al. 2005). These groups often can sample more streams at shorter intervals than federal or state environmental agencies, providing a more complete coverage of watersheds and expediting identification of point-source pollutants (Engel and Voshell 2002). Developing effective and efficient bioassessment protocols is essential for the success and sustainability of such volunteer monitoring efforts.

Bioassessments of streams based on macrobenthos have some limitations. First, volunteer groups often lack the resources for training their members how to identify macrobenthos beyond family, or in some cases, beyond order (Engel and Voshell 2002). Fortunately, bioassessments based on coarser taxonomic resolution are often in general agreement with those based on finer taxonomic resolution (Fore et al. 2001, Engel and Voshell 2002). Second, regardless of the taxonomic resolution, most standard bioassessment protocols require a large time investment (up to four person-hours per reach; B.J. Mattsson, personal observation). Obtaining accurate indices of biotic integrity requires arduous tasks of gathering the organic benthic material, followed by separating, identifying, and tallying macrobenthos. Third, much of the general public does not emotionally connect with invertebrates, which comprise the majority of macrobenthos. For example, while a reduction in the number of genera in the insect orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) is a valuable indicator of degraded water quality (Roy *et al.* 2003), this metric alone communicates little to a lay audience. Thus, tools for bioassessment that include measurements other than macroinvertebrates would be valuable additions to volunteer monitoring protocols.

We evaluated the usefulness of two potential indicators of stream biotic integrity. First, we surveyed Louisiana Waterthrushes (waterthrushes, *Seiurus motacilla*) which are forest-interior, Neotropical migratory songbirds that require streams for food and nesting sites (Robinson 1995). Their diet includes larval salamanders (B.J. Mattsson, personal observations) and benthic macroinvertebrates, including sensitive taxa such as EPT (Eaton 1958, Craig 1987). Their predominant foraging method is picking leaf litter while walking along rocks and other stable substrates along riffles of headwater streams (Craig 1987). They normally breed along inland forested streams throughout the eastern U.S. (Robinson 1995). Due to their dependence on streams for food and nesting, we predict that their presence along a stream reach will provide some indication of the stream biotic integrity. Second, we used standard protocols for rapid visual habitat assessments which have been designed for use by volunteer watershed groups and environmental agencies alike (e.g., Bjorkland et al. 2001), and are usually based on the U.S. Environmental Protection Agency (EPA) Visual Habitat Assessment (VHA, Barbour *et al.* 1999). These habitat assessments have shown good correspondence with stream biotic integrity (Sullivan et al. 2004, Hall and Killen 2005, Stone et al. 2005), and thus provide a baseline for comparison with waterthrushes.

Based on our literature review and logic, we developed four alternative hypotheses: 1) waterthrushes alone best predict stream biotic integrity, 2) habitat alone best predicts stream biotic integrity, 3) waterthrushes and habitat together best predict biotic stream biotic integrity, and 4) neither habitat nor waterthrushes best predict stream biotic integrity. If waterthrushes and/or habitat scores relate closely to more costly measures of biotic integrity, then this would justify incorporating waterthrush and/or habitat measurements into monitoring protocols to ensure cost-effective sampling. To evaluate our hypotheses and predictions, we sampled macrobenthos, surveyed waterthrushes, and measured habitat characteristics along 39 headwater reaches across 17 drainages of the Georgia Piedmont ranging from forested to heavily urbanized or grazed by cattle.

METHODS

Study region.-We sampled headwater stream networks with drainage areas ranging from 0.41 to 4.20 km^2 in the Piedmont ecoregion of Georgia, U.S.A. These drainages are located within 25 km of Athens-Clarke County (northern study area) and within 15 km of Piedmont National Wildlife Refuge (southern study area) north of Macon (Fig. 3.1). These areas include three river basins in the southern Piedmont of Georgia and parts of the Oconee National Forest. The Upper Ocmulgee, Upper Oconee and Broad River basins are in the southwestern portion of the southern Piedmont, which extends from east-central Alabama through north-central Georgia, then northeast through western South Carolina and central North Carolina. The Piedmont of Georgia is characterized by rolling hills and predominantly acid crystalline and metamorphic rock. Presettlement vegetation consisted of mixed deciduous and pine forest, and was cleared for agriculture and timber during the 1800's. Topsoil eroded from cleared fields and caused floodplains to fill with sediment and stream beds to become aggraded (Trimble 1974). Between the 1930's and the 1980's, cotton farms were abandoned following economic failure, and farmers moved to cities. As a result, urban land cover tripled from 1% to 3%, agricultural land cover decreased from 30% to 12%, and the remaining land was planted mostly with loblolly pine, or regenerated to deciduous/mixed forest (Turner and Ruscher 1988).

Site selection.-In 2002, we chose ten rural drainages characterized by low (< 2%) urban land cover and dominated by either cattle pastures, pine plantations, or mixed deciduous/evergreen forest. We selected these ten rural drainages from a larger pool of potential drainages that were forested >15 m on both sides from the headwaters throughout >2.5 km of stream as determined from the most recent digital orthophoto quadrangles (DOQQs) available at the time (USGS 1995) and overlaid stream lines (Georgia Department of Transportation 1997). All of these drainages had at least one pair of breeding waterthrushes despite varying amounts of forest, pasture and recent clearcuts within the surrounding landscape beyond the >15 m buffer. Cattle had access to two of the 10 stream networks. In 2003, we added six urbanized drainages in the Upper Oconee River Basin that had intact forest >15 m on both sides for at least 1 km but were often bisected by roads or other disturbances in the headwaters. We randomly selected two urban drainages that fell into one of the following categories of percent impervious surfaces within the drainage: 5-9%, 10-14%, and 15-19%. These percentages were determined from the most recent land cover map available at the time (NARSAL 2002). In 2004, we revisited the 13 drainages with breeding waterthrushes, including three of the six urban drainages and all ten rural drainages. We added an additional urban drainage with breeding waterthrushes in 2004 (Table 3.1).

Based on a satellite-derived 1998 land cover map (NARSAL 2002), urban land uses covered 0-38%, while impervious surfaces covered 0-18% of the land surface within these drainages. Biotic integrity in streams declines sharply beyond 15-20% urban land cover (Roy et al. 2003, King et al. 2005) and declines gradually (Booth *et al.* 2002) or sharply (Walsh 2004) beyond 10% impervious surfaces. Thus, we monitored streams that were likely to contain macrobenthos communities that range from degraded to intact.

Waterthrush surveys.-We visited drainages between sunrise and 4 hr after sunrise at least once between late March and early April, and again between late May and early June from 2002-2004. Based on a concurrent study of waterthrush reproduction, the earliest incubation date during this study was 7 April 2004 (B.J. Mattsson unpublished data). Waterthrush males sing frequently throughout the day near the stream upon arrival on the breeding grounds, defending their territories (≈ 500 m stream length) and advertising for mates (Robinson 1995). Once paired, the male sings less frequently and instead moves throughout the territory with his mate while they build the nest and she prepares to lay eggs (Robinson 1995). The pair is observable during this period of at least 1 week as they court and forage along the stream bed most of the day (B.J. Mattsson unpublished data). Thus, we conducted our surveys during the period when waterthrush males and females were most detectable.

During each survey, we walked slowly along the 1-3 km stream network while maintaining a clear view of the stream bed. For each survey, we recorded locations of singing male waterthrushes and breeding pairs both during and between point counts. For drainages that were visited more than once during either the early or late spring periods, we used the survey occasions closest to the median date for drainages visited only twice when including waterthrush occupancy in the analyses.

Macrobenthos sampling.-Between late May and mid June 2002, we sampled macrobenthos inside two randomly selected waterthrush territories within each rural drainage. In particular, we sampled riffles where we had observed waterthrushes foraging. Benthic macroinvertebrate assemblages in riffle habitats are more sensitive to degradation of stream water quality than those in other microhabitats (Roy *et al.* 2003). We resampled riffles in rural drainages and sampled additional riffles in both the rural and urban drainages in 2003 and 2004. Due to logistical constraints, we sampled the urban drainages in 2003 during July rather than in late spring. We sampled riffles within some of the urban drainages where there were no waterthrushes detected within 1 km of stream. We also sampled riffles in urban drainages where we did not observe a breeding pair.

We collected macrobenthos using a Surber sampler (30.5 cm x 30.5 cm, 1 mm mesh) at the downstream portion of two riffles (each at least 1 m x 1 m in area) in each sampling reach ≈ 50 m in length. We scrubbed all rocks (> 8 cm in diam) and disturbed the sediment 2 cm below the stream bed and within the Surber frame for a total of 3 minutes. We elutriated each sample separately in the field and stored all organic matter in 70% ethanol. All animals were carefully separated from other organic matter in each sample. We then identified, tallied, and recorded lengths (1 mm precision) of these animals using a dissecting microscope (10-45× magnification).

We identified insects to genus for orders Ephemeroptera, Plecoptera, and Trichoptera (EPT), with the exception of Leuctridae (Order Plecoptera) which were too small to identify to genus, and all other orders to family using standard dichotomous keys (e.g., Merritt and Cummins 1996). We calculated the EPT richness, % EPT as the ratio of EPT to total macrobenthos abundance, the Family Biotic Index (FBI, Hilsenhoff 1988), and macrobenthos biomass using length-mass regressions (Table 2, Benke et al. 1999). We averaged data from the two riffles in each sampling reach for statistical analyses.

Habitat surveys.-We conducted the EPA Visual Habitat Assessment (VHA) to obtain a total score for a reach that extended 20× channel width and encompassed the corresponding riffles where we sampled macrobenthos (Barbour *et al.* 1999). The total score for a reach increases with improving habitat quality (range: 0 – 200), and is based on 10 component scores for specific habitat characteristics including epifaunal substrate, embeddedness, velocity/depth regime, sediment deposition, channel flow status, channel alteration, frequency of riffles, bank stability, vegetative protection, and riparian zone width. We recorded the actual riparian vegetation cover width by pacing if the distance was < 17 m. Otherwise, we used ArcView GIS (ESRI 1999) to measure the distance from the sampling point to the nearest uphill canopy edge as shown on 1999 DOQQs (USGS 2002).

Statistical analysis.-Then, we constructed a linear regression model that contained four variables predicted to be good indicators of the four macrobenthos metrics (henceforth, global model; Table 3). To reduce the number of variables in the global model, we chose to include only riparian buffer width along with the total score in the initial analysis rather than all of the components of the EPA VHA. If, however, EPA VHA was included in one of the best models for one of the metrics, then we constructed post-hoc models that included individual component scores we believed to be best linked to integrity of riffle-dwelling macrobenthos: epifaunal substrate, embeddedness, velocity/depth regime, sediment deposition, and frequency of riffles. We standardized the EPA VHA and buffer width variables (mean = 0, SD = 1) to facilitate model convergence.

We evaluated goodness-of-fit for each of the global models by dividing the chi-square statistic by the error degrees of freedom to ensure adequate goodness-of-fit (i.e., $\hat{c} \approx 1$, Burnham and Anderson 2002). Next, we checked for spatial dependence in each global model by evaluating whether the 95% confidence intervals surrounding residuals were disparate among sampling reaches. All the global models exhibited some spatial dependence, and so we added stream reach as a random effect (i.e., measure of unexplained variation among physical locations of samples) to all models except macrobenthos occupancy which would not converge. Adding this random effect enabled us to later quantify the variation among stream reaches that was not accounted for by the combination of fixed effects. We then compared Akaike's Information Criterion (AICc, which includes a small sample size correction, Burnham and Anderson 2002) for each model with a more complex model that included year or sampling date (i.e., temporal effects; Table 3). If the model with the temporal effect had a Δ $\mathrm{AIC_c}$ value ≤ 4 when compared to the simpler model, then we included the temporal effect as a fixed effect in all subsequent models of that response variable. Finally, after log-transforming macrobenthos biomass (i.e., log(x+1) to account for samples with no macrobenthos), we confirmed that all global models had normally distributed residuals. We collected four samples with no macrobenthos, and these were excluded from regressions of log-transformed biomass estimates.

From the global models discussed above, we developed a set of eight *a priori* candidate models for each of the five macrobenthos variables. A model with no indicator variables (henceforth, null model) was included in each candidate set. For some model sets, temporal effects were included in all models including the null. We used an information-theoretic approach to assign weights of evidence to subsets of each global model using AIC_c (Burnham and Anderson 2002). Models with fewer predictors have higher AIC_c weights than those with the same fit but more predictors (Burnham and Anderson 2002). Thus, we ranked models according to their relative AIC_c weights, so that models with higher weights were more parsimonious. Models with a AIC_c weight ≥ 13.5 % of the AIC_c weight for the top model (i.e., $\Delta AIC_c \leq 4$) were included in the confidence set, which represents models that had a high probability of being the best model (Burnham and Anderson 2002: pg 171). We used box plots, scatter plots, and confidence intervals surrounding the slope of each predictor found in the confidence set to assess the strength and direction of effects on each of the five response variables. When possible, we used pure maximum likelihood methods with a maximum Fisher score of 5 to estimate model parameters in each set. If one or more models in a set failed to converge, then we used restricted maximum likelihood methods throughout that candidate set. We used PROC MIXED to carry out the analyses for macrobenthos occupancy and all other response variables, respectively (SAS Institute Inc 2004).

RESULTS

We observed a wide variety of macrobenthic communities in our samples (n=79) including those along dry or heavily polluted stream channels (no macrobenthos detected) to those with high biomass (>183 mg/m^2), high EPT richness (>20 genera), high proportion of EPT taxa (90%), and those indicative of low organic pollution (FBI < 2; Table 3). In addition to EPT taxa, we regularly found larval salamanders, bivalves, oligochaete worms, dipteran larvae, coleopteran larvae, and odonate nymphs. We observed a waterthrush male on 89% and a breeding pair of waterthrushes on 83% of the 66 sampling occasions along 39 reaches during the 3 years of the study (Table 3.2). We also observed a wide range of habitat and temporal variables used in models of the macrobenthos community (Table 3.2).

Variation in mean EPT richness per reach was best explained by a model that included only EPA VHA and year (AIC weight = 90%; Table 4). In a post-hoc analysis, this model was also superior (AIC_c weight = 93%) to models that contained one or all of the component scores of the EPA VHA. Each of the component scores, however, was correlated with the total score (Pearson correlation range: 0.32 – 0.53). The remaining models in the *a priori* candidate set that included waterthrush, buffer, or just year fell outside the confidence set of models (Δ AIC > 4), and had low weights of evidence ($w_i < 0.1$; Table 4). The random effect of physical location (i.e., sampling reach) in the top model had a confidence interval above zero (Appendix 2.1), indicating variation in EPT richness among stream reaches unaccounted for by EPA VHA. The 95% confidence interval surrounding the slope estimate for EPA VHA was above zero, indicating a strong positive association with EPT richness (Appendix 2.1), and this effect was consistent across years (Fig. 3.2).

Mean percent EPT within each reach was best explained by the global model that contained all four predictors (Table 3.3). In a post-hoc analysis, this model was also superior (AIC_c weight = 89%) to models that contained one or all of the component scores of the EPA VHA. The remaining models in the *a priori* candidate set were outside the confidence set of models and had low weights of evidence. Furthermore, there was no evidence of reach-level variation in % EPT beyond that explained by variables in the top model, as the confidence interval for the random effect of reach was centred on zero (Appendix 2.1). Neither the occupancy of a waterthrush nor buffer width had a clear association with % EPT, as the confidence intervals surrounding these slopes were nearly centred on zero (Appendix 2.1). Occupancy of a waterthrush pair and EPA VHA, however, had strong positive associations with % EPT (Fig. 3.3), as the confidence interval for theses slopes were completely above zero (Appendix 2.1). The interquartile ranges for % EPT did not overlap when comparing reaches with and without a waterthrush pair (Fig. 3.4). Although we did not evaluate this, a simpler model with just occupancy of a waterthrush pair and EPA VHA score would likely outperform the global model which dominated this particular candidate set.

All models except the global model were included in the confidence set for explaining variability in FBI (Table 3.3). Most notable was the null model, which carried a substantial weight of evidence (16%), indicating good support for the hypothesis that none of the predictors are useful for predicting FBI; i.e., the mean. As with the confidence set predicting EPT richness, there was evidence for reach-level variation in FBI values that remains unexplained by predictors in the top models. There was a tendency for FBI to be lower along reaches with waterthrushes (Fig. 3.4), wide riparian buffers, and/or higher EPA VHA scores, as confidence intervals for their slopes were mostly below zero (Appendix 2.1). These associations, however, remain uncertain.

The confidence set for explaining variability in the log of macrobenthos biomass (henceforth, biomass) was similar to that of FBI, as it included all models except the global model. Most notably, the confidence set included the null model with only temporal effects (Table 3.3). There was also evidence for reach-level variation in biomass that was unexplained by variables in the confidence set, as most of the random effects in these models had confidence intervals above zero (Appendix 2.1). There was a tendency for biomass to be greater along reaches with waterthrushes, higher EPA VHA scores, and/or wider riparian buffers, as confidence intervals for these effects were mostly above zero (Appendix 2.1). Indeed, the interquartile ranges of biomass did not overlap when comparing reaches without waterthrushes to those with waterthrush males or breeding pairs (Fig. 3.4). As with models of FBI, these associations remain uncertain. Biomass was lowest in 2003, as its confidence interval was below zero. In addition, biomass declined as the season progressed, and this effect was consistent across years (Fig. 3.5).

In a post-hoc logistic regression model, we found that buffer width was positively associated with waterthrush occupancy ($\hat{\beta}_{\text{buffer}}=3.69\pm3.60$, 95% CI). In particular, waterthrush occupancy averaged 99% when buffer width exceeded 120 m (Fig. 3.6). A stream with a buffer <40 m wide, however, averaged <80% occupancy. The relationship between waterthrush occupancy and the EPA VHA score, however, was unclear ($\hat{\beta}_{\text{EPAVHA}}=0.0195\pm0.0239$, 95% CI). This model was much more parsimonious than a model without covariates ($\Delta AIC_c = 15.1$).

DISCUSSION

Performance of waterthrush and habitat surveys as indicators of biotic integrity.-Our study demonstrates the relative usefulness of two simple indicators of several biotic integrity metrics in headwater streams. The EPA Visual Habitat Assessment (EPA VHA) was more useful as an indicator of EPT richness, while waterthrush occupancy was more useful as an indicator of indices that corresponded to relative abundances of macrobenthic taxa (i.e., % EPT, biomass). The EPA VHA and occupancy of a waterthrush pair were more useful when used in conjunction as indicators of % EPT. Riparian buffer width alone was a poor indicator of macrobenthic integrity, and the other component EPA VHA scores were much less useful as indicators of EPT richness or % EPT when compared to the total score. These findings support hypothesis 2, which states that waterthrushes and habitat are useful together for explaining variability of biotic integrity in streams. We would only add that waterthrushes and habitat surveys are useful in different ways.

Other studies have found positive associations between reach-scale habitat features and EPT measured by richness and by abundance (Richards et al. 1996, Roy et al. 2003). Through random effects modelling, however, we determined there was substantial variation in EPT richness that was unexplained by reach-scale habitat features. EPT richness is closely associated with other measurements like specific conductivity and percent urban land use in the drainage (Roy *et al.* 2003), and so reach-scale habitat measurements alone may be insufficient as indicators of EPT richness. Despite the development of robust methods to detect urbanization (Fung and Siu 2000, Weber and Puissant 2003), these rely on advanced knowledge of remote sensing and access to expensive satellite imagery. Measurements of specific conductance also require expensive equipment that may be unavailable to some volunteer groups. Thus, visual habitat assessments remain a valuable, cost-effective tool for monitoring biotic integrity of streams.

From an ecological standpoint, there is no reason to believe that waterthrushes would select streams with higher EPT richness per se. More conceivably, they respond to a numerical shift in the community toward their preferred prey (Stucker 2000), which include EPT taxa (Eaton 1958, Craig 1987). Indeed, we found that occupancy of a waterthrush pair was a useful indicator of measures of biotic integrity that are sensitive to abundances of macrobenthos including % EPT, FBI, and log of macrobenthos biomass. As in our study, occupancy of Louisiana Waterthrushes and American Dippers (*Cinclus mexicanus*) was positively associated with % EPT along headwater streams of southern Minnesota and western Wyoming, respectively (Stucker 2000, Feck and Hall 2004). We found, however that the best indicator of % EPT includes both waterthrush occupancy and EPA VHA.

There was a negative tendency between waterthrush occupancy and the tolerance index for macroinvertebrates (i.e., FBI) in our study, but the direction of this relationship remains uncertain. This is in agreement with findings comparing FBI between streams with and without waterthrushes in southern Minnesota (Stucker 2000). American Dipper occupancy along headwater streams of Wyoming, however, exhibited a clear negative association with a tolerance index for macroinvertebrates of the intermountain region of the U.S., but not with FBI which was developed in Wisconsin (Hilsenhoff 1988, Feck and Hall 2004). Likewise, Sorace et al. (2002) reported that European Dippers (*C. cinclus*) occurred only along streams of central Italy that had low tolerance indices for macroinvertebrates of the Mediterranean. Collectively, these findings emphasize the value of stream-dwelling birds as indicators of tolerance indices for macroinvertebrates in the region of interest.

There remains much variation in FBI among streams in our study that remains unexplained by waterthrush occupancy, however. As with EPT richness, FBI is associated with specific conductance and catchment-scale land use in the Georgia Piedmont (Roy *et al.* 2003). This importance of landscape processes further justifies developing workshops and open-access software to facilitate volunteer groups incorporating GIS analysis as an additional tool for their monitoring programs. Furthermore, we found waterthrushes breeding along forested reaches that were heavily impacted by cattle grazing. Monitoring programs in agricultural landscapes should take into account the possibility that their streams are impacted by cattle grazing, which may not be well represented by surveys of habitat or waterthrushes.

Stream-dependent songbirds would be expected to avoid breeding along reaches with insufficient macrobenthic biomass to support reproduction (Gray 1993, Iwata et al. 2003). Waterthrush occupancy in our study had a weak but positive association with macrobenthos biomass. Our urban stream sampling in 2003 followed the second wettest May and June on record for north central Georgia (NWSFO 2004). This excess rainfall was probably responsible for elevated macrobenthos biomass and EPT richness throughout these small headwater streams in 2004 (D.B. Batzer, University of Georgia, personal communication). Another potential confounding factor was that biomass of our macrobenthos samples from different streams declined as the season progressed, and this may have further obscured the association between biomass and waterthrush occupancy.

Dippers (family Cinclidae) forage almost exclusively on aquatic prey (Ormerod and Tyler 1993, Kingery 1996), while waterthrushes switch from predominantly aquatic prey early in the breeding season to predominantly terrestrial prey following leaf emergence (Craig 1984). Thus, we expected waterthrushes to have a weaker association with macrobenthos biomass when compared with dippers, especially following leaf emergence. In fact, occupancy and abundance of European Dippers were clearly lower along acidified streams with correspondingly low macroinvertebrate biomass (Ormerod and Tyler 1993). Along streams in western Wyoming, American Dipper occupancy increased with density of their preferred prey, but not with total macroinvertebrate density (Feck and Hall 2004). Finally, the distribution of eight Himilayan river bird species was more closely tied to habitat structure than invertebrate abundance (Manel et al. 2000). Occupancy of stream-dependent birds may reflect the density or biomass of their preferred prey, but probably not that of the macrobenthos community as a whole. Furthermore, total macrobenthos biomass or density is generally a poor indicator of water quality in streams (Roy et al. 2003, Sullivan et al. 2004, Stone et al. 2005).

