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Territories,Territoriality, and Conservation of the Louisiana Waterthrush and its Habitat, the Watershed of the Upper Buffalo National River

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TERRITORIES, TERRITORIALITY, AND CONSERVATION OF THE LOUISIANA WATERTHRUSH AND ITS HABITAT, THE WATERSHED OF THE UPPER BUFFALO NATIONAL RIVER

TERRITORIES, TERRITORIALITY, AND CONSERVATION OF THE LOUISIANA WATERTHRUSH AND ITS HABITAT, THE WATERSHED OF THE UPPER BUFFALO NATIONAL RIVER

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

By

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ABSTRACT

The Louisiana Waterthrush, *Parkesia motacilla*, is a migratory wood-warbler and breeding season resident of the eastern United States. Males defend breeding territories that extend linearly along clear, fast-flowing, gravel-bottomed, forest streams. Defense includes two song types, primary and extended song. As riverine specialists, birds rely upon aquatic invertebrates as prey and riparian habitat features for nesting. They use a unique foraging maneuver, leaf-pulling, that involves picking up or pulling a leaf from water, and turning it over to search for prey. Their relationship with riparian habitat introduces potential for Louisiana Waterthrushes to serve as indicators of stream health. The first objective was to determine if, during territorial defense, males exhibit the ‘dear-enemy’ effect with neighbors, strangers, and neighbors at incorrect boundaries. The second was to determine physical properties of extended song with different levels of aggression to test Morton’s (1977) motivational-structure rules of vocalizations. The third objective was to determine prey available in stream corridors as the result of leaf-pulling. The final objective was to determine how Louisiana Waterthrushes are affected by anthropogenic change in the watershed of the Buffalo National River and if functional relationships existed between territory size and common measures of riparian habitat quality. Territories were mapped and monitored on three watershed streams with legally protected and unprotected reaches. Birds were federally and color-banded and records of fidelity and nest-success were kept. Playback studies were run to test for neighbor-stranger and neighbor-neighbor discrimination and extended songs were analyzed alongside behavior. Territories were sampled for prey by simulating leaf-pulling. Bioassessment metrics were calculated. Males discriminated among neighbors, strangers, and neighbors at incorrect boundaries. Extended songs in more aggressive contexts had lower low-frequency components and longer suffixes of harsh, low-frequency components. Differences in prey were found among different areas in the stream corridor and different configurations of leaves. Aquatic invertebrate taxa differed with degrees of anthropogenic change. A functional relationship was found with lengths of territories and metrics indicative of riparian habitat quality and indicating that Louisiana Waterthrushes, as riverine specialists, could be useful bioindicators in the watershed of the Buffalo National River.

Keywords: Louisiana Waterthrush, *Parkesia motacilla*, riverine specialist, primary song, extended song, dear-enemy effect, neighbor-stranger discrimination, neighbor-neighbor discrimination, anthropogenic change, aquatic invertebrates, Buffalo National River, bioassessment metrics

This dissertation is approved for
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DEDICATION

I would like to dedicate this dissertation to the memories of my friend and conservationist, Martha Milburn, and my grandfather, Vaughn Hopper.

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Chapter 1:

Introduction

Territoriality can be defined in light of behavior as the action of defense of an area to exclude others, or it can be defined ecologically as the outcome of the behavior of defense in which an area is exclusively occupied (Maher and Lott 1995). The first definition is useful to those interested in how territories are established and maintained and the second is useful to those interested in the allocation of resources among individuals. Territory was first defined in studies of birds as any defended area (Howard 1920, Nice 1937, Noble 1939), with most bird studies involving passerines that defended their territories with song (Maher and Lott 1995). My study strives to understand the behavior of territoriality in both its behavioral and ecological frameworks.

Subject and Life History Traits

The Louisiana Waterthrush, *Parkesia motacilla*, a passerine and Nearctic-Neotropical migrant establishes linear breeding territories in the eastern United States along gravel-bottomed, fast-flowing, forested streams (Robinson 1995, Buckton and Ormerod 2002, Mattsson et al. 2009). It is a large, heavy-bodied wood-warbler, brown above, white underneath with dark streaking, with a buffy wash on its flanks and a prominent white supercillium, and a distinctive behavioral trait of teetering almost constantly (Eaton 1958, Casperson 1999). Male and female are similar, but, in the hand, they may be differentiated by bill size, with a male having a 5% larger bill, and a longer tail and wings. Adults can be distinguished from juveniles and second-year birds by small white spots on the tips of the adult's tail feathers and a white median crown stripe. Juveniles and immature birds also show rusty tips on the tertials and juvenal plumage has distinct, buffy wing-bars (Robinson 1995, Pyle et al. 1997).

In the Ozark Mountains of northwest Arkansas, Louisiana Waterthrushes are one of the earliest spring arrivals along with other early migrants, Black and White Warbler (*Mniotilta varia*) and Yellow-throated Warbler (*Setophaga dominica*). Spring arrival occurs prior to leaf-out in mid-March and fall migration begins as early as July (James and Neal 1986, Neal 2009). On arrival, males begin to sing and counter-sing to establish territory boundaries and to attract mates (Robinson 1995, Mattsson et al. 2009). Linear breeding territories are defended vigorously (Eaton 1958, Smith and Smith 1996, Mattsson et al. 2009). Defense includes counter-singing, chases accompanied by song, threat displays, and escalation to physical combat (Robinson 1995, Smith and Smith 1996, Mattsson et al. 2009). Boundaries are maintained upstream and downstream of a territory and occasionally occur where secondary streams, and thus territories, join. Compared to other wood-warblers, male Louisiana Waterthrushes have relatively few territory boundaries to defend. Upper and lower boundaries have been reported to be as little as 90 m apart, to as many as 1,200 m apart.

Two song types, primary song and extended song, are used by males with each having a different behavioral correlate. Smith and Smith (1996) provide an in depth description of Louisiana Waterthrush song. Both primary and extended songs begin with approximately two to four introductory notes in the form of wide chevrons, v-shapes, or a combination of both. This introduction is followed by briefer components of sharply descending frequency sweeps and rapidly descending and ascending v-shaped units. If, at this point, the song ends with an abrupt termination in the form of a chevron or couplet it is considered primary song. Primary song is most commonly given when a male is singing alone, and is thought to function equally to attract mates, advertise the singer’s presence on a territory, and counter-singing signals its intention to defend its territory. Each male has a unique song-signature within the introductory components of its song that can be easily identified by researchers by ear and on a spectrogram according to shape of the primary song components (Smith and Smith 1996).

When primary song continues with an extending suffix of notes that are lower pitched, rapid, and brief, the song is then considered the extended song type. Extended song is most commonly given when males are directly and aggressively interacting with one another in territorial defense, particularly when a male is approaching another male (Eaton 1958, Spector 1992, Smith and Smith 1996). The number of components and thus the length of the extended suffix often differ among extended songs. Birds tend to incorporate within the suffix a series of notes that may be repeated (Smith and Smith 1996) further extending the suffix. When the suffix of extended song becomes very long, it can be defined as a run-on pattern of singing. Run-on chains of singing have been documented to contain as many as 197 notes (Smith and Smith 1996).

The repertoire of the male Louisiana Waterthrush also incorporates non-song vocalizations including call-notes described as cheks, tps, buzzes, and brief vocalizations or bursts that are similar to components found in the endings of extended song (Smith and Smith 1996). Other infrequent vocalizations include a dusk flight song and accompanying flight display and soft song in which either primary or extended song types are sung at lower amplitudes. Females also use non-song vocalizations and have been heard to sing a very soft and somewhat broken primary song on leaving the nest during incubation recesses. Males arrive quickly to escort a female during these incubation recesses (Robinson 1995) and (Pers. Obs.) and her song may be important in advising him of her status.

Territoriality, as a measure of defense in the Louisiana Waterthrush, includes the initial arrival to the area, the establishment of territories by males returning to territories of the previous year, or by new males to new territories, and the continued maintenance of those territories. In my second and third chapters I focused upon the study of territoriality as the behavior of defense of an area in an effort to exclude others (Maher and Lott 1995). This included defense of an area with specific boundaries through self-advertisement, (song), and overt aggression, (approach, searching out an intruder, and display).

Chapter II: Behavior, song, and motivation of male Louisiana Waterthrushes, P*arkesia motacilla*, in response to neighbors, strangers, and neighbors at incorrect boundaries

The defense of territory is energetically costly and studies have shown that animals may exert energy to different degrees depending upon the costs and benefits of defense in different situations. Territories are often occupied by individuals that have gained previous knowledge of one another through experience. As a result, territory owners may be capable of discriminating known individuals as “neighbors” and unknown individuals as “strangers”, with each class of individual representing a different degree of threat to the owner of a territory. When a territory holder responds to a stranger with more aggression than it does a neighbor, this response is referred to as the ‘dear enemy’ effect (Fisher 1954). This behavior is believed to increase fitness of a territory holder by allowing them to efficiently allocate their time and energy (Falls 1969, Krebs 1971, 1982, Getty 1987, Beletsky and Orians 1989, Getty 1989, Godard 1993, Stoddard 1996) because neighbors and strangers differ in the relative amount of threat they present to a territory holder (Temeles 1994). Neighbors are less threatening because territory boundaries have previously been established between two individuals. Strangers are a greater threat because they are likely looking to usurp space for a territory within a territory holder’s boundaries. Therefore, more energy should be allocated to aggression toward a stranger than to a neighbor (Jaeger 1981, Getty 1989). Neighbor-stranger discrimination is a relatively common phenomenon, particularly in taxa where individuals hold and defend breeding, multi-purpose territories (Temeles 1994). Neighbor-stranger discrimination has been documented in insects (Gordon 1989, Thomas et al. 1999), amphibians (Davis 1987, Bee and Gerhardt 2001), fish (McGregor and Westby 1992), reptiles (Whiting 1999), mammals (Cheney and Seyfarth 1988, Mitani et al. 1996, Rosell and Bjørkøyli 2002), and birds (reviews in: Falls 1982, Lambrechts and Dhondt 1995, Stoddard 1996, see also: Lovell and Lein 2004, Mackin 2005, Hardouin et al. 2006, Skierczynski et al. 2007).

Territory owners may also be able to recognize and thus discriminate between individuals. This type of discrimination is more complicated than neighbor-stranger discrimination which requires an individual only to discern between a familiar and an unfamiliar signal (Axelrod and Hamilton 1981, Stoddard 1996) because individual discrimination of neighbors requires an individual to discern multiple individuals by using several approximately familiar stimuli in addition to location (Falls 1982, Stoddard 1996, Wiley 2005). Other species, such as amphibians (Bee and Gerhardt 2002), fish (Myrberg and Riggio 1985, McGregor and Westby 1992) and mammals (Cheney and Seyfarth 1982) have been shown to be capable of individual discrimination. Individual recognition has been documented in birds for parent-offspring recognition (Beer 1970, Falls 1982, Wiley et al. 1991, Lampe and Slagsvold 1998) and discrimination between individual neighbors (Falls 1982, Lambrechts and Dhondt 1995, Stoddard 1996, Lovell and Lein 2004, see also: Lovell and Lein 2005). If a bird responds with a similar degree of aggression to a neighbor singing at an incorrect boundary as it does to a stranger's song, then it is considered to be showing individual discrimination. This indicates that the territorial male associates a particular song with a particular location (Lovell and Lein 2005).

The individually distinctive primary songs of the Louisiana Waterthrush should allow identification by other males.

My objectives for Chapter 2 were to determine whether territorial male Louisiana Waterthrushes exhibit different behaviors in response to songs of strangers, songs of neighbors at correct boundaries, and songs of neighbors present at incorrect boundaries (i.e. the opposite boundary on a linear territory). I also wanted to determine whether there were differences in use of extended and primary song types as the breeding season progressed and males were involved in different breeding activities. My hypotheses were that there would be differences in behaviors that correlated with strangers presenting the greatest threat, correct neighbors presenting the least threat, and incorrect neighbors presenting a threat within these two extremes. Aggressive responses were expected to wane as a breeding season continued through its cycles of arrival, mate attraction and pair bonding, through reproductive states of nesting, feeding of nestlings and fledglings, and in some cases, predation of offspring and a renewed effort at reproduction.

Chapter III: Motivation-structural code and extended song acoustic structure in territorial male Louisiana Waterthrushes (*Parkesia motacilla*)

Vocalizations increase the amount of information that can be attained concerning an animal's motivational state. Morton (1977) presented motivation-structural rules based upon the premise that through natural selection vocalizations of birds and mammals have undergone convergent evolution such that, in an interaction, when two animals are in sight of one another, harsh, low-frequency vocalizations are honest signals that the producer of the vocalization is hostile, while pure-tone like sounds signal that it is frightened or appeasing. There are two dimensions to a single vocalization. The first is frequency and the second is harshness. The physiology of the vocal apparatus results in these two dimensions tending to be dependent on one another. A low-frequency sound will tend to be harsh and a high-frequency sound will tend to be pure-tone like. The structure of the majority of vocalizations generally lies somewhere on a continuum between the harshest and most low-frequency vocalization, for example, a growl and the highest pitch, most pure-tone vocalization, for example, a whine. A vocalization intermediate to these to endpoints tends to rise and fall in frequency, and illustrates that an individual has recognized something of interest and is neither retreating nor approaching the stimulus. A good example of this type of vocalization is a bark. Compound vocalizations lie not only upon this two-dimensional continuum of frequency and harshness, but also on a third and fourth dimension of rate of delivery and amplitude (Owings and Morton 1998). Thus, even simple vocalizations can confer a great deal of information and illustrate active changes in an animal's motivational state as a social situation plays out through time and with changes in stimuli.

The extended song of the Louisiana Waterthrush is an example of a compound vocalization produced as an extension of the primary song type. The frequency of the primary song components and the number of harsh low-frequency components found in extended song and run-on variants of extended song may serve to indicate the intensity with which males are interacting and the degree of aggression in the interaction. Therefore, my objectives for Chapter 3 were to determine whether there were differences in the acoustic structure of primary and extended song types, and prefix and suffix components of extended song in birds responding to songs of strangers, songs of neighbors at correct boundaries, and songs of neighbors present at incorrect boundaries. Song structures were also compared to determine if there were changes in the acoustic structure as time into the breeding season progressed and birds participated in different reproductive activities. Comparison of songs given by males in situations in which different levels of aggression were expected, allowed us to test the hypothesis that increased levels of aggression correlate to the number and structure of harsh, low frequency components in their song as predicted by Morton's (1977) motivation-structural rules of vocalizations.

Chapter IV: Leaf-pulling by Louisiana Waterthrushes: prey availability due to a unique foraging maneuver in a stream environment

The outcome of defensive behavior is exclusion of conspecifics from the resources within the focal male's breeding territory. Resources in the territory include nest sites and sufficient food resources to support the territory owner, its mate, and potential offspring (Robinson 1995, Mattsson et al. 2009). Birds spend a large percentage of their time each day foraging for aquatic insects (Robinson 1990). Analysis of stomach contents (Eaton 1958) and observation (Craig 1984, 1987) indicate prey include trichopterans, dipterans, ephemeropterans, oligochaetes, chironomids, stratiomyiids, tipulids, coleopterans, hemipterans, neuropterans, plecopterans, diplopods, and isopods, as well as odonate nymphs, dytiscid beetle larvae, cicadas, spiders, scorpions, crustaceans, earthworms, salamanders (Bent 1953, Mulvihill et al. 2008, Mattsson et al. 2009), small fish and decapods (Pers. Obs.). Craig (1984) reported that birds show preference for ephemeropterans, trichopterans, and dipterans, and avoid isopods. Correlations have been found with the percentage of riffle habitat, biomass availability of prey, and relative abundances of Ephemeroptera, Plecoptera, and Trichoptera (Stucker 2000, Mattsson 2006, Mulvihill et al. 2008) that are more commonly found within healthy stream reaches and riffle habitats (Brussock et al. 1985, Smith 1986, Brown and Brussock 1991, Kobayashi and Kagaya 2002, Roy et al. 2003).

Louisiana Waterthrushes primarily use two methods of foraging; picking (short rapid thrust of the bill directed to the water, ground, or foliage) and leaf-pulling (picking up or pulling a leaf from leaf litter or more commonly from shallow areas of the stream (<2cm) and turning it over to search its underside for prey (Craig 1981, Robinson 1990). Birds also opportunistically glean (remove prey with bill from foliage, twigs, or bark while perched), hawk (fly rapidly from perch to capture prey in bill opportunistically), and hover (fly from perch or ground to remove prey item from substrate in flight, seen when birds take prey from the surface of deep water or when gleaning insects from foliage too high to reach when perched) (Craig 1981, Robinson 1990). Leaf-pulling is the most common foraging maneuver prior to leaf-out in the spring (Craig 1984) and prior to incubation (Robinson 1990).

The objectives for Chapter 4 were to determine prey available to Waterthrushes in the stream corridor by simulating their foraging maneuver and pulling isolated leaves from the stream and the first five leaves from tops of leaf packs at edges of riffles, centers of riffles, and edges of pools to determine density, biomass, and assemblage of potential Louisiana Waterthrush prey. Prey availability was compared between isolated leaves and leaf packs, among locations within the stream corridor, and among Louisiana Waterthrush territories on three streams within the upper Buffalo National River Watershed with varying degrees of anthropogenic disturbance.

Chapter V. Louisiana Waterthrush (*Parkesia motacilla*) of the Buffalo National River Watershed and Their Relationship to a Changing Riparian Habitat

The Buffalo River in the Arkansas Ozarks was designated as the first National River in 1972. It is one of only five free-flowing rivers that have been federally protected through special acts of Congress (Benke 1990). The U.S. House of Representatives report of that year states, ‘Because it is a pure, free-flowing stream which has not been significantly altered by industry or man, it is considered to be one of the country’s last significant natural rivers’. National Rivers generally have wide segments of protected areas along their riparian corridors (Benke 1990). The Buffalo National River does not. Its headwaters form in the Boston Mountains, and it winds 150 miles east through the Ozark Uplands of northwestern and central Arkansas. Of its length, 135 miles are protected as National River, with widths of only one-half to four miles of its riparian border included in this protection. In addition, 29% of watershed is under State of Arkansas or United States Forest Service protection, leaving 60% of the watershed privately owned. Anthropogenic land-use changes on private lands within the Buffalo National River's watershed include gravel-mining, construction and use of dirt and gravel roads through streams and removal of forests for establishment of pasture (Mott and Laurans 2004). It is the conversion of forested land to pasture that poses the greatest threat to water quality (Mott and Steele 1991, Scott and Hofer 1995, Mott and Laurans 2004).

These activities within the watershed result in increased sediment load with storm runoff and habitat destruction to tributary streams and the river itself (Mott and Laurans 2004). The removal of forested land allows for greater amounts of sediment to enter streams during rain events. In addition, cattle are commonly allowed access to water along lengths of streams (Weeks 1987, Holleman 1992) creating 'sacrifice areas' that become filthy from trampling, urination, and defecation (Braun 1986, Weeks 1987). Pastures are often fertilized through the application of chicken manure (Holleman 1992), and together watering holes and fertilization of pasture result in high concentrations of nutrients and fecal coliform bacteria in watershed streams and the river (Dale et al. 1978, Weeks 1987, Mott and Steele 1991, Mott and Laurans 2004).

Increased sedimentation of streams, addition of nutrients, fecal coliform bacteria, and increased sunlight alter stream habitat and affect suitability of habitat for aquatic invertebrates (Mathis 1990, Wood and Armitage 1997, Roy et al. 2003, Suberkropp et al. 2010) and Louisiana Waterthrushes may be affected in turn. This predator-prey relationship, along with the bird's habit of nesting within stream banks, makes them vulnerable to changes in both stream water quality and riparian land-use and potentially informative as to the ecological integrity and health of the stream environment (Ormerod and Rundle 1998, Prosser and Brooks 1998, Stucker 2000, Mattsson and Cooper 2006, Mulvihill et al. 2008).

Food value theory (Stenger 1958, Wilson 1975) proposes that the function of territoriality is to ensure enough space for an adequate food supply to rear young. Thus, territories of different sizes may be indicative of differences in abundance and quality of prey (Smith and Shugart 1987, Marshall and Cooper 2004). If food is the limiting factor in size of territories, areas with lower abundances of prey or prey of lesser quality may necessitate increasing the size of a territory to increase fitness. Alternatively, areas of greater prey density and higher food-value may increase intraspecific competition among the predator population and result in smaller territory sizes (Smith and Shugart 1987, Marshall and Cooper 2004), though this may not apply as strongly to Waterthrushes who generally have only two territorial boundaries to defend compared to terrestrial species whose territories are bounded on all sides (Mattsson and Cooper 2006).

Previous studies have shown correlations between pollution-intolerant aquatic invertebrate taxa and presence and absence of Louisiana Waterthrushes (Stucker 2000, Mattsson 2006, Mattsson and Cooper 2006). Mulvihill et al. (2008) found a significant relationship between pollution-intolerant taxa and territory size. Territories on acidified streams in southwestern Pennsylvania were nearly twice the length of those on circumneutral streams. In addition, breeding birds on acidified streams had smaller clutches and decreased site fidelity to those territories. In the Georgia Piedmont a decline in nestling survival occurred as territory length increased and the riffle habitat for pollution-intolerant taxa decreased (Mattsson 2006).

My first objective for the 5th chapter was to map and monitor Louisiana Waterthrush territories on three watershed streams in the Buffalo National River watershed with legally protected and unprotected reaches and different degrees of anthropogenic change so that comparisons could be made between measures of stream and habitat ecological integrity, lengths of Louisiana Waterthrush territories, nest success and site fidelity. My second objective was to determine if functional relationships existed between lengths of territories and measures of riparian habitat quality so that Louisiana Waterthrushes might serve as a measure of stream ecological integrity in the Buffalo National River and its watershed.

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Chapter 2:

Behavior, song, and motivation of male Louisiana Waterthrushes, P*arkesia motacilla*, in response to neighbors, strangers, and neighbors at incorrect boundaries

Abstract

Neighbor-stranger discrimination is common in taxa where individuals defend breeding territories. A territory holder responding to a stranger with more aggression than it does a neighbor is increasing its fitness by allocating appropriate amounts of energy to different degrees of threat to its territory. Individual discrimination is less well documented. It requires an individual to discern multiple individuals by using several approximately familiar stimuli and location. Individual discrimination also increases fitness through correct allocation of energy. The Louisiana Waterthrush is a Nearctic-Neotropical migratory wood-warbler which breeds in the eastern United States. It establishes and defends linear territories along corridors of gravel-bottomed streams. Its vocal repertoire includes two song types used in different contexts. Individuals are easily recognized by song signatures. Playback studies were performed to mimic different types of intrusion and thus determine if males could discriminate between neighbors, strangers, and individuals as neighbors at incorrect boundaries. Males responded to songs of strangers and neighbors at incorrect boundaries with more aggressive behavior than to songs of neighbors at correct boundaries. In responses to strangers' songs, males used more extended song, responded with extended song more rapidly, and made more flights in search of a perceived intruder. Soft song was used in response to a stranger's song more often and earlier in the breeding season. Responses, including relative use of song types, changed with progression of the breeding season. Extended song correlated with more aggressive behavior and approach. Primary song correlated with less aggressive behavior.

Keywords: Louisiana Waterthrush, *Parkesia motacilla,* neighbor-stranger discrimination, neighbor-neighbor discrimination, breeding season, soft song

Introduction

Neighbor-stranger discrimination is a relatively common phenomenon, particularly in taxa where individuals hold and defend breeding, multi-purpose territories (Temeles 1994). When a territory holder responds to a stranger with more aggression than it does a neighbor, this response is referred to as the ‘dear enemy’ effect (Fisher 1954). This behavior is believed to increase the fitness of territorial animals by allowing them to efficiently allocate their time and energy (Falls 1969, Krebs 1971, 1982, Getty 1987, Beletsky and Orians 1989, Getty 1989, Godard 1993, Stoddard 1996). Neighbors and strangers differ in the relative amount of threat that they present to a territory holder (Temeles 1994). Neighbors are less threatening because territory boundaries have previously been established between the two individuals. Strangers are a greater threat because they are more likely to attempt to usurp space for a territory within the territory holder’s boundaries. Therefore, more energy should be allocated to aggression toward the stranger to which more could be lost than to a neighbor (Jaeger 1981, Getty 1989).

Neighbor-stranger discrimination requires an individual to discern only between a familiar and an unfamiliar signal (Axelrod and Hamilton 1981, Stoddard 1996). In contrast, individual discrimination of neighbors requires an individual to discern multiple individuals by using both familiar acoustic stimuli and location (Falls 1982, Stoddard 1996, Wiley 2005). Individual recognition has been documented in birds for parent-offspring recognition (Beer 1970, Falls 1982, Wiley et al. 1991, Lampe and Slagsvold 1998) and discrimination between individual neighbors (Falls 1982, Lambrechts and Dhondt 1995, Stoddard 1996, Lovell and Lein 2004, see also: Lovell and Lein 2005).

If a bird responds with a similar degree of aggression to a neighbor singing at an incorrect boundary as it does to a stranger’s song, then it is considered to be showing individual discrimination. This indicates that the territorial male associates a particular song with a particular location (Lovell and Lein 2005). A neighbor singing at an incorrect boundary might be looking to expand its territory (Stoddard 1996).

The learned behavior of discrimination may develop via the simplest form of learning, habituation (Wiley and Wiley 1977, Falls 1982, Stoddard 1996, Bee and Gerhardt 2002), or through more complex forms of associative learning (Richards 1979, Beecher et al. 1996, Stoddard 1996, Hyman and Hughes 2006). Birds have been shown to exhibit both short-term (Godard 1993) and long-term memory (Godard 1991). Long-term memory has been illustrated in that hooded warbler males, *Wilsonia citrina*, that had shared territorial boundaries in previous years, recognized each other even after a period of eight months in which the birds completed their migratory journeys and returned to breeding territories. Those males that had held territories adjacent to one another in previous years showed a reduced response to one another at the very onset of the breeding season (Godard 1991). The long-term memory of neighbors from the previous breeding season is adaptive in that it frees energy and time that might have been used for territorial establishment and other activities including courtship and pair-bonding with females (Godard 1991).