Waterthrushes satisfy most of the criteria for a useful indicator of stream biotic integrity as described by Ormerod and Tyler (1993). First, % EPT was greater where waterthrushes were present (Fig. 3.3). This satisfies portions of criteria 1 and 3: A good indicator reflects stream biotic integrity and should respond consistently across space. We monitored reaches for only one year (i.e., 2003) where waterthrushes were absent, and so we are unable to determine whether this pattern remains consistent among years. We conducted two waterthrush surveys per reach in about 30 minutes each to document established breeding territories (B.J. Mattsson unpublished data). This satisfies criterion 2: A good indicator reflects variables which are easily measured and are informative. Models of % EPT that contained waterthrush occupancy performed as well or better than those with habitat variables. This satisfies criterion 4: a good indicator performs as well or better than other potential indicators of stream biotic integrity.

We expect that habitat would affect the occupancy of waterthrushes in some of the same ways that habitat affects the macrobenthos community. For example, cobble substrate provides both interstitial spaces for macrobenthos (Wood and Armitage 1997) and foraging perches for waterthrushes (Robinson 1995). The observation that habitat features affect waterthrush occurrence does not necessarily invalidate the usefulness of waterthrush as an indicator. It would be difficult to discern whether waterthrushes are affected by macrobenthos directly or only indirectly through the habitat features upon which the macrobenthos depend, as they are inextricably linked. Thus, we will exclude criterion 5: Status of a good indicator will change in response to certain components of stream biotic integrity, and this response is readily separable from effects of other components and from effects of habitat features. Instead, we propose that waterthrushes may be absent from a reach due to metapopulation processes rather than a particular avoidance of a degraded macrobenthic community. For example, a patch of forested headwaters that is isolated by human developments may be less likely to be colonized than one that is connected with adjacent patches of intact riparian forest (Radford and Bennett 2004, Alderman et al. 2005).

Our findings combined with publications on life history attributes (Eaton 1958, Robinson 1995), foraging ecology (Craig 1984, Craig 1987), and breeding biology (Mulvihill 1999, Stucker 2000) provide much of the logic behind using waterthrushes as indicators of stream biotic integrity. This satisfies criterion 6: Ecology of a good indicator is well understood, so that we can identify the connections involved in criteria 1-5. Birders are happy to participate in local, long-term surveys (Greenwood 2003, Sauer et al. 2003). This satisfies the final criterion: It is advantageous for a good indicator to be colourful, big, charismatic or unusual so that it attracts sufficient public interest for the monitoring programme to be sustained and the results heeded.

Incorporating riparian birds into cost-effective bioassessments.-As indicators of stream biotic integrity, birds possess many of the advantages of fish (Karr 1991) and macroinvertebrates (Rosenberg and Resh 1993), plus several additional advantages. First, rather than conducting laborious sampling of benthic stream material, trained amateurs can identify bird species through passive observation or playback recordings of focal species (e.g., McLaren and Cadman 1999, e.g., Rosenberg et al. 1999). Second, the general public will better identify with birds than invertebrates. For example, there was great public support behind the reduction of logging of forests in the Pacific Northwest to benefit Spotted Owls (Garber-Yonts et al. 2004). According to a 2001 survey by the U.S. Fish and Wildlife Service (2002), over 10 million Americans go birdwatching away from residential areas, Americans spend on average over $300 per year observing wildlife, and birding is the most popular of the wildlife-watching activities. This demonstrates a strong interest in birds among the general public. Third, long-term monitoring programs involving volunteer birdwatchers have produced useful information for conservation and management in the U.S. and U.K. (Greenwood 2003, Sauer et al. 2003). Fourth, birds occupy headwater sections where many fish species are absent (Vannote *et al.* 1980). Finally, songbirds associated with streams have been shown to decline with increasing acidification in the headwaters (Ormerod and Tyler 1993, Mulvihill 1999).

Presence or absence of a single bird species or group of bird species may not necessarily mean that stream has high or low biotic integrity (Ormerod and Tyler 1993). Metapopulation processes may operate independently from avoidance or preference for instream conditions (Radford and Bennett 2004, Alderman et al. 2005). Thus, absences of birds should be considered as potential warning signals of degradation that should lead to direct measurements of macrobenthos and catchment-scale land use. As the general public becomes educated about the importance of riparian forests for birds such as waterthrushes and dippers, the target for bioassessment may shift from fish and macrobenthos to birds. Another approach might be to develop indices of biotic integrity based on the entire assemblage of birds that are detected along streams (O'Connell et al. 2000, Bryce et al. 2002).

Until such indices are developed, a simple approach would be to survey stream-dependent songbirds such as Louisiana Waterthrushes in eastern North America (Robinson 1995), dippers in Europe (Ormerod and Tyler 1993) or in western North America (Feck and Hall 2004), or the multitude of riparian obligate birds throughout other parts of the world (Buckton and Ormerod 2002). Ideally, experienced birders would conduct these surveys on at least two separate occasions, within 4 hr of sunrise, and between the time when females of the focal species arrive on the breeding grounds and when they begin incubating. Volunteers may be trained to do these surveys as well. In any case, integrating bird surveys into stream monitoring programs will improve our ability to detect perturbations in headwater ecosystems.

CONCLUSIONS

While several studies have documented relationships among water quality, stream biotic integrity, and dipper occupancy (Ormerod and Tyler 1993, Sorace et al. 2002, Feck and Hall 2004), few have investigated how stream biotic integrity relates to habitat assessments and waterthrush occupancy (Mulvihill 1999, Stucker 2000). We found that waterthrush occupancy and habitat surveys were useful independently or in concert as indicators of biotic integrity in headwater streams. Surveys of waterthrushes would complement existing rapid bioassessment protocols used by many existing volunteer watershed monitoring groups (Kerr et al. 1994, Lathrop and Markowitz 1995, Danielsen et al. 2005). These surveys could extend throughout the inland portions of the eastern U.S. where waterthrushes normally breed (Robinson 1995). Birding is the most popular wildlife-watching activity in the U.S. (US FWS 2002), and many birders are happy to volunteer their time conducting local surveys for waterthrushes (B.J. Mattsson, personal observation). While macrobenthos remain the most useful as direct indicators of stream water quality, stream bird surveys and reach-scale habitat assessments can serve as indicators of the macrobenthos themselves. Using stream-dependent birds as an early warning signal for degradation of stream biotic integrity could improve the efficiency of watershed monitoring programs in detecting and identifying perturbations within the watershed.

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Table 3.1. Schedule for surveying waterthrushes and sampling macroinvertebrates during spring or summer in the Georgia Piedmont from 2002-2004.

Drainage type	No. drainages	≥ 1 waterthrush pair detected?	Time of macroinvertebrate sampling 2002	2003	2004
Rural	8	Yes	Spring	Spring	Spring
Rural	2 *	Yes	Spring	Summer	Spring
Urban	2	Yes	No	Summer	Spring
Urban	4	No	No	Summer	No
Urban	1	Yes	No	No	Spring

* One of the two reaches was also sampled during spring 2003.

Table 3.2. Descriptions of variables used in models of the macroinvertebrate communities of headwater streams in the Georgia Piedmont during spring 2002-2004. Summary statistics were calculated across all 79 samples.

Model parameters	Description	Mean	Range			SE
Response variables						
EPT richness	Number of genera in Ephemeroptera, Plecoptora, and Trichoptera	6.36	0.00	-	20.50	0.61
% EPT	Proportion of EPT abundance relative to total macrobenthos abundance	0.35	0.00	-	0.90	0.03
FBI	Tolerance value from Hilsenhoff Family Biotic Index	3.72	1.16	-	7.00	0.16
Biomass	Biomass (g) of benthic macroinvertebrates and larval salamanders	0.57	0.00	-	17.13	0.29
Macrobenthos	Occupancy of macrobenthos in sample	0.94	0	or	1	NA
Potential indicators						
Waterthrush	Occupancy of Louisiana Waterthrush, including unpaired males	0.89	0	or	1	NA
Pair	Occupancy of Louisiana Waterthrush mated pair	0.83	0	or	1	NA
EPA	Total score from EPA Visual Habitat Assessment	135.2	85.58	-	175.48	2.69
Buffer	Distance (m) to nearest canopy edge uphill from macrobenthos sample	146.1	5.00	-	331.00	12.62
Temporal effects						
Day of year	Julian date of year for macrobenthos sample	156.4	133.00	-	212.00	3.31
Year	Class variable for year of sample measurements	NA	2002	-	2004	NA

Table 3.3. Model selection results for five response variables relating to the macroinvertebrate communities of headwater streams in the Georgia Piedmont during spring 2002-2004. Model parameters are described in Table 3.

Model	K^a	$AIC_c{}^b$	$\log(L)^c$	Δ^d	$w_i{}^e$
EPT richness[f] =					
EPA, Year	6	356.1	-171.4	0.00	0.897
Waterthrush, Year	6	362.0	-174.3	5.88	0.047
Buffer, EPA, Year	7	363.8	-173.9	7.68	0.019
Pair, Waterthrush, Buffer, EPA, Year	9	364.6	-171.7	8.45	0.013
Pair, Waterthrush, Year	7	364.9	-174.5	8.75	0.011
Pair, Year	6	366.1	-176.3	9.92	0.006
Year	5	366.2	-177.6	10.04	0.006
Buffer, Year	6	372.5	-179.6	16.40	0.000

Table 3.3. Continued

Model	K^a	AIC_c^b	$\log (L)^c$	Δ^d	w_i^e
% EPT =					
Pair, Waterthrush, Buffer, EPA	7	-6.3	11.1	0.00	0.887
Pair	4	-0.4	4.5	5.85	0.048
EPA	4	0.5	4.1	6.78	0.030
Buffer, EPA	5	1.5	4.7	7.80	0.018
Pair, Waterthrush	5	1.9	4.5	8.19	0.015
Waterthrush	4	5.0	1.8	11.28	0.003
Null	3	13.3	-3.4	19.54	0.000
Buffer	4	14.5	-2.9	20.78	0.000
FBI =					
EPA	4	206.2	-98.8	0.00	0.235
Waterthrush	4	206.4	-98.9	0.20	0.212
Null	3	207.0	-100.3	0.72	0.164
Buffer, EPA	5	207.6	-98.3	1.39	0.117
Pair	4	208.3	-99.8	2.03	0.085
Pair, Waterthrush	5	208.3	-98.6	2.07	0.083
Buffer	4	208.5	-99.9	2.25	0.076
Pair, Waterthrush, Buffer, EPA	7	210.6	-97.2	4.37	0.026

Table 5. Continued.

Model	K^a	AIC_c^b	$\log(L)^c$	Δ^d	w_i^e
Log (Macrobenthos biomass) =					
Year, Day of year	6	262.6	-124.6	0.00	0.285
Buffer, Year, Day of year	7	263.3	-123.7	0.66	0.205
Buffer, EPA, Year, Day of year	8	264.2	-122.8	1.58	0.129
Waterthrush, Year, Day of year	7	264.3	-124.2	1.64	0.125
EPA, Year, Day of year	7	264.4	-124.2	1.79	0.116
Pair, Year, Day of year	7	264.7	-124.4	2.08	0.101

[a] Number of parameters in model, includes intercept and error term (except for macroinvertebrate model, which is logistic regression)

[b] Akaike's Information Criterion corrected for small sample size (Burnham & Anderson 2002).

[c] Log likelihood, larger values indicate greater goodness of fit.

[d] Difference between AIC_c of top model.

[e] AIC_c weight of evidence, or probability that particular model is the best one of the set.

[f] Parameters in models of EPT richness were estimated using restricted maximum likelihood methods, as one model would not converge using pure maximum likelihood methods.

Appendix 2.1. Parameter estimates for models of five metrics describing macroinvertebrate communities of headwater streams in the Georgia Piedmont during spring 2002-2004. Model parameters are defined in Table 3.

Model parameters	Parameter estimate	Standard error	95% CI
EPT richness* =			
EPA, Year			
Intercept	0.09	0.02	(0.05 , 0.13)
EPA	0.09	0.02	(0.05 , 0.13)
Year 2002	3.63	1.19	(1.30 , 5.97)
Year 2003	5.28	1.01	(3.30 , 7.27)
Reach (random effect)	12.13	2.20	(7.82 , 16.43)
% EPT =			
Pair, Waterthrush, Buffer, EPA			
Intercept	0.13	0.09	(-0.04 , 0.30)
Waterthrush	-0.06	0.15	(-0.35 , 0.23)
Pair	0.33	0.12	(0.09 , 0.57)
Buffer	0.00	0.03	(-0.06 , 0.06)
EPA	0.10	0.03	(0.05 , 0.15)
Reach (random effect)	0.00	0.01	(-0.01 , 0.01)
FBI =			
EPA			
Intercept	3.73	0.16	(3.43 , 4.04)
EPA	-0.28	0.16	(-0.59 , 0.03)
Reach (random effect)	0.89	0.27	(0.36 , 1.42)
Waterthrush			
Intercept	4.61	0.55	(3.53 , 5.68)
Waterthrush	-0.97	0.57	(-2.09 , 0.15)
Reach (random effect)	0.90	0.27	(0.37 , 1.43)
Null			
Intercept	3.72	0.16	(3.40 , 4.03)
Reach (random effect)	0.96	0.28	(0.40 , 1.51)
Buffer, EPA			
Intercept	3.74	0.16	(3.44 , 4.05)
Buffer	-0.16	0.16	(-0.47 , 0.15)
EPA	-0.29	0.16	(-0.60 , 0.02)
Reach (random effect)	0.87	0.27	(0.35 , 1.39)

Appendix 2.1. Continued.

Model parameters	Parameter estimate	Standard error	95% CI
FBI =			
Pair			
Intercept	4.16	0.47	(3.24 , 5.08)
Pair	-0.50	0.50	(-1.47 , 0.48)
Reach (random effect)	0.94	0.28	(0.39 , 1.48)
Pair, Waterthrush			
Intercept	4.61	0.54	(3.54 , 5.68)
Pair	0.63	0.88	(-1.09 , 2.35)
Waterthrush	-1.57	1.02	(-3.57 , 0.43)
Reach (random effect)	0.89	0.27	(0.36 , 1.41)
Buffer			
Intercept	3.73	0.16	(3.41 , 4.04)
Buffer	-0.14	0.16	(-0.46 , 0.18)
Reach (random effect)	0.94	0.28	(0.39 , 1.49)
Ln (Macroinvertebrate biomass) =			
Year, Day of year			
Intercept	9.36	1.75	(5.93 , 12.80)
Year 2002	-0.79	0.58	(-1.93 , 0.35)
Year 2003	-2.23	0.69	(-3.57 , -0.88)
Day of year	-0.03	0.01	(-0.05 , -0.01)
Reach (random effect)	3.01	0.53	(1.97 , 4.05)
Buffer, Year, Day of Year			
Intercept	9.05	1.79	(5.55 , 12.55)
Buffer	0.10	0.13	(-0.15 , 0.36)
Year 2002	-0.86	0.59	(-2.01 , 0.29)
Year 2003	-2.33	0.69	(-3.70 , -0.97)
Day of year	-0.03	0.01	(-0.05 , 0.00)
Reach (random effect)	2.98	0.53	(1.95 , 4.01)
Buffer, EPA, Year, Day of year			
Intercept	7.50	2.54	(2.52 , 12.48)
Buffer	0.04	0.08	(-0.12 , 0.20)
EPA	0.01	0.01	(-0.01 , 0.03)
Year 2002	-0.70	0.59	(-1.86 , 0.45)
Year 2003	-2.22	0.69	(-3.56 , -0.87)
Day of year	-0.03	0.01	(-0.05 , 0.00)
Reach (random effect)	-0.03	0.01	(-0.05 , 0.00)

Appendix 2.1. Continued.

Model parameters	Parameter estimate	Standard error	95% CI
Log (Macroinvertebrate biomass) =			
Waterthrush, Year, Day of Year			
Intercept	7.37	2.74	(2.00 , 12.74)
Waterthrush	0.92	0.98	(-1.00 , 2.85)
Year 2002	-0.79	0.58	(-1.92 , 0.35)
Year 2003	-2.28	0.68	(-3.63 , -0.94)
Day of year	-0.02	0.01	(-0.05 , 0.01)
Reach (random effect)	2.97	0.52	(1.94 , 4.00)
Intercept	7.37	2.74	(2.00 , 12.74)
EPA, Year, Day of Year			
Intercept	7.63	2.53	(2.66 , 12.60)
EPA	0.01	0.01	(-0.01 , 0.03)
Year 2002	-0.68	0.59	(-1.84 , 0.48)
Year 2003	-2.17	0.68	(-3.51 , -0.84)
Day of year	-0.03	0.01	(-0.05 , 0.00)
Reach (random effect)	2.97	0.52	(1.94 , 4.00)
Pair, Year, Day of year			
Intercept	9.36	1.76	(5.92 , 12.80)
Pair	0.00	0.04	(-0.08 , 0.09)
Year 2002	-0.79	0.58	(-1.93 , 0.35)
Year 2003	-2.23	0.69	(-3.57 , -0.88)
Day of year	-0.03	0.01	(-0.05 , -0.01)
Reach (random effect)	3.01	0.53	(1.97 , 4.05)

[*] Parameters were estimated using restricted maximum likelihood methods.

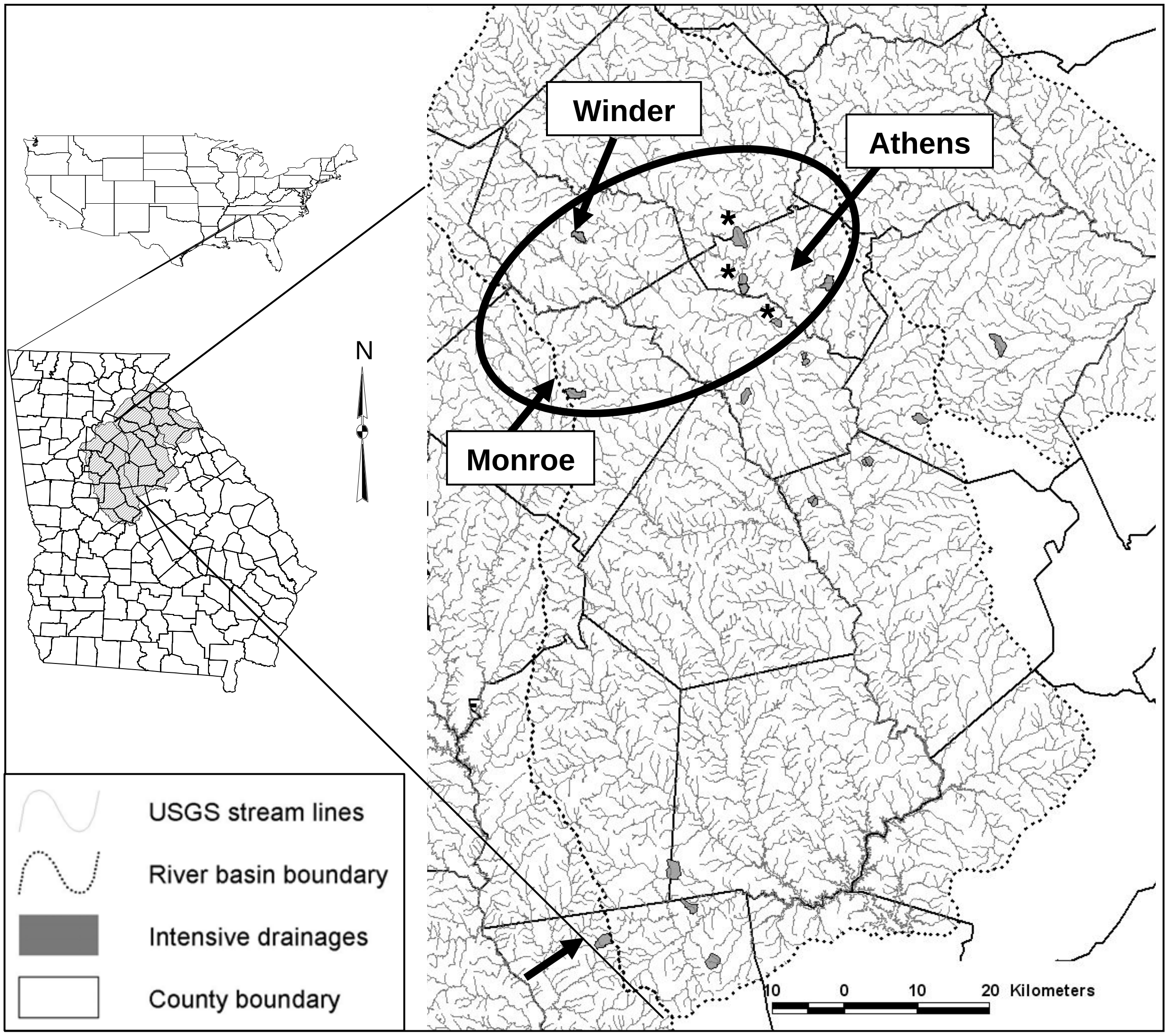

Fig. 3.1. Map of 17 drainages selected for waterthrush surveys and macrobenthos samples in the Upper Ocmulgee, Upper Oconee, and Broad River Basins of Georgia, USA, as viewed from east to west. The seven drainages inside ellipse were in the cities of Monroe, Winder, and Athens. These urban drainages had ≥ 5% urban land cover, while the ten drainages beyond the ellipse were dominated by rural land uses and had < 5% urban land cover. One of the four southern drainages was on Piedmont National Wildlife Refuge (PNWR), while the remaining three were just east of the refuge. The three urban drainages with an asterisk (*) had breeding waterthrushes, and all rural drainages had breeding waterthrushes.

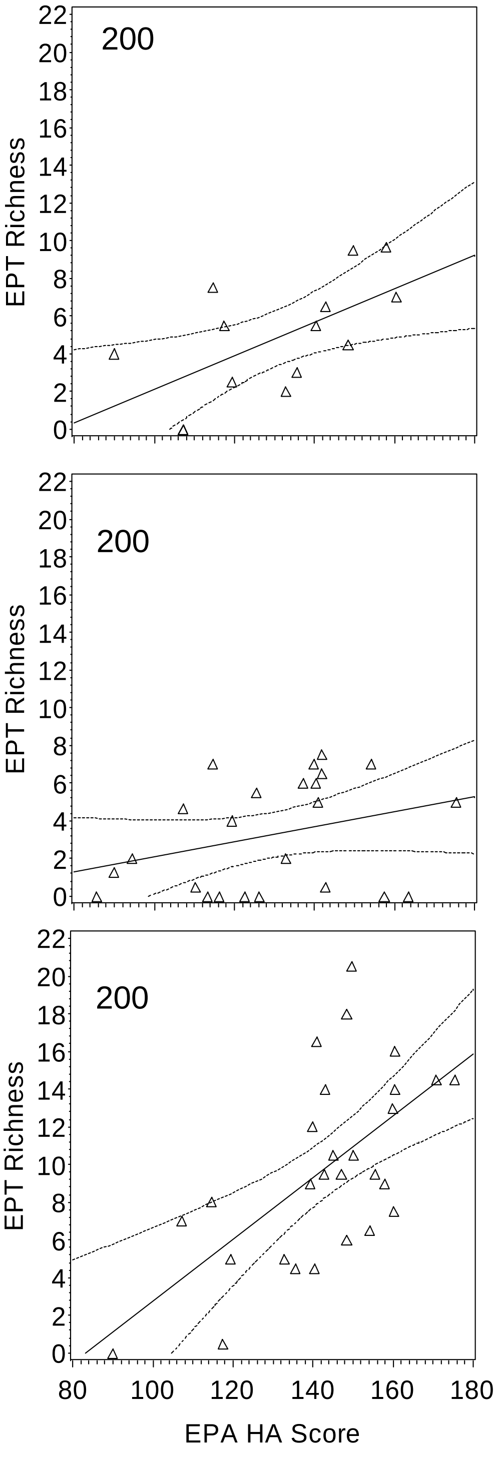

Fig. 3.2. Mean EPT richness per reach increased as a function of the EPA Visual Habitat Assessment (VHA) score in all years of the study, including 2002, 2003, and 2004, with the final year having higher EPT richness than the first two years. Lines through points are mean slopes and 95% confidence limits from a model that included EPA VHA and the intercept. Waterthrush and buffer variables were relatively unimportant in models of EPT richness. See Tables 3 and 4 for parameters in all candidate models.

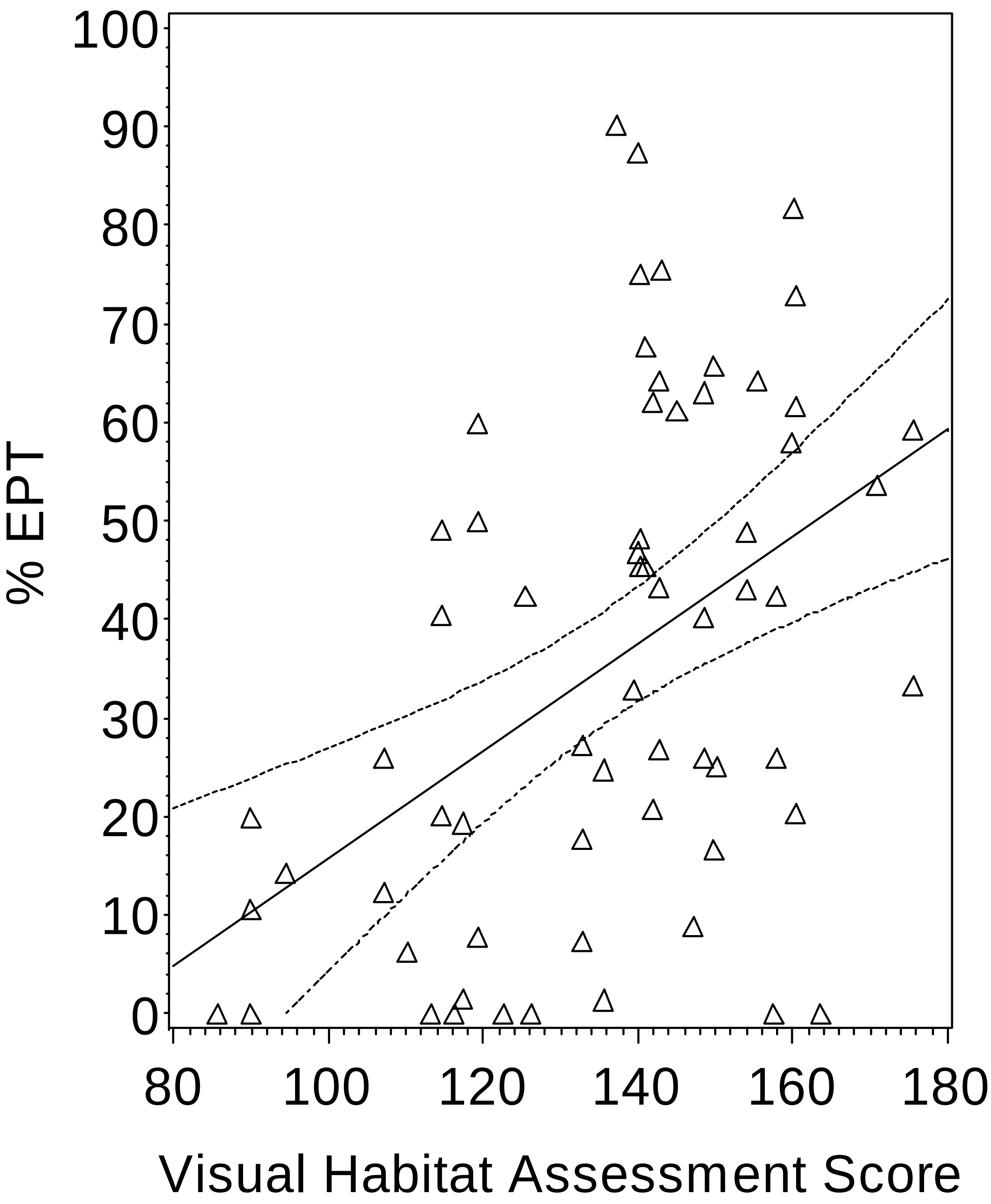

Fig. 3.3. Mean percent EPT per reach increased as a function of the EPA Visual Habitat Assessment (VHA) score. Lines through points are mean slopes and 95% confidence limits from a model that included EPA VHA and the intercept. Male waterthrush and buffer variables were relatively unimportant in models of EPT richness. See Tables 3 and 4 for parameters in all candidate models.

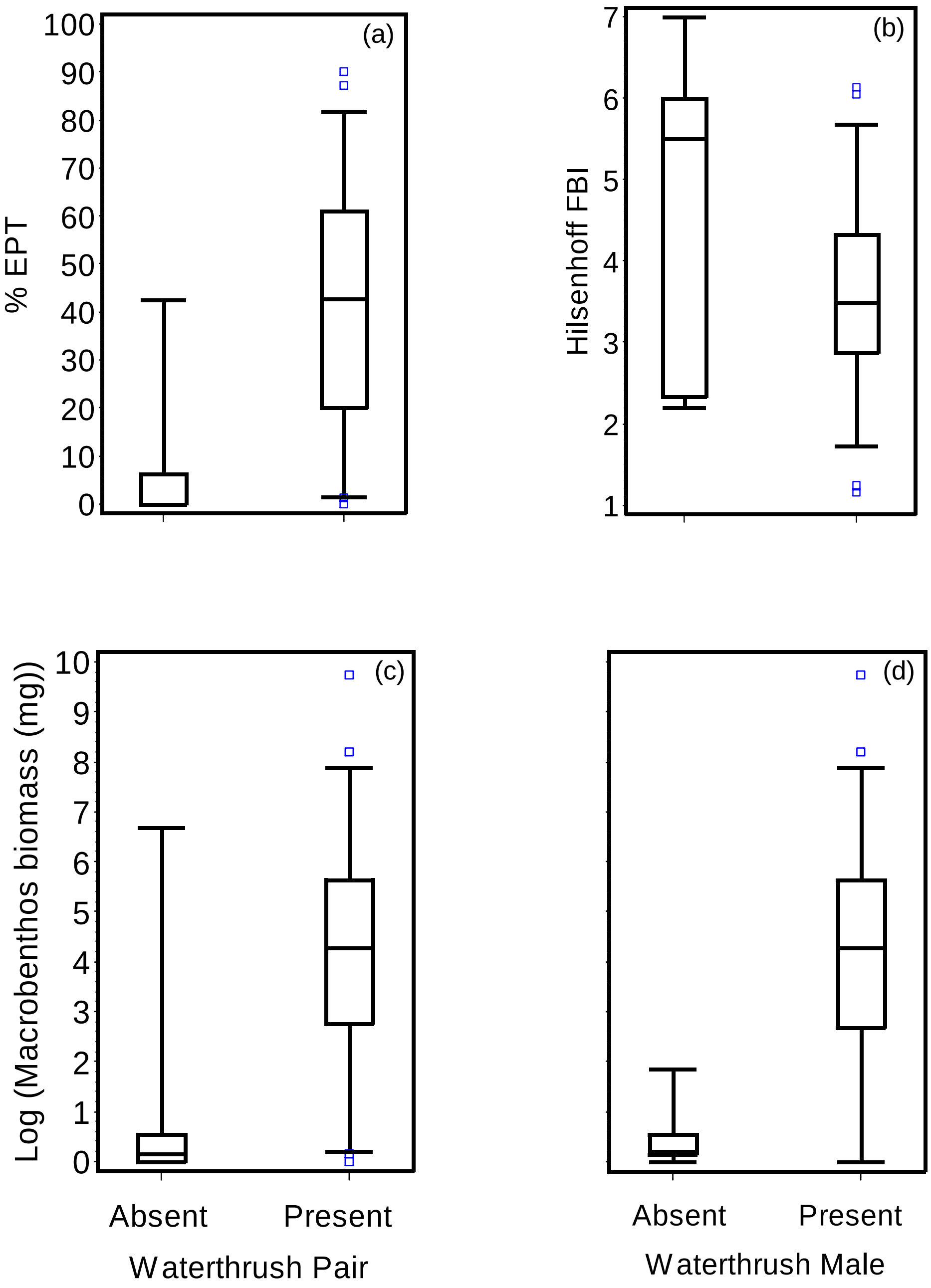

Fig. 3.4. Percent EPT (a) was greater in territories of breeding waterthrush pairs, while the Family Biotic Index (FBI, b) was lower along reaches where waterthrush males were present. Log-transformed macrobenthos biomass (c, d) was greater along reaches where waterthrush males or females were present compared to areas where they were absent. The bottom and top edges of each box represent the 25th and 75th percentiles, each centre horizontal line represents the median, and the lower and upper whiskers represent the 5th and 95th percentiles, respectively. Values beyond these percentiles are represented by squares. Habitat variables were relatively unimportant in models of macrobenthos biomass, percent EPT, and FBI.

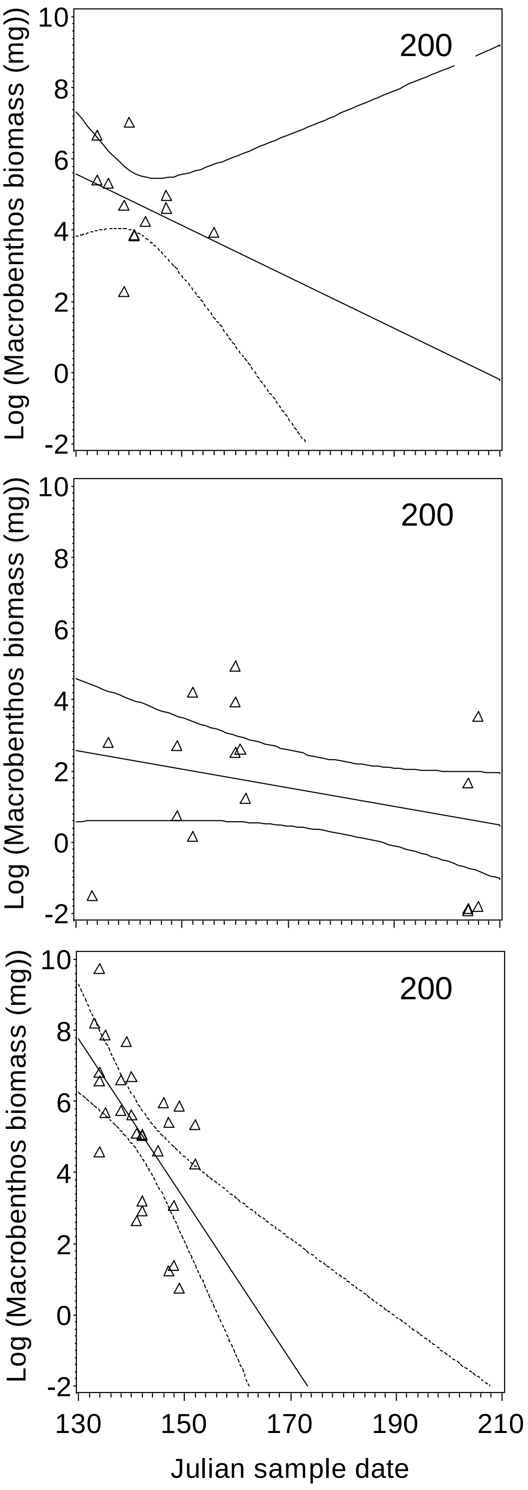

Fig. 3.5. Log-transformed macrobenthos biomass decreased as a function of Julian sampling date in all years of the study, including (a) 2002, (b) 2003, and (c) 2004. Lines through points are mean slopes and 95% confidence limits from a model that included sampling date and the intercept. Habitat variables were relatively unimportant in models of macrobenthos biomass. See Table 4 for a complete list of candidate models.

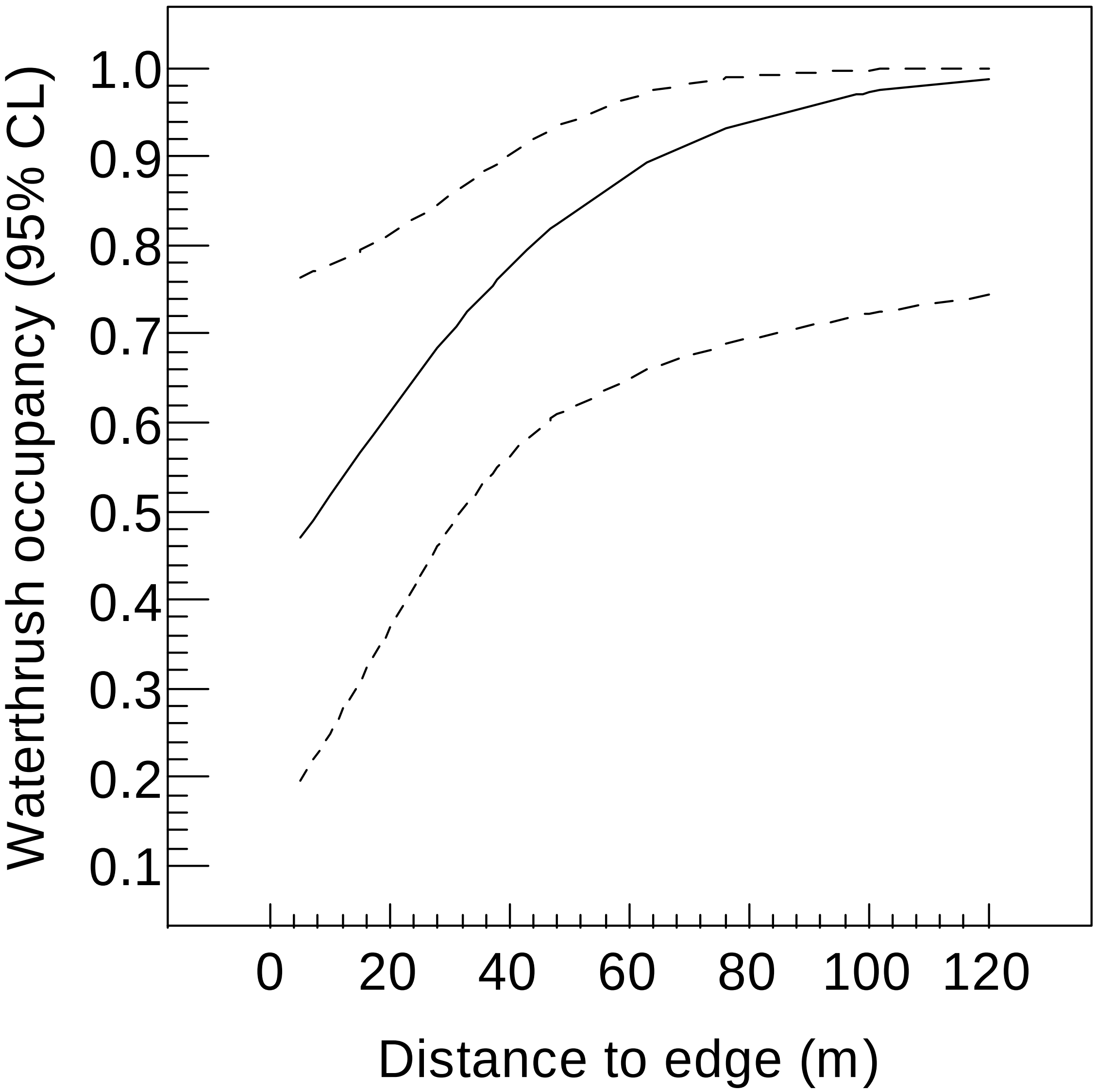

Fig. 3.6. Waterthrush occupancy increased as a function of distance from stream to forest canopy edge. The solid line represents the mean, while dashed lines represent upper and lower 95% confidence limits.

CHAPTER 4

WHICH LIFE HISTORY COMPONENTS DETERMINE BREEDING PRODUCTIVITY FOR INDIVIDUAL SONGBIRDS? A CASE STUDY OF THE LOUISIANA WATERTHRUSH[1]

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[1] Mattsson, B.J., and R. J. Cooper. Submitted to *The Auk*, 10/28/2005

ABSTRACT.- Population dynamics of small songbirds are driven in part by fecundity (i.e., the number of young that reach fledging age per female in a breeding season) or productivity (i.e., the number of young that survive the dependent stage per adult female within a breeding season). Due to the challenges associated with estimating productivity or fecundity directly, some researchers estimate fecundity indirectly using either the Donovan (Donovan et al. 1995), P-G (Pease and Grzybowski 1995), or F-S (Farnsworth and Simons 2005) approach, all of which produce a single point estimate. We developed an individual-based (I-B) model which estimates variability in productivity of Louisiana Waterthrushes (waterthrushes; *Seiurus motacilla*) based on various aspects of their breeding cycle. Our empirical estimate of waterthrush productivity ($\bar{x}$ =1.50, 1.45 SD) was similar to that provided by our I-B model ($\bar{x}$ = 1.07, 1.24 SD). Contrary to emerging arguments about the importance of renesting for reproduction, waterthrush productivity was most sensitive to and increased dramatically with increasing fledgling survival, daily nest survival, followed by nestling survival. Productivity increased less dramatically with increasing renesting probability, second brood probability, and maximum days to lay. The remaining four factors had no detectable effects on productivity. When compared with our I-B model, the Donovan and P-G approaches often overestimated fecundity, up to 2.1 young fledged per female. In contrast, the F-S approach often produced estimates that were similar to those from our I-B model. Our I-B model can be generalized to accomodate other breeding factors, including brood parasitism and temporal variability.

INTRODUCTION

Population dynamics of migratory songbirds depend on one of two main life history characteristics: survival of adults (overwinter and migration) and recruitment of individuals into the population. Recruitment includes immigration of new individuals (adults or juveniles) and production of young that survive to breed in their natal population. Difficulties in recapturing birds that disperse away from their site of capture in the subsequent year can prevent accurate estimates of adult survival and recruitment (Anders and Marshall 2005). As such, the most crucial factors driving populations of migratory songbirds remain largely unknown (Sillett and Holmes 2002).

In contrast, empirical estimates of productivity (i.e., the number of young that survive the dependent stage per adult female within a breeding season) exist for some populations of migratory songbirds (Powell et al. 1999, Gardali et al. 2000). Furthermore, productivity may be the most influential factor driving populations (Temple and Cary 1988, Noon and Sauer 1992). Some have argued that management efforts to improve other aspects of the life cycle such as survival during migration or on wintering grounds may be much less cost effective (Conroy et al. 1995, Donovan and Thompson 2001). Thus, regardless of what life cycle component drives migratory populations, productivity should be the focus of conservation efforts for species with declining populations.

Despite its importance, estimating productivity for individual migratory songbirds remains rare. Obtaining accurate estimates requires intensive tracking of females and juveniles to account for factors such as probability of renesting and fledgling survival. Migratory songbirds are often cryptic or disperse widely from the former nest site, making radio telemetry a necessity for obtaining accurate estimates of these factors. Until recently, high cost of small radio transmitters has prevented researchers from conducting telemetry for this purpose (Anders et al. 1997, Powell et al. 1999).

More commonly, researchers estimate fecundity (i.e., the number of young that reach fledging age per female in a breeding season), which does not require tracking of fledged young.

Obtaining accurate estimates of fecundity, however, does require an estimate of renesting probability based on intensive tracking of females using radio-telemetry (Walk et al. 2004), resighting of color-bands (Morrison and Bolger 2002), or territory mapping (Smith et al. 2002).

Due to the high costs required to track sufficient numbers of females intensively (Trine 1998), many researchers estimate fecundity indirectly. In particular, researchers adopt one of three approaches based on deterministic models, which provide a point estimate of fecundity for an average female. The first approach, introduced by Donovan et al. (1995, henceforth Donovan approach), includes point estimates of nest survival, number of young fledged per successful nest, and number of nest attempts per female. Pease and Grzybowski (1995, henceforth P-G approach) described another approach which assumes that the average female continues renesting until the breeding season expires while assuming that renesting intervals are constant. Like the Donovan approach, the P-G approach uses point estimates of nest survival and number of young fledged per successful nest. Farnsworth and Simons (2005, henceforth F-S approach) recently modified the P-G approach to incorporate renesting probability.

These models for estimating fecundity have some limitations. None of them provide estimates of variability in fecundity among individuals within the population. In addition, they each hold assumptions that could lead to biased estimates of fecundity by either underestimating or overestimating the number of renesting attempts per female. The Donovan approach may underestimate (Anders and Marshall 2005), while the P-G and F-S approaches may overestimate the number of renesting attempts per female (Jones et al. 2005). All of these approaches assume that all nests have the same survival rate and that all nests fledge the same number of young. The P-G and F-S approaches assume that all females have the same breeding season length and number of days between nest attempts. Finally, the F-S approach assumes that all females have the same likelihood of another nest attempt following their previous attempt, regardless of nest fate. Any of these assumptions may be violated when considering the natural variability in nest survival rate, breeding season length, days between nest attempts, and renesting probability. While some studies have evaluated relationships between some of these factors and annual variability in fecundity (Pease and Grzybowski 1995, Nagy and Holmes 2004), relationships between these factors and variability in fecundity among individuals remains unknown for many populations (Powell et al. 1999).

Accounting for this variability among individuals can be achieved using individual-based (I-B) models. This approach provides benefits that are unavailable using the population-level approaches described above (Grimm 1999). First, they provide ways for examining how different scenarios affect outcomes at the population level. Second, they provide a means to evaluate hypotheses about how factors affecting individuals translate into population-level processes. Researchers have used I-B models to address questions in avian ecology such as determining optimal clutch size in the face of brood parasitism (Takasu 2004) and identifying drivers of population dynamics (Letcher et al. 1998). In the case of songbird reproductive output, some have proposed that nest survival is overvalued while breeding season length (i.e., multi-brooding and renesting) is undervalued as drivers of fecundity (Pease and Grzybowski 1995, Murray 2000, Thompson et al. 2001). Using an I-B model, Powell et al (1999) found that Wood Thrush productivity was sensitive to survival of nests and fledglings but not breeding season length.