The Louisiana Waterthrush, *Parkesia motacilla*, is a Nearctic-Neotropical migratory wood-warbler which breeds in the eastern United States. It arrives prior to leaf-out in spring and aggressively establishes and defends linear breeding territories along corridors of gravel-bottomed streams (Eaton 1958, Smith and Smith 1996, Mattsson et al. 2009). Boundaries are upstream and downstream of a territory, and occasionally occur where secondary streams, and thus territories, join. As a result, males generally have relatively few territory boundaries to defend. Upper and lower boundaries have been reported to be as little as 90 m apart, to as many as 1,200 m apart. Defense includes counter-singing, chases accompanied by song, threat displays, and escalation to physical combat (Robinson 1995, Smith and Smith 1996, Mattsson et al. 2009).

The vocal repertoire of the Louisiana Waterthrush male includes primary and extended songs, contact notes, and a variety of brief vocalizations. Primary song consists of two to four introductory components followed by a twittering succession of notes, and ends with an abrupt termination. It is most commonly given when a male is singing alone. A bird singing primary song is not approaching another male and is taking the initiative only to advertise its presence (Smith and Smith 1996). Primary song is thought to function for both mate attraction and in territorial defense.

Extended song begins as primary song but proceeds beyond primary song's abrupt termination with a suffix of brief components of variable length. It is most commonly given when males are interacting directly with one another in territorial defense, particularly when a male is approaching another male (Bent 1953). The extended song in this context has been referred to as 'pursuit song' and at times the extended song can reach a length and composition that is referred to as 'run-on singing' (Bent 1953, Eaton 1958, Spector 1992, Smith and Smith 1996). Smith and Smith (1996) found that birds that approach with extended song, both to playback and in natural encounters, shortened extended song and lapsed back into primary song when they failed to find an intruder or, in the case of natural encounters, when the exchange between the two birds came to a 'stalemate'.

Call-notes are described onomatopoetically as 'cheks', 'chips', or 'tps'. Other non-song vocalizations include buzzes, zizzes, chuts, and churrs. Brief vocalizations are often given in 'bursts' and are similar to components found in the endings of extended song (Smith and Smith

1996). The vocal repertoire includes soft song and flight song. Both have the same composition as primary or extended song types, but soft song is sung at a lower amplitude and flight song is sung more rapidly while the bird is aloft (Smith and Smith 1996, Mattsson et al. 2009).

The breeding season and its associated hormonal changes appear to affect the behavior of singing (Voigt and Leitner 2008). With spring arrival, males are heard singing and counter-singing throughout the day (Eaton 1958). Song declines greatly with establishment of pair-bonds (Craig 1981). The decline continues as the season wanes, and after breeding and with molt, very little singing occurs. Just prior to fall migration there is a small resurgence of song (Eaton 1958).

Individuals have song signatures that are easily identified by researchers according to shape of the initial components of their primary song (Smith and Smith 1996). No geographic variation has been found in the song of this species (Smith and Smith 1996). Although individuals are recognizable by their song, it is yet to be determined whether males discriminate between songs of strangers and territorial neighbors (Robinson 1995). The individually distinctive primary songs of the Louisiana Waterthrush should allow identification by other males.

My objectives were to determine whether territorial male Louisiana Waterthrushes exhibit different behaviors in response to songs of strangers and songs of neighbors at correct boundaries (i.e. neighbor-stranger discrimination), and songs of neighbors present at an incorrect boundary (i.e. neighbor-neighbor or individual discrimination). I also wanted to determine whether there are differences in use of extended and primary song types as the breeding season progresses and males are involved in different breeding activities. My hypotheses were that there are differences in behaviors that correlate with strangers presenting the greatest threat, correct neighbors presenting the least threat, and incorrect neighbors presenting a threat within these two extremes. Responses were analyzed for differences that may have occurred as the breeding season continued through its cycles of arrival, mate attraction and pair bonding, through reproductive states of nesting, feeding of nestlings and fledglings, and in some cases, predation of offspring and a renewed effort of reproductive stages.

Methods

Louisiana Waterthrush populations on 9 km of three streams within the Buffalo National River's watershed in the Arkansas Ozarks near Ponca (Newton County) were banded and monitored from 2006 to 2008 with a preliminary banding season in 2005. Twenty-six males held territories during that time. Each male was mist-netted and banded with color and federal bands; their songs were recorded and their territories mapped each year by observing encounters between males at territory boundaries and by mapping song perches. Because Louisiana Waterthrush territories are linear along a stream, they usually had only two neighbor boundaries, one at the upstream end of a territory and one at the downstream end. Territories averaged 300 to 500 m in length.

All recordings were made with an Audio-Technica 815 Shotgun microphone with a Rycote windscreen and shock mount handle. A Sony TC-D5 PROII cassette recorder was used in 2006, and a Marantz PMD 660 was used in 2007 and 2008. A Mineroff SME-AFS speaker and Phillips portable CD player were used for playback. Recordings were digitized via Raven Interactive Sound Analysis Software, Version 1.1: developed by the Bioacoustics Research Program, Cornell Laboratory for Ornithology. Playback stimuli for eliciting reactions from the five focal males were produced from recordings of primary song bouts of territorial males. Unwanted low-frequency noise was high-pass filtered from recordings. Song stimuli occurred at five songs per minute on the playback recordings for a total of three minutes which was the mean song rate calculated from 2006 and 2007 recordings of males singing alone (without the stimulation of a counter-singing male). Songs used for stimuli were played at amplitude of 85 to 88 dB at 1m from the speaker (Smith and Smith 1996). The speaker faced into a territory within 5 m of the territory boundary at a height of 2 m on a tripod. Either the downstream boundary or upstream boundary was chosen randomly for each trial.

Six trials were attempted for each focal male. They were playback of the upstream neighbor's song at the upstream boundary (correct neighbor), playback of the downstream neighbor's song at the upstream boundary (incorrect neighbor), and playback of a stranger's song at the upstream boundary (stranger), playback of the downstream neighbor's song at the downstream boundary (correct neighbor), playback of the upstream neighbor's song at the downstream boundary (incorrect neighbor), and playback of a stranger's song at the downstream boundary (stranger) (Fig. 2.1). One trial was run each day for six contiguous days if possible. Choices of which of boundary and whether to use the correct neighbor, incorrect neighbor, or stranger song were made randomly to control for order of presentation and bias. The same neighbors were not used on consecutive days. To avoid pseudo replication (Kroodsma 1989) experiments used unique stranger song for a single male, and that male was used only in one set of trials in one year. Strangers were defined as individuals holding territories on different streams.

Playback began 10 min after the experimenter located territorial males near the territorial boundary where playback was to occur, and their behaviors were documented for 5 min before beginning playback. I required that males had not interacted with neighbors for those 10 min and that neighbors had remained silent for 5 min before playback began so that behavior was not influenced by their interaction. Trials were run every 24 h at least 1 h after dawn so that responses were not influenced by dawn chorus or previous experimentation and habituation (Lovell and Lein 2005). If a neighbor sang within 40 m of the playback speaker, if the focal male was never sighted near the correct boundary for experimentation, or if the weather precluded experimentation, the trial was abandoned and repeated the following day, and other trials were moved forward by one day (Molles and Vehrencamp 2001). Trials were run for each male within a year from within one day to as many as 18 days of one another. Trials were run for each male within a year from within one day to as many as 18 days of one another (Table 2.1). Long intervals between trials were a result of birds never approaching the randomly chosen boundary. There were long distances between an upstream and downstream boundary, and birds tended to interact more often at one boundary than another. This appeared to depend on placement of the nest in the territory, foraging behavior of females during incubation recesses, and interactions between neighboring males, particularly when a boundary was being contested regularly with a boundary neighbor. As many as six hours were spent waiting for the bird to appear at the randomly chosen boundary before the trial was abandoned for the day. Trials were run from within 39 days of the mean spring arrival date of March 14 to 108 days thereafter. This encompassed periods of nest construction, incubation, tending nestlings, tending fledglings, and depredation.

Each trial lasted 12 min with 3 min of preplayback, 3 min of playback and 6 min of post-playback recording the response of the subject (Lovell and Lein 2005). Timing of behavioral and vocal responses were transcribed from recordings with Etholog 2.25 Behavioral Observation Transcription software (Ottoni 2000).

Behavioral response measures included movements and approach, singing, and chek, tp, and buzz vocalizations (Smith and Smith 1996). They specifically included: latency to first approach within 10 m of the speaker (s); closest approach to speaker (m); latency to first flight toward speaker (s); total time within 10 m of the speaker (s); number of flights; number of primary songs; latency to first primary song (s); number of primary songs without terminations; latency to first primary song without termination (s); number of soft primary songs; latency to first soft primary song (s); number of soft extended songs; latency to first soft extended song (s); number of extended songs; latency to first extended song (s); number of cheks; latency to first chek (s); number of tps; latency to first tp (s); number of buzzes; latency to first buzz (s); number of foraging bouts, and latency to first foraging bout (s) and its duration (s).

Measurements of physical components and properties of extended songs were calculated for separate analysis (see Chapter 3) and included number of introductory notes in the primary segment, its length (s), lowest frequency (Hz), highest frequency (Hz), and bandwidth (Hz). Measures of the suffix included the number of components, length (s), lowest frequency (Hz), highest frequency (Hz), peak frequency (Hz), and bandwidth (Hz). Run-on song was treated as extended song.

The 24 behavioral response variables were reduced to 17. Cheks, tps, and buzzes or zeets were rare, but when given they occurred in bursts, and often in series with one another. Occasionally they were incorporated into a song's prefix or suffix. Therefore, I chose to lump these into a single variable identified as 'brief vocalizations'. Primary soft songs had a tendency to trail off in amplitude and may have instead been extended song with components that could not be heard in the recording. Therefore, soft primary and soft extended songs were lumped into a single variable 'soft song'. Foraging bouts were generally interrupted only by short flights which misleadingly elevated the number of these bouts. Therefore, 'foraging bouts' was deleted from the statistical evaluation. Latency and Closest Approach Variables were transformed by subtracting the actual values from the maximum possible values (540 s and 30 m, respectively) so that larger values indicated a stronger response (McGregor 1992). Thirty meters was chosen as the longest distance measurement as it was approximately the furthest along the stream a bird could be sighted.

Data collected comparing responses to neighbors and strangers and data collected to compare responses to correct and incorrect neighbors were grouped for separate statistical analysis. Within groupings, the seventeen behavioral responses were analyzed separately from the eleven physical components and properties of vocal responses. Response variables tended to be correlated. Therefore, a principal components analysis (PCA) was conducted to control for collinearity (Manly 1986). Principal components were then analyzed as a two-factor factorial ANCOVA (Milliken and Johnson 1992) with day of the nesting cycle beyond spring arrival (March 14) as a covariant. Neighbor versus stranger, correct neighbor versus incorrect neighbor, and each focal male were treated as fixed effects. Least square means were used to determine differences when appropriate. Data analysis was done using SAS software, Version 9.2 (SAS Institute Inc., Cary, NC, USA). Differences were considered significant at $p = 0.05$ or less.

Results

Yearly migration return rates were high. In 2007 there was an 80 % return rate, but 2008 had only 60 % of the previous year's males returning. Of the returning males, each year 100 % returned to their previous territory. Territory boundaries remained similar if not identical between males that had shared boundaries the previous year. Five focal males (FM) were chosen randomly and the stage of their breeding cycle was noted. Two of the five were tested in both 2007 and 2008 (Table 2.1). One male banded in 2006 was known to have the same neighbors throughout the three years of the study. Another three males were banded in 2006, and each shared one common boundary with the same neighbor from 2006 through 2008 while the opposite boundary was occupied by a new male in the year of experimentation. The last male was not banded until 2008, but he was recognized by a very clear and unusual song signature that was recorded from 2006 through 2008. He was known to have shared at least one common boundary with the same neighbor since the first year of his experimentation in 2007. The breeding cycle of each male was followed through the time the male served as a focal subject.

A total of 33 experiments were run with the five focal males over a period of two years (2007, 2008) during which 396 min of behavior and recordings of 614 measurable vocalizations were made. Of the five focal males, one did not actively respond to playback (Table 2.2). This bird was unlike the others in that, during three consecutive years of study, he had the same pair of neighbors every year and territorial boundaries remained in the same place year after year. All other males had at least one new neighbor at a boundary in the year trials took place. Therefore, analyses were run twice (Table 2.2 and Table 2.3). With his removal, the number of experiments used for statistical analysis was reduced to 24 (Table 2.1), including 288 min of behavior, and recordings of 560 vocalizations. Only this latter analysis is reported here.

Principal components analysis (PCA) for comparing responses to neighbors and strangers, (neighbor vs. stranger trials n = 17), produced five principal components (PCs) with eigenvalues greater than 1.0, explaining 83.9 % of variation in responses among trials. PCA for comparing behavioral responses to correct and incorrect neighbors, (correct vs. incorrect neighbor trials, n = 16), also produced five PCs with eigenvalues greater than 1.0, explaining 86.0 % of the variation.

Approach, Movement and Latency to Response

Neighbor-Stranger and Neighbor-Neighbor Discrimination

The first PC from both neighbor vs. stranger and correct vs. incorrect neighbor trials explained a similar amount of variation in the responses of focal males, 40.0 % and 37.6 %, respectively. In both trial types the PC was positively correlated with a focal male's approach, movement about the playback speaker, and latency of response to playback, including latency to the first extended song sung (Table 2.4 and Table 2.5). In contrast, time to return to and spent foraging had high negative correlations. The more positively correlated variables are those associated with what I consider a more aggressive response, with males actively approaching and interacting with what they perceive to be another male at their territory boundary. The opposite, and thus more negatively correlated response for this PC, occurs with focal males turning their attention from those actions related to territorial defense to foraging for themselves or their offspring.

Simple means of response values show differences among trial types in the variables associated with the first PC (Table 2.3). Focal males approached the playback area and replied with extended song more rapidly in response to stranger song. They also approached the playback speaker more closely, and took longer to begin foraging in response to a stranger. The averages suggest similar differences in responses of focal males to the playback of neighbors at correct versus incorrect boundaries, but the differences were not as large. However, sample sizes were small and thus standard errors large. No significant differences were found in the first PC between responses to neighbor and stranger stimuli, but neared significance at the p = 0.05 significance level ($F_{1, 16} = 4.57$, p = 0.06, $LSM_{Neighbor} = -0.278$ SE = 0.75, and $LSM_{Stranger} = 1.358$ SE = 0.76), or in comparison of responses among focal males ($F_{3, 16} = 1.67$, p = 0.23). Also, significant differences were not found between responses to neighbors at correct and incorrect boundaries ($F_{1, 16} = 0.26$, p = 0.62, $LSM_{Correct} = 0.145$ SE = 0.79, and $LSM_{Incorrect} = 0.731$ SE =

0.83). Comparison of responses between focal males to correct and incorrect neighbor stimuli were also not significant, but neared significance ($F_{3, 16} = 3.13$, $p = 0.088$).

These near significant differences found among the behavior of the four focal males was affected strongly by the behavior of two focal males. Focal Male S, did not approach the speaker in one of a total of four trials, and continued to forage for nestlings throughout that trial ($LSM_{FMS} = -0.793$). Focal Male A, did not approach the speaker in two of five trials and in four of five he never approached within 10 m of the speaker. In all but one of these trials he continued to forage to feed fledglings, ($LSM_{FMA} = -1.721$). This resulted in negative coefficients for those birds and significant differences between them and the most actively approaching and responding bird, Focal Male O, ($LSM_{FMO} = 3.103$) who was tested earliest in the breeding season during a period when he was unencumbered by parental duties.

Soft Song

Neighbor-Stranger Discrimination

In trials comparing responses of focal males to neighbor and strangers, the third PC had an eigenvalue of 2.25, and explained 12.3 % of variation in responses. This PC was positively correlated with latency to the first brief vocalization uttered, number of soft songs sung, and latency to when the first soft song was sung (Table 2.4). In contrast, it was negatively correlated with number of brief vocalizations uttered. Significant differences were found between focal males ($F_{3, 16} = 4.13$, $p = 0.03$) and with a covariate of days ($F_{1, 16} = 5.55$, $p = 0.04$). This covariate had a negative slope over time (Fig. 2.2) suggesting that, the response of males changed such that their use of soft song waned until it was no longer sung when birds were tested in the end stages of the breeding season when they were either feeding fledglings or had been reproductively unsuccessful for that year.

Soft Song and Primary Song

Neighbor-Neighbor Discrimination

In trials comparing responses to neighbors at correct and incorrect boundaries the third PC, like that found for trials comparing responses to neighbors and strangers, had an eigenvalue of 2.41 and explained 14.2 % of variation in response. It was different from the neighbor vs. stranger analysis in that it had its highest negative correlations with number of soft songs and time until soft song was sung (Table 2.5). Conversely, high positive correlations were related to the time it took for a bird to sing primary song and number of primary songs sung. This contrast illustrates differences in motivation of birds singing soft song, compared to the motivation of birds that were singing primary song.

Soft song and primary song reflect contrasting degrees of motivation and aggression. Soft song is considered a more aggressive response (Nice 1943, Searcy et al. 2006, Hof and Hazlett 2010) compared to primary song. In most cases soft songs are extended or run-on songs sung at lower amplitudes. Males are generally approaching and actively searching to participate in territorial defense when soft song is sung. Soft song was recorded more often at or near the beginning of a male's response to a perceived intruder. As the initial reaction of seeking out an intruder and defending a territory wanes during the trial, decreased aggression occurs, and the male lapses into primary song. Males lapsing into primary song more quickly and thus singing more primary songs during a trial resulted in larger positive coefficients.

The results of the ANCOVA were somewhat different compared to those testing for differences in responses to neighbors and strangers because of the weight of the variables related to primary song being placed into the third PC. Responses were affected by the covariate of days into the nesting season (Fig. 2.3). How the covariate affected the response was significantly different according to which focal male was being tested ($F_{3, 15} = 33.35$, $p = 0.008$), and according to whether a bird was responding to a neighbor at a correct or an incorrect boundary ($F_{3, 15}$ =13.78, p = 0.03). With the influence of the covariate removed, focal males responded differently from one another ($F_{3, 15}$ = 37.15, p = 0.007), and there was a significant difference in response to correct vs. incorrect neighbors ($F_{1, 15}$ = 15.68, p = 0.007). There was no interaction between which male was responding and to what type of neighbor a focal male was responding ($F_{3, 15}$ = 4.85, p = 0.11).

As the breeding season progressed, males lapsed from extended into primary song more quickly, and sang more primary songs overall. Males were more likely to sing primary song in response to a neighbor at an incorrect boundary than in response to a neighbor at a correct boundary. Of the males who sang soft song, two sang it more frequently in response to a stranger. The third was tested earliest in the breeding season, and sang soft song in response to playback regardless of whether he was responding to correct neighbor, stranger, or incorrect neighbor song (Table 2.6). In each of these trials, on his arrival to the area of the playback speaker, he perched and sang soft song before continuing any further response. The soft song he sang in response to a stranger had a longer suffix (45 components/ 5.8 s in length) than those given in response to a neighbor at the incorrect boundary and the neighbor given at an incorrect boundary (12.5 components/1.5 s in length; Table 2.6).

Primary Song

Neighbor-Stranger Discrimination

In trials comparing responses of focal males to neighbors and strangers, the fourth PC had its highest positive correlations with number of primary songs sung. The second highest correlation was latency to when the first primary song was sung. Similar to the third PC in the analysis of responses of focal males to correct and incorrect neighbors, negative correlations included number of brief vocalizations and latency to the first soft song sung (Table 2.4). However, number of soft songs sung did not weigh heavily in this PC.

More primary song was sung in response to a stranger's song compared to a correct neighbor's song (Table 2.3), but this difference was not found to be significant within the analysis of this principal component ($F_{1, 16} = 0.54$, $p = 0.48$). Overall, more song was sung in response to a stranger, but the greatest portion of those songs sung were extended song. Without the influence of number of soft songs sung the covariate of days into nesting season was not significant ($F_{1, 16} = 0.95$, $p = 0.36$). Also, there was no interaction between which male was being tested and whether a neighbor or stranger song was being played ($F_{3, 16} = 2.40$, $p = 0.14$). There was a difference in responses when comparing males to one another ($F_{4, 16} = 8.55$, $p = 0.05$).

Focal males showed more negative loadings for this PC early in the breeding season ($LSM_{FMO} = -1.296$ and $LSM_{FMS} = -1.481$) meaning that they sang fewer primary songs and responded with more brief vocalizations, and sang soft song sooner compared to those whose trials were ran later in the breeding season ($LSM_{FMF} = 0.842$ and $LSM_{FMA} = 0.830$). Males who were tested later in the season were more likely to begin their response with primary song or lapse more quickly from extended to primary song.

Extended Song, Primary Song without Termination, and Brief Vocalizations

Neighbor-Neighbor Discrimination

The second principal component explained 17.2 % of the variation in responses of males to correct and incorrect neighbor song. It was associated with responses that I considered to be related to a general state of alarm, with brief vocalizations and primary songs without termination and extended song (Table 2.5). Number of primary songs sung without termination and latency to when they were first sung had the highest correlations to this PC. Number of extended songs and number of brief vocalizations such as cheks, tps, and zeets had a lower positive correlation.

There was no effect of the covariate of days into the nesting season ($F_{1, 15} = 0.01$, $p = 0.93$). Though there appeared to be differences in at least number of extended songs sung in response to correct and incorrect neighbor song (Table 2.3), no significant differences were found with this PC ($F_{1, 15} = 0.26$, $p = 0.63$). There was no significant interaction between males and which type song they were responding to ($F_{3, 15} = 0.81$, $p = 0.52$). There was a near significant difference between males with these response measures ($F_{3, 15} = 3.08$, $p = 0.09$). These results were driven by the male tested earliest in the breeding season responding with more of all these type vocalizations more rapidly, particularly extended song, compared to the other males who were tested later in the breeding season.

Extended Song, Flights, Brief Vocalizations, and Soft Song

Neighbor-Stranger Discrimination

The seventh PC explained only 4.6 % of the variation in responses, but was included in the analysis because of my interest in its biological interpretation (McGregor 1992). It allowed comparison of the behavior of singing extended song and number of flights about the playback speaker in response to a stranger and a correct neighbor (Table 2.7). This behavior is considered one of aggression, with a male seeking to interact with a perceived intruder in his territory (Smith and Smith 1996). Extended song and number of flights about the playback speaker were similarly weighted coefficients with this PC. Both measures were negatively correlated, and numbers of brief vocalizations were positively correlated to a similarly weighted coefficient. Smaller correlations occurred with soft song and the time it took for a bird to sing a primary song lacking termination (Table 2.4).

There was no effect of the covariate of days into the nesting season ($F_{1, 16} = 0.00$, $p = 0.97$). There was a significant difference in responses to neighbors at the correct boundary and strangers ($F_{1, 16} = 9.59$, $p = 0.01$). There was no significant difference between males for this response ($F_{3, 16} = 1.98$, $p = 0.19$), though there was an indication of an interaction between which male was responding and whether he was responding to a neighbor or a stranger ($F_{3, 16} = 2.97$, $p = 0.09$).

In all trials, regardless of which male was responding or the number of days into the nesting season, males responded to a stranger's song at their territory boundary with multiple flights and extended song. Number of flights and number of extended songs were often similar. Males responded to a correct neighbor's song with extended song in only five of nine trials. In response to a correct neighbor, there were instances when a male approached the playback speaker but did not sing extended song, and alternatively, there were instances when a male sang two to five extended songs but never approached the speaker. In most cases, there were more extended songs, flight, and brief vocalizations in response to a stranger. The male tested earliest in the breeding season was an exception. He moved about the playback speaker and sang more extended songs with a correct neighbor than with a stranger. This may be a result of his trial with correct neighbor song being on the 39th day after his approximate arrival, and his trial with a stranger song being on the 56th day after his approximate arrival.

Discussion

The ability of individuals to discriminate between neighbors and strangers is relatively common (Temeles 1994), and is based upon the evolution of a system that allows birds to allocate time and energy correctly to maintenance of a territory and other breeding activities (Falls 1969;

Krebs 1971; Krebs 1982; Getty 1987; Beletsky and Orians 1989; Getty 1989; Godard 1993; Stoddard 1996). Differences in response and allocation of energy in response to one individual compared to another indicate that one presents more threat to a territory than does the other (Temeles 1994). In the case of the Louisiana Waterthrush a stranger singing at a territory boundary would more likely be looking to establish a territory than a neighbor doing the same. In the linear territories held by Louisiana Waterthrushes, the loss of a territory could cost them their reproductive success and thus strangers elicit more aggressive behavior from the resident male. The energetic cost of this aggression would be appropriate to the situation (Jaeger 1981, Getty 1989, Temeles 1994).

A neighbor singing at a correct boundary presents less threat (Temeles 1994). Territorial boundaries are generally stable, however, in Louisiana Waterthrushes, neighbors may extend the length of their territory. The focal male would have experience and memory of neighbors, (Godard 1991, 1993) and the allocation of energy to defense of the territorial boundary would be more appropriate to the degree of threat that individual presented. Neighbors that have wandered widely enough to be singing at the incorrect boundary of a focal male's territory are likely less threat than a stranger, but more threat than if they were singing at their own territory boundary. In this situation, that neighbor would be encroaching widely upon its neighbor's territory and would thus more likely be to attempt to usurp territory (Stoddard 1996). More energy should be allocated in this situation.

My hypotheses were upheld in that Louisiana Waterthrushes in my study responded to songs of strangers and neighbors at incorrect boundaries differently than to songs of neighbors at correct boundaries. The differences in response were more apparent in comparisons of neighbors and strangers, than in comparison of responses to neighbors at correct and incorrect boundaries.