We developed a similar I-B model which allows us to estimate productivity of Louisiana Waterthrushes (waterthrushes; *Seiurus motacilla*) based on various aspects of their breeding cycle including nest survival, clutch size, renesting, and fledgling survival. Waterthrushes provide an excellent opportunity for such a modeling effort. They nest in banks along forested, headwater streams (Robinson 1995), allowing us to readily locate, monitor, and band entire families. Furthermore, waterthrush fledglings typically remain within 50 m of the stream and within the territory of their parents (Mattsson, unpublished data), making them relatively easy to resight without the aid of radio telemetry. Using the I-B model in conjunction with field data, we identify which breeding factors are most important for waterthrush productivity by varying each factor across its range of natural variation using sensitivity analyses. We then compare estimates produced by our I-B model with those produced by the Donovan, P-G, and F-S approaches. Finally, we suggest how our I-B model may be applied to other birds that exhibit repeated nesting attempts in a season.

METHODS

Study sites.- Our study took place in 13 forested, headwater drainages of the southern Piedmont in north-central Georgia. Nine of the drainages are in the Upper Oconee River basin near Watkinsville, Georgia, and four are in the Upper Ocmulgee River basin in Piedmont National Wildlife Refuge, Georgia. We monitored nests on ten rural drainages from 2002-2004, and we added 3 sites in 2004 that were surrounded by more urban land use.

White oak (*Quercus alba*), red maple (*Acer rubra*), yellow poplar (*Liriodendron tulipifera*), American sweetgum (*Liquidambar styraciflua*), sourwood (*Oxydendrum arboreum*) and hickory (*Carya* spp.) dominated the canopies along study streams, although 15 other species were also present as canopy trees. Understories were generally shaded and sparse and included flowering dogwood (*Cornus florida*), American hornbeam (*Carpinus caroliniana*), black cherry (*Prunus serotina*), blueberry (*Vaccinium corymbosum*), Eastern red cedar (*Juniperus virginiana*), Georgia buckeye (*Aesculus sylvatica*), willow oak (*Quercus phellos*), and paw paw (*Asimina triloba*).

Canopy gaps were dominated by muscadine (*Vitis rotundifolia*), spicebush (*Lindera benzoin*), greenbriar (*Smilax* spp.), and blackberry (*Rubus argutus*). Chinese privet (*Ligustrum sinense*), American holly (*Ilex opaca*), and river cane (*Arundinaria gigantea*) occurred in floodplains or disturbed soils.

Data collection.- From late March through early June of 2002, 2003, and 2004, we located waterthrush nests by following adults as they constructed their nests or fed young, and by systematically searching bank crevices. Once nests were located, observers monitored them every 2-4 days, recording number of eggs or nestlings and documenting evidence of nest failure or fledging. We assumed no partial egg loss during egg laying when estimating clutch size. We determined hatch date by morphology of nestlings (e.g., size relative to the egg). For the purpose of analysis, observation days began when the nest was found or when the clutch was filled, and the observation period ended at the midpoint between the last check while active and the first day the nest was observed to be empty for nests with known fates. For nests with uncertain fate, the last observation date was the last date the nest was observed active. This was to minimize bias in the estimate of nest success (see Manolis et al. 2000).

When possible, we captured adult females using mist nets or butterfly hoop nets at the nest. We also banded all nestlings from each monitored nest 1-3 days before fledging. Each waterthrush received unique combinations of colored leg bands and a USGS aluminum band, which enabled us to track the female or fledged broods following nest predation or fledging every 2-7 days. In cases where an unbanded female renested, we assumed that she was the same female as the previous nest unless > 2 weeks had elapsed between attempts. Otherwise, we assumed this was a different female (Budnik et al. 2000). If nestlings flapped, chirped, or had pins unsheathed > 5 mm during the last nest check, then we considered them ready to fledge (usually day 8 or 9 post-hatching; Mattsson pers. obs.). Otherwise, we determined fledging status based on our observations of fresh fecal sacs near the nest, banded juveniles, or adults scolding or with food during subsequent visits to the territory. If we resighted fledglings > 1 week after fledging, then we considered them to be successful juveniles. Juveniles are likely most at risk of predation during the first week after fledging (Anders et al. 1997).

Simulation model.-After identifying 11 factors (henceforth breeding factors; Table 1) that describe many aspects of the breeding cycle, we developed an individual-based stochastic model that enabled us to estimate fecundity and productivity for a hypothetical female waterthrush (Fig. 4.1). Using this approach, we induced heterogeneity in breeding factors (e.g., nest survival rate, clutch size) to represent variability within the population using probability distributions derived from empirical data. The I-B model required as input the means, process variances (i.e., variance among nest attempts), and 5th - 95th percentiles of each breeding factor, based on data from each nest monitored (Table 4.1). For drawing simulated values of breeding factors, we chose a probability distribution appropriate to the parameter of interest, and we confirmed the selection against field data using goodness of fit measures. Each iteration represented an individual female and began by drawing random rates and probabilities from a beta distribution using field estimates for mean and nest-wise variance of each rate including egg laying, daily nest survival, nestling survival, renesting, and double-brooding. Nest cycle length and maximum days to lay were randomly generated in similar fashion, except they were drawn from a normal distribution. Intervals between nests (both renests and second broods) were drawn randomly from a gamma distribution. Next, clutch size for the first nest was drawn randomly from a random binomial distribution using the egg laying rate and the number of trials, represented by the maximum number of eggs in a clutch (i.e., 5 for waterthrushes). Daily nest fate (fledged or failed) was then drawn from the binomial distribution, based on daily nest survival rate. In an iterative fashion, the nest was exposed to failure on a daily basis until egg laying and nest cycle were completed. If the nest survived the nest cycle, then it was considered fledged. In this case, the number of fledglings was drawn randomly from a binomial distribution using the nestling survival rate and the number of trials, represented by clutch size. The number of juveniles was then drawn in a similar fashion, except using the fledgling survival rate and number of fledglings as trials. Next, the decision to renest (for failed nests) or double-brood (for fledged nests) was drawn randomly from a binomial distribution using the probability of renesting or double-brooding. While we did not measure survival rates of females directly, nest survival and renesting was an indication that the female survived and remained on the study site. Thus, daily nest survival and renesting probability are reflections of female survival in our model. The bird could begin laying eggs at the renesting rate if 1) the number of days elapsed did not exceed the maximum days to lay, and 2) they had less than 3 previous nesting attempts. The model included a total of 11 stochastic variables and 2 constants (i.e., maximum clutch size and maximum number of nesting attempts).

Sensitivity analysis.- For each set of simulations, the model held one factor constant while the others varied randomly based on the input values for their means and variances for 200 iterations. For example, nest survival was held constant at 11 different values between its 5th and 95th percentiles (henceforth, range of natural variation) while the other 10 factors varied randomly. We plotted the mean productivity from each set of simulations, and we used these plots to determine how productivity changed when altering a specific breeding factor across its range of natural variation.

Comparisons with other approaches.- To allow a comparison with our direct estimate of productivity from actual field data, we ran one simulation where all the factors varied stochastically around their means based on their respective variances. We calculated the mean fecundity predicted by our stochastic model and compared this to those predicted by the other three approaches (i.e., Donovan, P-G, and F-S). Finally, we used a sensitivity analysis to compare our I-B model to the other three approaches following the methods above, except we excluded fledgling survival from the analysis.

RESULTS

We captured and resighted most adult female waterthrushes (n = 131 of 151, 86.8%) from 173 nests, and the number of observation days from these nests totaled 2,429. Of these broods, 101 (58%) reached fledging age, and 83 (48%) included at least one juvenile that survived > 1 week after fledging (Table 4.1). Of these families, four (4.8%) females began a second brood. We observed banded adults with unbanded fledglings from first broods in four territories during the study. Thus, we monitored the vast majority of fledged nests on our plots, and we have no reason to believe these data are not representative of the population.

Of 75 nests (including renests and second broods) that either failed or did not produce successful juveniles, 36 (49%) were followed by a renesting attempt (Table 4.1). Third (n = 3) and fourth (n = 1) nesting attempts were uncommon. Of the 32 renests with known egg laying date (Table 4.1), 66% had a clutch of 4 eggs and 22% had 3 eggs. In contrast, 77% of the 97 first nests had 5 eggs, while 19% had 4 eggs. Of the 449 eggs laid in nests that eventually fledged at least one young, 90% hatched successfully and reached fledging age (Table 4.1). Of the 101 fledged nests, 33% fledged fewer young than eggs laid, including unhatched eggs and disappearance of eggs or young.

Despite the presence of Brown-headed Cowbirds (*Molothrus ater*), we did not observe any parasitized waterthrush nests. Of the 64 nests that failed before young were ready to fledge, predation was the primary cause of failure (n = 51, 79.7%), 10 nests were abandoned with eggs or young, 2 nests were washed out during floods, and 1 nest was buried by natural bank slumping. Of the 10 abandoned nests, four were followed by renests, while the remaining six were suspected to be due to adult mortality based on the absence of females during subsequent visits to the territory.

Our direct field estimate of productivity (i.e., number of young that disperse from the nest area per adult female) was 1.50 (n = 130, 1.45 SD, range: 0 - 5), while a simple stochastic run in our simulation model produced an estimate of 1.07 (n = 200, 1.24 SD, range: 0 - 5). Productivity was most sensitive to and increased dramatically with increasing fledgling survival, daily nest survival, followed by nestling survival (Fig. 4.2). Productivity increased less dramatically with increasing renesting probability, second brood probability, and maximum days to lay (Fig. 4.2). Productivity peaked twice when varying nest cycle length, once near 21 days and again near 23 days (Fig. 4.2). Egg laying rate (i.e., number of eggs per clutch), renesting interval, and second brood interval had no detectable effect on productivity (Fig. 4.2).

Our field estimate for mean fecundity was 2.89 (n = 130, 1.86 SD). A simple stochastic run produced a mean fecundity estimate (number of young fledged per adult female) of 2.42 (n = 200, 2.11 SD), while the Donovan, F-S, and P-G approaches rendered point estimates of 2.93, 2.31, and 3.25, respectively. Using our I-B model as a baseline in a sensitivity analysis, the Donovan approach often overestimated fecundity, up to 1.6 young fledged per female (Fig. 4.3). This was most evident when nestling survival was low (rate ≤ 0.5), when the breeding season was short (last day to lay ≤ 16), and to a lesser degree when renesting was infrequent (probability ≤ 0.5). Likewise, the P-G approach often overestimated fecundity, up to 2.1 young fledged per female (Fig. 4.3). Overestimation was greatest when the breeding season was long (≥ 37 days), renesting was infrequent (probability ≤ 0.29), and to a lesser degree when renest clutches were large (egg laying rate ≥ 0.83). In contrast, the F-S approach often produced estimates that were similar to those from our I-B model, except for mild underestimation when renest clutches were small (egg laying rate ≤ 0.52; Fig. 4.3).

DISCUSSION

Determinants of productivity.- According to our individual-based model, productivity of individual females was most sensitive to measured variation in survival of fledged young, nests, and, to a lesser degree, survival of eggs and young in the nest. Other factors such as nest cycle length, clutch size, interval between nests, renesting probability, and breeding season length were much less important for productivity. Based on our findings, predation on eggs and young is likely limiting productivity for individual waterthrushes. Predation on the first nest attempt is probably more influential than subsequent attempts, as renesting had little effect on productivity. If they can protect their offspring and themselves from predation during the first attempt of the season, then females can maintain sufficiently high productivity each year. If food were limiting, we would expect to see factors such as egg laying rate or nestling survival influence productivity more dramatically. Insectivorous birds may spend less time foraging and more time guarding the nest when arthropods are abundant, so there may be some interaction between availability of arthropods and predation (Zanette et al. 2003, Mattsson and Niemi 2006). This hypothesis remains to be evaluated for waterthrushes.

Using a similar I-B model, Powell et al. (1999) found that Wood Thrush productivity was sensitive to variation in renesting interval, nest success, fledglings per successful nest, and survival of adults and juveniles. Although their study system was similar, their model differs from ours in the following ways: 1) clutch size and nestling survival are combined into a single breeding factor (i.e., number of fledglings per successful nest), 2) females themselves are exposed to predation, 3) juveniles are exposed to predation on a daily basis through the entire dependent stage, and 4) females always renest if they are still alive after a previous nest attempt (unless the last day to lay had passed). They used radio telemetry to estimate daily survival rates for females and juveniles. We lacked such data, so we modeled juvenile survival as an instantaneous number survived after one week out of the nest, and we modeled female survival indirectly through our estimate of renesting probability. Powell et al. (1999) were able to track females between nest attempts, sometimes 5 km from their previous attempt. As our study sites were < 3 km long, we may have underestimated renesting probability for waterthrushes. Despite these differences, we found that productivity was sensitive to a similar set of breeding factors.

Using a 21-year data set of direct fecundity estimates for Wood Thrushes, Underwood and Roth (2002) found that annual variability in seasonal fecundity was explained best by May fecundity, and to a lesser degree the number of nest attempts and nest success. This analysis increases our knowledge about songbird breeding biology, but lumping individual fecundity estimates into an annual mean disguises potentially important individual-level variability. In a similar analysis, Nagy and Holmes (2004) found that annual variability in fecundity for Black-throated Blue Warblers during a 16 year period was best explained by a model that included nest survival, double brooding, renesting probability, and food availability. Unfortunately, neither of these studies considered the influence of other factors they measured like season length, nest cycle length, renesting interval, or clutch size. These two data sets (Underwood and Roth 2002, Nagy and Holmes 2004) present great opportunities for investigating more closely the factors that drive individual variation in fecundity for songbirds using an I-B model.

Alternative methods for estimating fecundity.- Two of the three deterministic approaches to modeling fecundity produced point estimates that were similar to our empirical and stochastic mean estimates of waterthrush fecundity. When considering variability in the underlying breeding factors, however, they exhibited some bias. First, the Donovan approach slightly overestimated fecundity, and this was consistent with Anders and Marshall (2005). This method was most problematic when nestling survival was low, when the breeding season was short, or when renesting was infrequent. In general, the Donovan approach overestimated breeding productivity or the number of young fledged per female. Anders and Marshall (2005) also found that this approach overestimates fecundity. This bias stems from assuming a fixed number of renesting attempts (in this case, one) and a fixed number young fledged per successful nest. Second, the F-S approach, though it produced a point estimate similar to our stochastic estimate, slightly underestimated fecundity when clutches in renests were small. The P-G approach, on the other hand, grossly overestimated fecundity. Like the Donovan approach, this method does not restrict renesting probability. This failure to account for restricted renesting also led to overestimation when the breeding season was long.

While the P-G and F-S approaches limited breeding season length, they did not link clutch size to nest survival. This probably led to overestimation of fecundity by the P-G approach and underestimation of fecundity by the F-S approach for large and small renest clutches, respectively. When clutch sizes are large, nests are exposed longer to failure, whereas small clutches are exposed less to failure. The I-B model takes this into account so that females with extremely large clutches fledge fewer young than would be expected without accounting for increased exposure times. Despite considerable complexity in the F-S and P-G models (10 constants as input parameters), neither method produces an estimate for the variability in fecundity among individuals in the population. The I-B model approach, however, does provide an estimate of variance without adding much model complexity (11 stochastic variables and 2 constants as input parameters).

Potential additions to our I-B model.- Our I-B model can be expanded to suit life history characteristics of other populations. For example, while brood parasitism was non-existent in this population of waterthrushes, this has important consequences for fecundity in some populations of songbirds (Pease and Grzybowski 1995, Dececco et al. 2000, Smith et al. 2002). Depending on the frequency of brood parasitism, researchers could expand our I-B model to include parasitism when applying the model to other populations. Second, our model assumes normal, gamma and binomial distributions for input parameters, but these distributions may not fit data collected elsewhere. Thus, our I-B model could be expanded to allow more user control of which distributions are used for random sampling. Finally, our I-B model assumes the following are constant throughout the season: nest survival rate, nestling survival rate, fledgling survival rate, renesting probability, and renesting interval. Nest survival, for example, has been shown to vary temporally in some populations (Shaffer 2004). Our finding that productivity was less sensitive to renesting factors may be biased if renesting probability or intervals changed throughout the season. Depending on the number of time steps, however, allowing these factors to vary temporally would add considerable complexity to the I-B model. While we saw no evidence for temporal variation in any breeding factors for waterthrushes in our study, it may be wise to include this for other populations.

Conclusion.- Discovering which factors influence fecundity and productivity can provide more detailed insight into the factors driving population dynamics of birds. Contrary to emerging arguments that multi-brooding and renesting are important drivers of fecundity (Pease and Grzybowski 1995, Murray 2000, Thompson et al. 2001), we found that factors relating to survival of nests and fledglings were much more influential than those relating to renesting, double-brooding, and breeding season length for fecundity and productivity of Louisiana Waterthrushes. Employing a stochastic model was essential to evaluate this question, as deterministic approaches provide only a point estimate of fecundity, which may be biased. Empirical approaches provide no way of examining the sensitivity of their estimates to individual breeding factors. In particular, analyses of long-term data sets that substitute years for individuals may obscure important individual-level variation. The power of our individual-based model is that researchers can expand it to account for characteristics of individuals in other populations including brood parasitism, alternative statistical distributions for stochastic factors, and temporal variation in breeding factors.

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Table 4.1. Descriptions of breeding factors used in sensitivity analysis for productivity of Louisiana Waterthrushes in the Georgia Piedmont (2002-2004).

Field measurement	Description or individual-based calculation
Egg laying - 1st nest [a]	No. eggs laid in 1st nest / maximum clutch size of 5 eggs
Egg laying - renest [a,b]	No. eggs laid in renest / maximum clutch size of 5 eggs
Daily nest survival	Daily nest survival rate (Hazler 2004)
Nestling survival [c]	No. young fledged / no. eggs laid
Fledgling survival [c]	No. fledglings observed >1 week after fledging / no. fledged
Renesting probability [d]	Probability that female renests after nest failure
2nd brood probability [d]	Probability that female lays eggs while 1st brood juvenile lives
Renest interval [a,b]	No. days between previous attempt failed and egg laid in renest
2nd brood interval [a,b]	No. days between 1st brood fledging and 2nd brood egg laying
Nest cycle [a,e]	No. days from completion of egg laying to fledging
Max. days to lay [a,f]	
Mean	No. days between mean egg laying date for 1st nests and final nests
SSE	Sum of standard errors for egg laying date for 1st nests and final nests
95% CL	Mean +/- 1.96 * SSE
95th Percentile	Subtract 5th percentile for 1st nest egg laying dates from 95th
5th Percentile	Set at 1, no renesting allowed, represents females that arrive late

[a] Hatch or lay date known

[b] Monitored previous nest by banded female

[c] Certain at least one young ready to fledge

[d] Revisited at least weekly for 4 weeks after nest failed or fledged

[e] Both hatch and lay date known

[f] Final nest must be a final renest or 2nd brood

Table 5.1. Estimates for breeding factors used in sensitivity analysis for productivity of Louisiana Waterthrushes in the Georgia Piedmont (2002-2004).

Field measurement	Distribution	Nests	Trials [a]	Mean	5-95th Percentiles	95% CL[b]	Variance [b]
Egg laying - 1st nest	Beta-binomial	97	485	0.94	0.80 - 1.00	0.92 - 0.96	0.011
Egg laying - renest	Beta-binomial	32	160	0.74	0.40 - 1.00	0.66 - 0.80	0.039
Daily nest survival	Beta-binomial	173	2429	0.97	0.67 - 1.00	0.97 - 0.98	0.000
Nestling survival	Beta-binomial	101	449	0.90	0.50 - 1.00	0.87 - 0.92	0.000
Fledgling survival	Beta-binomial	101	394	0.48	0.00 - 1.00	0.45 - 0.54	0.001
Renesting probability	Beta-binomial	75	75	0.49	0.00 - 1.00	0.38 - 0.60	0.003
2nd brood probability	Beta-binomial	83	83	0.08	0.00 - 1.00	0.04 - 0.17	0.001
Renest interval	Gamma	29	-	6.59	4.00 - 12.00	5.83 - 7.56	0.010
Second brood interval	Gamma	4	-	12.75	8.00 - 17.00	9.77 - 18.35	0.012
Incubation + nestling pd.	Normal	32	-	21.66	20.00 - 24.00	21.29 - 22.02	1.007
Last day to lay	Normal	27	-	28.64	1.00 - 52.00	24.00 - 33.00	6.134

[a] Sum of the total possible number of eggs, nest observation days, fledglings, juveniles, renests, or second broods.

[b] Variance and confidence intervals were calculated based on variability among individual nest attempts.

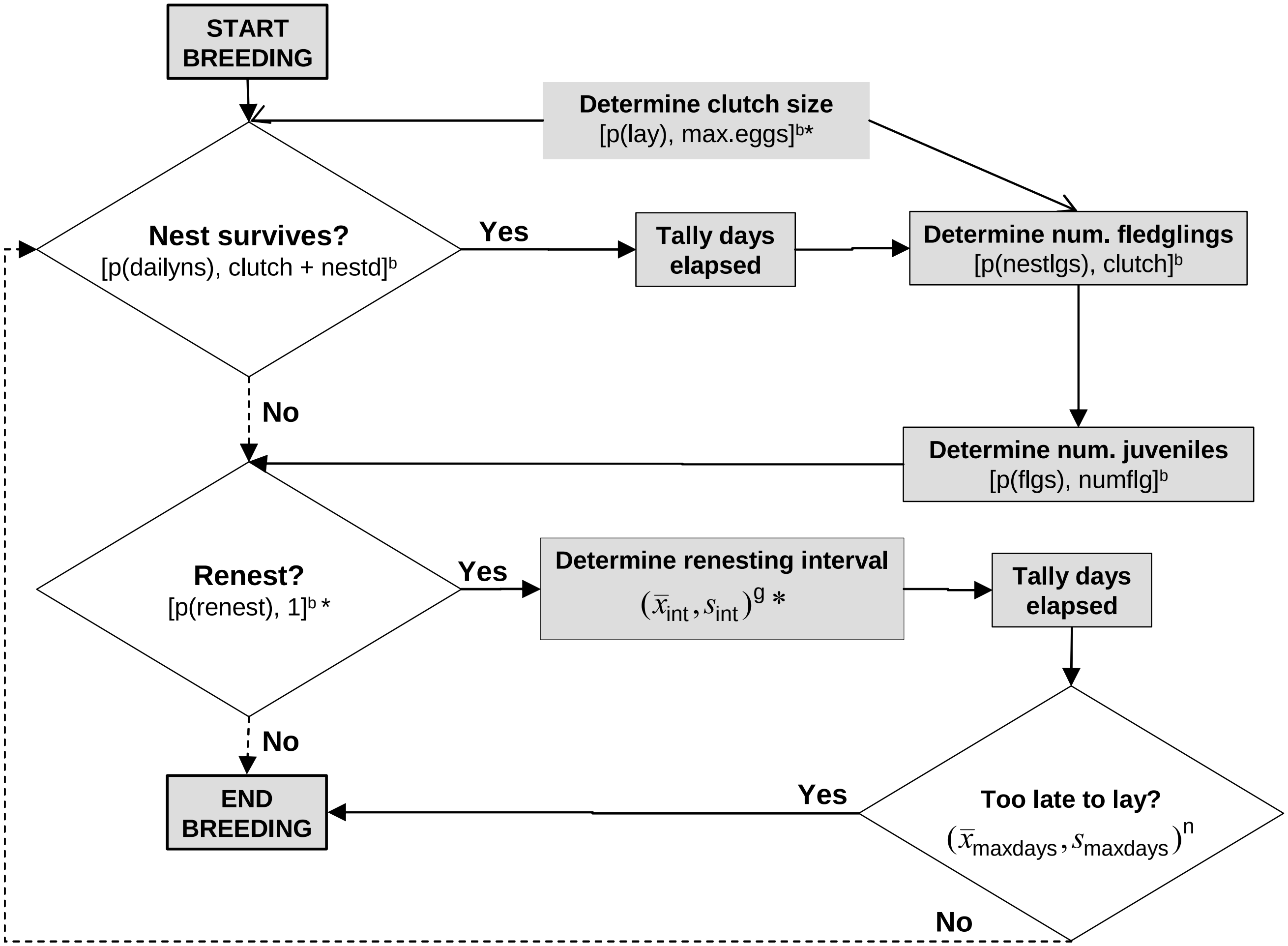


Fig. 4.1. Flow diagram describing simulated reproduction for an individual female songbird. Random statistical distributions are indicated as follows: b = beta-binomial; n = normal; g = gamma. Probabilities are abbreviated as follows: p(lay) = probability of egg laying; p(dailyns) = daily nest survival rate; p(nestlgs) = nestling survival rate; p(flgs) = fledgling survival rate; p(renest) = probability of nesting again. Other variables are abbreviated as follows: max.eggs = maximum clutch size (i.e., 5); nestd = the nest cycle length; numflg = number of fledglings; int = interval between nest attempts; maxdays = maximum days to lay. Functions with an asterisk (*) had different parameters for individuals that raised one brood successfully.