Focal males exhibited different behaviors in response to songs of strangers and songs of neighbors at correct boundaries (i.e. neighbor-stranger discrimination). The four focal males in this experiment appeared to approach stranger song stimuli more closely and more rapidly than the song of a correct neighbor. There was also an indication that they reacted with extended song more quickly and took longer to return to foraging after responding to stranger stimuli than after responding to the stimulus of a correct neighbor's song. However, data analysis did not show these responses to be significantly different from one another at a .05 level of significance.

As in many of studies of this type (Gerhardt 1992) the number of birds tested was small, and thus the power (ability to detect differences) was low, and probability of a type II error was high. There is a very high probability that I am not detecting differences with a traditional 0.05 % level of significance. Variables associated with latency to response may have been biased to some degree by the distance a male was from the playback speaker when the stimulus began (Stoddard 1996). Louisiana Waterthrush territories tend to be very long and winding as they follow the stream corridor. Also, the birds are often foraging directly within the stream. When water levels are high in early spring it would be more difficult for foraging birds to hear song from the playback speaker.

It was clear at a 0.05 % level of significance that birds discriminated between a neighbor and a stranger in that those reacting to a stranger's song sang significantly more extended song and made more flights about the playback speaker in search of a perceived intruder than they did in response to a neighbor's song. There were also differences in use of extended and primary song types as the breeding season progressed and males were involved in different breeding activities. Males who were tested later in the season were more likely to begin their response with primary song or lapse more quickly from extended to primary song. This upholds the finding of Smith and Smith (1996) that birds sing extended song while searching for a perceived intruder and then lapse into primary song once an intruder cannot be found. More aggressive birds earlier in the season spent more time searching and singing extended song than those responding to the same stimulus later in the season.

Soft song is thought to be one of the most clearly aggressive signals given by males as aggressors (Nice 1943, Searcy et al. 2006, Hof and Hazlett 2010). Soft song occurred more often and more rapidly during trials with males tested earlier in the breeding season, and occurred more often in response to strangers, except in the case of the male tested earliest in the season who responded in all trials with soft song, regardless of which type song he was responding to. The use of soft song waned as the season progressed until it was no longer sung when birds were tested in the end stages of the breeding season at which point they were either feeding fledglings or had been reproductively unsuccessful for that year. It was more difficult to recognize this difference in responses to neighbors and strangers in the early part of the breeding season because there was an overall high aggressive response to all individuals. As the season continued, relationships were established at territory boundaries, and other breeding activities took priority, aggression decreased (Van Duyse et al. 2003), and differences between responses to neighbors and strangers became more apparent.

The four focal males exhibited different behaviors in response to songs of neighbors at correct boundaries compared to songs of neighbors present at an incorrect boundary (i.e. neighbor-neighbor or individual discrimination). The responses to incorrect neighbors were much like the responses to strangers. Again, differences in the behavior of approaching the playback speaker, closest approach, and latency to extended song were not significantly different at the 0.05 % level, but there was a significant difference between males at the 0.10 %

significance level. The difference between males seemed to be driven by their breeding activities.

Birds responding to an incorrect neighbor's song appeared to be more affected by what they were doing at the time than birds responding to a stranger. During those trials with a reduced response to an incorrect neighbor, males were engaged in a breeding activity in which the needs of offspring appeared to trump the need for territorial defense. A good example was one case in which the focal male arrived and sang with food in his mouth, left to feed his nestlings, and then returned to sing with his mouth empty. These differences were seen in comparisons among males for responses involving all song types and brief vocalizations. Primary song was used more often in response to incorrect neighbors and as the breeding season progressed, males lapsed from extended to primary song more rapidly. Soft song was used similarly with its use waning as the season progressed.

Though the sample sizes were small, and the trials were often separated by long stretches of time in the breeding season, the study afforded an intimate glimpse into the lives of the four focal males. Treating focal males as fixed effects allowed us to determine differences occurring among individuals, at the cost of being able to generalize beyond those particular individuals. The life of each male was followed very closely, and early in the study I became aware of the trade-off males were making between important breeding activities such as feeding nestlings and responding to a threat to their territorial boundary.

Aggression changes with the breeding season. Earlier in the season, when birds are arriving on territories from the previous year or establishing new territories, attracting females, mating, and in stages when females are incubating, they are not only hormonally driven to be more aggressive (Catchpole and Slater 2008, Voigt and Leitner 2008), but they are also less encumbered with the responsibilities of parenthood (Wingfield et al. 1990, Van Duyse et al. 2003). Thus, males are much more likely to be available to respond to a threat to a territory boundary at the beginning of the breeding season. Activities associated with feeding nestlings and fledglings occur later in the season when less aggression is expected and when birds are, of a greater necessity, foraging for these offspring. This was no more apparent than when a male whose nestlings had hatched that day arrived at the playback with his mouth full to sing extended song. He then disappeared for a short period of time and returned with his mouth empty and continued with his response. Another male, busy in the stream with his division of fledglings responded with extended songs as he might have if approaching, but continued foraging and feeding his fledglings and never approached the playback speaker. However, changes in hormonally driven aggressive behavior throughout the nesting season occur periodically. Males that are feeding fledgling are expected to have higher degrees of hormonally-driven aggression, probably because they are preparing for the possibility of a second brood (Wingfield et al. 1990, Van Duyse et al. 2003)

I was also aware of activities occurring on the length of the streams which caused a shuffling of boundaries above and below the territory of the male involved in trials, as well as changes in territory holders from year to year. In one situation, males were regularly engaged in the slow progression of movement of territory boundaries when a young male began acquiring small amounts of a new territory on a single stream. Over the period of a season this young male held his place and the male at the upstream boundary moved further up into a portion of a territory where the previous territory male had been killed by a cat. The male at the lower boundary where the young male was intruding held his boundary throughout the season. When a territorial male disappears from his territory, or when a young male makes an attempt to establish a territory, the effects are felt on either side, and perhaps up and down the stream.

It is known that birds remember neighbors and boundaries from previous years (Godard 1991). Certainly, a neighbor who has been a neighbor for three years is more familiar than a neighbor that has arrived and taken place on an adjoining territory in the same year as trials are taking place. Unfortunately, I was uncertain of the status of one of the focal male's neighbors across the three years of the study so I could not analyze the effects of familiarity. However, the male who responded with an unusually weak response to playback was unique according to my records in that he had the same neighbors at both upstream and downstream boundaries for three consecutive years.

Future study should be undertaken with an awareness of the inherent difficulties of working with a species with very long linear territories within the noisy environment of headwater streams. Treatments should be directly compared only within the early part of the breeding season when activities associated with nestlings and fledglings have not yet begun or treatments should be confined to the period in which females are incubating their first clutch and there has been a period of time that has elapsed allowing males to develop relationships with one another at territorial boundaries. Also, it would be a benefit to the experimenter to be aware of the familiarity and current relationship of territorial males and their neighbors with one another throughout multiple years.

In conclusion, my hypotheses were upheld in that four male Louisiana Waterthrushes responded to the songs of strangers and neighbors at incorrect boundaries with more aggressive behavior than to the songs of neighbors at correct boundaries. The differences in response were more apparent in comparisons of neighbors and strangers, than in comparison of responses to neighbors at correct and incorrect boundaries. Responses, including the use of extended and primary song types, changed with progression of the breeding season and correlated with more and less aggressive activities. Soft song was sung in the most aggressive responses.

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Table 2.1. Dates of trials ran with focal males at upstream and downstream boundaries and with correct neighbor song, stranger song, and incorrect neighbor song

Focal Male Y = Passive Trials

Correct Neighbor	Boundary	Stranger	Boundary	Incorrect Neighbor	Boundary
5/18/07	upstream	6/4/07	upstream	5/28/07	upstream
5/20/07	downstream	6/11/07	downstream	6/6/07	downstream
4/27/08	upstream	4/23/08	upstream		
		5/12/08	downstream		

Focal Male O Trials

Correct Neighbor	Boundary	Stranger	Boundary	Incorrect Neighbor	Boundary
4/22/08	upstream	5/9/08	upstream	4/23/08	downstream
				5/3/08	upstream

Focal Male S Trials

Correct Neighbor	Boundary	Stranger	Boundary	Incorrect Neighbor	Boundary
5/13/08	downstream	5/2/08	upstream	5/29/08	downstream
5/21/08	upstream	5/22/08	downstream	5/31/08	upstream

Focal Male F Trials

Correct Neighbor	Boundary	Stranger	Boundary	Incorrect Neighbor	Boundary
6/1/08	upstream	5/28/08	upstream	5/30/08	upstream
6/30/08	downstream	6/12/08	downstream	6/10/08	downstream

Focal Male A Trials

Correct Neighbor	Boundary	Stranger	Boundary	Incorrect Neighbor	Boundary
5/29/07	downstream	5/31/07	upstream	6/5/07	downstream
6/9/07	downstream	6/2/07	downstream		
6/12/07	upstream	6/19/08	downstream		
6/18/08	downstream				

Table 2.2. Means and single standard error measurements of responses by five focal males to neighbor at the correct boundary song, stranger song, and neighbor at the incorrect boundary song. Includes passive bird

Response Measure	Correct Neighbor		Stranger		Incorrect Neighbor	
	mean	SE	mean	SE	mean	SE
Latency to first approach within 10 m (s)	279.50	69.87	225.42	68.36	216.17	81.40
Closest approach to speaker (m)	15.58	2.87	12.42	2.93	12.11	3.58
Latency to first approach toward speaker (s)	167.75	65.65	133.02	56.09	151.03	74.15
Total time spent within 10 meters (s)	91.89	35.54	154.31	46.10	163.43	75.80
Number of flights	10.50	2.95	9.42	2.18	8.22	2.34
Number of primary songs	6.83	2.45	11.08	3.50	9.89	4.93
Latency to first primary song sung (s)	213.10	70.57	200.98	63.46	156.93	73.45
Number of primary songs lacking terminations	0.33	0.26	0.50	0.26	0.89	0.65
Latency to first primary song lacking termination (s)	501.53	25.94	418.05	55.97	442.99	53.63
Number of extended songs	5.17	2.92	13.58	3.12	10.89	4.43
Latency to first extended song sung (s)	303.73	69.28	147.38	56.94	211.54	82.61
Number of brief vocalizations	3.92	1.96	4.00	1.54	1.89	1.22
Latency to first brief vocalization (s)	308.66	71.15	344.45	61.34	411.02	69.22
Number of soft songs	0.42	0.23	1.75	0.88	0.22	0.22
Latency to first soft song sung (s)	433.78	56.32	390.82	64.24	497.50	42.50
Latency to foraging (s)	331.39	67.99	395.91	47.09	441.78	45.88
Time spent foraging (s)	168.56	64.20	100.01	45.13	62.65	37.75

Table 2.3. Means and single standard error measurements of responses by four focal males to neighbor at the correct boundary song, stranger song, and neighbor at the incorrect boundary song. Does not include passive bird

	Correct Neighbor		Stranger		Incorrect Neighbor	
Response Measure	mean	SE	mean	SE	mean	SE
Latency to first approach within 10 m (s)	295.53	82.51	68.14	20.34	123.65	70.28
Closest approach to speaker (m)	16.33	3.73	6.13	1.20	7.00	1.56
Latency to first approach toward speaker (s)	201.28	84.92	46.87	13.68	39.90	12.71
Total time spent within 10 meters (s)	119.10	44.04	231.46	49.58	210.13	90.64
Number of flights	10.22	3.85	12.88	2.30	10.57	2.29
Number of primary songs	8.33	3.07	13.88	4.69	12.71	5.97
Latency to first primary song sung (s)	157.96	73.74	163.03	62.68	47.48	16.27
Number of primary songs lacking terminations	0.44	0.34	0.75	0.37	1.14	0.83
Latency to first primary song lacking termination (s)	488.71	33.93	357.07	76.09	415.28	65.99
Number of extended songs	5.00	2.94	19.63	2.69	14.00	5.13
Latency to first extended song sung (s)	223.49	71.81	58.84	25.58	117.69	71.37
Number of brief vocalizations	3.11	1.84	6.00	1.96	2.43	1.53
Latency to first brief vocalization (s)	289.40	81.15	246.67	69.08	374.17	84.82
Number of soft songs	0.33	0.24	2.00	1.21	0.29	0.29
Latency to first soft song sung (s)	450.63	60.21	361.20	87.29	485.36	54.64
Latency to foraging (s)	327.28	86.83	414.14	40.16	413.72	54.94
Time spent foraging (s)	187.49	83.79	71.10	29.43	80.55	46.93

Table 2.4. Factor loadings in the Principal Components Analysis of behavioral responses in neighbor vs stranger trials (NSD). Includes only PCs in which significant differences were found

Response Measure	PC1	PC3	PC4	PC7
Latency to first approach within 10 m (s)	0.3446	-0.0355	0.0933	0.1857
Closest approach to speaker (m)	0.3643	-0.0237	-0.0534	0.1244
Latency to first approach toward speaker (s)	0.3388	-0.0941	0.0508	0.0932
Total time spent within 10 meters (s)	0.2823	0.0897	-0.1795	0.2314
Number of flights	0.3035	0.0903	-0.2269	-0.4538
Number of primary songs	0.1232	0.2607	0.4957	0.1984
Latency to first primary song sung (s)	0.0872	-0.2463	0.4459	-0.0399
Number of primary songs lacking terminations	0.1149	-0.0165	0.0704	-0.1744
Latency to first primary song lacking termination (s)	0.0684	-0.0791	0.0676	0.3107
Number of extended songs	0.2608	-0.2246	0.0073	-0.4114
Latency to first extended song sung (s)	0.3046	-0.1281	0.2677	0.0789
Number of brief vocalizations	-0.0299	-0.3928	-0.4003	0.4615
Latency to first brief vocalization (s)	-0.0561	0.5188	0.2363	0.0176
Number of soft songs	0.1368	0.4873	-0.2097	0.3001
Latency to first soft song sung (s)	0.2105	0.3275	-0.3410	-0.1737
Latency to foraging (s)	-0.2980	0.0328	0.0090	0.0471
Time spent foraging (s)	-0.3236	0.0438	0.0065	-0.0521
% Variation in Responses	40.0	12.3	11.5	4.6

Table 2.5. Factor loadings in the Principal Components Analysis of behavioral responses in correct vs. incorrect neighbor trials (NND). Includes only PCs in which significant differences were found

Response Measure	PC1	PC2	PC3
Latency to first approach within 10 m (s)	0.3306	0.0008	0.1151
Closest approach to speaker (m)	0.3638	-0.1382	-0.0273
Latency to first approach toward speaker (s)	0.3251	-0.1933	0.0487
Total time spent within 10 meters (s)	0.2691	-0.0345	0.0485
Number of flights	0.3232	0.1366	-0.2722
Number of primary songs	0.0891	-0.2682	0.3643
Latency to first primary song sung (s)	0.1747	0.0498	0.4418
Number of primary songs lacking terminations	0.1644	0.4444	0.0418
Latency to first primary song lacking termination (s)	0.1164	0.4162	0.0913
Number of extended songs	0.2629	0.3734	-0.0599
Latency to first extended song sung (s)	0.3022	0.0838	0.2380
Number of brief vocalizations	-0.0928	0.3134	0.1509
Latency to first brief vocalization (s)	0.0624	0.2796	0.0686
Number of soft songs	0.0774	-0.0455	-0.5676
Latency to first soft song sung (s)	0.1876	0.1208	-0.3946
Latency to foraging (s)	-0.2966	0.2537	0.0546
Time spent foraging (s)	-0.3076	0.2733	0.0276
% Variation in Responses	37.6	17.2	14.2

Table 2.6. Summary data on soft song given by 3 focal males (labeled “O”,”S”,”F”) in response to songs of strangers, neighbors at correct boundaries, and neighbors at incorrect boundaries

Response to Stranger				
Focal Male	"O"	"S"	"S"	"F"
Number of Soft Songs	1	8	1	7
Day into nesting season	56	49	69	75
Latency to First Soft Song (s)	105	64	78	49
Number of Components in Suffix	45.0	47.4	*	7.0
Length (s) of Suffix	5.784	6.386	*	1.114

Response to Neighbor at Correct Boundary		
Focal Male	"O"	"S"
Number of Soft Songs	1	2
Day into nesting season	39	60
Latency to First Soft Song (s)	69	387
Number of Components in Suffix	12.0	56.0
Length (s) of Suffix	1.374	8.058

Response to Neighbor at Incorrect Boundary	
Focal Male	"O"
Number of Soft Songs	1
Day into nesting season	50
Latency to First Soft Song (s)	157
Number of Components in Suffix	13.0
Length (s) of Suffix	1.604

* amplitude too low to measure characteristics adequately

Table 2.7. Number of extended songs, flights, and brief vocalizations given in each trial in response to stranger song and correct neighbor song at upstream and downstream boundaries

Focal Male	Boundary	Trial	Flights	Extended Songs	Brief Vocalizations
O	upstream	Stranger	14	22	13
S	upstream	Stranger	10	5	5
S	downstream	Stranger	23	25	14
F	upstream	Stranger	22	20	0
F	downstream	Stranger	11	14	8
A	upstream	Stranger	11	29	1
A	downstream	Stranger	6	17	0
A	downstream	Stranger	6	25	7
		Average	**12.9**	**19.6**	**6.0**
		SE	2.3	2.7	2.0

Focal Male	Boundary	Trial	Flights	Extended Songs	Brief Vocalizations
O	upstream	Correct	34	33	1
S	downstream	Correct	19	0	0
S	upstream	Correct	0	0	0
F	upstream	Correct	10	4	0
F	downstream	Correct	14	2	5
A	downstream	Correct	14	18	1
A	downstream	Correct	0	0	17
A	upstream	Correct	0	2	0
A	downstream	Correct	1	0	4
		Average	**10.2**	**6.6**	**3.1**
		SE	3.9	3.8	1.8

Figure 2.1. Schematic diagram indicating where trials occurred on focal male territories

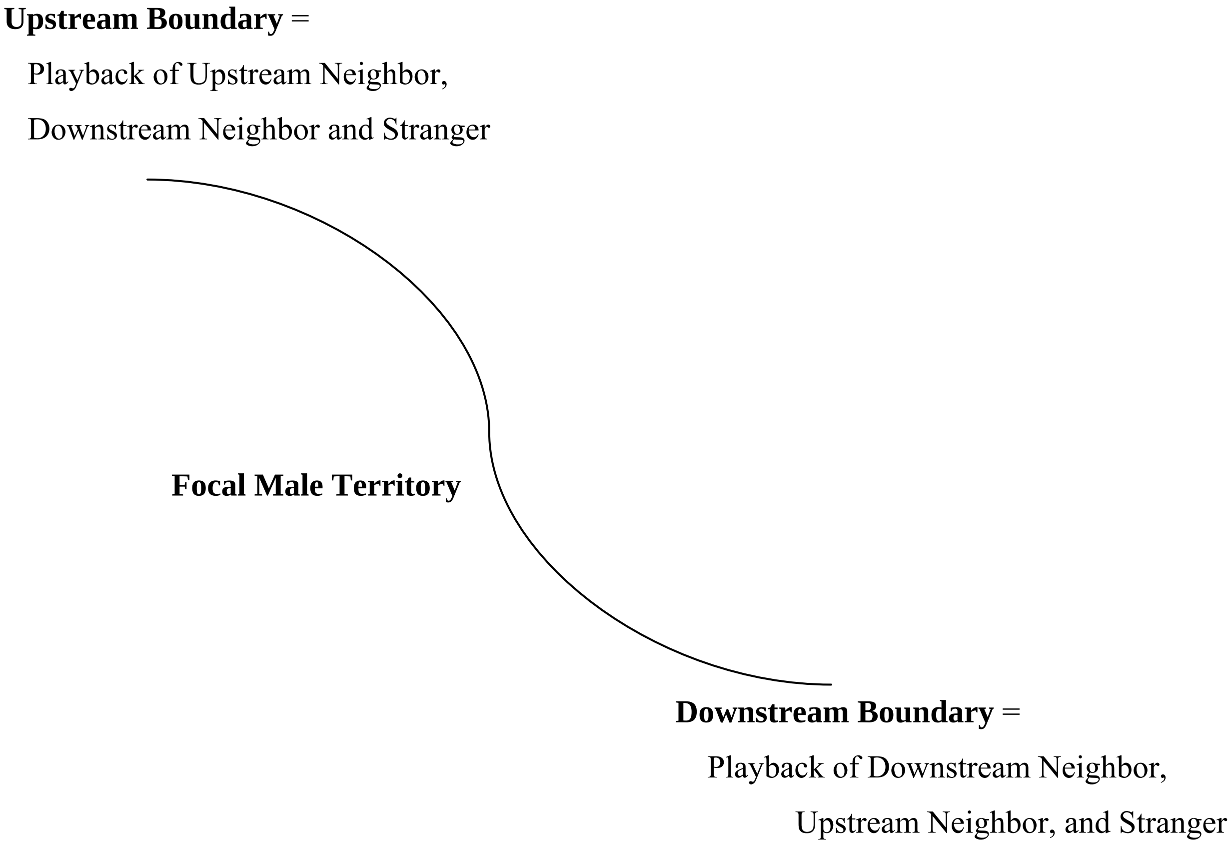


Figure 2.2. Effect of covariate of days into nesting season on PC 3 comparing focal male responses in neighbor-stranger discrimination trials; PC3 associated positively with latency to brief vocalizations, number of soft songs, and latency to soft song, and negatively with the number of brief vocalizations (Table 2.4)

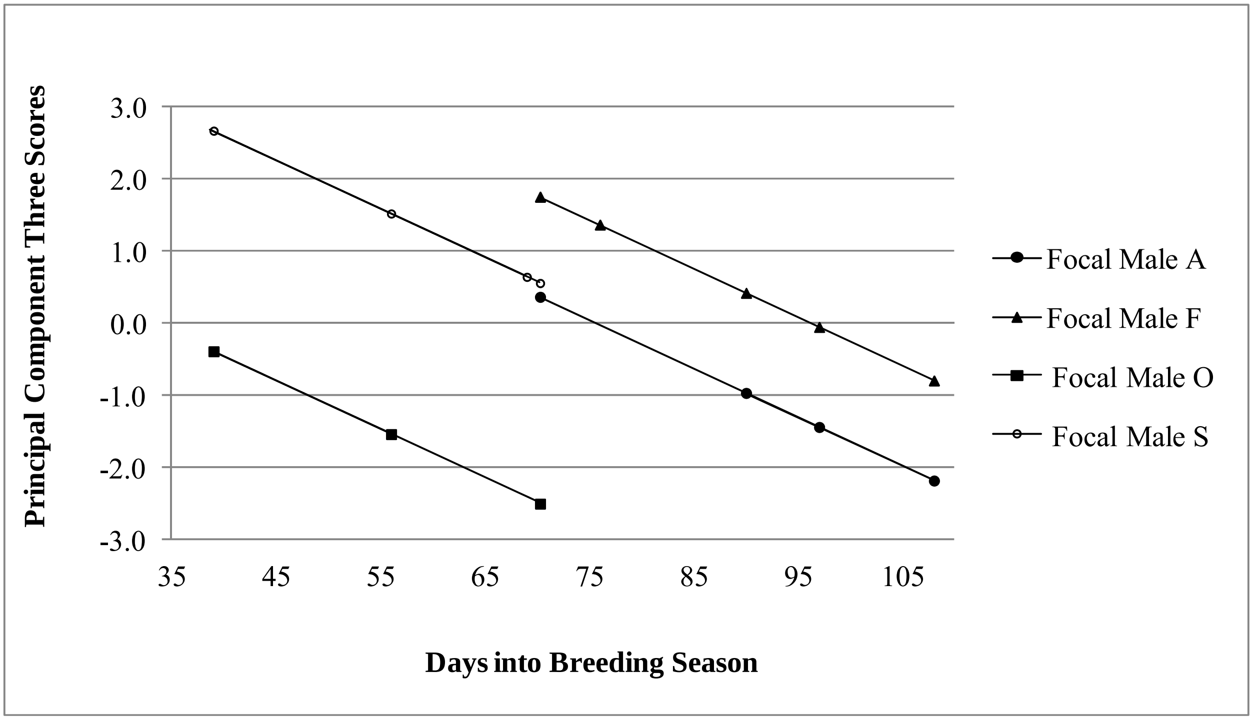
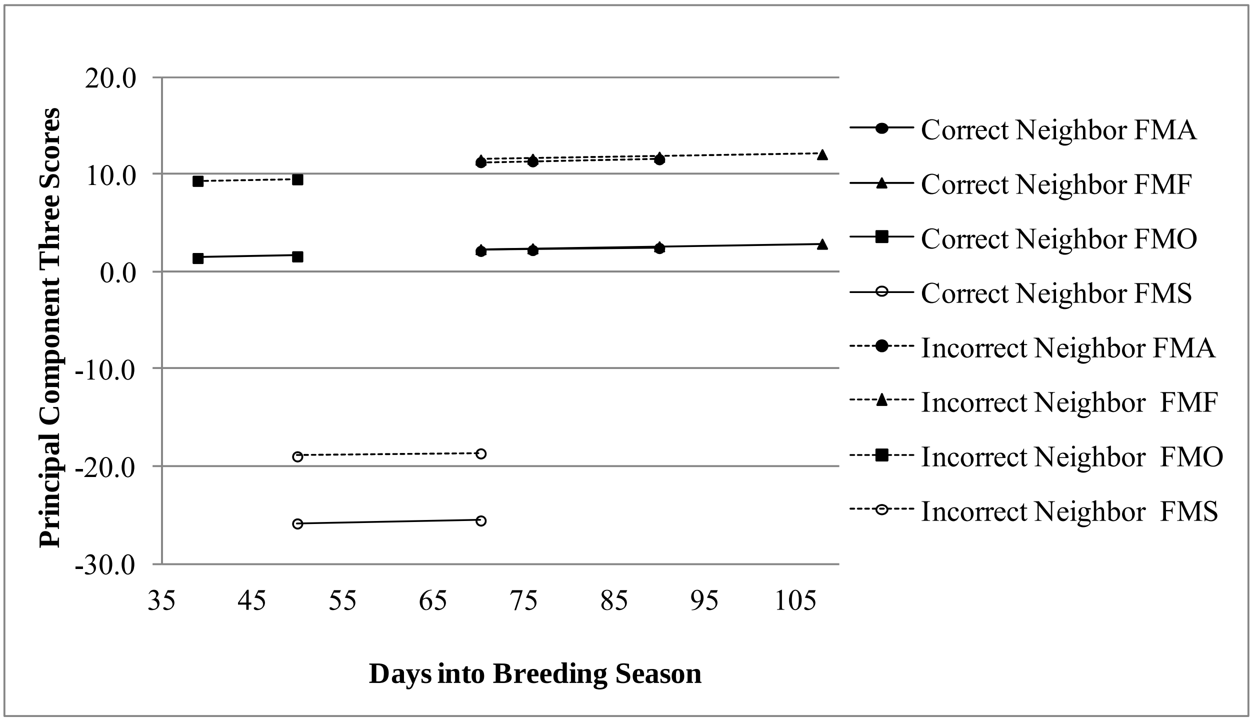


Figure 2.3. Effect of covariate of days into nesting season on PC 3 comparing focal males and their responses to neighbors at correct boundaries and neighbors at incorrect boundaries; PC3 correlated positively with latency to the first primary song sung and the number of primary songs sung and negatively with the number of soft songs sung and the latency to the first soft sung



Chapter 3:

Motivation-structural code and extended song acoustic structure in territorial male Louisiana Waterthrushes (*Parkesia motacilla*)

Abstract

The Louisiana Waterthrush is a Nearctic-Neotropical migratory wood-warbler. It breeds in streamside habitats in the eastern United States. Males have primary and extended song types. Primary song begins with approximately two to four introductory components followed by briefer components and an abrupt termination. Characteristics of these components constitute an individual's song signature. Extended song begins with primary song and continues beyond it with an extending suffix of components which are harsh, low frequency, rapid, and brief. Playback studies showed that male Louisiana Waterthrushes discriminate between neighbors, strangers, and neighbors at incorrect boundaries and respond with different degrees of aggression as predicted by the amount of threat perceived. I analyzed extended songs given alongside behavioral responses in these playback studies. Differences were found as predicted by Morton's motivation-structural rules of vocalizations. Increased levels of aggression correlated with differences in the acoustic structure of the extended song type when comparing songs in response to neighbors, strangers, and neighbors at incorrect boundaries. Differences included lower average low frequencies in both primary segments and extended song suffixes, as well as with number of harsh, low frequency components that comprised suffixes in more aggressive interactions. Differences related to aggression were more evident in neighbors-stranger discrimination. Higher levels of aggression early in the breeding season resulted in lower low frequency components, longer song suffixes, and less discrimination between neighbors, strangers and neighbors at incorrect boundaries. Decreasing levels of aggression with breeding season correlated with shorter suffixes and primary segments with higher high frequencies and lower low frequencies.

Keywords: extended song, song types, Louisiana Waterthrush, Morton's motivation-structural rules of vocalizations, neighbor-stranger discrimination, neighbor-neighbor discrimination

Introduction

Morton (1977) presented motivation-structural rules that allow insight into the motivational state of vocalizing animals according to the physical structure of the sounds they produce. Through natural selection, close-range vocalizations have undergone convergent evolution across taxa such that there are two endpoints within repertoires of animal vocalizations. Harsh, low-frequency sounds, for example, growls, indicate that a sender is hostile, while pure tone-like sounds, for example, 'whines', indicate that a sender is frightened, appeasing, or approaching in a friendly manner (Morton 1977). The structure of vocalizations generally lie somewhere on a continuum between these two endpoints. A good example of an intermediate vocalization is a 'bark', which is characterized by a rise and fall in frequency, and illustrates that an individual has recognized something of interest and is neither retreating nor approaching the stimulus.

Vocalizations lie not only on this two-dimensional continuum of frequency and harshness, but also on a third and fourth dimension of rate of delivery and amplitude that illustrate motivation (Owings and Morton 1998). These multiple dimensions allow a great deal of information to be coded into even very simple vocalizations and changes along the continuums of these four dimensions illustrate active changes in an animal's motivational state as a social situation plays out through time and with changes in stimuli.

Compound vocalizations allow for the inclusion of more information about motivation within a single vocalization (Owings and Morton 1998). A good example of this is the 'chickadee' call used by the black-capped chickadee *(Parus atricapillus)*. The 'chickadee' call is a compound vocalization in that its notes may be used separately or together in a bird's repertoire (Owings and Morton 1998) and notes may be used in various combinations and repeated within the vocalization (Foote et al. 2010). It is complex in that it is used in a variety of situations

(Foote et al. 2010) and different properties of notes illustrate different motivational states upon a continuum (Owings and Morton 1998).

The “chicka” beginning of the song is composed of two to four chevron shaped notes that decrease in frequency (Ficken et al. 1978). The placement of these notes upon the continuum of dimensions in motivation-structural code indicates that the singer has recognized something of interest, the singer is not approaching or retreating from the stimulus, and as a result, the attention of others is brought to the singer. The decreasing frequency of the ‘chicka’ notes indicates increasing aggressiveness. The ending ‘dee’ notes of the vocalization are harsher and lower in frequency and illustrate a more aggressive motivation, though they are not at the aggressive endpoint of this species repertoire (Owings and Morton 1998). When given during the mobbing of a predator there are often long strings of ‘dee’ notes suffixed to the call (Odum 1942). In captive flocks, birds were found to add more ‘dee’ notes in the presence of smaller, more threatening predators. These birds also responded with stronger responses to playback of ‘chickadee’ calls that contained more ‘dees’ (Templeton et al. 2005).

The Louisiana Waterthrush, *Parkesia motacilla*, is a Nearctic-Neotropical migratory wood-warbler that breeds in the eastern United States. Its breeding habitat is one of fast-flowing streams in areas of often steep terrain. It is one of the earliest spring migrants, and its average arrival date in the Ozark Mountains of northwest Arkansas centers around the second week of March (James and Neal 1986, Neal 2009). At the time of their arrival, and with subsequent breeding activities, the sound environment is dominated by rushing water. Therefore, the streamside habitat has resulted in the evolution of songs and chek vocalizations that are loud and ringing (Mattsson et al. 2009a).

Louisiana Waterthrushes, like other genera in Family Parulidae*, Protonotaria, Helmitheros, Limnothlypis, Seiurus, Oporornis, and Geothlypis* (Spector 1992), have a song repertoire that contains two song types, a primary song and an extended song type. Generally, there is only one primary song type per male, though there may be some subtle variability within a male's song (Spector 1992). The extended song type is produced as an extension of the primary song type. They are characterized by acoustic structure and by distinct behavioral correlates. The primary song has been described by Smith and Smith (1996) as beginning with approximately two to four introductory notes in the form of wide chevrons, v-shapes, or a combination of both. This introductory section is followed by briefer components of sharply descending frequency sweeps and rapidly descending and ascending v-shaped units. The primary song ends at this point with an abrupt termination in the form of a chevron or couplet. All males have complete primary song, but males may leave out components at the beginning and ending of the song in any given rendition. If the song continues beyond this point it is considered extended song.

Extended song begins with primary song and then continues with an extending suffix of notes that are lower pitched, rapid, and brief. The number of notes in the suffix has been reported to vary from as few as one to as many as 25. The birds tend to incorporate the notes in a series that may be repeated, and across renditions by a given male, there are usually more deletions and additions of components within the extending suffix than in primary song (Smith and Smith 1996). The extended song may therefore be considered a compound vocalization.

When the extended segment of extended song becomes very long, it becomes a run-on pattern of singing. Most run-on singing begins with the introductory notes of primary song and extended song, but the ending is repeated. The components of the extending segment may be repeated to show a recurring pattern. Within these repetitions, however, components of the song are often deleted, inserted and/or interspersed with non-song vocalizations. Primary notes used at the beginning of the song are occasionally used again in run-on singing. Run-on chains of singing have been documented to contain as many as 197 components (Smith and Smith 1996). When primary, extended, or run-on song types are sung at lower amplitudes they are considered soft song (Nice 1943). In many species, soft song is indicative of aggressive intent (Searcy et al. 2006, Marshall 2011) and serves as a reliable indicator of attack in at least one species of North American wood-warbler (Hof and Hazlett 2010).

The behavioral correlates of the two song types of the Louisiana Waterthrush are related to different situations and degrees of aggression (Spector 1992, Smith and Smith 1996, Marshall 2011). Primary song is the most common of the two types (Spector 1992) and is sung more often when a male is alone (Smith and Smith 1996). Extended song is given when males are interacting, particularly when one male is approaching or attempting to interact in close contact with another (Smith and Smith 1996) and, as such, is used more often in territorial disputes (Spector 1992, Smith and Smith 1996, Marshall 2011).

Longer songs have been shown to be indicative of stronger aggressive reactions in a species with single song repertoires (Lattin and Ritchison 2009, Beckett and Ritchison 2010) and in species with multi-song repertoires (McGregor and Horn 1992). Also, playback of longer songs resulted in stronger reactions from territorial males compared to their reactions to shorter songs (Balsby and Dabelsteen 2001, Lattin and Ritchison 2009). Increasing the number of phrases and thus song complexity without increasing the length of the song type has also been shown to be correlated to increased aggression (Leitao et al. 2006, Lattin and Ritchison 2009).

Louisiana Waterthrushes interact with perceived territorial intruders with more aggression and extended song early in the breeding season (Marshall 2011) and the use of extended song declines as the breeding season wanes. During territorial disputes, as the interaction comes to a stalemate, or, in the case of playback, the territorial intruder cannot be found, the intensity of an encounter decreases and males switch from extended to primary song (Smith and Smith 1996, Marshall 2011).

Louisiana Waterthrushes are capable of discriminating between neighbors, strangers, and neighbors at incorrect boundaries based on song (Marshall 2011). They show different degrees of aggression with the most aggressive responses to the songs of strangers at territorial boundaries and the least aggressive responses to correct neighbors. Responses to neighbors at incorrect boundaries appear to fall between the two. This is a relatively common occurrence in species that maintain and hold breeding territories (Temeles 1994). Neighbor-stranger and individual discrimination of where a certain territorial neighbor should be allows the territory holder to correctly allocate time and energy to territorial defense based upon the degree of threat presented by different types of individuals at a territory boundary (Temeles 1994). Individuals considered a greater threat are met with stronger degrees of aggressive response (Jaeger 1981, Getty 1989). This correct allocation of energy thus increases the territory owner's fitness (Falls 1969, Krebs 1971, 1982, Getty 1987, Beletsky and Orians 1989, Getty 1989, Godard 1993, Stoddard 1996).

The responses of Louisiana Waterthrushes to playback of the songs of neighbors and strangers included the use of extended and primary song types. The relative amount of each song type used varied with the degree of aggression observed, with more extended song sung in response to what would be considered the greater threat, strangers at a territorial boundary (Marshall 2011). There was also a change in the use of these song types during playback tests with progression of the breeding season, with extended song being used more frequently at the onset of the breeding season, and less frequently as the season continued. Extended song use also declined through the progression of individual playback trials, with males switching from extended to primary song types as the time into the trial continued and birds, having not found an intruder, returned to nonaggressive activities. Soft song too was sung in more aggressive responses and more often earlier in the breeding season (Marshall 2011).

My objectives were to determine whether there were differences in the acoustic structure of primary segments and suffix components of extended song of Louisiana Waterthrushes responding to songs of strangers, songs of neighbors at correct boundaries, and songs of neighbors present at an incorrect boundary (i.e. the opposite boundary on a linear territory). Songs were also compared to determine if there were changes in the acoustic structure as time into the breeding season progressed and birds participated in different reproductive activities. Comparison of songs given by males in situations in which different levels of aggression were expected allowed us to test the hypothesis that increased levels of aggression correlate to the number and structure of harsh, low frequency components in their song as predicted by Morton's (1977) motivation-structural rules of vocalizations.

Methods

Louisiana Waterthrush populations on 9 km of three streams within the Buffalo National River's watershed in the Arkansas Ozarks were banded and monitored from 2006 to 2008 with a preliminary banding season in 2005. Twenty-six males held territories during that time. Each male was mist-netted, and banded with color and federal bands, their songs were recorded, and their territories mapped each year by observing encounters between males at territory boundaries and by mapping song perches. Because Louisiana Waterthrush territories are linear along a stream, they usually had only two neighbor boundaries, one at the upstream end of a territory, and one at the downstream end. Territories averaged 300 to 500 m in length.

Yearly migration return rates were high. In 2007 there was an 80% return rate, but 2008 had only 60% of the previous year's males returning. Of the returning males, each year 100% returned to their previous territory. Territory boundaries remained similar if not identical between males that had shared boundaries the previous year. Five focal males (FM) were chosen randomly and the stage of their breeding cycle was noted. Two of the five were tested in both 2007 and 2008. One male banded in 2006 was known to have the same neighbors throughout the three years of the study. Another three males were banded in 2006, and each shared one common boundary with the same neighbor from 2006 through 2008 while the opposite boundary was occupied by a new male in the year of experimentation. The last male was not banded until 2008, but he was recognized by a very clear and unusual song signature that was recorded from 2006 through 2008. He was known to have shared at least one common boundary with the same neighbor since the first year of his experimentation in 2007. The breeding cycle of each male was followed through the time the male served as a focal subject.

All recordings were made with an Audio-Technica 815 Shotgun microphone with a Rycote windscreen and shock mount handle. A Sony TC-D5 PROII cassette recorder was used in 2006, and a Marantz PMD 660 was used in 2007 and 2008. A Mineroff SME-AFS speaker and Phillips portable CD player were used for playback. Recordings were digitized using a sampling rate of 48,000 Hz at a 16-bit resolution via Raven Interactive Sound Analysis Software, Version 1.1: developed by the Bioacoustics Research Program, Cornell Laboratory for Ornithology. Playback stimuli for eliciting reactions from the five focal males were produced from recordings of primary song bouts of territorial males. Unwanted low-frequency noise was high-pass filtered from recordings. Song stimuli occurred at five songs per minute on the playback recordings for a total of three minutes which was the mean song rate calculated from 2006 and 2007 recordings of males singing alone (without the stimulation of a counter-singing male). Songs used for stimuli were played at amplitude of 85 to 88 dB at 1m from the speaker (Smith and Smith 1996). The speaker faced into a territory within 5 m of the territory boundary at a height of 2 m on a tripod. Either the downstream boundary or upstream boundary was chosen randomly for each trial.

Six trials were attempted for each focal male. They were playback of the upstream neighbor's song at the upstream boundary (correct neighbor), playback of the downstream neighbor's song at the upstream boundary (incorrect neighbor), and playback of a stranger's song at the upstream boundary (stranger), playback of the downstream neighbor's song at the downstream boundary (correct neighbor), playback of the upstream neighbor's song at the downstream boundary (incorrect neighbor), and playback of a stranger's song at the downstream boundary (stranger) (Fig 1). One trial was run each day for six contiguous days if possible. Choices of boundary and whether to use correct neighbor, incorrect neighbor, or stranger song were made randomly to control for order of presentation and bias. The same neighbors were not used on consecutive days. To avoid pseudo replication (Kroodsma 1989) experiments used unique stranger song for a single male, and that male was used only in one set of trials in one year. Strangers were defined as individuals holding territories on different streams.

Playback began 10 min after the experimenter located territorial males near the territorial boundary where playback was to occur, and their behaviors were documented for 5 min before beginning playback. I required that males had not interacted with neighbors for those ten min and that neighbors had remained silent for 5 min before playback began so that behavior was not influenced by their interaction. Trials were run every 24 h at least 1 h after dawn so that responses were not influenced by dawn chorus or previous experimentation and habituation (Lovell and Lein 2005). If a neighbor sang within 40 m of the playback speaker, if the focal male was never sighted near the correct boundary for experimentation, or if the weather precluded experimentation, the trial was abandoned and repeated the following day, and other trials were moved forward by one day (Molles and Vehrencamp 2001). Within each year trials were run for each male within one day to as many as 18 days apart. Long intervals between trials were a result of birds never approaching the randomly chosen boundary. There were long distances between an upstream and downstream boundary, and birds tended to interact more often at one boundary than another. This appeared to depend on placement of the nest in the territory, foraging behavior of females during incubation recesses, and interactions between neighboring males, particularly when a boundary was being contested regularly with a boundary neighbor. As many as six hours were spent waiting for the bird to appear at the randomly chosen boundary before the trial was abandoned for the day. Trials were run from within 39 days of the mean spring arrival date of March 14 to 108 days thereafter. This encompassed periods of nest construction, incubation, tending nestlings, tending fledglings, and depredation.

Each trial lasted 12 min with 3 min of preplayback, 3 min of playback and 6 min of post-playback recording the response of the subject (Lovell and Lein 2005). Timing of behavioral and vocal responses was transcribed from recordings with Etholog 2.25 Behavioral Observation Transcription software (Ottoni 2000). Extended and soft extended songs were measured using Raven Interactive Sound Analysis Software, Version 1.1. using the default 1.3 power scale preset for spectrograms. The primary section and song signature of each male's song (Figure 3.1) was determined previous to measurements of vocalizations according to the definition given by Smith and Smith (1996). Afterward, the number of introductory notes, length of the primary segment (s), lowest frequency (Hz), highest frequency (Hz), and bandwidth (Hz) were measured manually on the sound window by selecting the primary segment components in their entirety with the cursor including the first and last of the components and highest (maximum) and lowest (minimum) frequency values. I manually counted the number of components within the segment according to Smith and Smith (1996) and the sound analysis software calculated length and frequency values.

Similarly, extended and soft extended song were measured for the number of components in the suffix, length of the suffix (s), lowest frequency (Hz), highest frequency (Hz), peak frequency (Hz), and bandwidth (Hz) of the suffix. Run-on song was treated as extended song. Extended song suffixes, like the primary component of the extended song, were also measured by creating a selection that encompassed the beginning of the extended song suffix, manually measuring the number of components within the suffix, and the sound analysis software measuring length and frequency values. In addition, the peak frequency (Hz) measurement of the extended song suffix was calculated automatically by the software.

Data collected comparing responses to neighbors and strangers and data collected to compare responses to correct and incorrect neighbors were grouped for separate statistical analysis. Variables from measurements of vocalizations were highly correlated. Therefore, a principal components analysis (PCA) was conducted to control for collinearity (McGregor 1992). Principal components were then analyzed as a two-factor factorial ANCOVA (Milliken and Johnson 1992) with day of the breeding cycle beyond spring arrival (March 14) as a covariant. Neighbor versus stranger, correct neighbor versus incorrect neighbor, and each focal male were treated as fixed effects. Least square means were used to determine differences when appropriate. Data analysis was generated using SAS software, Version 9.2 (SAS Institute Inc., Cary, NC, USA). Differences were considered significant at p = 0.05 or less.

Results

A total of 33 experiments were run with five focal males over a period of two years (2007, 2008) during which 396 min of behavior were documented and recordings of 614 measurable vocalizations were made. One focal male was removed from analysis. He was unusual in that he exhibited a much weaker response to playback than the other males (Marshall 2011). The only known difference in this male and others was the constancy of his associations with his neighbors. Over a period of three years his neighbors and territorial boundaries remained identical. With his removal, the number of experiments used for statistical analysis was reduced to 24, to documentation of 288 min of behavior, and recordings of 560 vocalizations.

Principal Components Analysis of Extended Song Responses

PCA of physical characteristics of vocal responses to neighbor versus stranger trials, n = 13, produced four PCs with eigenvalues greater than 1.0 explaining 94.55 % of the variation and the full complement of variables measured in extended song. PCA of physical characteristics of vocal responses to correct versus incorrect neighbor trials, n = 10, produced three PCs with eigenvalues greater than 1.0 and explaining 88.8 % of the variation, the fourth PCs was added to the analysis to explain 96.01 % of variation in responses.

Neighbor-Stranger Discrimination

Primary Segment: Length and Number of Components

Suffix: High Frequency, Bandwidth, and Number of Components

The first PC for neighbor vs. stranger trials had an eigenvalue of 4.92, and explained 44.7 % of variation in responses. The highest positive factor loadings were high frequencies and bandwidth of the extended song suffix, followed by the number of components in the suffix (Table 3.1). There was a negative correlation with number of components within the prefix and prefix length. No significant differences were found comparing responses to neighbor vs. stranger stimuli. There were significant differences according to these attributes of the vocalizations between focal males ($F_{3, 12} = 5.15$ $p = 0.04$). Males differed in number and length of components in the primary song segment. The average number of components ranged from 9 to 12 with an average length from 1.7 to 2.3 s respectively (Table 3.2). Males also differed according to length of their extended song suffix with males tested earlier in the season having more components in their suffix than those tested later in the season (Table 3.3).

The high frequencies and bandwidth within song suffixes had the highest positive correlations with the first PC. Only one of the four focal males $LSM_{FMF} = -2.310$ was significantly different from the others. He tended to have vocalizations with lower high frequencies and smaller bandwidths compared to $LSM_{FMA} = 1.220$, $p = 0.01$ and $LSM_{FMO} = 1.982$, $p = 0.02$. His trials were run after his having lost his nest to predation and his last trial was run very late in the breeding season. He sang little in response to playback, and thus the trial had a small sample size that might have played a role in driving his values to be different from those of the others.

Neighbor-Neighbor Discrimination

Primary Segment: Length and Components

Suffix: Length and Number of Components, High Frequency and Bandwidth

The first PC in correct vs. incorrect neighbor trials had an eigenvalue of 4.98 and explained 45.3 % of variation in responses. The number of components and length of the song suffix had high positive correlations with this PC, followed by the high frequency and bandwidth of the suffix. High negative correlations, equal in magnitude to those associated with the extended song suffix, were found with the number of components and length of the primary segment. Values of this PC differed significantly between focal males ($F_{3,9} = 6.70$ $p = 0.05$). There were no significant differences found in comparisons between reactions to correct and incorrect neighbors ($F_{1,9} = 0.03$ $p = 0.86$), and no interaction between males responding and the type of neighbors they were responding to ($F_{1,9} = 0.06$ $p = 0.82$).

As seen in the neighbor vs. stranger trials, each male had a characteristic length and number of components within its primary song segment (Table 3.2). Males also differed according to length of their suffix, with average number of components and length of suffixes of the two males tested earliest in the season having more components and longer suffixes, than those tested later in the season (Table 3.2). There was also a difference in focal males when high frequencies within song suffixes were compared. Though there was no effect of the covariate of days into the season, those males tested earlier in the season had higher frequencies in their suffixes compared to males tested later in the season (Table 3.2). Again, the focal male tested later in the season, after his nest had been lost to predation, had the shortest suffixes, lowest high frequencies, and smallest bandwidths in his trials.

Two focal males that had two trials with the same type of neighbor, correct or incorrect, responded differently depending on the boundary at which the trial was run, but not according to the type of neighbor. The first of these focal males (FMA) was tested on days 76 and 90, and his response on day 90 was different in that he sang measureable extended song only once. He never approached the playback speaker, but continued foraging with his fledglings and sang primary song at a rate similar to that of day 76. The second focal male (FMS) was tested on days 76 and 78. He had been very actively defending both ends of his territories from new neighbors that season. The intrusion by another male at the upstream boundary had only just begun during these trial periods and this may have affected his responses at that boundary. He sang twice as many extended songs at the upstream boundary and averaged three times the number of components and length in the suffixes of these songs. The high frequency of his extended song suffixes was also measurably higher at the boundary where he was interacting to the most recent intruder regardless of whether the playback was of his correct or incorrect neighbor (Table 3.2).

Neighbor-Stranger Discrimination: PC2

Primary Segment: Low Frequency, High Frequency, and Bandwidth

Suffix: Length

The second PC had an eigenvalue of 3.13, and explained 28.5 % of variation. The lowest frequency of the primary segment and length of the suffix had high positive loadings, while the highest frequency and bandwidth of the primary segment had high negative loadings (Table 3.1). There was a significant interaction of the covariate of days into the breeding season with responses to neighbor and stranger stimuli ($F_{1, 12} = 59.56$ $p = 0.02$), and with comparisons between focal males ($F_{2, 12} = 21.67$, $p = 0.04$). Removing the influence of the covariate revealed significant differences in responses to neighbor and stranger stimuli ($F_{1, 12} = 62.90$, $p = 0.02$), and between responses of focal males ($F_{3, 12} = 24.15$, $p = 0.04$), with no interaction between the two factors ($F_{1, 12} = 2.34$, $p = 0.27$).

The primary segment of songs sung in response to stranger stimuli had a lower low frequency, lower high frequency, and smaller bandwidth compared to the primary segment of songs in response to correct neighbor stimuli (Table 3.2). As the breeding season wore on, the average high frequency within prefixes became higher, the low frequency lower, and the bandwidth larger. Song suffixes were longer in response to strangers and in males tested earlier in the season (Table 3.3). One male, while foraging with fledglings, sang only one long extended song in response to a correct neighbor's song.

Neighbor-Neighbor Discrimination: PC 2

Primary Segment: Low Frequency, High Frequency, and Bandwidth

Suffix: Low Frequency and Bandwidth

The second PC comparing extended song in the presence of correct and incorrect neighbors had an eigenvalue of 3.65 and explained 33.2 % of the variation of responses. The highest positive factor loadings were bandwidth of both the primary segment and the suffix of the song, followed by the highest frequency of the primary segment (Table 3.1). Highest negative correlations were with low frequencies in the primary song segment and the suffix. Significant differences were found with the covariate of days into the breeding season ($F_{1,9} = 9.38$ $p = 0.03$).With effect of the covariate removed, significant differences were found between focal males ($F_{3,9} = 12.36$ $p = 0.01$), but no significant differences were found between responses to correct and incorrect neighbors.