Fig. 4.2. Sensitivity of productivity to 11 component breeding factors across the range of natural variation for Louisiana Waterthrushes in the Georgia Piedmont (2002-2004). Triangles at the base of each graph indicate means and arrows indicate 95% confidence limits from field data for the focal breeding factor. The upper confidence limit for second brood interval (18.35) was beyond the natural range of variation. Each circle is the mean productivity (i.e., number of fledglings that survive > 1 week per female), and each dash is +1 standard deviation based on 200 iterations of the simulation model at each setting of the focal breeding factor. Graphs fill the following two pages.

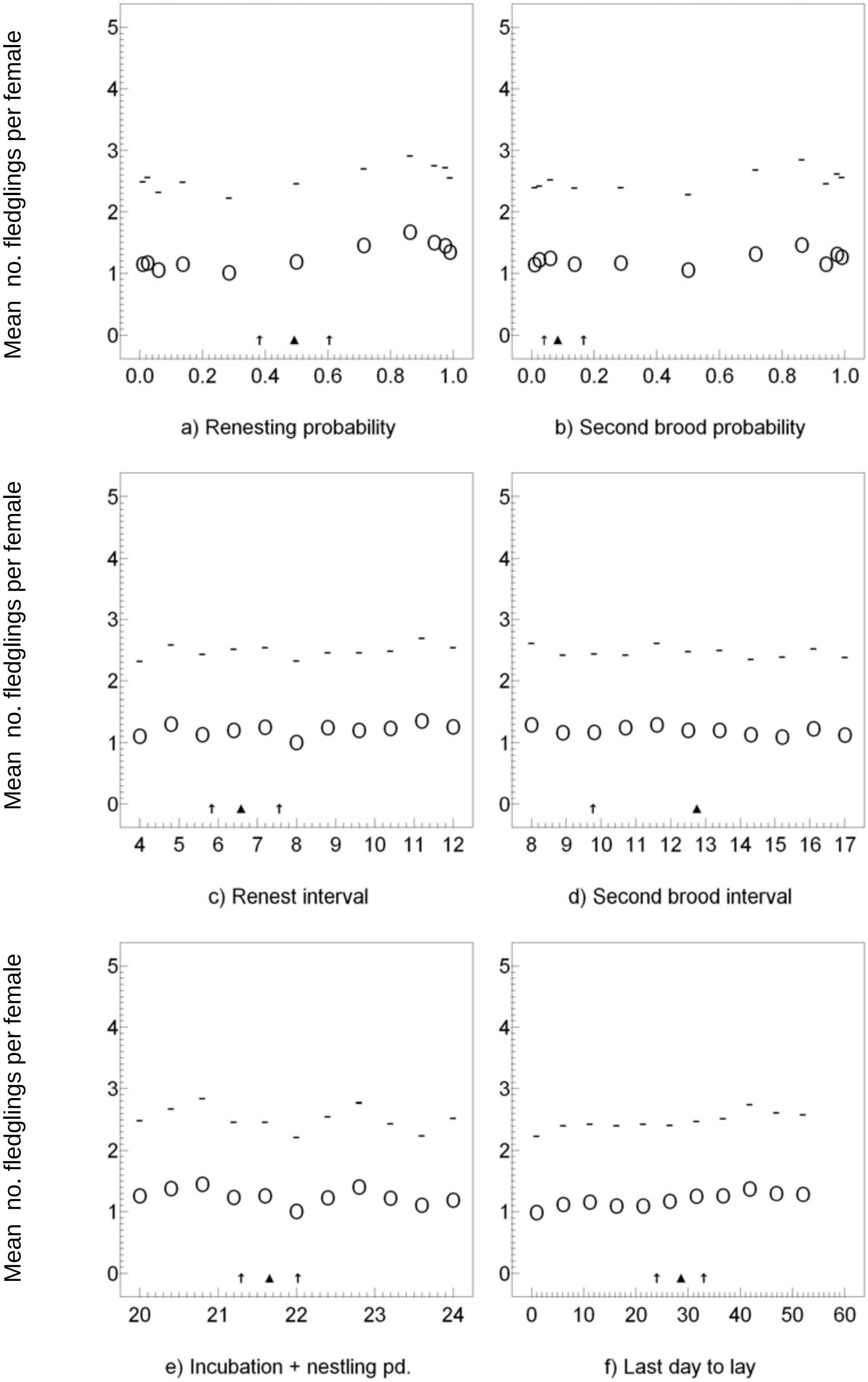
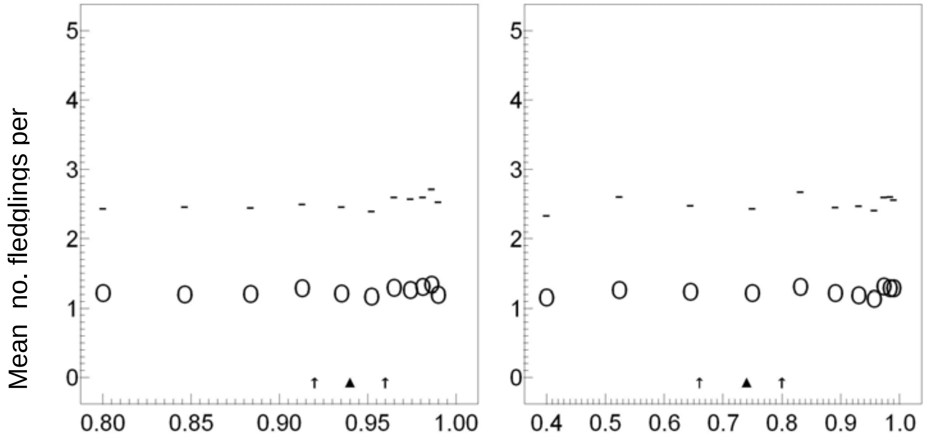
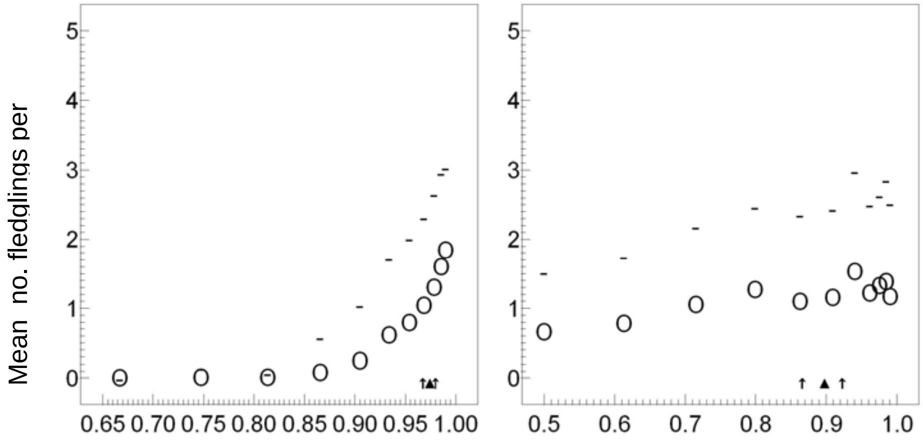


Fig. 4.2.Part 1 of 2, see legend on previous page.



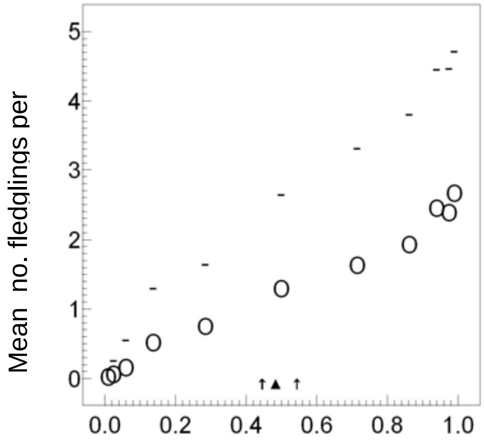
g) Egg laying (first nest)

h) Egg laying (renest)



i) Daily nest survival

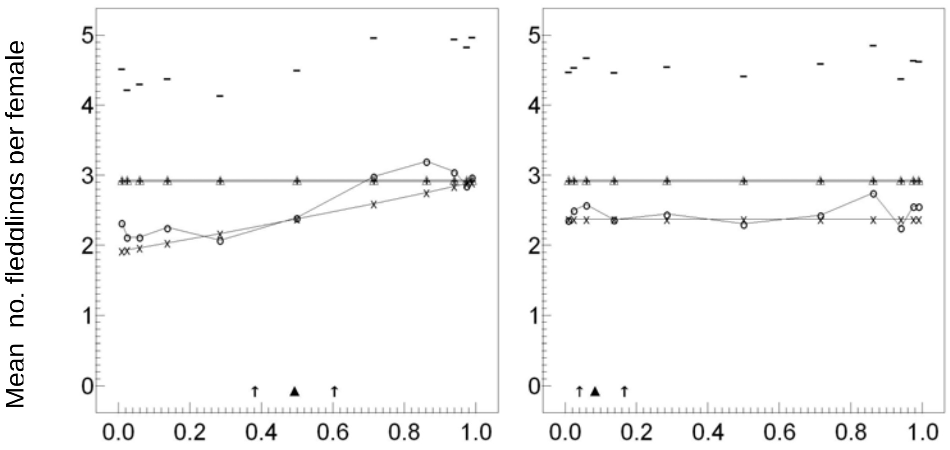
j) Nestling survival



k) Fledgling survival

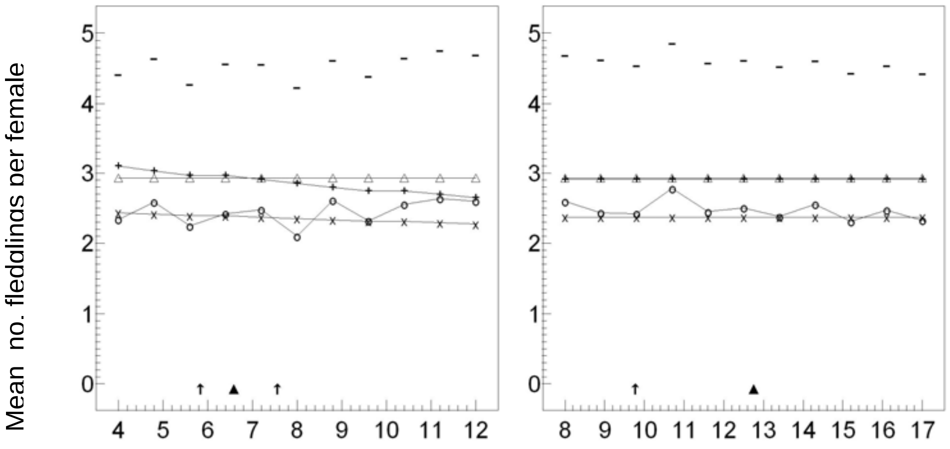
Fig. 4.2. Part 2 of 2, see legend on previous page.

Fig. 4.3. Comparisons of four different approaches to estimating fecundity while perturbing 10 of its component breeding factors across their range of natural variability for Louisiana Waterthrushes in the Georgia Piedmont (2002-2004). Triangles at the base of each graph indicate means and arrows indicate 95% confidence limits from field data for the focal breeding factor. The upper confidence limit for second brood interval (18.35) was beyond the natural range of variation. Each dash is +1 standard deviation above mean fecundity for the IBM based on 200 iterations at each setting of the focal breeding factor. Graphs fill the following two pages.



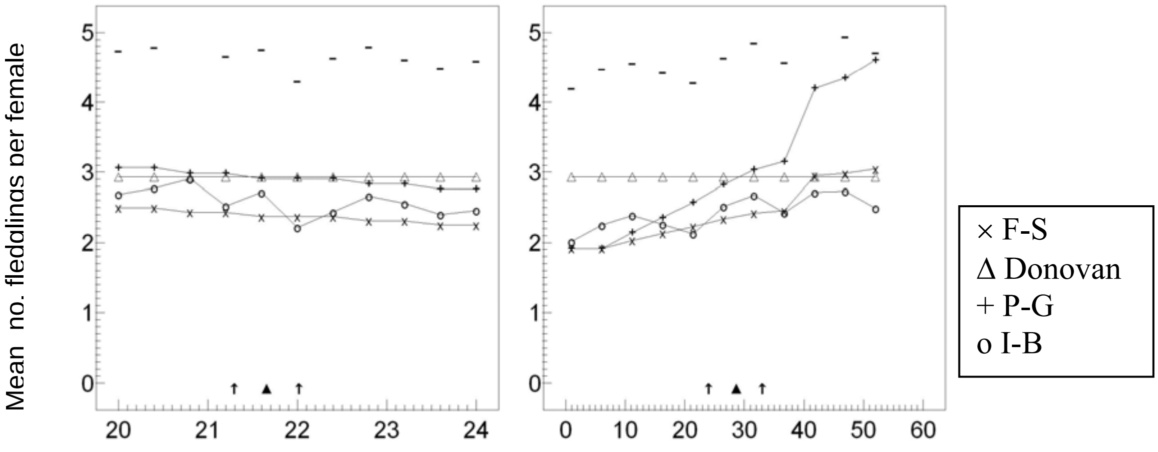
a) Renesting probability

b) Second brood probability



c) Renest interval

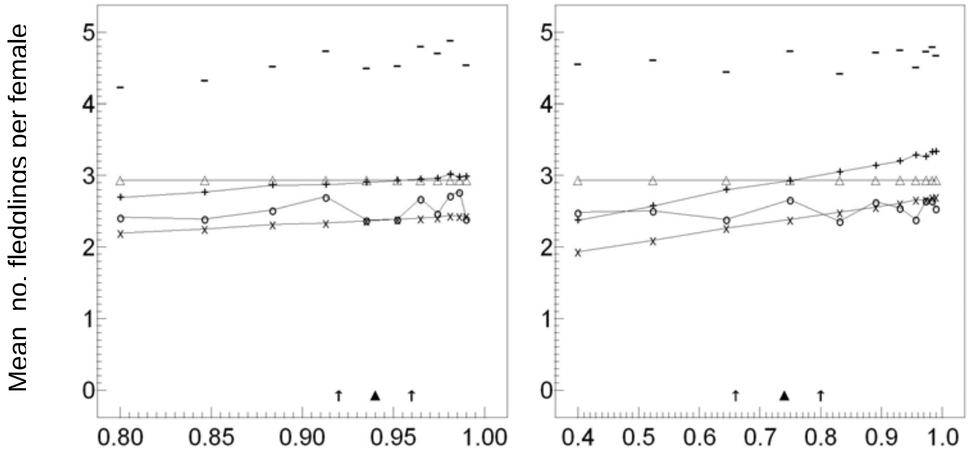
d) Second brood interval



e) Incubation + nestling pd.

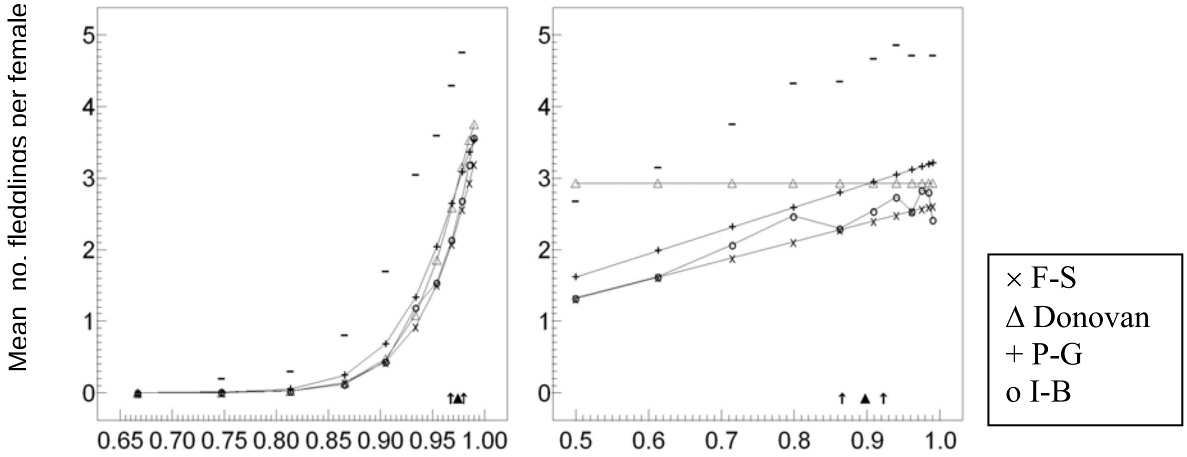
f) Last day to lay

Fig. 4.3. Part 1 of 2, see legend on previous page.



g) Egg laying (first nest)

h) Egg laying (renest)



i) Daily nest survival

j) Nestling survival

Fig. 4.3. Part 2 of 2, see legend on previous page.

CHAPTER 5

TERRITORY CHARACTERISTICS AND SUBSEASONAL VARIATION IN RAINFALL INFLUENCE REPRODUCTION BY A RIPARIAN OBLIGATE SONGBIRD, THE LOUISIANA WATERTHRUSH (*SEIURUS MOTACILLA*)[1]

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[1] Mattsson, B.J., and R. J. Cooper. To be submitted to *Oecologia*

ABSTRACT.-We studied the reproductive ecology of the Louisiana Waterthrush, *Seiurus motacilla*, a riparian obligate songbird that breeds in the eastern U.S. Our aim was to identify and quantify environmental factors that were associated with the crucial components of individual fecundity, using an information-theoretic approach. We monitored 190 nests in 139 territories within 13 drainages during 4 breeding seasons. We also tracked 357 color-banded young from 87 of 112 fledged broods during the dependent stage. Mean rainfall during the nesting period had a strong positive effect on waterthrush daily nest survival (Range: 0.966-0.998) and nestling survival (0.73-0.97), while understory cover had a strong negative effect on weekly site tenacity of fledgling waterthrushes (0.72-0.99). In addition, nestling survival (0.16-0.98) declined with increasing territory size. Other factors, including land use surrounding drainages, proximity to edges, measures of food availability, differences among years, and timing of nesting had weak, if any, effects on waterthrush reproduction. These findings provide support for the hypotheses that nesting success of riparian obligates is strongly associated with the variation in rainfall within the season and with territory size. Improved field methods for detecting waterthrush fledglings could help distinguish permanent emigration from mortality, and elucidate relationships between environmental variables and true survival during the dependent stage. Continued monitoring of waterthrush reproduction and improved estimates of juvenile and adult survival will provide the ingredients needed to predict their responses to changing land use and climate.

INTRODUCTION

Identifying and quantifying the extrinsic factors that drive fecundity is an essential step toward understanding how populations respond to changing environmental conditions (Anders and Marshall 2005). Many passerine species that breed in North America and winter in the

Neotropics have undergone population fluctuations during the past several decades (Sauer and Link 2002). Despite the awareness about changes in these populations, little is known about the causes for such fluctuations in many of these migratory bird species. While factors during migration and winter may be important for population dynamics (Sillett and Holmes 2002), these impacts are relatively diffuse and thus difficult to measure and manipulate (Conroy et al. 1995). Focusing on the reproductive portion of the avian life cycle, however, could provide crucial information about the factors driving population dynamics in migratory songbirds.

Riparian obligates are of particular concern due to their dependence on habitats that often abut human land uses, including urbanization, agriculture, and silviculture (Poff et al. 1997, Allan 2004). Landscape-scale alterations can lead to dramatic effects on stream chemistry, hydrology, and associated aquatic organisms (Richards et al. 1996, Roth et al. 1996, Roy et al. 2003, Allan 2004). Impacts of these land uses on terrestrial riparian obligates, however, remain largely unknown (Price and Bock 1983, Warkentin et al. 2003). While such habitat alterations may be important, patterns of precipitation may also have dramatic effects on these species. Riparian systems often consist of ephemeral channels and wetlands that only become active during storm events (Wood et al. 2005), bringing to life some of the biota that would otherwise remain dormant in these areas. Furthermore, stream channels are subject to flooding, which can destroy nests (Price and Bock 1983, Stucker 2000) and reduce aquatic food availability for birds that nest and forage in stream channels (Bond and Downes 2003, Negishi and Richardson 2006). Our objective was to investigate the relationships between reproduction of a riparian obligate songbird and environmental variation as measured by amount and proximity of anthropogenic land uses, territory quality and quantity, and rainfall.

While little is known about many taxon-specific responses to land use change in riparian systems, relationships between habitat conditions and songbird reproduction in general have been described at multiple spatial scales. At the landscape scale, the amount of urbanization, agriculture, and silviculture in the landscape may influence predator numbers (Chalfoun et al. 2002) and ultimately may affect songbird reproduction (Stephens et al. 2004, Lloyd et al. 2005, Patten, 2003 #68). While the amount may be important, the proximity of this predator habitat may accentuate the negative effects on breeding songbirds (Donovan et al. 1997, Lahti 2001, Driscoll and Donovan 2004). At the patch scale, territories with high quality foraging habitat may confer better reproduction than those with low quality foraging habitat (Price and Bock 1983, Duguay et al. 2000). According to the food value theory (Stenger 1958), territory sizes decrease with elevated food availability (Smith and Shugart 1987, Feck and Hall 2004, Marshall and Cooper 2004). When food resources (rather than nest sites) are limiting, the optimal territory size is one that maximizes fitness by balancing time required for territory maintenance and time required for foraging (Both and Visser 2003).