The male tested earliest in the season averaged the highest low frequency, lowest high frequency, and smallest bandwidth in his prefix (Table 3.2). Males were different from one another in frequency of their primary segment components on the frequency scale. There was a tendency overall for components of the primary segment to show increases in high frequency, decreases in low frequency, and larger bandwidths as the breeding season wore on. The suffix of the male tested earliest in the breeding season had the highest low frequency with low frequency becoming higher as the season progressed (Table 3.3). Overall, the low frequencies tended to decrease and bandwidths of the song suffix to become smaller with the breeding season. The focal male with two trials with the same type of neighbor, which responded differently depending on the boundary at which the trial was run, but not according to the type of neighbor, had a lower average low frequency at the boundary where he had been more actively involved in boundary disputes.

Neighbor-Stranger Discrimination: PC3
Primary Segment: Length, Components, and Low Frequency
Suffix: Length, Components, and Low Frequency

The third PC in the neighbor vs. stranger trials had an eigenvalue of 1.33, and explained 12.1 % of the variation in responses. Positive correlations occurred with length and number of components in the primary segment, and length and number of components in the suffix. Negative correlations occurred with low frequency in both primary segment and suffix. There was a significant effect of the covariate of days into the nesting season and interactions of the covariate with responses to neighbors vs. strangers and focal males ($F_{1, 12} = 171.05$ $p = 0.05$). With the influence of the covariate removed, a significant interaction was found between responses to neighbors vs. stranger stimuli and which focal male was responding ($F_{1, 12} = 137.62$ $p = 0.05$).

Focal males tended to respond to strangers with lower low frequencies in the primary song segment and suffixes. Length and components of the primary segment varied as expected by focal male, and longer suffixes occurred in focal males tested earlier in the season. The male tested earliest in the season averaged a lower low frequency in his suffix in response to a stranger, while males tested later in the season showed higher low frequencies in the suffix in response to a stranger.

Neighbor-Neighbor Discrimination and Extended Song: PC3
Primary Segment: Low and High Frequency
Suffix: Length, Components, and Low Frequency

The third PC from the correct vs. incorrect neighbor trials had an eigenvalue of 1.14, and explained 10.3 % of variation in responses. Highest positive correlations were found with the high frequency of the primary song segment, the lowest frequency of the suffix, and the lowest frequency of the primary segment. Negative correlations had lighter loadings, and were associated with the number of components and length of the suffix (Table 3.1). The variables associated with this PC showed a non-significant effect of the covariant of days into the breeding season ($F_{1,9} = 10.13$ $p = 0.09$) and significant differences among responses of focal males ($F_{3,9} = 33.77$ $p = 0.03$). The covariant affected each of the focal males differently ($F_{3,9} = 28.10$ $p = 0.03$).

As stated previously, the male tested earliest in the season averaged the highest low frequencies and lowest high frequencies in his primary song segment (Table 3.2). There was a tendency for those components to show increases in high frequency and decreases in low frequency as the breeding season progressed. Males also differed in the length of their extended song suffix with the two males tested earliest in the season having more components and a longer suffix than those tested later in the season (Table 3.3). The suffix of the male tested earliest in the breeding season had the highest low frequency in his suffix with the low frequency becoming higher as the season progressed. On average, low frequencies in the suffix tended to decrease as the breeding season waned.

The male that had been actively defending his territory against a new male that had just moved in between him and a neighbor at his upstream boundary responded with a higher frequency in the primary segment of his extended songs and much lower average low frequencies in his primary segment and suffix, with his suffixed averaging nearly three times as long as at the downstream boundary.

Neighbor-Stranger Discrimination: PC4

Suffix: Peak Frequency

The fourth PC in the neighbor vs. stranger trials had an eigenvalue of 1.02 and explained 9.3% of the variation in responses. Peak frequency had the highest loading, more than double that of the two next highest correlations, number of components in the primary segment, and lowest frequency of the extended song suffix (Table 3.1). There was a non-significant effect of the covariate of days into the nesting season according to neighbor vs. stranger and with focal males ($F_{1, 12} = 63.27$, $p = 0.08$). Removing the influence of the covariate, a significant interaction was found between response to neighbors and strangers and focal males ($F_{1, 12} = 153.55$, $p = 0.05$). Significant differences were also found separately in responses to neighbor and stranger stimuli ($F_{1, 12} = 1530.47$, $p = 0.02$), and between responses of focal males ($F_{2, 12} = 1353.26$, $p = 0.02$).

When responses to neighbor and stranger stimuli were compared, males with trials earlier in the season responded with higher peak frequencies and lower low frequencies in the extended song suffix in response to a stranger (Table 3.2). The opposite was true of males tested in the latter part of the season. They tended to have lower peak frequencies with strangers and higher low frequencies with strangers. Focal Male F, the male who had lost his nest, had a strong influence on the analysis, in that, in his two correct neighbor trials, he sang only three extended songs in the first trial with only two or three components in the suffix that gave an average peak frequency of 6062.5 Hz and two songs in the second trial conducted much later in the season where he sang two songs with only one to three components in the suffix that gave an average peak frequency of 2531.5Hz.

Neighbor-Neighbor Discrimination

Suffix: Peak Frequency

The fourth PC in the correct vs. incorrect neighbor trials had an eigenvalue of 0.79 and explained 7.01 % of the variation in responses. Peak frequency of the extended song suffix had the highest loading, more than double that of the next highest correlation, the length of the primary song segment (Table 3.1). There was an indication of an effect of the covariate of days into the breeding season with focal males ($F_{1, 10} = 4.86$ $p = 0.08$). However, with the effect of the covariate removed no significant differences were found among the males' responses ($F3_{,10}$ = 3.13 p = 0.12).

Discussion

Differences were found in the acoustic structure of primary segments and suffixes of extended song of Louisiana Waterthrushes responding to songs of neighbors and songs of strangers. Increased levels of aggression were correlated with an increase in the number of harsh low frequency notes in the extended song suffix as predicted by Morton's (1977) motivation-structural rules of vocalizations. Differences were also found in frequency measurements of primary segments and suffixes of extended songs. These acoustic structures also changed with progression of the breeding season.

I found this to be particularly apparent in two of the focal males. The first was removed from the analysis as a result of his dampened response. He was unique compared to other focal males in that he had the same neighbors with boundaries in the same place for three years. The second male was not removed from analysis, though he behaved and vocalized differently in response to incorrect neighbors at his upstream and downstream boundary. During the time period when the last of his trials were run, a stranger appeared at the upstream boundary between the focal male and his upstream neighbor. The stranger continued to hold his place on the stream while the original upstream neighbor of the focal male moved further up into a territory whose owner had been recently killed by a cat. Playback trials of incorrect neighbor song were run two days apart at the upstream and then at the downstream boundary. The focal male who had been sustaining his territory boundary with the intruding male responded at that boundary (the upstream boundary) to incorrect neighbor song with twice as many extended songs with suffixes that averaged three times the length of those used at the downstream boundary, and with lower low and higher high frequencies in both his suffix and primary song segments. This increased aggression at that territory boundary was likely a result of the constant aggressive interactions with the strange male.

As predicted by Morton's motivation-structural rules (Morton, 1977), I found that extended song suffixes, composed of harsh low-frequency components, were overall significantly longer when males were responding to strangers compared to males responding to correct neighbors. In comparing extended song responses of males to correct and incorrect neighbors, the differences were not significant. Song suffixes were longer in songs of males tested earlier in the season compared to those tested later in the season in both neighbor-stranger and neighbor-neighbor discrimination trials, and also differed among individual males in both studies.

Overall high levels of aggression in the early breeding season likely resulted in less discrimination and a similar number of notes within, and length of, song suffixes regardless of whether the response was to a correct neighbor or a stranger. This notion is upheld in that discrimination of focal males between neighbors and strangers became increasingly more evident as the season wore on, and then increasingly less evident. Higher degrees of hormonally-driven aggression occur earlier in the season (Wingfield and Hahn 1994, Catchpole and Slater 2008, Voigt and Leitner 2008). Aggression may also be affected in part by the memory of birds as neighbors from previous years (Godard 1991). Even if a male became the correct neighbor at a given boundary, if it was not the same neighbor from the previous year there might still be a higher degree of aggression between neighboring males at the beginning of the breeding season's establishment or reestablishment of territories.

The number of notes and length of primary segments of extended song were unique for each of the four focal males. Though notes were occasionally added or deleted from the primary segment there was little variation. This stereotypy was expected (Smith and Smith 1996). Because these properties are less variable within males and this primary structure is basically the same as the primary song produced when a bird is singing alone on its territory, it is these features that are likely most important to recognition of a bird by species (Marler 1960, Becker 1982) and as an individual. The intervals between notes were not measured in this study, but could also prove to be important in recognition (Emlen 1972). See review in Catchpole and Slater (2008).

Individuals can often be identified by ear and from spectrograms (Figure 1) according to the unique notes within the primary segment of their songs (Smith and Smith 1996). In contrast, though still showing properties relative to the individuality of males and species recognition (Nelson 1988, Weisman and Ratcliffe 1989), frequency parameters of the primary song segment varied not only with individuals, but with differences in aggression in response to neighbors, strangers, and neighbors at incorrect boundaries. Overall, therefore, primary song might encode not only information about individual and species identity, but also information about motivation.

The frequency parameters of the primary segment of extended song were more variable than its number of components and overall length. These frequency parameters might therefore be more capable of conveying information concerning the motivational state of a singer among individuals in close proximity to one another (Morton 1977, Spector 1992). In neighbor-stranger discrimination trials, primary segments of extended song responses to strangers averaged lower low frequencies, lower high frequencies, and smaller bandwidths compared to primary segments of song sung in response to correct neighbors. Lower frequency levels of these pure-toned notes might be an indication of higher levels of hostile motivation and aggression (Morton 1977) in response to a stranger compared to a correct neighbor.

In addition, days into the breeding season affected the frequency parameters of the primary segment of extended songs sung by males in response to stranger songs. As the season wore on, the average high frequency of the primary segment of extended songs tended to increase, the average low frequencies to decrease, and bandwidth to become larger. In comparison to responses to stranger song, the songs that were sung in response to a correct neighbor did not show significant changes in these characteristics as the season wore on. This suggests that motivation in response to strangers may change as the breeding season progresses, testosterone levels decrease, and males become more active in providing care to offspring. On the other hand, motivation behind a response to neighbor song remains similar as the season progresses.

In discrimination between neighbors at correct boundaries and at incorrect boundaries, differences were not attributable to the type of neighbor a focal male was responding to, but to individuality among each of the four focal males. However, frequency characteristics of the primary song segment showed overall similar changes as seen in neighbor and stranger trials with low frequencies declining and high frequencies increasing as the season wore on.

Most of the variation in frequency parameters of extended song suffixes appeared to be attributable to individuality among males as well, though there were indications of differences in low frequencies of the suffix when comparing responses to neighbors and strangers, such that focal males responding to strangers did so with lower low frequencies. There were also changes with the progression of the breeding season, with the average low frequency declining over time as was also seen in primary song segments.

The decline in low frequency of the primary song segment and the extended song suffix with the breeding season does not support Morton's motivation-structural rules. If the focal males were becoming increasingly less aggressive as the season progressed then it would be expected that the low frequency would instead increase with days into the season. One explanation is that frequency differences were a result of signal-to-noise ratios and measurements of the recordings. A relative-amplitude criterion was not used in identifying minimum and maximum frequencies. The background noise on any given day on the stream was relatively louder or quieter based upon the amount of water in the stream. As a result, louder songs on quieter days may have been measured as having lower minimum and higher maximum frequencies. This would explain the lower minimum frequencies and higher maximum frequencies measured within songs as days progressed from early in the season when water and its associated noise was at its highest, to later in the season when water was at its lowest and quietest.

In addition, lack of clear differences in the frequency properties of the components of extended song suffixes may have been a result of the method employed in the measurement of the components of the suffix. Unlike the more stereotyped primary segment of extended song, the extended song suffix contains a variable number of notes of many different frequencies. Many of the components are uttered at lower amplitudes and the suffix has a tendency to 'trail off' making measurement of components much more difficult. Frequency measures of each extended suffix component were made, but not included in this analysis. Their comparison would provide more information to a researcher than the overall measurement of high, low, and peak frequencies across the suffix. The number of components within an extended song suffix also played a large role in mean frequency measures. Shorter suffixes and thus fewer components in the segment contribute more to overall averages. They likely indicated lower and higher average frequencies within a suffix than did suffixes with a fuller complement of components.

If my observations reflect true changes or differences in frequency between trials and across dates then the within-male song variation in frequency parameters is indicative of males having repertoires of frequency types within their song type, or birds matching frequencies to the song of the bird they are responding to (Morton and Young 1986). Smith and Smith (1996) tested for song matching by using extended and primary song types in playback, but they only considered matching to be occurring if males responded to either song type with the same song type while comparison of frequencies was not tested.

In conclusion, increased levels of aggression were correlated with differences in the acoustic structure of the extended song type of four male Louisiana Waterthrushes when comparing songs used in responses to neighbors, strangers, and (to a more limited extent) neighbors at incorrect boundaries. Extended song segments varied on a continuum of length and number of harsh, low-frequency components following the introductory notes of the primary segment in reference to the degree of aggressive motivation. Differences also included lower average low frequencies in both the primary segment and extended song suffix, as well as with the number of harsh, low-frequency components that comprise the suffixes of extended song in more aggressive interactions as predicted by Morton's (1977) motivation-structural rules of vocalizations. Differences were more evident when comparing songs given in response to neighbors and strangers than when comparing songs given in response to neighbors at correct and incorrect boundaries. Changing levels of aggression across the breeding season were related to predicted changes in song structure with decreasing levels of aggressive motivation.

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Table 3.1. Principal Components Analysis of physical components of extended song responses in neighbor vs stranger trials (NSD) and correct vs. incorrect neighbor trials, and their associated correlations (loadings) with response variables. Includes only those PCs found to have siginificant differences in one or more of the comparisons made in the study

	PC1		PC2		PC3		PC4	
Response Measure	NSD	NND	NSD	NND	NSD	NND	NSD	NND
Number of Components in Prefix	-0.3332	-0.3854	-0.1603	0.1907	0.4390	-0.2449	0.3066	0.2266
Length(s) of Prefix	-0.3471	-0.4010	-0.1170	0.1116	0.4385	-0.2093	0.2540	0.3174
Lowest Frequency (Hz) in Prefix	-0.0229	0.2157	0.4710	-0.3821	-0.3831	0.3660	0.2106	0.1115
Highest Frequency (Hz) in Prefix	0.1928	-0.0138	-0.4621	0.4075	-0.2679	0.5311	0.0952	-0.2669
Bandwidth (Hz) of Prefix	0.1610	-0.1076	-0.5146	0.4722	-0.0953	0.2248	0.0108	-0.2465
Number of Components in Suffix	0.3370	0.4126	0.2588	0.0281	0.3801	-0.3229	-0.1613	-0.0894
Length (s) of Suffix	0.2819	0.3978	0.3248	-0.0549	0.3687	-0.3227	-0.1371	-0.0368
Lowest Frequency (Hz) in Suffix	-0.2711	-0.0293	0.2859	-0.4153	-0.3092	0.4297	0.3066	0.2173
Highest Frequency (Hz) in Suffix	0.4272	0.3851	0.0094	0.2438	-0.0189	0.0756	0.2359	0.1345
Bandwidth (Hz) of Suffix	0.4351	0.3494	-0.0643	0.3144	0.0621	-0.0337	0.1248	0.0685
Peak Frequency (Hz) in Suffix	0.2579	0.1804	0.0444	0.2855	0.0849	0.1726	0.7602	0.7900
% Variation in Responses	44.7	45.3	28.5	33.2	12.1	10.3	9.3	7.0

Table 3.2. Means and single standard error measurements of the primary segments of extended song produced by focal males in responses to songs of neighbors, strangers, and incorrect neighbors

Focal Male "O"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	39			56			40, 50		
Response Measure	n	mean	SE	n	mean	SE	n	mean	SE
Number of Components	26	8.9	0.1	17	8.9	0.2	25	8.7	0.1
Length (s)	26	1.740	0.021	17	1.729	0.040	25	1.719	0.028
Lowest Frequency (Hz)	26	2274.8	60.3	17	2011.5	79.5	25	2275.9	77.8
Highest Frequency (Hz)	26	9216.1	29.9	17	8958.8	113.2	25	9126.5	122.6
Bandwidth (Hz)	26	6941.3	74.8	17	6947.3	138.7	25	6850.6	157.6

Focal Male "S"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	60, 68			49,69			76, 78		
Response Measure	no extended song			n	mean	SE	n	mean	SE
Number of Components				26	11.6	0.1	25	11.7	0.1
Length (s)				26	2.191	0.027	25	2.182	0.033
Lowest Frequency (Hz)				26	1740.2	78.4	25	1424.4	70.7
Highest Frequency (Hz)				26	9224.9	71.2	25	9316.1	310.9
Bandwidth (Hz)				26	7484.7	128.3	25	7891.8	324.4

Focal Male "F"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	79, 108			75, 90			77		
Response Measure	n	mean	SE	n	mean	SE	n	mean	SE
Number of Components	5	12	0.0	22	11.9	0.1	4	12	0.0
Length (s)	5	2.338	0.012	22	2.327	0.023	4	2.398	0.094
Lowest Frequency (Hz)	5	1778.8	88.3	22	1744.1	108.5	4	1698.2	83.0
Highest Frequency (Hz)	5	9430.6	219.1	22	8742.1	197.5	4	9606.7	37.7
Bandwidth (Hz)	5	7651.8	232.3	22	6998.0	289.4	4	7908.5	53.4

Focal Male "A"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	76, 87, 90, 96			78, 80, 97			83		
Response Measure	n	mean	SE	n	mean	SE	no extended song		
Number of Components	15	10.47	0.19	75	10.23	0.06			
Length (s)	15	1.893	0.045	75	1.942	0.018			
Lowest Frequency (Hz)	15	1557.2	30.1	75	1702.8	21.8			
Highest Frequency (Hz)	15	10835.1	331.4	75	9975.6	79.5			
Bandwidth (Hz)	15	9277.9	324.1	75	8272.8	82.5			

Table 3.3. Means and single standard error measurements of suffixes of extended songs produced by focal males in response to songs of neighbors, strangers, and incorrect neighbors

Focal Male "O"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	39			56			40, 50		
Response Measure	n	mean	SE	n	mean	SE	n	mean	SE
Number of Components in Suffix	26	11.15	0.91	17	12.24	0.95	25	10.15	0.95
Length (s) of Suffix	26	1.284	0.112	17	1.355	0.153	25	1.218	0.124
Lowest Frequency (Hz) in Suffix	26	2052.3	63.0	17	1753.7	117.0	25	2307.4	161.2
Highest Frequency (Hz) in Suffix	26	10443.9	141.0	17	10113.5	161.7	25	9523.5	201.7
Bandwidth (Hz) of Suffix	26	8391.6	155.0	17	8359.9	212.9	25	7216.1	298.9
Peak Frequency (Hz) in Suffix	26	4932.7	189.4	17	5106.6	192.6	25	5059.1	151.1

Focal Male "S"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	60, 68			49,69			76, 78		
Response Measure	no extended song			n	mean	SE	n	mean	SE
Number of Components in Suffix				26	11.00	1.53	25	8.68	1.36
Length (s) of Suffix				26	1.386	0.195	25	1.106	0.161
Lowest Frequency (Hz) in Suffix				26	2059.6	97.3	25	1745.9	75.4
Highest Frequency (Hz) in Suffix				26	9344.3	174.8	25	9508.3	126.7
Bandwidth (Hz) of Suffix				26	7284.8	259.1	25	7762.4	182.4
Peak Frequency (Hz) in Suffix				26	5816.0	320.6	25	5572.5	237.1

Focal Male "F"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	79, 108			75, 90			77		
Response Measure	n	mean	SE	n	mean	SE	n	mean	SE
Number of Components in Suffix	5	2.2	0.4	22	7.4	0.9	4	2.3	0.4
Length (s) of Suffix	5	0.243	0.091	22	0.886	0.104	4	0.205	0.034
Lowest Frequency (Hz) in Suffix	5	1852.5	99.3	22	2019.4	163.6	4	1915.4	103.8
Highest Frequency (Hz) in Suffix	5	7737.6	1135.8	22	8565.2	346.9	4	7581.9	164.0
Bandwidth (Hz) of Suffix	5	5885.1	1173.7	22	6546.2	426.0	4	5666.5	157.4
Peak Frequency (Hz) in Suffix	5	4650.0	886.2	22	4576.7	189.0	4	5343.8	583.6

Focal Male "A"	Correct Neighbor			Stranger			Incorrect Neighbor		
Days into Season	76, 87, 90, 96			78, 80, 97			83		
Response Measure	n	mean	SE	n	mean	SE	no extended song		
Number of Components in Suffix	15	5.8	0.9	75	5.4	0.3			
Length (s) of Suffix	15	0.578	0.091	75	0.664	0.039			
Lowest Frequency (Hz) in Suffix	15	1657.1	111.1	75	1861.1	45.7			
Highest Frequency (Hz) in Suffix	15	10283.5	384.7	75	9469.8	94.6			
Bandwidth (Hz) of Suffix	15	8626.5	421.6	75	7608.7	118.3			
Peak Frequency (Hz) in Suffix	15	5120.1	239.8	75	4810.0	34.0			

Fig 3.1. Illustration of where trials occurred on focal male territories

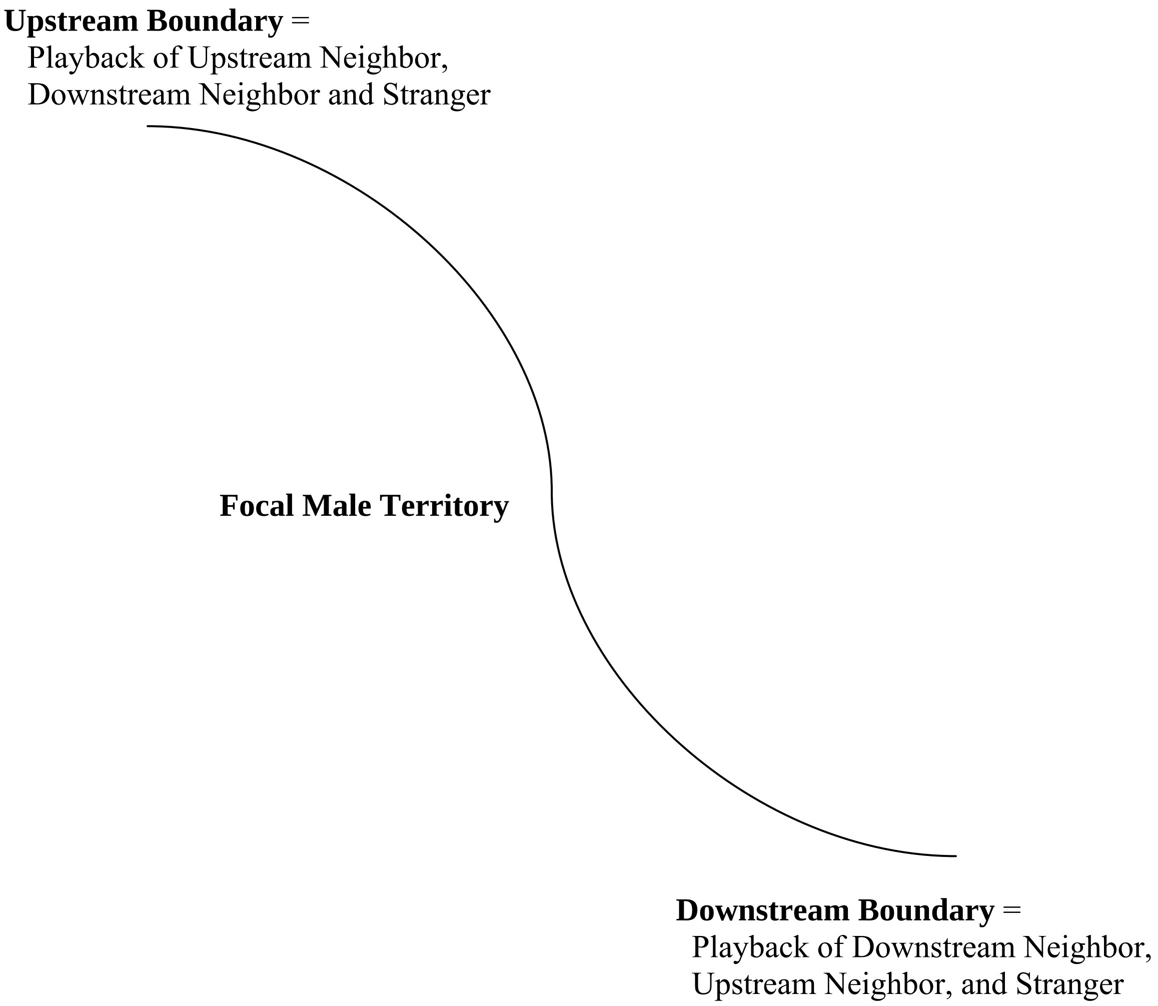
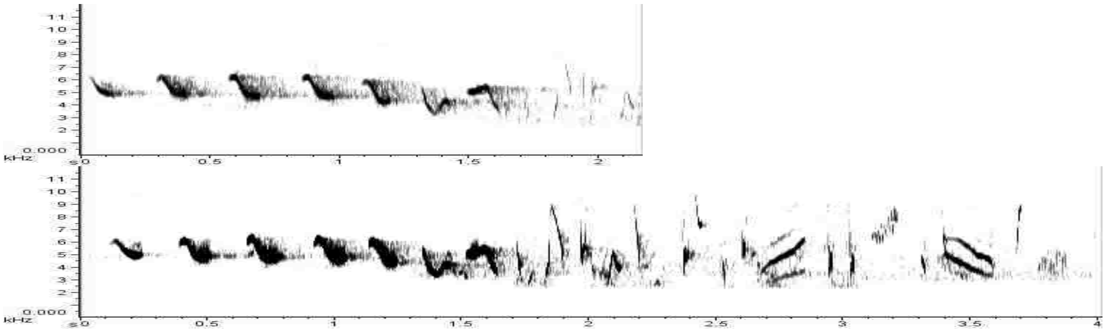
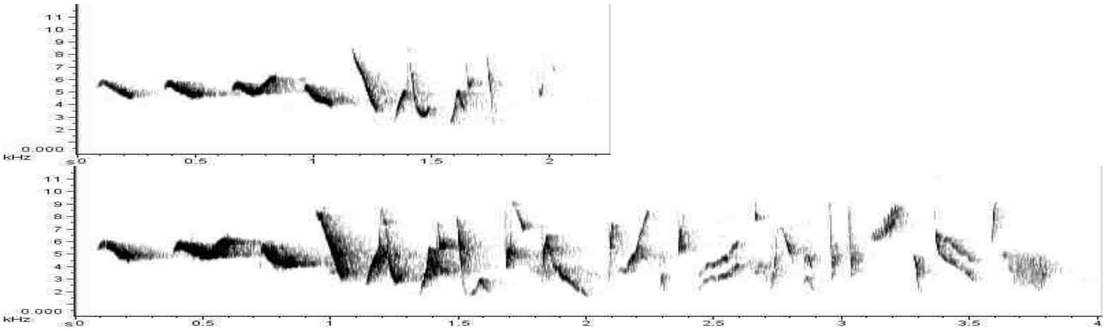


Figure 3.2. Spectrograms of primary song sound signatures and extended song of four focal males

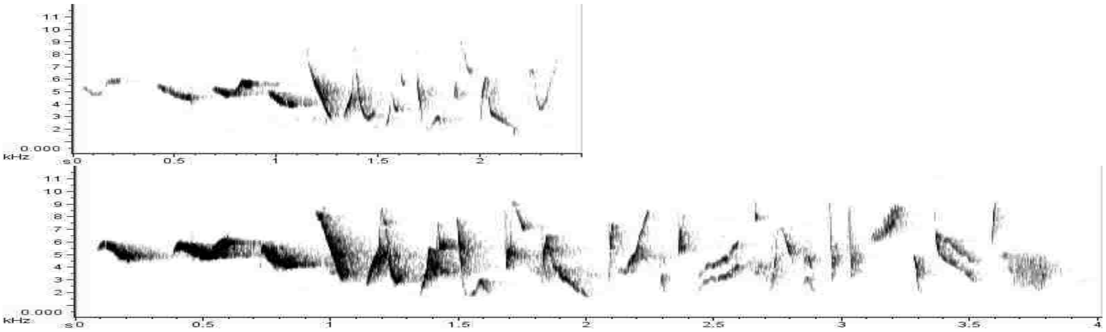
Focal Male "O"



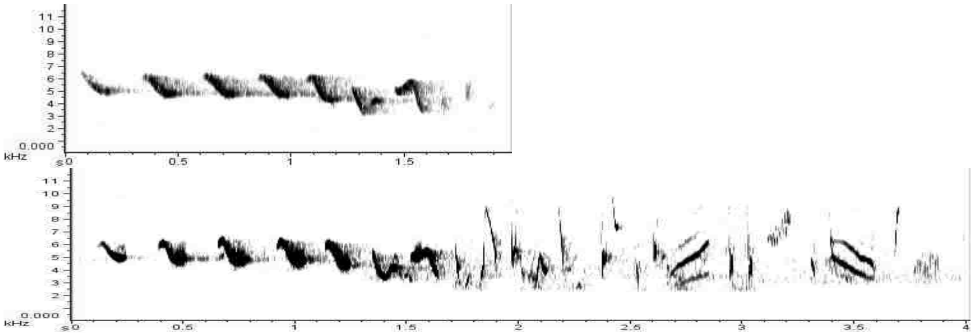
Focal Male "S"



Focal Male "F"



Focal Male "A"



Chapter 4:

Leaf-pulling by Louisiana Waterthrushes: prey availability due to a unique foraging maneuver in a stream environment

Abstract

Leaves and leaf packs create patches of habitat and refugia for aquatic invertebrates in streams. The Louisiana Waterthrush is an obligate riparian species that forages in streams by wading no deeper than 2 cm, pulling isolated leaves or leaves in leaf packs from the water, flipping them over, and searching for invertebrate prey. My objective was to simulate this foraging maneuver to determine density, biomass, and assemblage of prey associated with isolated leaves and leaves in top layers of packs, according to their position in the stream. Twenty-three Waterthrush territories were mapped, and one adjoining riffle and pool within each was sampled. From those, 20 isolated leaves and the first five leaves from five leaf packs were pulled from edges of riffles, centers of riffles no deeper than 2 cm, and from edges of adjoining pools. A total of 1,725 samples were taken from 23 territories. From those, invertebrates were found associated with 704 samples. A total of 4,933 organisms were collected from leaves and leaf packs within the 23 territories on three streams. Two representative subsamples were then randomly chosen from each territory, position, and configuration of leaves. In addition, three territories, on representing each stream at a similar distance had all samples analyzed. Of the subsamples, 2,878 organisms were identified. The greatest density of prey was found within centers of riffles in packs of leaves (F =17.13, df = 2 and 138, P = <0.0001). Overall, the greatest biomass, not including gastropods and tipulids, was found in centers of riffles (F = 4.95, df = 2 and 322, P = 0.01). Differences in biomass, density, and distribution of taxa occurred among territories with different degrees of nutrient and sediment input. An optimally foraging Louisiana Waterthrush would be more successful pulling leaves from packs in centers of shallow riffles in healthy stream reaches within constraints of nutrient availability of prey and the potential of its own predation. In more polluted reaches success of foraging by leaf-pulling should correlate foraging choices with the ubiquitous nature of pollution-tolerant taxa and facultative taxa seeking refuge across multiple areas of the stream environment.

Keywords: Louisiana Waterthrush, *Parkesia motacilla,* foraging behavior, obligate riparian songbird, invertebrate prey, leaf packs

Introduction

Louisiana Waterthrushes, *Parkesia Motacilla*, depend upon clear, fast-flowing, forest streams (Prosser and Brooks 1998) where they feed primarily upon invertebrates taken within the stream channel (Robinson 1990, 1995, Master and Mulvihill 2009). Analysis of stomach contents (Eaton 1958) and observation (Craig 1984, 1987) indicate prey include trichopterans, dipterans, ephemeropterans, oligochaetes, chironomids, stratiomyiids, tipulids, coleopterans, hemipterans, neuropterans, plecopterans, diplopods, and isopods. They have also been reported to prey upon odonate nymphs, dytiscid beetle larvae, cicadas, spiders, scorpions, crustaceans, earthworms, and salamanders (Bent 1953, Mulvihill et al. 2008, Mattsson et al. 2009). In addition, they have been seen feeding upon small fish and decapods (Pers. Obs.). Craig (1984) reported that Louisiana Waterthrushes prey-handle trichopterans by pulling them from their cases. He found that large centipedes were prey-handled up to 3 min by beating them against the ground. In addition he found that the birds show preference for ephemeropterans, trichopterans, and dipterans, and avoid isopods. Their presence has been found to correspond to riffle habitat, biomass availability of invertebrate prey, and relative abundances of Ephemeroptera, Plecoptera, and Trichoptera (Stucker 2000, Mattsson 2006, Mulvihill et al. 2008) that are more commonly found within healthy stream reaches and riffle habitats (Brussock et al. 1985, Smith 1986, Brown and Brussock 1991, Kobayashi and Kagaya 2002, Roy et al. 2003).

Louisiana Waterthrushes forage by opportunistically gleaning (removing prey with bill from foliage, twigs, or bark while perched), hawking (flying rapidly from perch to capture prey in bill opportunistically), hovering (flying from perch or ground to remove prey item from substrate while hovering, seen when birds take prey from the surface of deep water or when gleaning insects from foliage too high to reach when perched), leaf-pulling (picking up or pulling a leaf from the leaf litter, or more commonly from water, and turning it over to search its underside for prey), and picking (short rapid thrust of the bill directed to the water, ground, or foliage) (Craig 1981, Robinson 1990, Master and Mulvihill 2009). Of these, picks and leaf-pulling were most commonly employed (Craig 1981, Robinson 1990) with picks being used more frequently (Robinson 1990, Master and Mulvihill 2009). These methods were directed at both water ($\leq$ 2cm depth) and ground, though water was used more frequently prior to incubation (Robinson 1990). Leaf-pulling was used most frequently prior to leaf-out (Craig 1984) and prior to incubation (Robinson 1990). In Minnesota, streams that support Louisiana Waterthrush populations tend to have significantly more edge, riffle habitat and rockier areas within the stream compared to streams that do not support Louisiana Waterthrush populations (Stucker 2000). A predominance of these habitats and rocks within the stream would increase the number of shallow foraging areas. Both Craig (1984) and Robinson (1990) focused their efforts on the study of prey taken as the result of picking, and little is known concerning what is taken as a result of leaf-pulling.

Headwater streams (1st and 2nd order) of the Buffalo National River lie within the Boston Mountain Ozark Plateau, which is characterized by sharp vertical relief in erosional karst topography. Streams begin on hillsides in oak-hickory forests and steeply descend to the river through riparian corridors (Smith 1977, Sagers and Lyon 1997). North-facing slopes are characterized by Carolina beech (*Fagus grandifola*), mockernut hickory (*Carya tomentosa*), and sweet gum (*Liquidambar stryaciflua*). South-facing slopes are characterized by post oak (*Quercus stellata*), and black hickory (*Carya texana*). White oak (*Quercus alba*), shagbark hickory (*Carya ovata*), and sugar maple (*Acer saccharum*) occur on both slopes. Leaves of these deciduous trees fall into streams and are carried along by current until lodged along edges of riffles and pools and within shallow areas of riffles. As a result of their shape and flexibility and the velocity of water, they often form tightly compacted layers referred to as leaf packs. The isolated leaves and leaf packs create patches within the stream environment that provide food and refugia for bacterial and fungal decomposers and, consequently, for invertebrates known as shredders that feed upon leaves and their microbial colonists. In addition, invertebrates find refuge from predators and stream flow by associating themselves with leaves and leaf packs (Pringle et al. 1988, Palmer et al. 2000, Kobayashi and Kagaya 2004). Arrangement of patches, such as those created by leaves in the stream landscape, is thought to affect the number of invertebrates associated with them (Palmer 1995, Palmer et al. 1996, Murphy et al. 1998, Lancaster 2000, Palmer et al. 2000, Silver et al. 2000). Greater density, biomass, and faunal richness of invertebrates have been associated with riffles as opposed to pools (Brussock et al. 1985, Smith 1986, Brown and Brussock 1991, Kobayashi and Kagaya 2002, Roy et al. 2003).

An additional constraint upon assemblage of invertebrate taxa is summer-seasonal conditions and drought that result in decreases in flow. As the season progresses from spring to summer, reaches of streams begin to dry to isolated pools. These intermittent reaches have been reported to have a lower density and diversity of invertebrates (Brown and Brussock 1991). A comparison of perennial and intermittent streams in the headwaters of the Buffalo National River showed a distinct difference in community structure between the two types (Dick 1998). Timing and degree of intermittency differ from year to year with precipitation, temperature, and evapotranspiration (Delucchi 1988, Feminella 1996, Dick 1998, Magoulick 2000). Species found in reaches that become intermittent are thought to have adapted shorter life histories or diapause (Brown and Brussock 1991) or have the ability to find refuge within the hyporheic zone (Feminella 1996).

Lastly, anthropogenic disturbances affect density, mass, and assemblage of aquatic invertebrates. The watershed of the Buffalo National River is largely unprotected (Mott and Laurans 2004). Only 39 % is protected by state and federal authorities. The remaining 61%, unprotected and mismanaged in private ownership, has resulted in an increasing trend of degraded water quality (Scott and Hofer 1995, Mott and Laurans 2004). Anthropogenic land-use changes within the Buffalo National River's watershed include gravel mining and construction and use of dirt and gravel roads through streams (Mott and Laurans 2004). These activities result in increased sediment load with storm runoff and habitat destruction to tributary streams and the river itself (Mott and Laurans 2004). Agricultural practices that involve the removal of forests for establishment of pasture have been denoted as the greatest threat to water quality (Mott and Steele 1991, Scott and Hofer 1995, Mott and Laurans 2004). The removal of forested land allows for greater amounts of sediment to enter streams during rain events. In addition, cattle are commonly allowed access to watering along lengths of streams (Weeks 1987, Holleman 1992). These places are known as 'sacrifice areas' and become filthy from trampling, urination, and defecation by herds of cattle on banks and in water (Braun 1986, Weeks 1987). In addition, pastures are fertilized through the application of chicken manure (Holleman 1992). Together watering holes and fertilization of pasture result in high concentrations of nutrients and fecal coliform bacteria in watershed streams and the river (Dale et al. 1978, Weeks 1987, Mott and Steele 1991, Mott and Laurans 2004). Increased sedimentation of streams, addition of nutrients, fecal coliform bacteria, and increased sunlight alter stream habitat and affect suitability of habitat for aquatic invertebrates (Mathis 1990, Wood and Armitage 1997, Roy et al. 2003, Suberkropp et al. 2010).

Riffle habitat and its associated taxa are particularly sensitive to sedimentation. Sedimentation occurs when fine particles fill the interstices between cobbles in a riffle. This results in reduction and destruction of riffle habitat (Wood and Armitage 1997). Different habitats within the stream, i.e. riffles, pools, and banks, contain different assemblages of aquatic insects. Some are obligate species to any one of these habitats, while others are facultative and capable of living in multiple habitats. Different habitats and taxa are affected differently by increased sedimentation and non-point source pollution (Roy et al. 2003). Facultative taxa commonly associated with riffles are capable of moving into bank habitat as refuge, while obligate taxa are lost from riffle assemblages. Shifts in distribution of taxa from riffles to banks may prove to be an important early indicator of degradation of stream habitat (Roy et al. 2003).

My objective was to simulate the foraging maneuver of leaf-pulling by Louisiana Waterthrushes by pulling isolated leaves from the stream and the first five leaves from tops of leaf packs to determine density, biomass, and assemblage of potential invertebrate prey. Prey associated with an isolated leaf was compared to prey associated with the top five leaves of leaf packs. I also compared potential prey among three places where foraging occurs, i.e. edges of riffles, centers of riffles, and edges of pools. Lastly, I made comparisons of potential prey among Louisiana Waterthrush territories on three streams with varying degrees of anthropogenic disturbance.

Site Description

Three 1st and 2nd order headwater streams were chosen for study in Newton County, Arkansas, within the upper Buffalo National River watershed: Adds, Leatherwood, and Steele creeks (Fig. 4.1). Adds Creek and Leatherwood Creek empty into the Buffalo National River at the Ponca low-water bridge. Leatherwood Creek runs north and Adds Creek south. Leatherwood Creek is a relatively pristine stream with the majority of its drainage within the park. It begins at altitudes of 610 m and descends 305 m to the river in a distance of approximately 4 km. The reach of Leatherwood Creek studied descends from 490 m to 310 m over a distance of 3 km. Upstream 1.9 km from its confluence with the Buffalo National River and at an elevation of 420 m, Leatherwood Creek becomes losing stream over a distance of approximately 345 m to an elevation of 463 m. Adds Creek begins at 671 m and descends 311 m, over a distance of 5.74 km. It flows through the small town of Ponca, AR for a distance of approximately 1.75 km, then through the National Park for another .5 km before entering the river. The reach of Adds Creek studied descends from 428 m to 308 m over a distance of 4.1 km. Steele Creek empties from the north into the Buffalo River downstream of the Steele Creek campground. It is characterized by moving through approximately 5 km or more gently sloping terrain (a descent of 244 m). The studied reach of Steele Creek descends from an elevation of 342 m to 298 m over a distance of 3.1 km. At least half of Steele Creek's drainage is in private lands containing many gravel roads and an increased human occupancy. All three streams lie within remnant beech, oak, and hickory forests.

Methods

Twenty-three linear Louisiana Waterthrush territories were mapped on three streams within the watershed of the upper Buffalo National River for a total of 9.8 km of stream reach. Territorial boundaries were determined according to song perches and frequent aggressive interactions at territorial boundaries between males. A preliminary observational study was completed prior to sampling to give an indication of the best sampling method to imitate the leaf-pulling maneuver used by Louisiana Waterthrushes. Birds were observed foraging in shallow water at the centers of riffles, edges of riffles, and edges of pools. As they walked along the stream they pulled leaves that were lying singly in the stream environment and also pulled multiple leaves from leaf packs one leaf at a time. In both cases, they would flip over each leaf and rapidly search its underside as well as the water that had been disturbed by moving the leaf.

Within each territory, one corresponding riffle-pool complex was randomly chosen and sampled. Sampling began on 12 April 2007 and extended through 24 April 2007. This timing precluded any high-water events that would have swept the stream free of isolated leaves and leaf packs. Choice of order in which territories were to be sampled was randomly determined.

Individual leaves and five leaves from the top of five leaf packs were removed from the stream in a manner simulating the leaf-pulling foraging maneuver of the Louisiana Waterthrush. Twenty isolated leaves and five leaves from the top of five packs were removed from the edge of riffle, the edge of a pool, and the center of a riffle, from water no deeper than 2 cm. An aquarium dip-net (12.5 cm width, 9.5 cm length, depth 11 cm, mesh size 0.2 mm) was held slightly downstream from the leaves removed to capture any potential prey that were dislodged by the movement. Upon removal, leaves and their associated taxa were placed in cylinders and a 70% ethanol solution was added. The samples were transported to the laboratory where leaves were rinsed and handpicked. A total of 1,725 samples were taken from 23 territories. From those, invertebrates were found associated with 704 samples. The number of insects within each of these samples was counted.

Two samples were randomly chosen from each territory, position and configuration of leaves; i.e., invertebrates, associated with isolated leaves from the edges of riffles, edges of pools, and from the center of riffles and with five leaves from leaf packs at the edges of riffles, edges of pools, and the center of riffles. In addition, three territories, one representing each stream at a similar distance, i.e. the second or third territory from the river, had all samples analyzed for a project conducted by an undergraduate researcher. They were identified and weighed as follows.

Invertebrates were identified to the lowest taxon possible (Merritt and Cummins 1996). Terrestrial adults, primarily emerging aquatic insects, were included in biomass and number calculations. Biomass measurements were attained by placing aquatic invertebrates in a 50-degree Celsius oven and drying them to a constant dry weight for no less than 24 hours. Large tipulid larvae were dried for no less than 72 hours. Gastropods were weighed with shell intact after no less than 72 hours. All invertebrates were measured in μgs with a Sartorius SC-2 microbalance**.** Biomass of invertebrates used for vouchers were measured by calculation of length-mass regressions (Sample et al. 1993, Benke et al. 1999). Total biomass of invertebrates within each treatment combination, territory, position and configuration of leaves were summed.

Statistical design was a three-factor factorial (stream × position × leaf configuration) with territory nested within stream. All factors were treated as fixed effects. Data were subjected to Analysis of Variance (ANOVA) by SAS software, Version 9.2 (SAS Institute Inc., Cary, NC, USA). Least-squares means were used to determine differences where appropriate. In addition, density and biomass of invertebrates found associated with pack leaves was divided by number of leaves in a pack (5) and analyzed as above to allow for a comparison of invertebrates found per leaf. Assemblage of the most common taxa, Class Gastropoda, and Orders Isopoda, Coleoptera, Diptera, Ephemeroptera, Plecoptera, and Trichoptera, were compared using Chi-Square tests for equality of distributions across streams, territories, and positions. Differences were considered significant at $P = 0.05$ or less.

Results

Assemblage

A total of 4,933 organisms were collected from leaves and leaf packs within the 23 territories on three streams. Of those, 2,878 organisms were identified (Appendix 1). Five phyla were represented in the collection: Phylum Annelida, Arthropoda, Chordata, Mollusca, and Nematoda.

Significant differences in the distributions were found when comparing the most common taxa, gastropods, isopods, coleopterans, dipterans, ephemeropterans, tricopterans, and plecopterans, among streams ($\chi 2 = 390.2$, df=12, $P = <0.0001$). Adds Creek and Steele Creek had similar numbers of gastropods while Leatherwood Creek was nearly lacking the taxa. Steele Creek had more ephemeropterans. Leatherwood Creek and Steele Creek supported more trichopterans than Adds Creek. Leatherwood Creek tended to have more Coleoptera than the other two streams. However, taxa were not always equally distributed across territories.

Significant differences were found in the frequency distributions of the seven most common taxa among territories ($\chi 2 = 1688.7$, df = 132, $P = <0.0001$) and positions within territories ($\chi 2 = 403.3$, df = 12, $P = <0.0001$). Territories on Steele Creek suffering from increased amounts of sediment and nutrients due to cattle pastured and allowed access to ‘watering holes’ had greater abundances of ephemeropterans and plecopterans at the edges of pools and riffles than all other territories. Of the Ephemeroptera in these territories, Family Leptophlebiidae was most common. This Family was also found in other cases where ephemeropterans were found at the edges of pools. Though Diptera tended to be most abundant at the centers of riffles, in the most degraded of the Steele Creek territories, they, like the Ephemeroptera, were more abundant at edges. In the upstream-most territory of Leatherwood the reach is very different from all other territories in that it is a bedrock-boulder debris-regulated reach. There were fewer taxa found within it overall except for a large number of isopods in the Family Asellidae. Leatherwood Creek was also different from the other two creeks in that there is nearly 100% canopy cover throughout. It contained a greater variety of taxa within Order Trichoptera. Few Trichoptera were found in Adds Creek. In Steele Creek, although Trichoptera were similar in abundance to Leatherwood Creek, there was less diversity. When Trichoptera were present, they were nearly always associated with riffles. Coleoptera were also greatest in density and diversity within Leatherwood Creek and were nearly always associated with the edges of riffles and pools.

Density

A significant interaction was found when comparing density of invertebrate prey associated with configurations of leaves and their positions within the stream (F =17.13, df = 2 and 138, P = <0.0001). More invertebrates were associated with leaves in packs than with isolated leaves, and pack leaves at centers of riffles had significantly more invertebrates compared to pack leaves in edges of riffles (Fig. 4.2). Pack leaves at edges of pools had significantly fewer invertebrates associated with them than packs found at the edges and centers of riffles. There were no significant differences found in density of invertebrates associated with isolated leaves regardless of their position.

In addition, there was a significant interaction between territories and configurations of leaves (F =2.25, df = 20 and 138, P = <0.01). In all territories pack leaves held significantly more invertebrate prey than isolated leaves, but there were significant differences among territories. These differences were sometimes, but not always, driven by the inclusion of chironomids which tend to be small and numerous. Two territories on Adds Creek were among four (Fig. 4.1) with the greatest density of invertebrates found in pack leaves. Significant differences in density were often seen when comparing one territory to the next linearly along a stream. Therefore, even though territories graded into one another linearly along the stream, density of invertebrates in territories adjacent to one another was not always similar (Table 4.1).

The uppermost Adds Creek territory was characterized by having a large number of chironomids, nearly twice that of other territories, while the territory furthest downstream, and thus nearest the confluence with the river, was driven by both a high percentage of chironomids and pulmonate gastropods. As with Adds Creek, The territory on Leatherwood Creek with the greatest density was the one nearest the stream's confluence with the river and was similar in having a higher percentage of chironomids than its other five territories. The two territories on Steele Creek nearest the river also had significantly higher densities of potential prey compared to its other territories. There, density was not a result of chironomids, but of Ephemeroptera, Plecoptera, and Trichoptera.

Division of Density

When numbers of potential prey associated with packs were divided to account for there being five leaves in every pack sample compared to samples taken from isolated leaves, there continued to be significant differences in density between the two configurations with most invertebrates found with a single leaf taken from a pack. An interaction was found between territories and number of invertebrates associated with isolated leaves compared to leaves associated with packs (F =2.18, df = 20 and 138, P = <0.02). Also, there was a significant interaction of territories in their density of potential prey and the position of leaves within the stream (F =1.93, df = 40 and 138, P = <0.02).

In 12 of 23 territories, despite reduction by a fifth, there continued to be significantly more prey available per leaf when a leaf was taken from a pack (Fig. 4.4). In no territory was there significantly more prey associated with an isolated leaf. Differences in territories were similar to those found without division of density in pack leaves. Steele Creek and Leatherwood Creek tended to have higher densities of prey in pack leaves than Adds Creek and the four aforementioned territories had the greatest densities in them. In 11 of the 23 territories significantly more prey were associated with leaves taken from centers of riffles compared to those taken from the edges of riffles and pools (Fig. 4.5). In no case did another position yield significantly more prey than centers of riffles. In only four territories did the leaves taken from edges of riffles yield significantly more prey than those taken from the edges of pools, and in only one territory was there more prey found at the edge of a pool.

Biomass

Significant interactions were found between the three streams sampled and their associated biomass within different configurations of leaves (*F* =3.72, df = 2 and 322, *P* = 0.03). Leaves associated with packs had greater biomass in Steele Creek compared to Leatherwood Creek and Adds Creek. Significant differences were also found when comparing territories (*F* = 1.75, df = 20 and 322, *P* = 0.03). Four of the 23 had significantly higher biomass of invertebrates overall compared to others (Fig. 4.6). The two with greatest biomass, the second territory on Adds Creek and the seventh territory on Steele Creek, were driven by a predominance of gastropods and habitat where canopy cover was removed and a water hole was formed where cattle herds often stood defecating and urinating within the stream. The mass of gastropods across all areas of the stream environment (Table 4.2) overwhelmed differences in biomass associated with position at centers of riffles, edges of riffles, and edges of pools (*F* = 1.34, df = 40 and 322, *P* = 0.09).