Models of fecundity often assume that reproductive rates remain constant throughout the nesting season (Donovan et al. 1995, Pease and Grzybowski 1995). The likelihood of breeding success, however, may vary throughout the season due to changes in food availability (Ormerod and Tyler 1993, Bradbury et al. 2003) and predator numbers and behavior (Schmidt 1999, Grant et al. 2005). There may be a peak in reproduction during the middle of the nesting season (Grant et al. 2005), or reproduction might change at a consistent rate throughout the nesting season (Wilson and Cooper 1998). If elevated rainfall negatively impacts songbird foraging efficiency (Radford et al. 2001), then reproduction might crash during periods of high rainfall (Siikamaki 1996, Donald et al. 2001, Takagi 2001, Dinsmore et al. 2002, Harris et al. 2005). Alternatively, reproduction might increase during wetter periods when there is a greater abundance of aquatic food items, but this has rarely been observed or evaluated for riparian obligate passerines (Petit and Petit 1996). Furthermore, deeper water below nests might preclude some predators from reaching nests (Gannon 2005, Hoover 2006). Similarly, reproduction might vary among years according to variation in climatic conditions (Renton and Salinas-Melgoza 2004, Bolger et al. 2005).

The Louisiana Waterthrush (waterthrush; *Seiurus motacilla*) requires forested streams for food and nesting (Robinson 1995). Waterthrushes provide an excellent model species for studying the factors influencing reproduction of riparian obligates. Their bank nests are very accessible and allowed us to readily locate, monitor, and mark entire families. Furthermore, waterthrush fledglings typically remain within 50 m of the stream and within the territory of their parents (Mattsson, unpublished data), making them relatively easy to resight without the aid of radio telemetry. They forage mostly in riffles along the stream bed, but move into the canopy of the adjoining riparian forest following leaf emergence (Craig 1984). Finally, the Louisiana Waterthrush has been proposed as an integrative indicator of riparian ecosystem integrity (Brooks et al. 1998), due to its dependence upon not only the stream itself but also the surrounding forest. Thus, responses in waterthrush reproduction may reflect how the ecosystem as a whole responds to environmental variation.

Our objective was to identify and quantify the factors associated most closely with their daily nest survival, nestling survival (i.e., probability of an offspring surviving from egg laying to fledging in a successful nest), and fledgling site tenacity. All of these are likely to be important for explaining variability in waterthrush fecundity (BJ Mattsson unpublished data). Following an information-theoretic framework (Burnham and Anderson 2002), we rank candidate models that correspond to *a priori* hypotheses that describe relationships between environmental factors and reproduction of an obligate riparian songbird.

MATERIALS AND METHODS

Study sites.-Our study took place in 13 forested, headwater drainages (1.12 to 4.20 km^2) of the southern Piedmont in north-central Georgia (Fig. 5.1). Most of the drainages (n=11) are in the Upper Oconee River basin, while one is the Upper Ocmulgee River basin and the other is in the Broad River basin. In 2002, we selected ten of the drainages from a larger pool of potential drainages that had contiguous forest buffers >15 m on both sides from the headwaters throughout >2.5 km of stream as determined from the most recent available digital orthophoto quadrangles (DOQQs, USGS 1995) and overlaid stream lines (Georgia Department of Transportation 1997). Dominant land uses within the ten rural drainages include cattle pastures (n=2), clearcuts and evergreen forest (n=7), and deciduous with some mixed deciduous and evergreen forest (n=1). For 2004 and 2005, we added three additional drainages that were dominated by urban land uses beyond the 15 m buffer, and these contained some road crossings. Thus, drainages were categorized into the following treatments: urban, field, silviculture, and native forest. We monitored waterthrush broods on the rural and urban drainages from 2002-2005 and 2004-2005, respectively.

White oak (*Quercus alba*), red maple (*Acer rubra*), yellow poplar (*Liriodendron tulipifera*), American sweetgum (*Liquidambar styraciflua*), sourwood (*Oxydendrum arboreum*) and hickory (*Carya* spp.) dominate the canopies along study streams, although 15 other species were also present as canopy trees. Shaded understories were generally sparse and included flowering dogwood (Cornus florida), American hornbeam (*Carpinus caroliniana*), black cherry (*Prunus serotina*), Eastern red cedar (*Juniperus virginiana*), Georgia buckeye (*Aesculus sylvatica*), willow oak (*Quercus phellos*), and paw paw (*Asimina triloba*). Canopy gaps were dominated by muscadine (*Vitis rotundifolia*), spicebush (*Lindera benzoin*), greenbriar (*Smilax* spp.), and blackberry (*Rubus argutus*). Chinese privet (*Ligustrum sinense*), American holly (*Ilex opaca*), and river cane (*Arundinaria gigantea*) occur in floodplains or disturbed soils.

Waterthrush monitoring.-To quantify breeding success, we located waterthrush nests by following adults as they constructed their nests or fed young, and by systematically searching bank crevices from late March through early June of 2002-2005. Once nests were located, observers monitored them every 2-4 days, recording number of eggs or nestlings and documenting evidence of nest failure or fledging. We determined hatch date and nestling age by morphology of nestlings (e.g., size relative to the egg, amount of feather unsheathing, chirping). We estimated date when the first egg was laid by subtracting from hatch date the mean incubation period (12 days, BJ Mattsson unpublished data). For nests that failed before hatching but were found after clutch completion (*n*=21), we assumed that they were found at the midpoint of the incubation period. For the purpose of nest survival analysis, observation days began when the nest was found or when the clutch was filled, and the observation period ended at the midpoint between the last check while active and the first day the nest was observed to be empty for nests with known fates. For nests with uncertain fate, the last observation date was the last date the nest was observed active. This was to minimize bias in the estimate of nest success (Manolis et al. 2000). We excluded two nests that were found with eggs that eventually expired and were likely abandoned beforehand based on no observations of adults tending to these nests.

We placed mist-nets over the stream and used play-backs of the waterthrush song to attract and capture males. We also captured adult waterthrushes passively in these nets or by walking toward them as they foraged along the stream. Once we located the nest, we captured incubating females using a butterfly hoop net. If these efforts failed, we captured adult waterthrushes in a mist net placed near the nest as they carried food to the nest. Each waterthrush received a unique combination of three colored leg bands and a USGS aluminum band. This enabled us to delineate territories using standard territory mapping techniques (International Bird Census Committee 1970). If territories of two males overlapped, we used observations of females to delineate the respective territories. If during a single season a female mated with multiple coexisting males that defended their own territories, then we delineated separate territories for each respective male. If during a single season a female mated with multiple males that did not coexist, then we considered the collective area defended by these males as a single territory. If a male mated with two females, then we considered the entire area defended as a single territory. Two nests were within territories that were poorly mapped, and we excluded these from the analysis.

When possible, we banded all nestlings from each monitored nest 1-3 days before fledging. Nestling waterthushes received a unique combination of two colored leg bands and a USGS aluminum band. This enabled us to track the brood following fledging every 2-7 days. If nestlings flapped, chirped, or had pin feathers unsheathed > 5 mm during the last nest check, then we considered an empty nest successful (usually day 8 or 9 post-hatching; Mattsson pers. obs.). Otherwise, we determined fledging status based on our observations of fresh fecal sacs near the nest, banded juveniles, or adults scolding or with food during subsequent visits to the territory.

We excluded some fledglings from the analysis of fledgling site tenacity for one of several reasons. First, we excluded young that were found dead in or within 5 m of the nest during the last nest check (*n*=6), which was also the first resighting attempt following banding of the nestlings. We also excluded young that were missing during the last check but were too young to fledge by that time based on their morphology on the penultimate nest check (n=4). One young escaped before banding, so we excluded it as well. We excluded another nest in which we banded the young early at 4-5 days old, and they were missing on the next check five days later. Thus, the fate of this nest was unknown. Finally, we attached radio transmitters to a total of 12 fledglings from a subset of broods (n=5) during 2003 as part of a concurrent study evaluating the efficacy of radio tracking fledglings to document dispersal patterns and to estimate survival rates (Mattsson et al. 2006). Due to potential biases induced by this procedure, we excluded these broods from the analysis of fledgling site tenacity.

Potential correlates of waterthrush reproduction.-During late March and early April, we recorded the presence of ≥ 1 m^2 riffles within 5-m intervals throughout each stream network. We then estimated percent riffles in each territory by dividing the number of intervals with riffles by the total number of intervals.

Between late May and mid June of 2002-2005, we estimated the biomass of benthic macroinvertebrates and larval salamanders in stream riffles (henceforth, macrobenthos; Table 1) where we had observed waterthrushes foraging within mapped territories. We collected macrobenthos using a Surber sampler (30.5 cm × 30.5 cm, 1 mm mesh) at the downstream portion of two riffles (each at least 1 m × 1 m in area) in each sampling reach $\approx$ 50 m in length. We scrubbed all rocks (> 8 cm in diam) and disturbed the sediment 2 cm below the stream bed and within the Surber frame for a total of 3 minutes. We elutriated each sample separately in the field and stored all organic matter in 70% ethanol. All animals were carefully separated from other organic matter in each sample. We then identified, tallied, and recorded lengths (1 mm precision) of these animals using a dissecting microscope (10-45× magnification). We identified insects to family using standard dichotomous keys (e.g., Merritt and Cummins 1996), and used these data to estimate macrobenthos biomass using length-mass regressions (Table 1, Benke et al. 1999). We averaged data from the two riffles in each sampling reach for statistical analyses. Due to logistical constraints, we sampled macrobenthos in only a subset of territories (*n*=50). As most drainages had >2 territories, we used the average biomass estimate for that drainage in that year for most territories with missing biomass data (*n*=64). For territories in drainages that lacked biomass data in a particular year (*n*=25), we used the average biomass estimate across years for that drainage.

During June and July, we estimated percent understory cover within territories using a 2 m × 0.5 m (h × w) cloth composed of four 0.25 m^2 checker squares (Table 5.1). An observer visually estimated the percent of each square obscured by vegetation, including tree trunks, foliage, and ground cover while standing 10 m from the cloth held by an assistant vertically from ground level at a central location. This procedure was repeated in four directions surrounding this location (i.e., upstream, downstream, bank edge, opposite bank edge), covering an area of 200 m^2 along the stream channel. We averaged the percent cover for each square across the four directions to obtain an estimate for each location. In 2002, we measured understory cover every 250 m along the stream on both sides of the channel. In 2003 and 2005, we measured understory cover at nests and at randomly selected juvenile locations for a subset of broods. We averaged all locations sampled within each territory for statistical analyses. For most territories with missing understory cover (*n*=14), we used the mean for that drainage. For two territories within a drainage that lacked understory measures, we used the mean across all territories.

We measured several habitat variables at three different spatial scales (nest, territory, drainage; Table 1) using ArcView® 3.2 (ESRI 1999). First, we used a Trimble® Global

Positioning System (GPS) to map the centerline of the stream network within each drainage. We also used the GPS to record locations for grid points every ~50 m along the stream channels, with an error radius of approximately 15 m. We then plotted each nest in ArcView® (ESRI 1999) using the GPS stream lines and grid points as references. Next, we estimated distances from nests to the nearest urban and rural edges observed on 1999 color-infrared DOQQs (Table 1, USGS 2002). Urban edges included roads ≥5 m wide and houses on >450 m^2 lots. Rural edges included >450 m^2 patches of recent clearcuts or evergreen forest and cattle pasture. To account for inaccuracies in the lengths of GPS stream lines, we measured territory sizes by summing 30-m pixels in a digital elevation model (USGS 1999) that intersected our GPS stream lines (Table 5.1). While this method produces a measurement of area, the target measurement was actually territory length. We generated 60-m buffers surrounding the GPS stream lines in ArcView® (ESRI 1999), and then estimated the total percent forest cover within this buffer for each mapped territory using the National Landcover Dataset (Table 1, Homer et al. 2004). Finally, we generated 1.75-km buffers (one-half the minimum distance between stream networks) for the GPS stream lines in order to estimate the percent urban, field, and silviculture cover classes (including clearcuts and evergreen forest) surrounding each drainage (Table 5.1).

Finally, we obtained estimates of daily rainfall that coincided with our nest observation dates from two weather stations, one located in Athens and the other in Macon, Georgia (National Weather Service Forecast Office 2005). We used data from the Athens and Macon weather stations for nests in the northern and southern study areas, such that the reference station was within 44 km of each nest. In particular, we calculated mean daily rainfall during the period of observation for each nest (Table 5.1). We pooled data from both weather stations when estimating mean daily rainfall throughout the spring of each year.

Modeling reproduction.-From the original list of five hypothesized factors that relate to waterthrush reproduction (Table 5.1), we constructed a set of 13 candidate statistical models. Rather than generating a list of all possible combinations of the five factors, we identified factors that could potentially interact with one another in an ecological context. In particular, we investigated potential interactions between territory amount and quality and between predator habitat amount and proximity. Thus, the candidate set included individual factors, additive factors, interactions, a quadratic term (i.e., mid-season peak in reproduction), and a model with no factors (NULL). We eliminated percent silviculture from the analysis, as it was inversely correlated with percent fields (r=-0.82) and percent riffles (r=-0.58). All of the remaining correlation coefficients between main effects were low ($|r|<0.50$). We used the same set of models for estimating nest survival, nestling survival, and fledgling site tenacity.

To model survival of nests and nestlings, we followed the Mayfield logistic regression procedure described by Hazler (2004). In particular, we obtained maximum-likelihood estimates for intercepts and slopes in each candidate model using PROC LOGISTIC (SAS Institute Inc 2004). This procedure allowed us to model survival as a binomial process. For nest survival, the outcome is either 0 (fledged successfully) or 1 (failed), and the number of trials was the number of days each nest was observed. For nestling survival, we only considered fledged nests where the number of successes was the number of young fledged, and the number of trials is the number of eggs laid. To evaluate goodness-of-fit for the survival models, we ran the null model in PROC LOGISTIC (SAS Institute Inc 2004) while aggregating the data by drainage and year (Hazler 2004). This approach allowed us to estimate the variance inflation factor ($\hat{c}$), where $\hat{c} \leq 1$ indicates that the model fits the data. We evaluated independence among years and drainages by examining residuals from the model with all covariates included. In particular, we plotted the

95% confidence intervals surrounding the residuals to enable pairwise comparisons of both streams and years. If the confidence intervals did not overlap for some comparisons, then this would indicate a lack of independence among these groups.

For modeling fledgling site tenacity, we computed maximum-likelihood estimates of intercepts and slopes in each candidate model using the Cormack-Jolly-Seber model type (Lebreton et al. 1992) in the program MARK (White and Burnham 1999). This model estimates detection probability (p_i) and site tenacity (ϕ_i) of color-banded waterthrush juveniles during the first 28 days after fledging. Fledgling waterthrushes remain dependent on adults for food for the first week after fledging, at which point they occasionally feed themselves while still dependent on adults for nourishment (Robinson 1995). Dispersal from the natal territory may occur after they can maintain sustained flight ≈10 days after fledging, or more likely after they become completely independent beyond four weeks after fledging (Robinson 1995). Given that a marked fledgling is alive and in the study drainage at age i, we defined p_i and ϕ_i as the probabilities that the individual is resighted at this age and remains in the drainage until age $i+1$, respectively. Thus, we could not distinguish mortality from permanent emigration from the study drainage. Encounter histories were based on four weekly intervals, or five total occasions. For broods visited multiple times within a given week, we only used the last visit of the week in the analysis. We fixed p_i to zero when there were no visits during that week for a particular brood (n=47). We inspected the highest dimension convergent model for overdispersion using the median $\hat{c}$ procedure in program MARK (White and Burnham 1999).

Using the maximized log-likelihood estimates for each model, we calculated Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002). We also corrected for overdispersion where appropriate using $QAIC_c$ (Burnham and Anderson 2002).

This information-theoretic approach determines models that best explain the data while incorporating the fewest parameters, i.e., models that are parsimonious. We then ranked each model by its AIC_c or $QAIC_c$ weight (i.e., strength of evidence that a model is the most parsimonious of the candidates), so that models with the highest Akaike weight are the most parsimonious (Burnham and Anderson 2002). Models with a ΔAIC_c or $\Delta QAIC_c \leq 4$ were included in the confidence set (Burnham and Anderson 2002: 217). To account for model selection uncertainty, we computed model-averaged parameter estimates using the Akaike weights for each candidate model where the parameter of interest occurred. We made inferences regarding effect size and direction for predictors based on the value of model-averaged estimates and their respective 95% confidence intervals (CIs), and estimates are presented as $\overline{\beta}$ = X±95% CI.

RESULTS

During spring of 2002-2005, we monitored 190 active waterthrush nests in 139 territories within 13 drainages. Of these nests, 112 fledged between 1 and 5 young over a total of 2,667 observation days. We color-banded 357 young as nestlings in 87 of the fledged nests. We also measured a wide range of values for variables in candidate models of daily nest survival, nestling survival, and weekly fledgling survival (Table 5.1). Potential predators that we observed included owls (Barred Owl [*Strix varia*], Great Horned Owl [*Bubo virginianus*], Eastern Screech-owl [*Megascops asio*]), Red-shouldered Hawk (*Buteo lineatus*), accipiters (Sharp-shinned Hawk [*Accipiter striatus*], Cooper's Hawk [*Accipiter cooperii*]), corvids (American Crow [*Corvus brachyrhynchos*] and Blue Jay [*Cyanocitta cristata*]), carnivores (raccoon [*Procyon lotor*], opossum [*Didelphis virginiana*], domestic cat [*Felis domesticus*]), sciurids (eastern gray squirrel [*Sciurus carolinensis*], fox squirrel [*Sciurus niger*], eastern chipmunk

[*Tamias striatus*]), white-tailed deer [*Odocoileus virginianus*], and snakes (copperhead [*Agkistrodon contortrix*], timber rattlesnake [*Crotalus horridus*], black rat snake [*Elaphe obsoleta*], black racer [*Coluber constrictor*], common kingsnake [*Lampropeltis getula*], water snake [*Nerodia erythrogaster*]). The most commonly observed predators in or near the stream channel were raccoons and snakes. We observed accipiters in aerial pursuit of adult waterthrushes on multiple occasions.

Nest survival.-Of the 68 nests that failed before young were ready to fledge, predation was the primary cause of failure (n = 55, 80.9%), 10 nests were abandoned with eggs or young, 2 nests were washed out during floods, and 1 nest was buried by natural bank slumping. Of the 10 abandoned nests, four were followed by renests, while the remaining six were suspected to be due to adult mortality based on the absence of females during subsequent visits to the territory. Despite the presence of Brown-headed Cowbirds (*Molothrus ater*), we did not observe any parasitized waterthrush nests. Several depredated nests were found extracted from their crevices, which is indicative of predation by mammals. At one depredated nest, we found a pile of adult waterthrush feathers on the opposite bank, indicative of predation by an accipiter.

A nest survival model without any covariates but aggregated by drainage and year for goodness-of-fit estimation fit the data (χ^2_{38}= 35.38, $\hat{c}$=0.9311, P=0.5911). This null model, however, had only slightly greater parsimony when compared to a model with only year as a fixed effect (ΔAIC_c=3.9), so we included year in all subsequent candidate models. We found no lack of independence among drainages or years based on 95% CIs surrounding deviance residuals for a model containing all of the continuous covariates in the candidate models (henceforth, global model).

Two of the three models in the confidence set for daily nest survival included rainfall (Table 5.2). While the model with a linear effect of egg laying date and mean rainfall carried the most support (AIC_c weight=45%), a model with only a year effect (i.e., null model) shared a substantial weight of evidence in the confidence set (AIC_c weight=16%). This provides some evidence that the null model might be the most parsimonious for predicting nest survival, or there may be more parsimonious models that we did not consider. While there was a strong positive association between nest survival and rainfall ($\bar{\beta}_{\text{RAIN}}$=0.184±0.172, Fig. 5.2), the relationship between egg laying date and nest survival was equivocal ($\bar{\beta}_{\text{LAYDATE}}$=0.045±0.144). A model with a lone effect of rainfall was not included in the *a priori* candidate set. A *post hoc* model that included a quadratic effect of rainfall ($\hat{\beta}_{\text{RAIN}}{}^2$=0.0490±0.0203, Fig. 5.2) was much more parsimonious than the best model in the *a priori* set of models (ΔAIC_c=13.5). Despite high annual variation in rainfall and the evidence in favor of including year in all models, nest survival was similar among years (Fig. 5.3).

Nestling survival.-A nestling survival model without any covariates but aggregated by drainage and year for goodness-of-fit estimation exhibited minor overdispersion (χ^2_{36}= 39.641, $\hat{c}$=1.101, P=0.3108). We deemed it unwise to use QAIC_c for this model set, as adding continuous covariates to the model further improves the goodness-of-fit (Cooch and White 2003). A model with a year effect was less parsimonious than the null model ($\Delta\text{AIC}_c > 4$), so we did not include year in subsequent candidate models. We found no lack of independence among years based on 95% CIs surrounding deviance residuals for the global model. We did, however, find a minor lack of independence among drainages, as a pairwise comparison of 95% CIs separated two of the drainages. This observation was insufficient to justify developing a hierarchical model for this analysis, but may introduce some downward bias in variances for parameter estimates.

The confidence set of models for nestling survival included several models (Table 5.2), demonstrating much uncertainty as to which model is the most parsimonious. The global model had the greatest weight of evidence ($\mathrm{AIC_c}$ weight=30%), while the null model had a substantial amount of support ($\mathrm{AIC_c}$ weight=9%). As with nest survival, rainfall had a strong positive association with nestling survival based on the model-averaged slope estimate ($\bar{\beta}_{\mathrm{RAIN}}=0.215\pm0.194$, Fig. 5.2). Nestling survival, however, was inversely related to territory size ($\bar{\beta}_{\mathrm{TERRL}}=-1.36\pm1.01$, Fig. 5.2). Two *post hoc* models revealed that quadratic effects of rainfall ($\hat{\beta}_{\mathrm{RAIN}}{}^{2}=-0.0122\pm0.0528$) and of territory size ($\hat{\beta}_{\mathrm{TERRL}}{}^{2}=-9.44\pm48.57$) were weak or absent.

We did find evidence of an interaction between territory size and percent riffles ($\bar{\beta}_{\mathrm{TERRA\times PRIFF}}=-3.86\pm1.15$), and an interaction between percent fields within 1.75 km and distance to nearest rural edge ($\bar{\beta}_{\mathrm{PFIELD\times DRURAL}}=-0.099\pm0.081$). These interactions were most evident when inspecting the contour plots of the upper 95% confidence limits for predicted nestling survival (Fig. 5.4). In particular, nestling survival rate was lowest for nests that were near rural edges in landscapes with high amounts of fields (i.e., low amounts of silviculture). Likewise, nestling survival rate was lowest for nests in larger territories with small amounts of riffles. The dominant effects in these interactions were distance to rural edge and percent riffles, respectively. The quadratic term for egg laying date ($\bar{\beta}_{\mathrm{LAYDATE}}{}^{2}=1.71\pm2.51$), macrobenthos biomass ($\bar{\beta}_{\mathrm{BUGM}}=0.800\pm1.23$), and percent urban within 1.75 km ($\bar{\beta}_{\mathrm{PURBAN}}=7.46\pm13.01$) had positive trends, while percent riffles ($\bar{\beta}_{\mathrm{PRIFF}}=-4.75\pm5.17$), distance to nearest rural edge

($\overline{\beta}_{\mathrm{DRURAL}}$= -0.0225±0.0272), and percent fields within 1.75 km ($\overline{\beta}_{\mathrm{PFIELD}}$=-6.30±7.79) had negative trends with nestling survival.