Excluding biomass of gastropods from analysis resulted in significant differences being found with the interaction of the three streams being sampled, the position of leaves in the stream environment, and configuration of leaves as either isolated or in packs (*F* = 3.70, df = 4 and 322, *P* = 0.01). Overall, the greatest biomass of invertebrates was associated with leaves in packs and within the center of a riffle. Steele Creek had a significantly higher biomass associated with pack leaves taken from the center of riffles compared to all other streams and configurations of leaves (Fig. 4.7). Otherwise, there were no significant differences within Steele Creek among positions and configurations. Leatherwood Creek showed significant differences with the greatest biomass of invertebrates associated with centers of riffles and packs of leaves compared to all configurations in Steele Creek other than the centers of riffles and to four of the six positions and configurations within Adds Creek. Unlike Steele Creek and Adds Creek, Leatherwood Creek showed a tendency in all cases for configurations of leaves within the stream to have a greater biomass of aquatic invertebrates associated with packs. Adds Creek had the greatest mass of invertebrates in packs in the centers of riffles and also in packs at the edges of pools.

A total of 18 tipulid larvae, varying in mass from .002 mg to 7.63 mg, were found in samples from all three streams. Steele Creek had the greatest mass with 7 individuals totaling 31.18 mg. Five of the seven were found within its second territory, in the center of a riffle, within packs of leaves. Leatherwood Creek was similar in having seven individuals totaling 15.49 mg all found within packs of leaves. Five were found within the third territory with two at the center of a riffle, two at the edge of a riffle, and one at the edge of a pool. Adds Creek had the fewest individuals, 4, and the lowest mass, 8.27 mg. It was unusual in that one relatively large tipulid, 2.62 mg, was found associated with an isolated leaf.

Excluding the mass of tipulid larvae from analysis, there continued to be a significant interaction with positions and configuration of leaves and the stream from which they were taken (*F* = 3.10, df = 4 and 322, *P* = 0.02). Steele Creek again showed significantly greater biomass associated with leaves in packs taken from centers of riffles (Fig.4.8). Leatherwood Creek showed more pronounced differences in biomass of invertebrates associated with leaves from packs compared to isolated leaves regardless of their position within the stream. Adds Creek had a greater biomass of invertebrates associated with leaves in packs at the edges of pools.

Division of Biomass

When biomass of invertebrates was divided by number of leaves removed from packs and compared to biomass of invertebrates found when removing an isolated leaf from the stream, significant differences were found among territories (Fig. 4.9) with a significant interaction between territories and configurations of leaves (*F* =1.93, df = 20 and 322, *P* = 0.01). Three territories showed significant differences in the biomass associated with isolated leaves versus one leaf taken from a pack. In the second and fourth territories of Adds Creek and the third territory of Steele Creek isolated leaves had a higher mass of invertebrates associated with them than did a leaf taken from a pack. This was driven in the second territory of Adds Creek by two large (22.63 mg) gastropods, in the fourth territory of Adds Creek it was also driven by two large (3.78mg) gastropods, and in the third territory of Steele Creek it was driven by three gastropods (7.06 mg).

After exclusion of biomass of gastropods and division of biomass to account for five leaves in each pack, a significant difference was found with interaction of the streams being sampled, the positions of leaves in the stream environment and the configuration of leaves as either isolated or within a pack (*F* = 2.90, df = 4 and 322, *P* = 0.02). With division of mass of invertebrates in packs by five and subsequent analysis there was no longer a clear difference seen between mass of invertebrates in packs and those associated with isolated leaves (Fig. 4.10), but, as with exclusion of gastropods, significant differences could be seen among different positions within the stream environment. As before, the centers of riffles tended, though not always significantly, to have a greater biomass of potential prey.

Excluding mass of tipulid larvae from analysis resulted in a significant difference in biomass of potential prey according to the positions of leaves taken from the stream ($F = 4.95$, df = 2 and 322, $P = 0.01$). Leaves within the centers of riffles held a significantly greater biomass of potential prey than edges of riffles and pools (Fig. 4.11). Differences in biomass of prey at edges of riffles and pools were not significant from one another, but neared significance.

Discussion

Simulating the foraging maneuver of leaf-pulling by Louisiana Waterthrush, I found that a greater density of potential invertebrate prey were found significantly more often associated with the top five leaves of leaf packs positioned within centers of riffles. This remained true when making comparisons between an isolated leaf and a single leaf from a pack. A greater biomass of potential prey was also found significantly more often in leaf packs within centers of riffles, but unlike prey density, biomass was not always greater when comparisons were made between an isolated leaf and a single leaf from a pack. However, it should be taken into consideration that analysis of density included a greater sample size and analysis of mass was a subsample taken from the samples used for density. Also my samples were stored in a 70% ethanol solution. Alcohol preservation affects mass by dissolving fats of different taxa to different degrees (Howmiller 1972, Stanford 1972, Dermott and Patterson 1974, Donald and Patterson 1977, Leuven et al. 1985, Wetzel et al. 2005). Because different taxa respond differently to preservation my results may be biased against those taxa which lose greater biomass with preservation. Unfortunately, correction factors do not exist for many taxa and thus, I made no effort to correct for only a percentage of the collection. In addition, caution should be used when comparing my mass estimates to those of other studies.

Differences in taxa occurred among the different positions of leaves and leaf packs within the stream environment with some taxa found more often associated with centers and edges of riffles and others more often associated with edges of riffles and pools. Differences in assemblage, density, and biomass were also found among Louisiana Waterthrush territories. Those territories suffering from anthropogenic degradation through sedimentation, increased nutrient input, and increased sunlight supported different densities of taxa and lacked others compared to less degraded territories. The physical characteristics of pollution-tolerant taxa affected biomass estimates for territories such that the degraded territories sometimes showed greater biomass.

To optimize foraging success, which is measured as energy gained and lost through foraging (Schoener 1971, Krebs 1973, Pyke et al. 1977), early in the breeding season, using the foraging maneuver of leaf-pulling, a Louisiana Waterthrush will find a greater density of potential invertebrate prey if it forages within packs of leaves at centers of shallow riffles. Thus, optimal foraging theory (Schoener 1971, Smith and Dawkins 1971, Charnov 1976, Pyke et al. 1977) suggests that Louisiana Waterthrushes may forage more efficiently and successfully within these central patches in the stream environment compared to edges of riffles and pools. Foraging success and efficiency may be increased by the bird remaining within the center of a riffle up to a point (Krebs et al. 1974, Charnov 1976), pulling multiple leaves from a single pack, and searching the nearest available sources of possible prey (Robinson and Holmes 1982). However, constraints exist, such as nutrient availability, toxicity, and the possibility of predation upon the forager (Schoener 1971, Curio 1976, Pyke et al. 1977, Werner et al. 1983, Stephens and Krebs 1986).

Adult Louisiana Waterthrushes are preyed upon by accipiters such as the sharp-shinned hawk, *Accipiter striatus*, (Mattsson et al. 2009) and small buteos, such as the broad-winged hawk, *Buteo platypterus* (Pers. Obs.). A bird foraging within the center of a riffle is likely to be more obvious to these predators. In addition, centers of riffles are further from the safety of cover found at edges of the stream channel. Waterthrushes, like many other species of birds that are adapted to a stream habitat, teeter (Orenstein 1975, Casperson 1999). As a Louisiana Waterthrush forages within the stream among the cobbles of a riffle, teetering movements and flashes of contrasting white plumage of the white belly, flanks, and under-tail coverts tend to blend with the background of flashing water tumbling over cobbles in riffles. Thus, the function of teetering may include prey defense through mimicry of water in the foraging habitat.

Preference for certain prey types may also affect the time spent foraging within different areas. Craig (1984) reported that, although Louisiana Waterthrushes have a wide range of diet, they show preference for ephemeropterans, trichopterans, and dipterans. In addition, Louisiana Waterthrush presence has been found to correspond to riffle habitat and relative abundances of Ephemeroptera, Plecoptera, and Trichoptera (Stucker 2000, Mattsson 2006, Mulvihill et al. 2008) that are more commonly found within healthy stream reaches in riffle habitat (Brussock et al. 1985, Smith 1986, Brown and Brussock 1991, Kobayashi and Kagaya 2002, Roy et al. 2003). My study found Trichoptera and Plecoptera more often among centers of shallow riffles, followed by edges of riffles, indicating increased potential of these areas as Louisiana Waterthrush foraging sites.

Louisiana Waterthrushes have been reported to spend different percentages of their time in different positions within the stream channel depending upon the stream. In northeastern Pennsylvania, where streams were deeper, a greater percentage of time was spent foraging on edges of banks (Master and Mulvihill 2009), while, conversely, in southwestern Pennsylvania, where streams were more shallow, birds spent a greater percentage of time foraging within the stream (Master and Mulvihill 2009). In addition, Stucker (2000) found that birds require riffles and rockier streams that create shallower areas for foraging. The amount of shallow or rocky habitat within streams has been incorporated into indices pertaining to accessibility of foraging microhabitat for Louisiana Waterthrushes relative to water surface, depth of the water, and exposed submerged rocks and large woody debris (Master et al. 2005).

The availability of nutrients (Pulliam 1975) may also constrain a foraging Louisiana Waterthrush to certain taxa and thus affect the percentage of time it spends foraging in different areas of the stream. Ephemeroptera, Plecoptera, and Trichoptera may be higher quality food resources than other taxa. Mulvihill et al. (2008) found that shortages of these prey on acidified streams correlated to smaller clutch sizes and smaller nestlings, though availability of calcium as a result of acidification was a confounding factor. Females may be particularly constrained by the availability of calcium in prey. Ormerod and Rundle (1998) state that female passerines along rivers rely upon crustaceans, mollusks, or fish fry for the calcium necessary for egg-forming because they are unable to gain sufficient calcium from feeding on insects.

A female Louisiana Waterthrush during periods of egg-laying may therefore show preference for gastropods. Territories on stream reaches with little canopy cover and/or a high degree of nutrient input had greater densities of pollution tolerant pulmonate gastropods evenly distributed across the stream environment. With greater degrees of sedimentation, fish fry may be reduced, and gastropods and crustaceans might become a more common prey item. As a result, foraging habits in these areas would differ when compared to foraging within areas of higher percentage canopy cover, less sediment, and less nutrient input. A foraging female might be particularly apt to be found more often in any one position in the stream environment compared to a foraging male.

The greater mass of a single tipulid larvae, compared to other potential prey, greatly biased biomass comparisons. If a tipulid was found in any one position, it quickly tipped the scale of greater mass to that area. A foraging Louisiana Waterthrush would also, energetically speaking, have the scale tipped in its favor after finding such a large prey item, assuming nutrient content correlated positively with size. There is a greater probability of finding large tipulid larvae within leaf packs in centers and edges of riffles and this may make these areas and pack leaves more attractive for foraging. However, it should be considered that a large prey item requires some energetic cost through prey-handling (Holling 1959). Waterthrushes, having found a large tipulid larva, carry it to the edge of the stream and beat it against a hard substrate prior to ingesting it, feeding it to a fledgling, or leaving to carry the food to nestlings (Pers. Obs.). There is also a caveat to a foraging bird finding abundant small prey items. For example, chironomids and early instars of ephemeropterans and plecopterans are often found in high densities among packs of leaves. When a bird has found a large number of such prey, it must make multiple foraging movements, picks, after leaf-pulling to make use of the prey available.

Optimal foraging theory and prey preference tend to place the Louisiana Waterthrush foraging within the center of riffles in healthy streams. Most EPT taxa are obligate to riffle habitats, the percentage of viable riffle found within a stream would correlate to increases in their density, biomass, and faunal richness and thus to an increase in Louisiana Waterthrushes foraging within the same places. On the other hand, reduction or destruction of riffle habitat results in decreased density and diversity within the riffle community (Waters 1995). Facultative taxa, which can move from riffle habitat to bank habitat for refuge, will do so when sedimentation increases and fills the interstices between cobbles in riffles (Roy et al. 2003). Thus, birds foraging within more degraded habitats may be found foraging more often at the edge of streams than at their center.

My results raise an important question and opportunity for future research with Louisiana Waterthrush. Can foraging habits of this species, with consideration of constraints of optimal foraging theory within territories on different stream reaches suffering different types of anthropogenic change, tell us something of the degree of movement of facultative prey to refugia, the loss of obligate prey, and the forced need for predation upon more ubiquitous and pollution-tolerant prey, and thus, give insight into the degree of a stream's degradation?

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Table 4.1. Density of total invertebrate prey found within each territory on three streams and percentages of common taxa that contributed to density

Territory	Creek	Total Density[a]	% EPT[b] Taxa	% Chironomid Taxa	% Gastropod Taxa
1	Leatherwood	148	29.05	49.32	0.00
2	Leatherwood	41	48.78	24.39	2.44
3	Leatherwood	212	33.02	20.28	0.00
4	Leatherwood	65	33.85	12.31	0.00
5	Leatherwood	104	11.54	49.04	0.00
6	Leatherwood	111	13.51	20.72	0.00
1	Steele	99	67.68	10.10	0.00
2	Steele	302	49.67	27.81	1.00
3	Steele	86	48.84	25.58	8.14
4	Steele	111	71.17	12.61	7.21
5	Steele	148	31.76	61.49	2.03
6	Steele	155	32.90	34.84	20.65
7	Steele	151	33.11	54.30	1.99
8	Steele	90	46.67	33.33	5.56
1	Adds	184	8.15	48.91	22.83
2	Adds	140	25.71	47.14	5.71
3	Adds	81	43.21	18.52	0.00
4	Adds	123	6.50	42.28	11.38
5	Adds	81	34.57	33.33	4.94
6	Adds	77	18.18	61.04	1.30
7	Adds	46	34.78	30.43	15.22
8	Adds	104	23.08	56.73	4.81
9	Adds	202	12.87	73.76	0.00

a = across all configurations and placements of leaves and leaf packs

b = Ephemeroptera, Plecoptera, and Trichoptera families

Table 4.2. Number of gastropods found associated with leaves in each of three streams according to their configuration, isolated = I, or in packs = P, and position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP

Creek	Leaf Position	Leaf Configuration	Number of Gastropods
Leatherwood	CR	Pack	0
Leatherwood	CR	Isolated	0
Leatherwood	EP	Pack	0
Leatherwood	EP	Isolated	2
Leatherwood	ER	Pack	0
Leatherwood	ER	Isolated	0
Steele	CR	Pack	4
Steele	CR	Isolated	5
Steele	EP	Pack	19
Steele	EP	Isolated	9
Steele	ER	Pack	13
Steele	ER	Isolated	16
Adds	CR	Pack	1
Adds	CR	Isolated	28
Adds	EP	Pack	15
Adds	EP	Isolated	6
Adds	ER	Pack	0
Adds	ER	Isolated	0

Figure 4.1. Study sites, Adds Creek, Leatherwood Creek, and Steele Creek, within the watershed of the upper Buffalo National River GPS Map detail = 500 m (Garmin Map Source 1999 – 2010, Version 6.15.11, Garmin LTD)

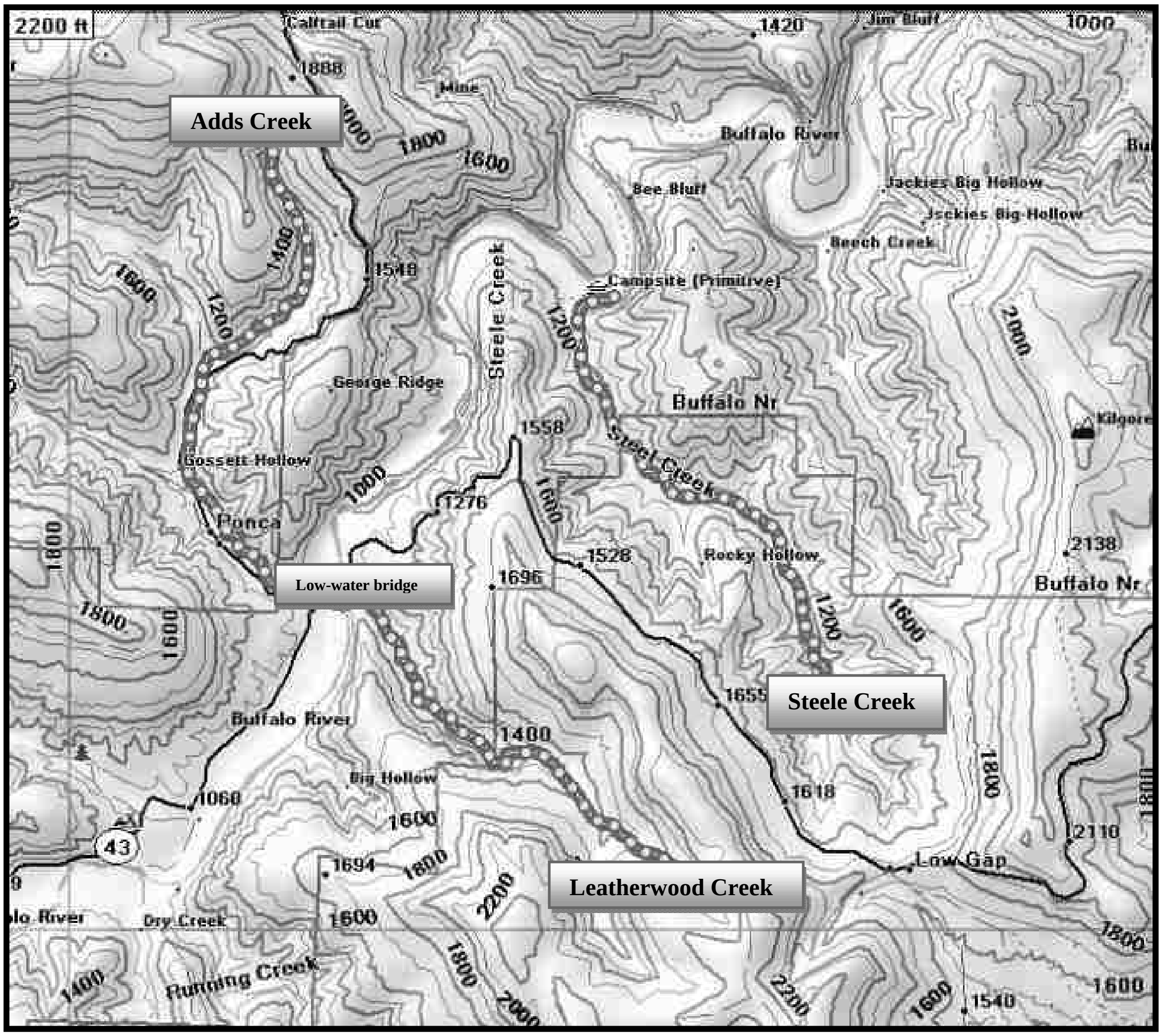


Figure 4.2. Least-squares means and SE of density of potential prey associated with leaves according to their configuration, isolated = I, or in packs = P, and their position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP

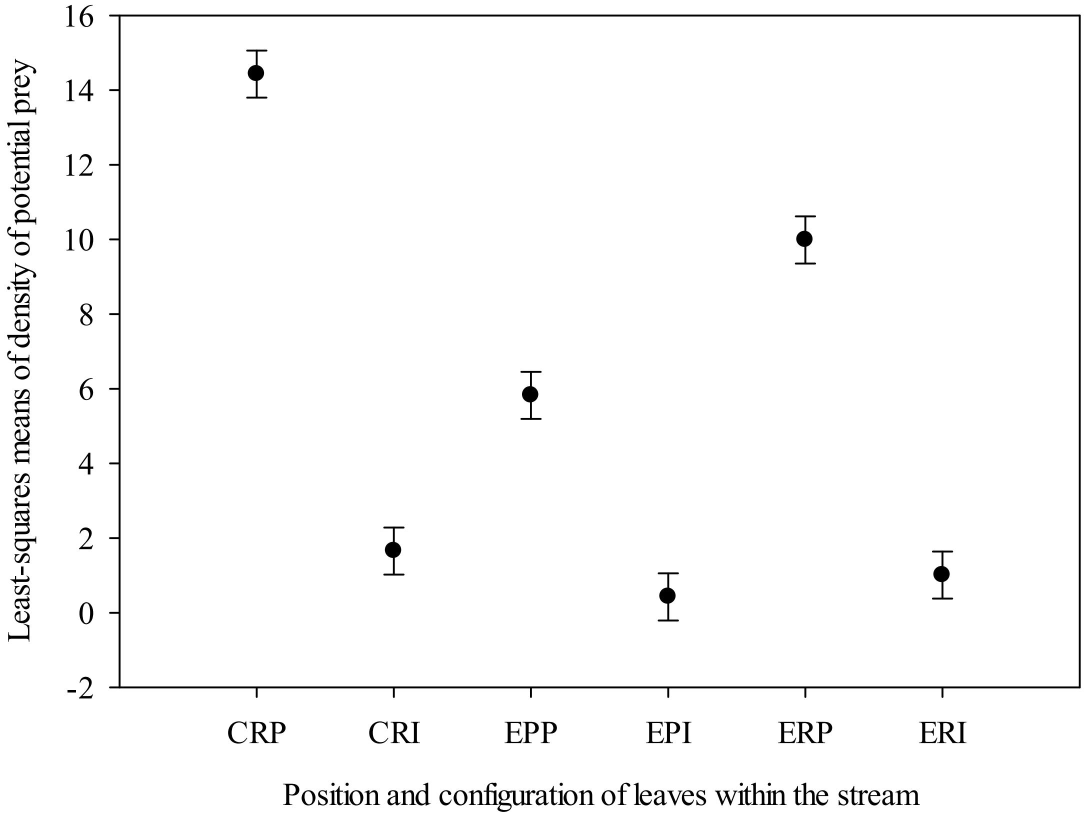


Figure 4.3. Least-squares means and SE of density of potential prey associated with leaves according to their configuration, isolated or in packs, within multiple territories on each of three streams, Adds Creek = A, Leatherwood Creek = L, or Steele Creek = S

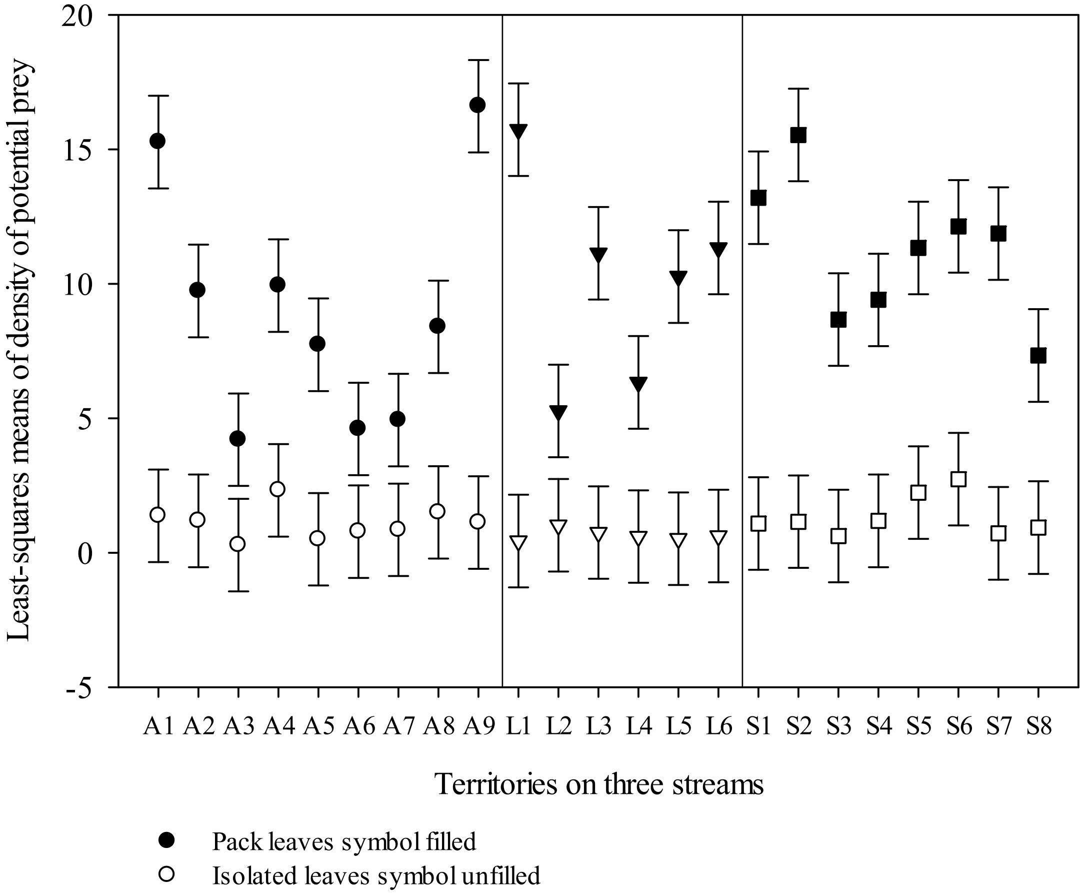


Figure 4.4. Least-squares means and SE of density of potential prey associated with leaves within multiple territories on each of three streams, Adds Creek = A, Leatherwood Creek = L, or Steele Creek = S, according to their configuration, isolated or in packs, with number of prey divided to account for multiple (5) leaves in packs