Fledgling site tenacity.-The most general categorical model that converged contained a year effect on weekly fledgling site tenacity and additive effects of treatment, year and week on fledgling resighting probability [φ(year)*p*(treatment+year+week)]. This model exhibited substantial overdispersion (median ĉ=1.417±0.055), and so we applied a variance inflation factor of 1.417 when estimating model parameters and used $\mathrm{QAIC_c}$ for ranking our candidate models. Adding continuous covariates to the subsequent candidate models reduced this overdispersion to an unknown degree. We therefore used a conservative approach which may overvalue simpler models in the candidate set (Cooch and White 2003).

A simpler categorical model [ϕ(year)*p*(year+week)] was the highest dimension model in the confidence set of categorical models ($\Delta\mathrm{QAIC_c}$=3.850), which included all possible combinations of year, treatment, and time effects on fledgling site tenacity and detection. None of the models converged when fledgling site tenacity depended upon week or treatment. A model where detection depended upon territory specific habitat features [foundation model, ϕ(year)*p*(PFOR60M+TERRA+PCOVR+year+week)] had a similar level of parsimony when compared to the simpler categorical model ($\Delta\mathrm{QAIC_c}$=0.7338). Thus, we used this model as the foundation for constructing candidate models of fledgling site tenacity. Due to problems with convergence, however, we were unable to obtain estimates for models that contained interaction terms.

The confidence set included several models of weekly fledgling site tenacity (Table 5.3), indicating some uncertainty as to which is the most parsimonious. While a model with only territory specific effects dominated the set (AICc weight=45%), a territory quality model (weight=27%), the null model (weight=10%), and a model with fledge date and rainfall (weight=7%) carried substantial weights of evidence. While there was a strong negative association between percent understory cover and fledgling site tenacity ($\bar{\beta}_{\text{PCOVR}}$=-5.53±4.40, Fig. 5.5), other effects in the confidence set remain less certain. There was, however, a positive trend with territory size ($\bar{\beta}_{\text{TERRA}}$=15.1±16.9) and a negative trend with rainfall ($\bar{\beta}_{\text{RAIN}}$=-7.93±11.8). While the foundation model contained a year effect, fledgling site tenacity was similar among years (i.e., model-averaged 95% CIs overlapped).

Weekly detection rates were low but greatest during 2004 (0.237±0.067) when compared to other years (e.g., 2003: 0.163±0.121). Detection rates were similar among weeks after fledging (i.e., model-averaged 95% CIs overlapped). Detection rates tended to be inversely related to both percent riparian forest ($\bar{\beta}_{\text{PFOR60M}}$=-1.96±2.17) and territory size ($\bar{\beta}_{\text{TERRA}}$=-5.86±8.83). The relationship with percent understory cover, however, remains equivocal ($\bar{\beta}_{\text{PCOVR}}$=2.75±5.33).

DISCUSSION

Nest survival was greatest at intermediate levels of rainfall during the nesting period, while nestling survival increased in a linear fashion with rainfall. In addition, nestling survival declined with increasing territory size. Finally, understory cover had a negative effect on site tenacity of fledgling waterthrushes. Other factors, including land use surrounding drainages, proximity to edges, measures of food availability, annual variation in climate, and timing of nesting had weak, if any, effects on waterthrush reproduction.

Rainfall and nest success.-The rainfall effect provides support for the hypothesis that variability in climatic conditions within the breeding season influences waterthrush nesting success. In our study, daily nest survival was highest during intermediate amounts of rainfall, while nest survival showed a more consistent increase across the rainfall gradient. Periods of drought may reduce food availability (Bolger et al. 2005), which could increase the probability of nest predation (Podolsky 2003), number of young fledged per successful nest (Preston and Rotenberry 2006), or both (Zanette et al. 2006). When rain levels are moderate, food availability increases, allowing adults to spend more time at the nest. More extreme rainstorms induce downstream drift of their aquatic prey (Bond and Downes 2003, Negishi and Richardson 2006), lowering food availability, and consequently less time is available for nest defense.

Furthermore, as seen in our study, nests may be flooded during such storm events. This has also been observed in other studies of bank-nesting birds (Price and Bock 1983, Stucker 2000). While such flood events appear to reduce nest survival, they had little or no effect on the number of young that fledged in our study. This observation supports the hypothesis that while some nests are lost to flooding during extreme storm events, food availability remains sufficiently high to maintain nestling survival in nests safe from flooding. Comparing nestling provisioning rates under varying climatic conditions will help elucidate the mechanism by which rainfall affects nesting success.

Our finding that within-season hydrologic variation influences nesting success is consistent with studies of other birds associated with wetlands. Snail Kites (*Rostrhamus sociabilis*) have reduced reproduction during periods of drought (Beissinger 1986), while Prothonotary Warblers (*Protonotaria citrea*) have a reproductive advantage when nesting over deeper water (Petit and Petit 1996, Hoover 2006). In contrast, rainfall has negative impacts on reproduction for birds that forage upon flying insects (Siikamaki 1996, Donald et al. 2001, Takagi 2001) or that nest in exposed areas (Dinsmore et al. 2002, Harris et al. 2005). American Dippers (*Cinclus mexicanus*) fledged fewer young, including failed nests, during extreme storm events (Price and Bock 1983). Thus, precipitation can have positive or negative consequences for reproduction, depending on the extremity of rainfall events and the life history strategy of particular species.

One surprising finding was that nest survival varied little among years despite substantial annual variation in rainfall. A possible explanation for this result is that rainfall varied more within a given year than among years, such that waterthrushes were more subject to climatic conditions at a finer temporal scale. Therefore, examining the variability in precipitation and food resources within the breeding season may be crucial for predicting survival of waterthrush nests and nestlings.

Territory size and nest success.-Our finding that nestling survival decreases with increasing male territory size, especially in territories with sparse riffles, is consistent with optimal territory size theory (Both and Visser 2003). In particular, males defending food resources (rather than nest sites) would be expected to allocate more time to maintaining the territory and less time toward reproduction after exceeding the optimal territory size. Studies of males defending food resources in terrestrial habitats have indicated the opposite trend, where multiple measures of reproduction increase with increasing male territory size (Sillett et al. 2004, Wilkin et al. 2006). These terrestrial territories are usually embedded within a matrix of territories, so that the number of neighbors increases as local population density increases and territory size decreases. Stream obligates, however, are probably less sensitive to local population density, as they defend linear territories that often adjoin only two neighboring territories. Thus, all else being equal, a large linear territory would be more costly to maintain than a smaller territory.

Territorial species that occupy restricted resources such as wetlands, however, show similar patterns as in our study (Pribil 2000, Sejberg et al. 2000). Indeed, our finding may also support the predictions of a resource defense polygyny mating system, where males of higher quality defend large territories for the purpose of defending multiple mates (Bensch 1997). While each female produces fewer young (Bensch 1997, Pribil 2000), the males maintain a fitness advantage by producing more broods than would be possible with a single mate. In effect, the male may deceive a second female into mating with him (Alatalo and Lundberg 1984). Indeed, male waterthrushes do occasionally defend large territories containing two nesting females (BJM unpublished data), and the secondary female often raises fewer young than the primary female (Pribil 2000, Mulvihill et al. 2002). Female American Dippers similarly engaged in polygynous territories had lower reproduction than those in monogamous territories (Price and Bock 1983). The costs of polygyny and large territories for reproduction can therefore have important consequences for population dynamics in riparian obligate species.

Habitat and nest success.-Many studies have found strong, consistent relationships between landscape-scale habitat features and nesting success of upland songbirds (for review see Lloyd et al. 2005). Such relationships, however, have rarely been examined for riparian songbirds. In our study, the only evidence for a landscape-scale effect was that nestling survival was lowest in areas that were near rural edges (clearcuts and fields) but were surrounded by high amounts of fields. This finding agrees with Driscoll and Donovan (2004), who found that Wood Thrush nest predation increased with proximity to agricultural edges in fragmented but not in contiguous forest landscapes. Tewksbury et al. (2006), however, found that songbird nest predation was greater along rivers with forest buffers than those without buffers in landscapes dominated by agriculture. Gannon (2005) found that songbird nest predation increased with increasing density of roads but decreased with increasing density of silvicultural edges in a bottomland forest. Finally, Peak et al. (2004) failed to detect any strong relationships between landscape-scale habitat features and nesting success of riparian songbirds in agricultural landscapes. Further examinations of landscape habitat associations with riparian songbird reproduction are needed before making any general conclusions.

While riparian forest characteristics relate to their distribution (Keller et al. 1993, Buffington et al. 1997, Prosser and Brooks 1998), we found that waterthrush reproduction had a weak, if any, association with percent riparian forest and understory cover. The former result is consistent with Gray Wagtails (*Motacilla cinerea*) nesting along streams surrounded by moorlands or agriculture (Tyler and Ormerod 1991). The latter result is consistent with findings for other ground-nesting songbirds (Rodewald and Yahner 2001), but contradicts predictions from an experiment where raccoons searched for eggs under varying understory conditions (Bowman and Harris 1980). Interior forest songbirds that nest in shrubs and trees, however, have shown positive associations with understory density (Holmes et al. 1996, Moorman et al. 2002, Driscoll et al. 2005). The differing search strategies employed by predators might explain why understory density relates to predation of nests in shrubs but not of nests on the ground (Martin and Roper 1988).

The lack of an association between the amount and proximity of surrounding urban land uses and waterthrush reproduction was surprising, as studies of upland forest songbirds have found negative effects of urbanization on nest survival (Kosinski 2001, Borgmann and Rodewald 2004, Phillips et al. 2005). To our knowledge, our study is the first to examine the influence of urbanization on reproductive success in a riparian forest songbird. While nest predators have been shown to be more abundant in smaller riparian buffers within urbanized areas (Sinclair et al. 2005, Smith and Wachob 2006), the relationship between urbanization and artificial nest predation is inconsistent among regions (reviewed in Jokimaki et al. 2005). More studies of forest songbirds in riparian and upland habitats are needed before generalizing impacts of urbanization on nest success.

Specialized attributes of streamside habitat might explain why songbirds nesting in riparian forests respond differently to altered patch and landscape conditions when compared to those nesting in upland forests (Marzluff et al. 2001). For example, streamside habitats possess greater humidity and plant biodiversity than upland forests (Brosofske et al. 1997, Naiman and Decamps 1997), and thus riparian forests may maintain sufficient levels of food availability despite habitat modifications beyond the riparian buffer. Furthermore, by nesting in stream banks, waterthrush nests may be sheltered from predation despite increased densities of nest predators in fragmented landscapes (Chalfoun et al. 2002). The complete lack of nest parasitism in our study supports this hypothesis. An alternative explanation is that due to widespread human land uses or other factors, the entire region is host to a homogenous community of predators. Thus, predation levels change little among drainages within the region, as has been suggested in other riparian habitats surrounded by agriculture (Peak et al. 2004). This explanation is less likely, as mammalian predators are more abundant in narrower riparian buffers within urbanized landscapes (Sinclair et al. 2005).

Fledgling site tenacity.-Unfortunately, we could not distinguish fledgling mortality from permanent emigration in our study, so our inferences about the factors influencing survival of juvenile waterthrushes are limited. There are at least two non-mutually-exclusive explanations for how understory cover reduces site tenacity by fledgling waterthrushes. First, dense patches of vegetation provide a refuge for juvenile songbirds (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006), potentially allowing for more efficient food provisioning by adults. This may spur faster growth rates and expedite fledgling dispersal from their natal drainage.

Second, predators may be attracted to areas of thick understory which are also often associated with edge habitat (Dijak and Thompson 2000, Blouin-Demers and Weatherhead 2001), leading to elevated rates of predation on fledglings in these areas. The first explanation seems more likely, as we found that proximity to edges had, at best, weak associations with nest survival, nestling survival, and even fledgling site tenacity.

Improved methods for studying waterthrush fledgling site tenacity could help distinguish permanent emigration from mortality, and thus provide estimates that are more representative of true survival. While waterthrush juveniles exhibit negative responses to radio-transmitters, adult waterthrushes and older fledglings carry radio-transmitters without any apparent ill effects (Mattsson et al. 2006). Using radio-telemetry to track adults can facilitate resighting of their fledged young, thus providing better estimates of fledgling site tenacity over separate time intervals.

CONCLUSIONS

Our study provides evidence that seasonal fluctuations in rainfall and territory characteristics are better predictors of waterthrush reproduction than annual variation in climate or landscape-scale habitat features. Climate models predict extended periods of drought and more extreme rainstorms in the Piedmont (Mulholland et al. 1997), which would likely have negative consequences for waterthrush nest success. Furthermore, projected human population increases and associated urbanization in the Piedmont (Wear and Greis 2002) could lead to local extirpation of breeding waterthrushes due to piping of streams and diminished riparian buffers (Poff et al. 1997). In this event, some female waterthrushes might be prevented from breeding due to crowding by conspecifics, reducing the effective population size. Their dependency upon aquatic food sources and stream banks for nesting makes waterthrushes especially vulnerable to removal of riparian buffers and climatic fluctuations. Management practices that promote large tracts of riparian forests and stable climatic conditions will help ensure breeding requirements are met for waterthrushes and other riparian obligates.

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Table 5.1. Hypotheses for environmental factors driving Louisiana Waterthrush reproduction, Georgia Piedmont, USA, 2002 - 2005.

Hypotheses, predictors, and descriptions		Mean	Range	SD
Drainage specific, *n* =13				
1. Amount of habitat preferred by predators within 1.75 km of stream network				
PURBAN	% Human developments	0.114	0.021 - 0.547	0.152
PFIELD	% Crops and pasture	0.188	0.065 - 0.428	0.124
PSILV	% Clearcuts and evergreen forest	0.306	0.090 - 0.518	0.157
Territory specific, *n* =139				
2. Territory amount; quantity of suitable breeding habitat for waterthrushes				
TERRA	Area (ha) of DEM stream pixels defended by male waterthrush	1.56	0.27 - 4.32	0.77
PFOR60M	% Deciduous and evergreen forest within 60 m of stream	0.874	0.366 - 1.000	0.163
3. Territory quality; quality of foraging habitat for waterthrushes				
PRIFF	% Riffles in stream created by gravel, cobbles, or boulders	0.358	0.000 - 0.771	0.213
PCOVR	% Vegetation obscuring cloth (2 m high x 0.5 m wide)	0.368	0.099 - 0.802	0.134
BUGM	Biomass (g) of benthic macroinvertebrates and larval salamanders	0.906	0.000 - 17.127	2.304
Nest specific, *n* =190				
4. Predator habitat proximity; distances from nests to nearest edges suitable for predators				
DRURAL	Field, clearcut, or evergreen forest	46	0 - 211	38
DURBAN	Human development	350	15 - 867	182
5. Climatic variation within the season relating to waterthrush food and predators				
RAIN	Average daily rainfall (mm) during period of nest observation	2.76	0.00 - 15.24	2.47
LAYDATE	Julian date when first egg laid	116	93 - 155	15
FLGDATE	Julian date when young fledged from nest	139	119 - 179	15

Table 5.2. Model selection results for survival of Louisiana Waterthrush nests (n=190) and nestlings from fledged nests (n=112), Georgia Piedmont, 2002-2005. All models of nest survival included a year effect (df=3). The global model included all predictor variables, while the null model included none. Hypotheses and predictor variables are described in Table 5.1.

Hyps.	Model	k	ΔAIC_c	Ln(L)	w_i
	Logit (Daily nest survival) =				
5	LAYDATE, RAINFALL	6	0.00	-310.3	0.446
5	LAYDATE, LAYDATE^2, RAINFALL	7	1.72	-310.1	0.188
	Null	4	2.10	-313.5	0.156
5	LAYDATE, LAYDATE^2	6	4.16	-312.4	0.056
3	PRIFF, PCOVR, BUGM	7	4.45	-311.5	0.048
2	PFOR60M, TERRA	6	5.21	-312.9	0.033
4	DURBAN, DRURAL	6	5.39	-313.0	0.030
1	PURBAN, PFIELD	6	6.02	-313.4	0.022
2, 3	PFOR60M, TERRA, PRIFF, BUGM, PCOVR	9	8.18	-311.2	0.007
1, 4	PURBAN, PFIELD, DURBAN, DRURAL, PFIELD×DRURAL, PURBAN×DURBAN	10	8.20	-310.1	0.007
1, 4	PURBAN, PFIELD, DURBAN, DRURAL	8	8.70	-312.5	0.006
2, 3	PFOR60M, TERRA, PRIFF, BUGM, PCOVR, TERRA×PRIFF, TERRA×BUGM, PFOR60M×PCOVR	12	11.45	-309.4	0.001
1-5	Global	21	18.09	-301.9	0.000
	Logit (Nestling survival) =				
1-5	Global	18	0.00	-136.5	0.305
1	PURBAN, PFIELD	3	1.21	-155.7	0.167
5	LAYDATE, RAINFALL	3	1.45	-155.8	0.147
1, 4	PURBAN, PFIELD, DURBAN, DRURAL, PFIELD×DRURAL, PURBAN×DURBAN	7	2.26	-151.8	0.098
5	LAYDATE, LAYDATE^2, RAINFALL	4	2.49	-155.2	0.088
	Null	1	2.50	-158.4	0.087
1, 4	PURBAN, PFIELD, DURBAN, DRURAL	5	4.57	-155.2	0.031
5	LAYDATE, LAYDATE^2	3	4.88	-157.5	0.027
3	PRIFF, PCOVR, BUGM	4	5.95	-157.0	0.016
4	DURBAN, DRURAL	3	6.31	-158.2	0.013
2	PFOR60M, TERRA	3	6.48	-158.3	0.012
2, 3	PFOR60M, TERRA, PRIFF, BUGM, PCOVR, TERRA×PRIFF, TERRA×BUGM, PFOR60M×PCOVR	9	7.45	-152.0	0.007
2, 3	PFOR60M, TERRA, PRIFF, BUGM, PCOVR	6	10.35	-156.9	0.002

Table 5.3. Model selection results for weekly site tenacity of 357 Louisiana Waterthrush fledglings from 87 fledged nests, Georgia Piedmont, 2002-2005. All models included a year effect (df=3) on both tenacity and detectability. In addition, all models included effects of week since fledging (df=3), territory size, understory cover, and % riparian forest on detection. Models were adjusted with a variance inflation factor of 1.42. Predictor variables are described in Table 5.1.

Hyps.	Model	*k*	$\Delta QAIC_c$	Deviance	w_i
2,3	PFOR60M, TERRL, PRIFF, BUGM, PCOVR	17	0.00	56284.2	0.447
3	PRIFF, BUGM, PCOVR	15	1.00	56289.4	0.271
	Null	12	3.07	56297.6	0.096
5	FDATE, RAINFALL	14	3.79	56294.2	0.067
1	PURBAN, PFIELD	14	4.81	56295.2	0.040
5	FDATE, $FDATE^2$, RAINFALL	15	5.85	56294.2	0.024
2	PFOR60M, TERRL	14	6.54	56297.0	0.017
5	FDATE, $FDATE^2$	14	6.93	56297.3	0.014
4	DURBAN, DRURAL	14	7.17	56297.6	0.012
1-5	Categorical global model	12	7.26	56301.8	0.012

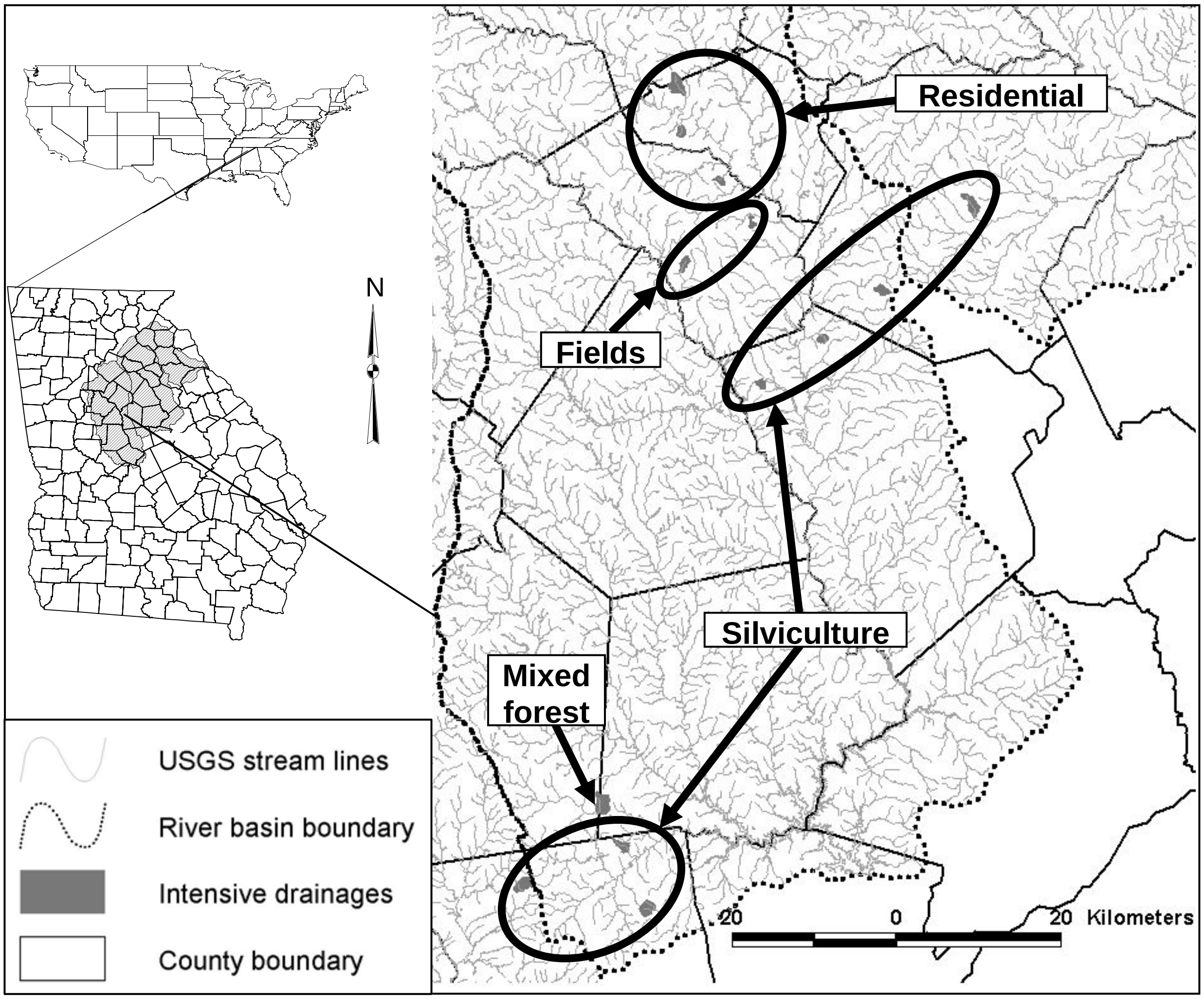

Fig. 5.1. Map of 13 drainages selected for breeding studies of Louisiana Waterthrushes in the Upper Ocmulgee, Upper Oconee, and Broad River Basins of Georgia, USA, as viewed from east to west. Drainages dominated by residential areas, fields, and mixed forest were located in the Athens area, cattle farms, and U.S. Forest Service land, respectively. Silvicultural drainages were located on timber company lands, U.S. Forest Service land, and Piedmont National Wildlife Refuge.

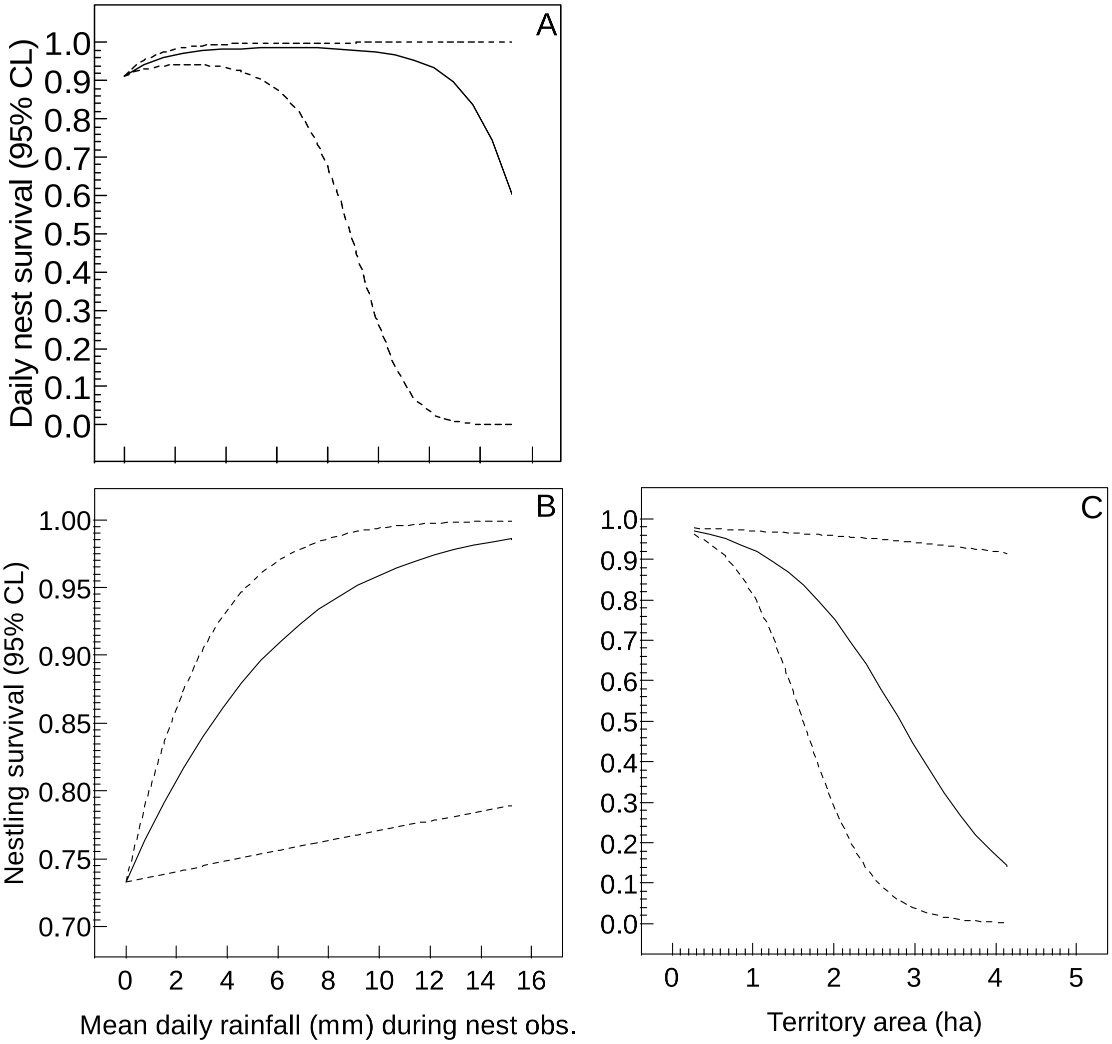

Fig. 5.2. Relationships between environmental variables and nesting success of Louisiana Waterthrushes breeding along headwaters of the Georgia Piedmont, USA. Nest survival was greatest during intermediate amounts of mean rainfall during the nest observation period (A). Nestling survival from egg laying to fledging in successful nests increased consistently with increasing amounts of rainfall (B), but decreased with increasing territory size (C). Uncertainty in nesting success increased with increasing values of predictors. All other parameters were held constant at their mean values. Dashed lines represent upper and lower 95% confidence limits surrounding model-averaged estimates.

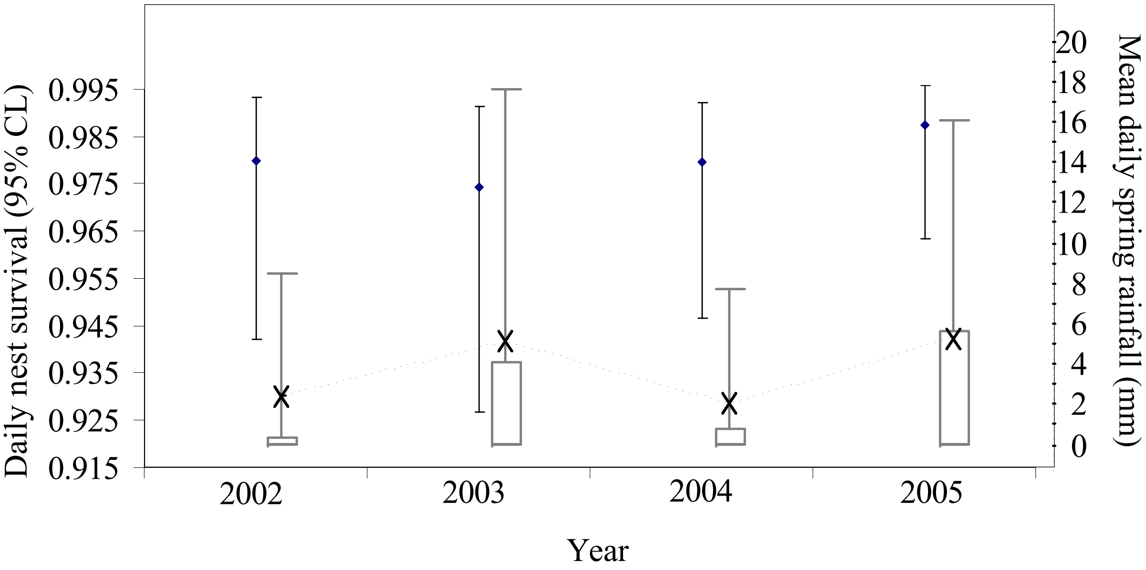

Fig. 5.3. Annual variation in spring rainfall (box plots) and daily nest survival (diamonds) for Louisiana Waterthrushes breeding along headwaters of the Georgia Piedmont, USA. *Error bars* for nest survival rates show 95% CIs. *Error bars* in box plots show 95th percentiles, each mean is marked with an X, and *boxes* represent 25th and 75th percentiles, respectively.

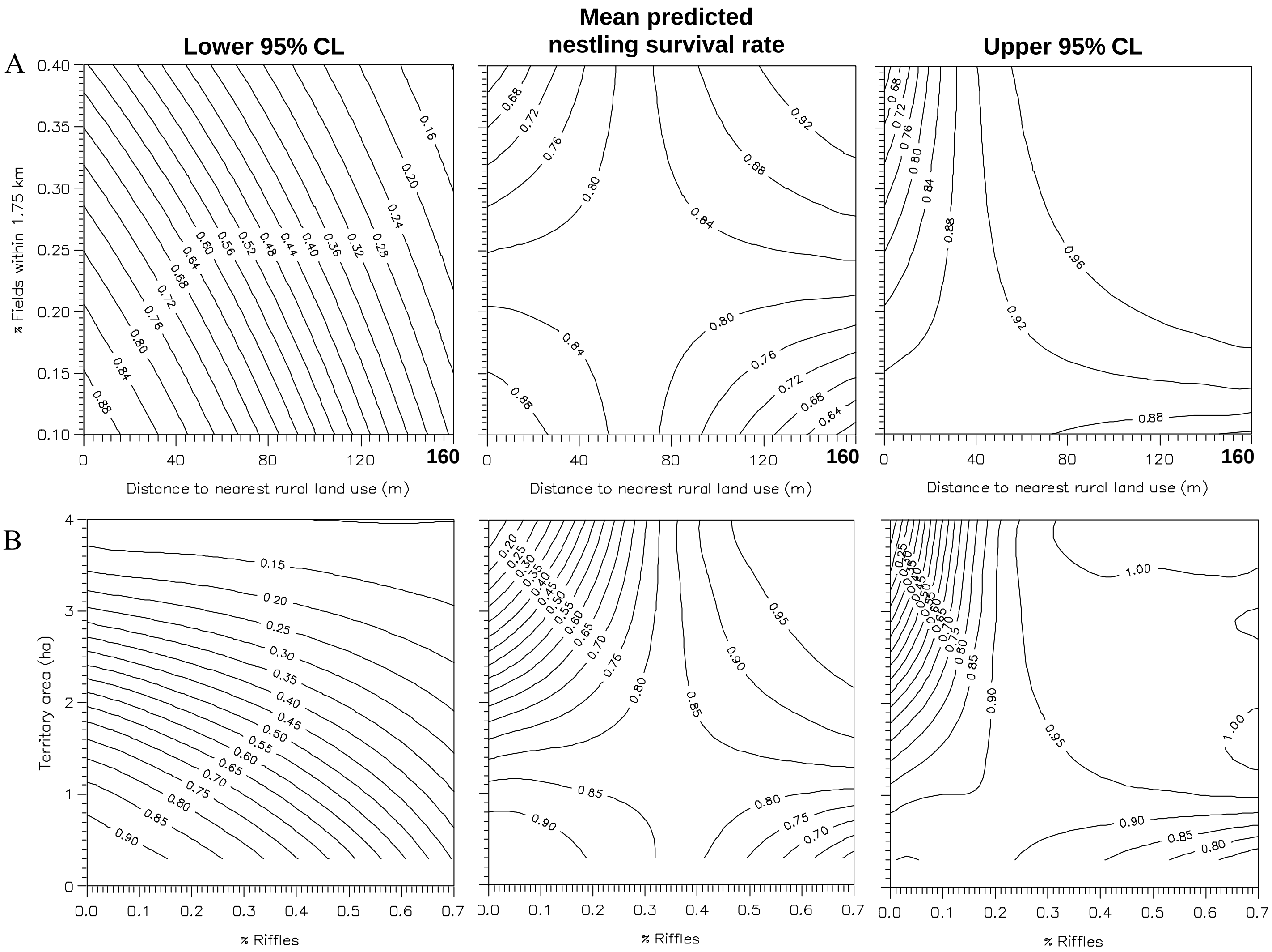

Fig. 5.4. Contour plots showing the interaction between percent fields and proximity to rural edges (A), and the interaction between territory size and percent riffles (B). All other parameters were held constant at their mean values. Contours represent the lower 95% confidence limits, means, and upper 95% confidence limits for model-averaged estimates of nestling survival rates, as viewed from left to right.

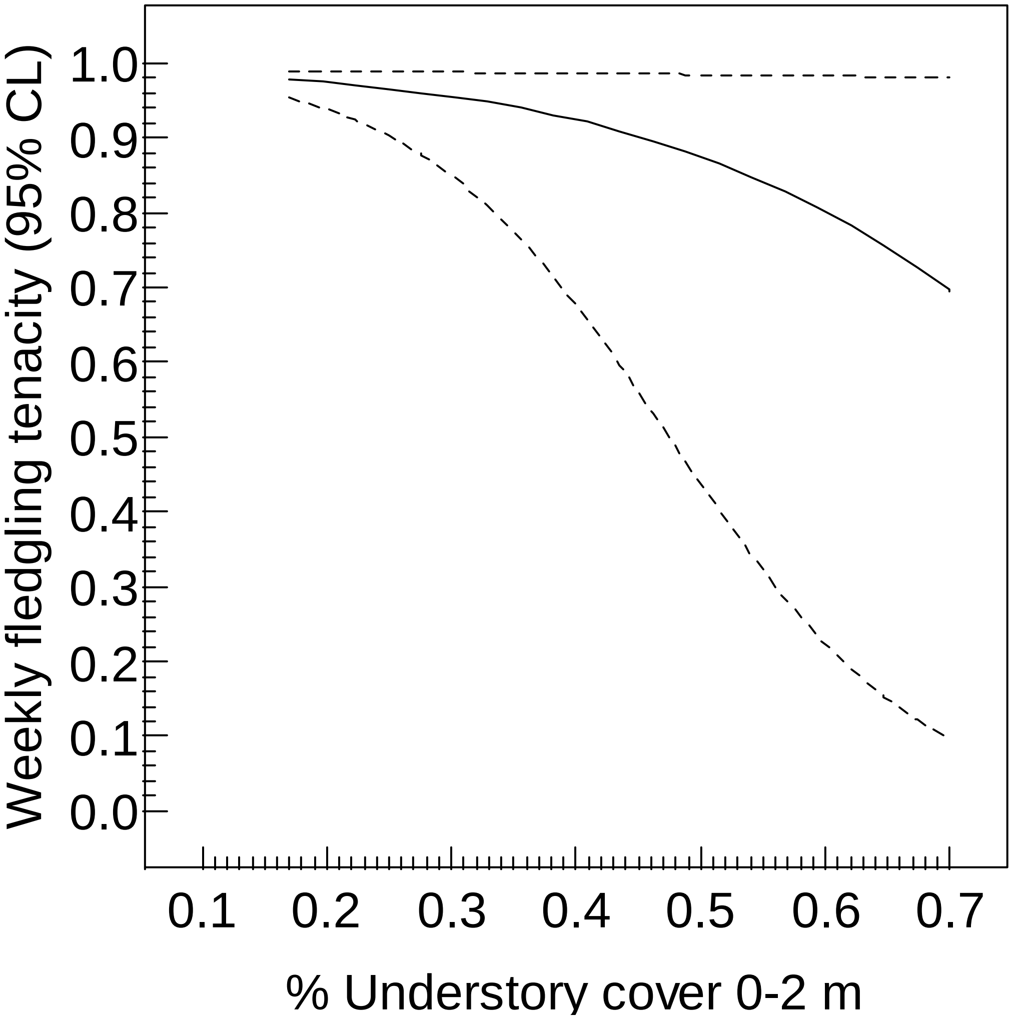

Fig. 5.5. Relationship between weekly fledgling site tenacity and percent understory cover while holding all other parameters constant at their mean values. Dashed lines represent upper and lower 95% confidence limits surrounding model-averaged estimates.

CHAPTER 6

A SUMMARY

I will first summarize my findings by returning to the original questions posed in the Introduction. Then, I will provide management recommendations based on these findings. Finally, I will suggest directions for future research on Louisiana Waterthrushes throughout their geographic range.

Summary of Findings

How well can waterthrushes serve as cost-effective indicators of stream biotic integrity?- Of the indicators considered, waterthrush occupancy was best for predicting relative abundances of macrobenthic taxa, while the EPA Visual Habitat Assessment (VHA) was best for predicting Ephemeroptera-Plecoptera-Trichoptera (EPT) richness. Individual components of EPA VHA scores were much less useful as indicators of EPT richness and % EPT when compared to the total score. Waterthrushes were found along streams with higher % EPT, a lower Family Biotic Index (FBI) pollution tolerance values, and greater macrobenthos biomass. Occupancy of waterthrushes was nearly 100% as buffer width exceeded 120 m. Stream benthic macrobenthos are good yet time-intensive indicators of stream water quality. Stream bird surveys and reach-scale habitat assessments, however, can serve as cost-effective indicators of macrobenthos. Using stream-dependent birds as an early warning signal for degradation of stream biotic integrity could improve the efficiency of watershed monitoring programs in detecting and identifying perturbations within the watershed.

Which life history characteristics determine reproduction for individual waterthrushes?- We developed an individual-based (I-B) model which estimates variability in productivity (i.e., the number of young that survive the dependent stage per adult female within a breeding season) of Louisiana Waterthrushes based on various aspects of their breeding cycle. Our empirical estimate of waterthrush productivity ($\bar{x}$=1.50, 1.45 SD) was similar to that provided by our I-B model ($\bar{x}$= 1.07, 1.24 SD). Contrary to emerging arguments about the importance of renesting for reproduction, simulated waterthrush productivity was most sensitive to and increased dramatically with increasing fledgling survival, daily nest survival, and, to a lesser extent, nestling survival. Productivity increased less dramatically with increasing renesting probability, second brood probability, and maximum days to lay. The remaining four factors had no detectable effects on productivity. When compared with our I-B model, the Donovan and Pease-Grzybowski approaches often overestimated fecundity (i.e., the number of young that reach fledging age per female in a breeding season) by up to 2.1 young fledged per female. In contrast, the Farnsworth-Simons approach often produced estimates that were similar to those from our I-B model. Our I-B model can be generalized to accommodate other breeding factors, including brood parasitism and temporal variability.

What environmental factors drive these crucial components of reproduction?-I used logistic regression and capture-recapture modeling in an information-theoretic approach to identify and quantify the environmental factors that predict the crucial components of individual fecundity for waterthrushes. I monitored 190 nests in 139 territories within 13 drainages during 4 springs. I also tracked 357 color-banded young from 87 of 112 fledged broods during the dependent stage. Nest survival (Range: 0.966-0.998) was greatest at intermediate levels of rainfall during the nesting period, while nestling survival (0.73-0.97) increased in a linear fashion with rainfall. In addition, nestling survival (0.16-0.98) declined with increasing territory size, and this relationship was exacerbated when riffles were sparse. Furthermore, nestling survival was lowest in areas that were near rural edges (clearcuts and fields) but were surrounded by high amounts of fields. Finally, understory cover had a negative effect on site tenacity of fledgling waterthrushes (0.72-0.99). Other factors, including measures of macrobenthos biomass, annual variation in climate, and timing of nesting had weak, if any, effects on waterthrush reproduction. These findings provide support for the hypothesis that nesting success of riparian obligates is subject to seasonal variation in climatic variables and is related to territory size. Improved field methods for studying waterthrush fledgling site tenacity could help distinguish permanent emigration from mortality, and elucidate relationships between environmental variables and true survival during the dependent stage. Continued monitoring of waterthrush reproduction and improved estimates of juvenile and adult survival will provide the ingredients needed to predict their responses to changing land use and climate.

Management Recommendations

Wide riparian buffers containing older hardwood or pine-hardwood forest along headwater stream networks (>1.5 km) will help maintain stability of Louisiana Waterthrush populations in the Georgia Piedmont. Based on Figure 3.6, a stream with >120 m of forest on both sides will average 99% male waterthrush occupancy. A stream with a buffer <40 m wide, however, will average <80% male waterthrush occupancy. According to Table 5.1, waterthrush nests averaged 46 ± 5 m (95% CI) from the nearest silvicultural stand or field, and waterthrush territories averaged 87 ± 3% forest within 60 m of the stream. Thus, extensive, buffered stream networks will likely provide suitable habitat for multiple breeding waterthrush pairs. This may facilitate both mate switching and extra-pair fertilizations (henceforth, polygamy), which could improve individual fitness and ultimately promote population stability. Water diversions, channelization, and dams also reduce stream habitat required by waterthrushes. Without these buffered stream networks, waterthrushes will be forced to occupy the remaining intact patches of riparian forest. This would likely lead to a reduced percentage of actual breeders in the population due to lack of required space for breeding territories, and thus population declines.

In addition to maintaining suitable habitat conditions, moderate rainfall during spring months (mean rainfall 3-8 mm day^{-1}) will likely lead to improved nesting success. Their dependency upon aquatic food sources and stream banks for nesting makes waterthrushes especially vulnerable to climatic fluctuations. On a global scale, management practices that minimize greenhouse gasses released into the atmosphere may help ensure stable climatic conditions in the Georgia Piedmont, thus maintaining waterthrush reproduction.

Future Research

Waterthrushes as indicators.-While I demonstrated that Louisiana Waterthrush occupancy provided information about stream macrobenthos beyond that which was indicated by visual habitat assessments alone, waterthrushes must be validated as indicators in other regions. One approach would be to survey waterthrushes along streams representing a wide gradient of land use impacts as evidenced by existing datasets on macrobenthos, water chemistry, and instream habitat conditions. Based on my experience, waterthrush surveys should include at least two visits along each perennial stream reach ($\geq$0.5 km) during the week preceding peak incubation initiation and within 4 hours after sunrise to ensure high rates of detection for both males and females. More visits may be required in regions for which peak incubation periods are unknown. Ideally, these surveys would be repeated annually to test for consistency among years. Once waterthrushes have been tested as indicators in other regions, then volunteer monitoring groups may begin to implement waterthrush surveys as part of their regular protocols.

Waterthrush population ecology.-While I have begun to fill some of the gaps in knowledge regarding Louisiana Waterthrush population ecology, several important research questions remain to be addressed and can be addressed with additional data collection and analysis of existing data. These include the following: 1) What environmental conditions influence the frequency of polygamy, and how does this influence reproduction by individual females? 2) What environmental conditions and intraspecific attributes (territory density, reproductive success) influence between-year colonization and evacuation of territories by individual females? 3) What factors (environmental conditions, family attributes) influence fledgling mortality during the dependent period?

Once these questions have been addressed, population viability analyses (PVAs) can be used to estimate waterthrush persistence in the Georgia Piedmont. The two approaches to PVA that I have identified are territory-based and individual-based. The former estimates the probability that all female breeding territories in the system become vacant and requires as input the number of available territories and rates of initial occupancy, colonization and evacuation of patches. A land cover database and a digital elevation model can be used in conjunction with my data on minimum territory sizes and capture and resighting of color-marked female waterthrushes to parameterize the territory-based PVA. This approach is analogous to a patch-based PVA, except that it defines a female territory as a patch.

The individual-based PVA estimates the probability that all females in the population become extinct and requires as input the initial population size, fecundity, and adult survival. The estimate for waterthrush population size in the Piedmont by the conservation group Partners in Flight could be used in conjunction with my data on fecundity, site tenacity of fledglings, and annual return rates of adult females to parameterize the model. This approach is a special case of a stage-based PVA, where there is only a single age group beyond the dependent period.

Although not outlined here, both approaches carry many assumptions that can be evaluated using existing literature on passerine population ecology and additional field data for waterthrushes. Sensitivity analyses would also help identify the crucial input parameters for each PVA approach. Then, predictive models that include environmental factors and intraspecific attributes selected by an information-theoretic approach could be applied to these crucial input parameters within each PVA. Comparing results from these two PVAs will provide more comprehensive knowledge about how changes in management and climate might affect waterthrush persistence in the Georgia Piedmont.