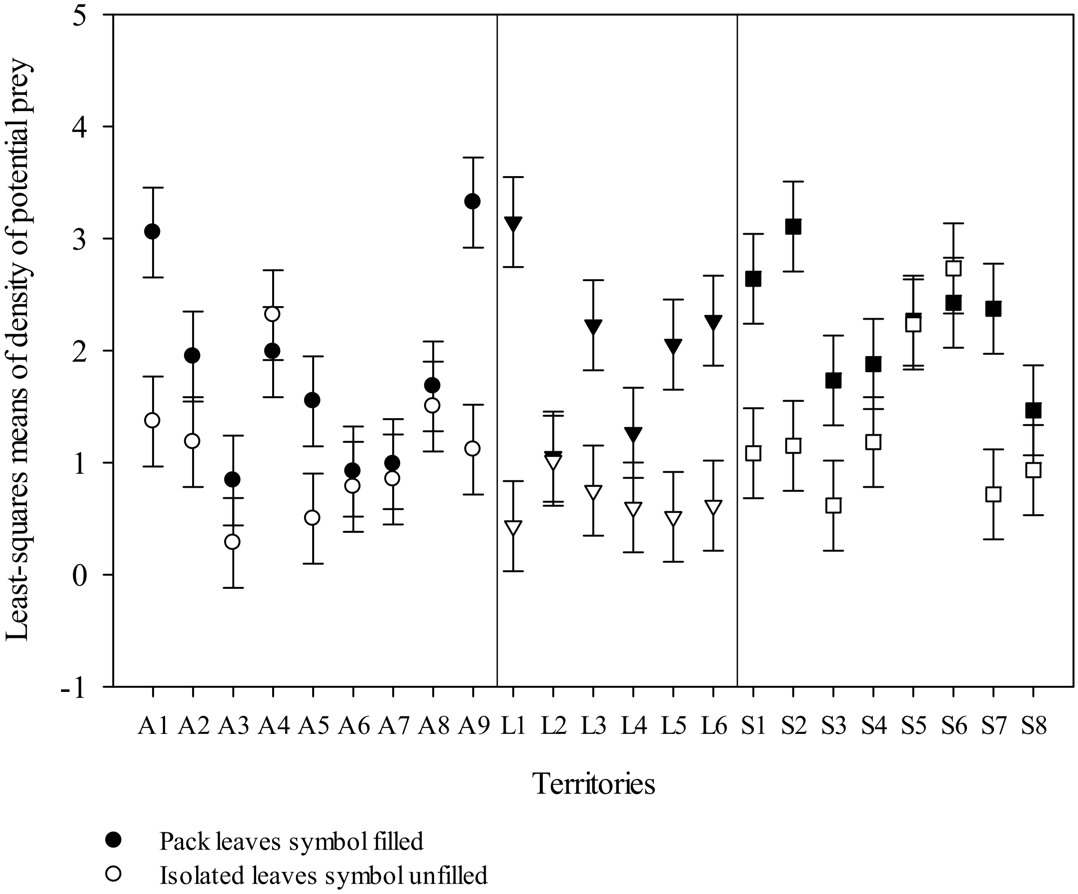


Figure 4.5. Least-squares means and SE of density of potential prey associated with leaves according to position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP, within multiple territories on three streams, Adds Creek = A, Leatherwood Creek = L, or Steele Creek = S, according to their configuration, isolated or in packs, with number of prey divided to account for multiple (5) leaves in packs

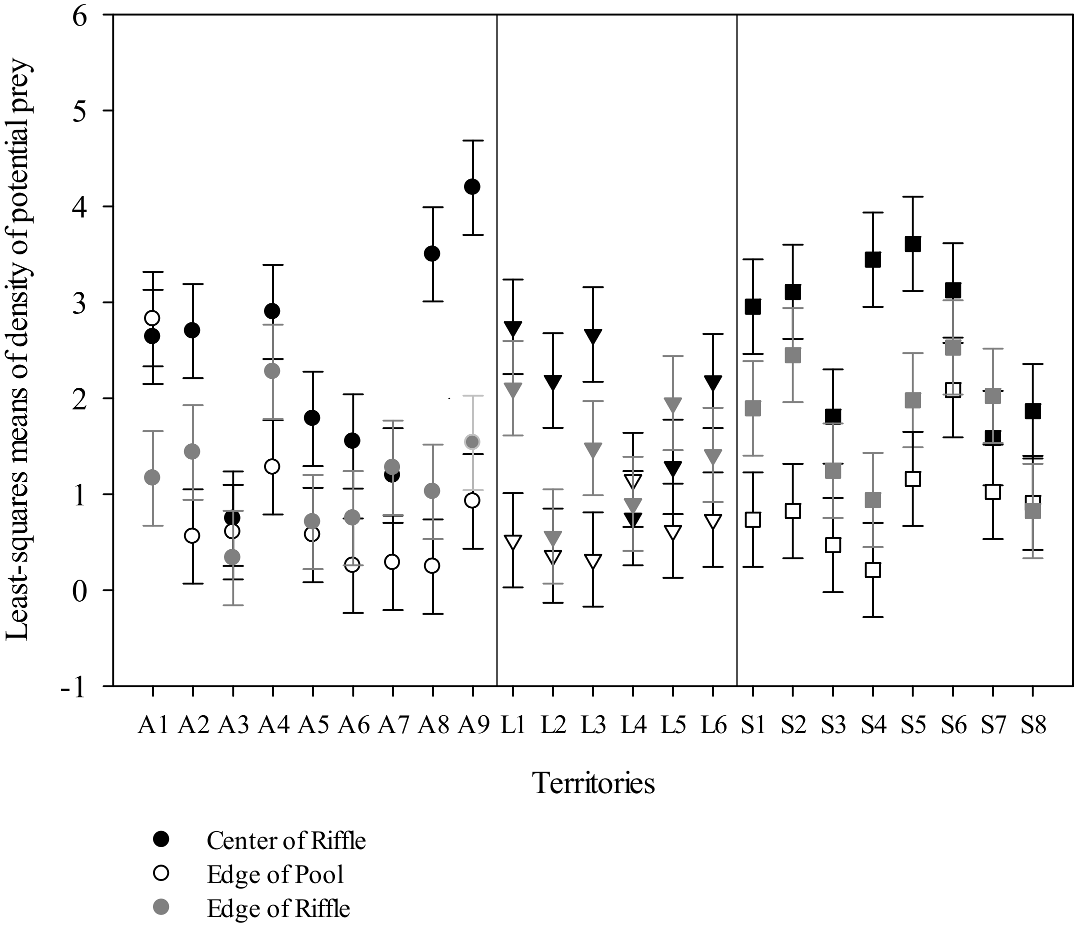


Figure 4.6. Least-squares means and SE of biomass (mg) of potential prey, including gastropods, associated with leaves within 23 Louisiana Waterthrush territories on three streams, Adds Creek = A, Leatherwood Creek = L, or Steele Creek = S

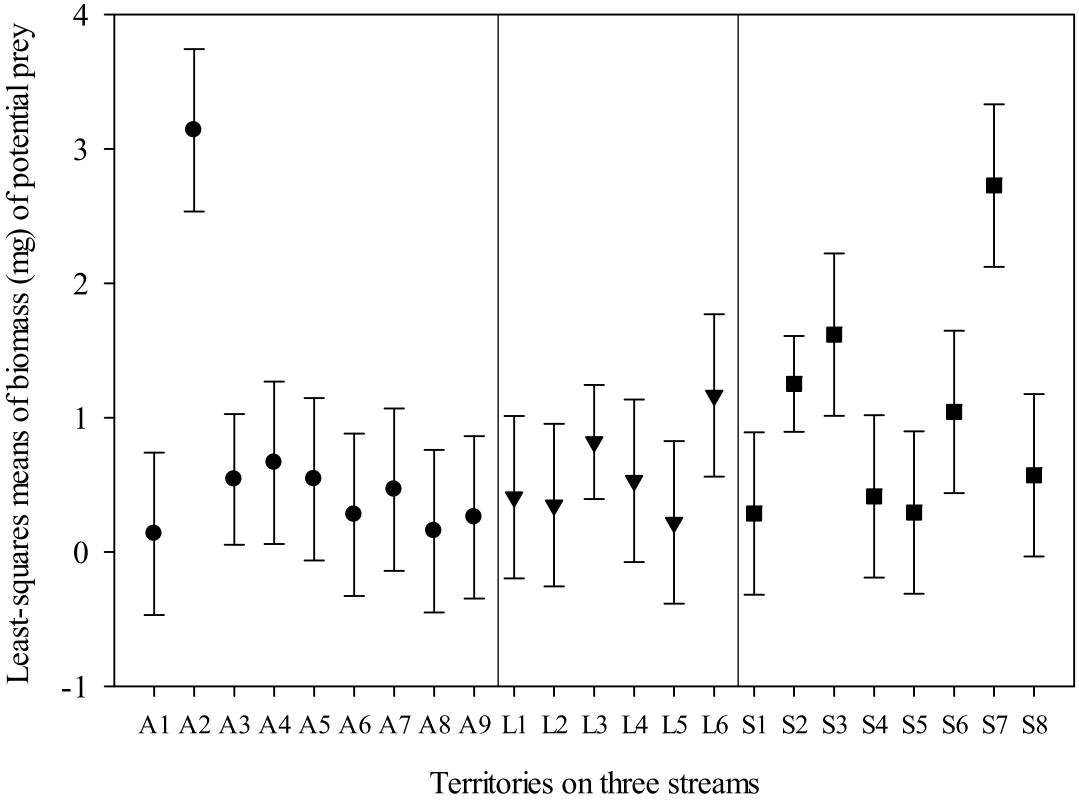


Figure 4.7. Least-squares means and SE of biomass (mg) of potential prey, excluding gastropods, in each of three streams, A=Adds Creek, L=Leatherwood Creek, S=Steele Creek, associated with leaves, according to their configuration, isolated = I or in packs = P, and position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP

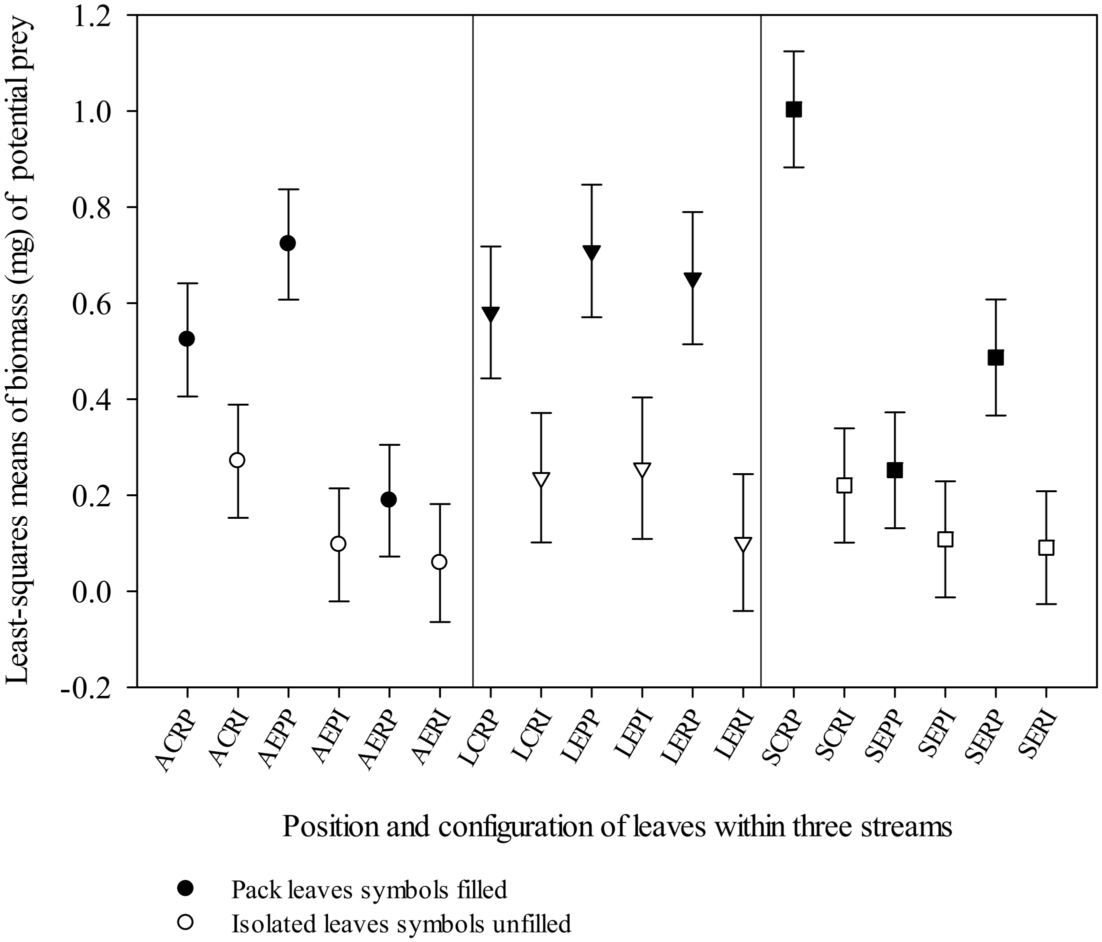


Figure 4.8. Least-squares means and SE of biomass (mg) of potential prey, excluding gastropods and tipulids, in each of three streams, A=Adds Creek, L=Leatherwood Creek, S=Steele Creek, associated with leaves, according to their configuration, isolated = I or in packs = P, and position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP

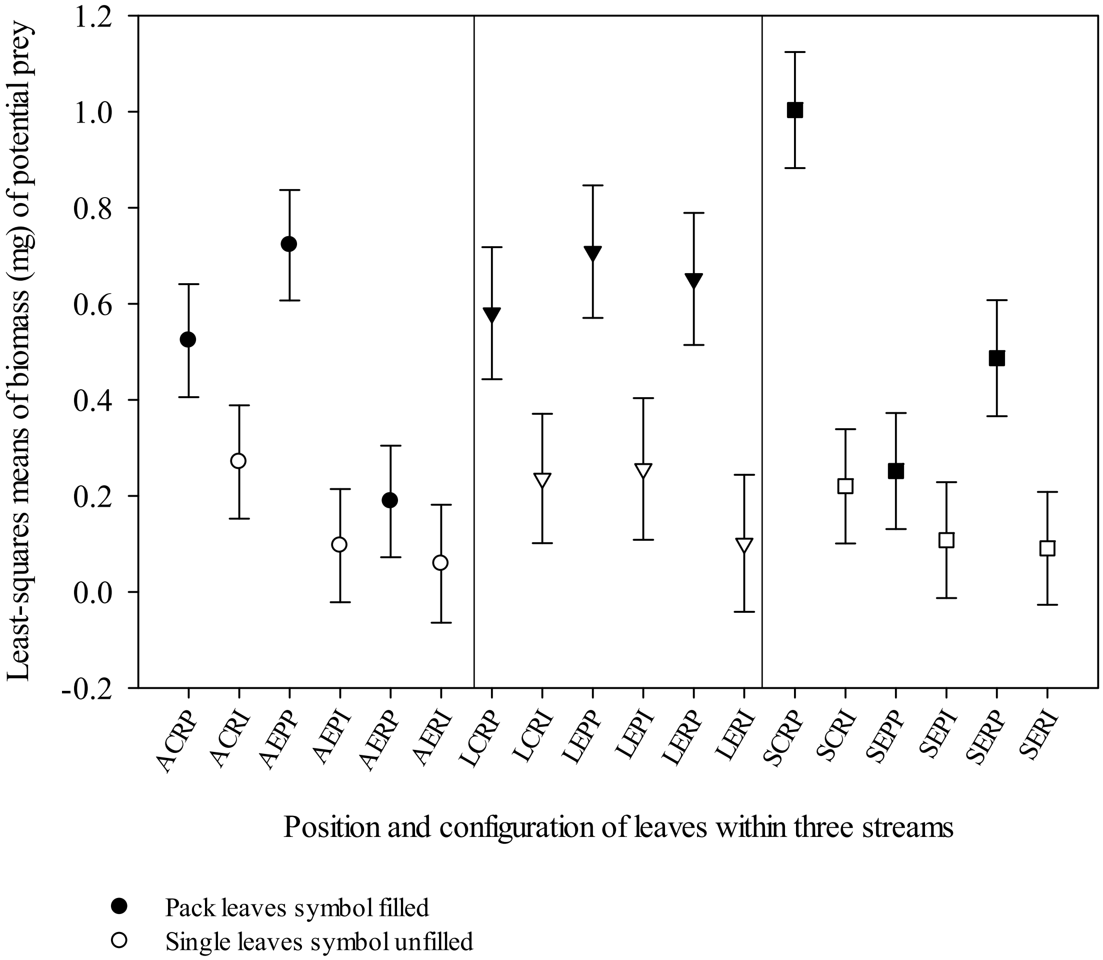


Figure 4.9. Least-squares means and SE of biomass (mg) of potential prey including gastropods, after division of biomass of packs by five, within multiple territories on each of three streams, A=Adds Creek, L=Leatherwood Creek, S=Steele Creek

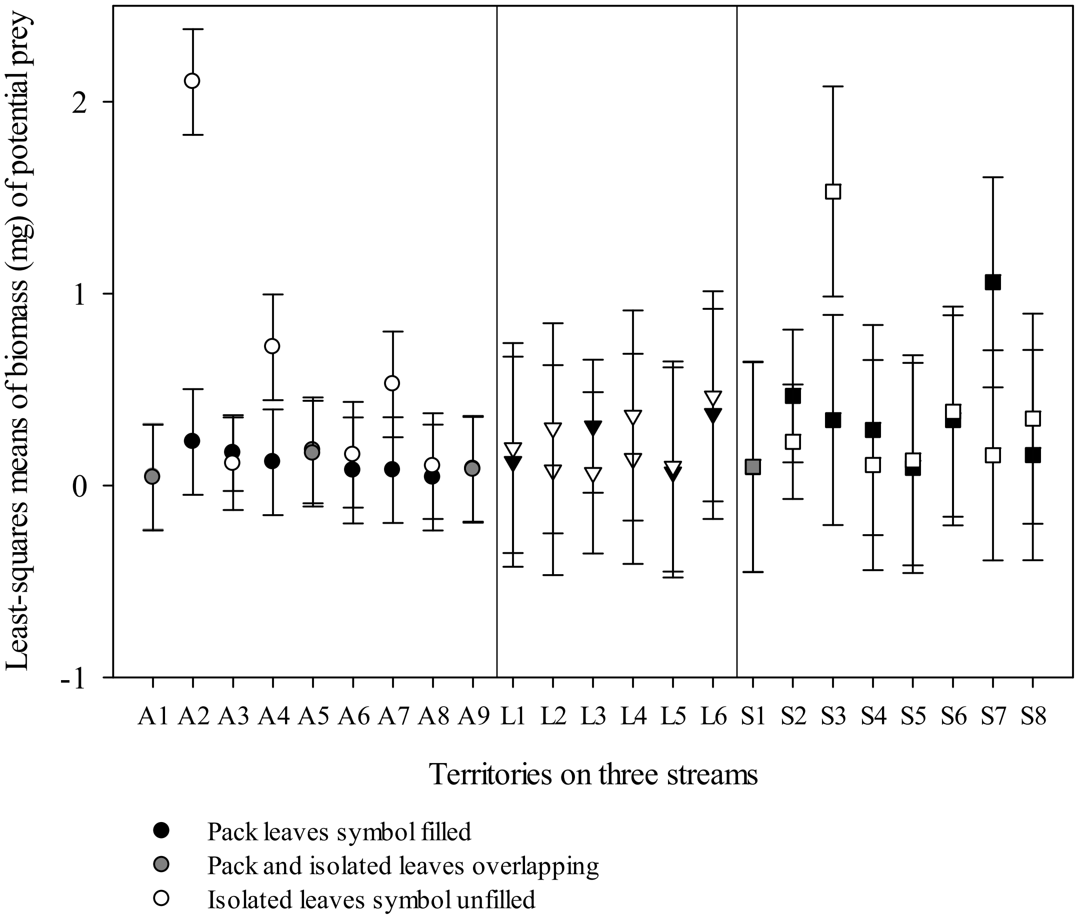


Figure 4.10. Least-squares means and SE of biomass (mg) of potential prey excluding gastropods, after division of biomass of packs by five, in each of three streams, A=Adds Creek, L=Leatherwood Creek, S=Steele Creek, associated with leaves, according to their configuration, isolated = I or in packs = P, and position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP

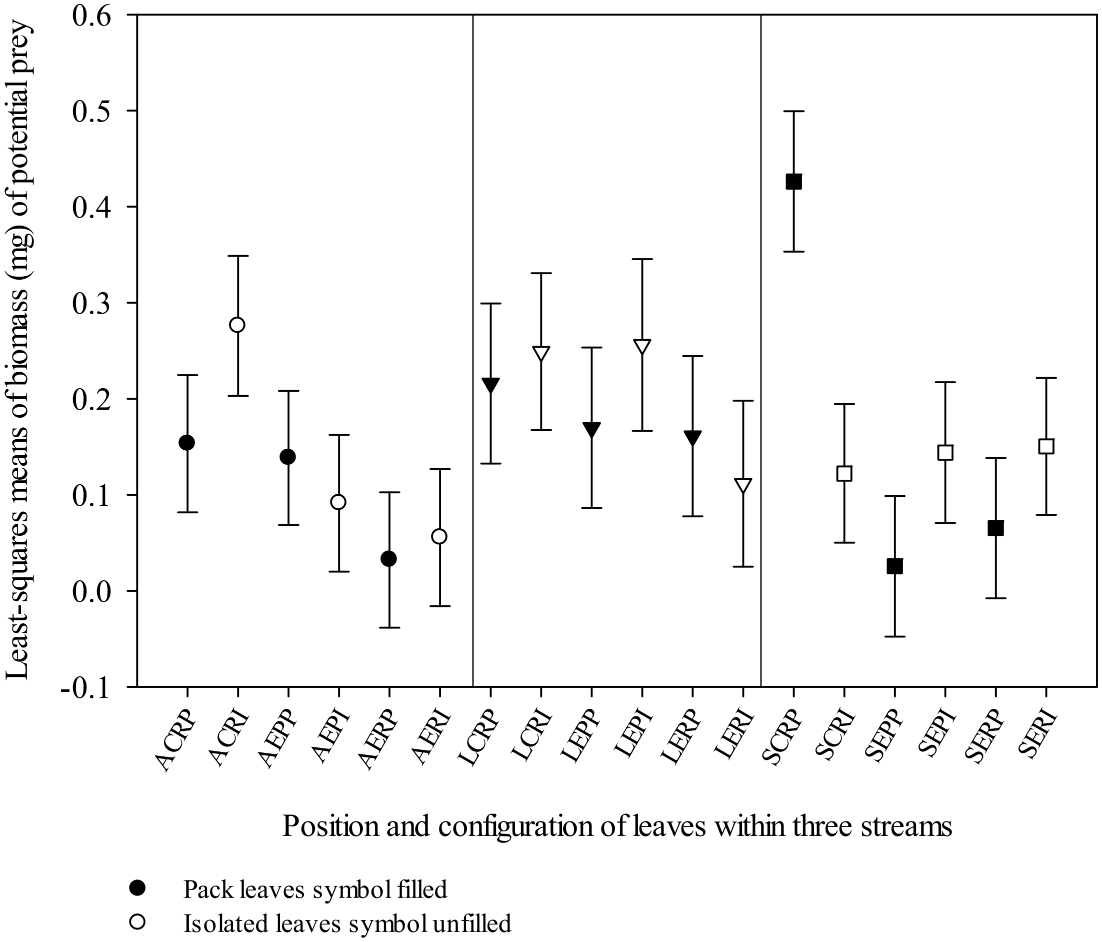
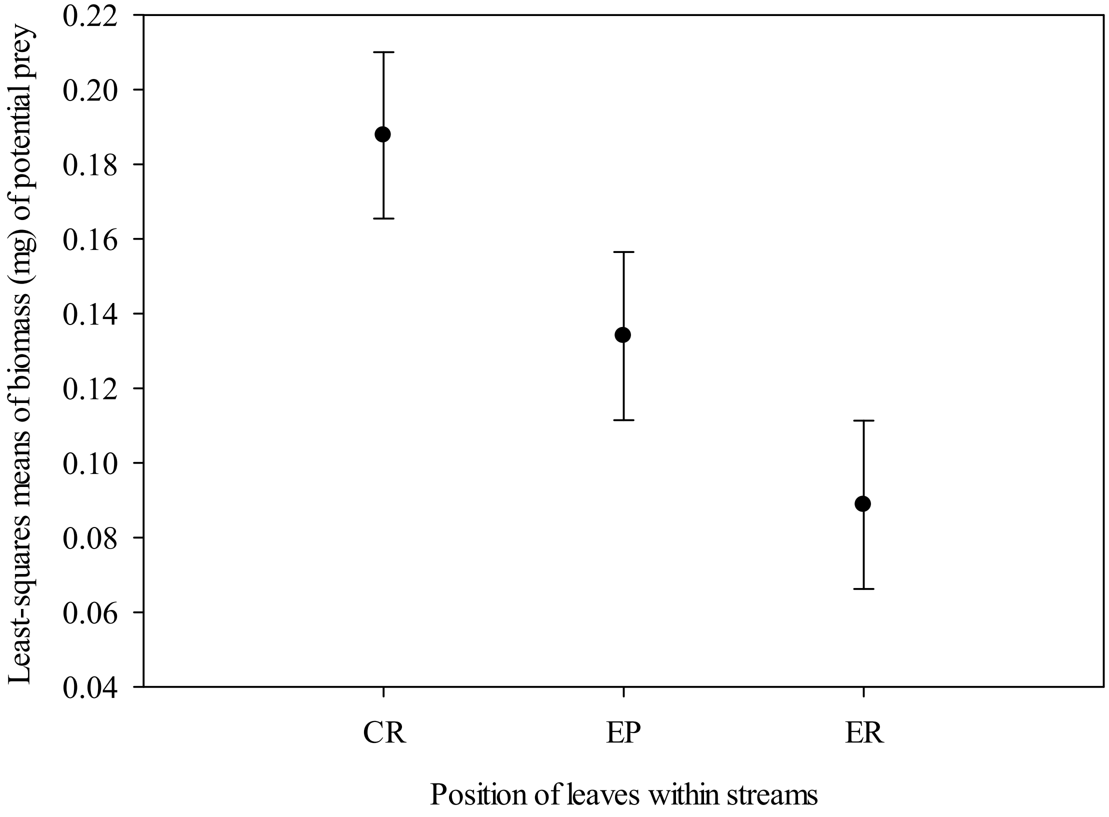


Figure 4.11. Least-squares means and SE of biomass (mg) of potential prey excluding gastropods and tipulids, after division of biomass of packs by five according to position within the stream environment, at centers of riffles = CR, edges of riffles = ER, or edges of pools = EP



Appendix 4.1. Listing of taxa associated with leaves and leaf packs in three streams in the watershed of the upper Buffalo National River

Phylum	**Subphylum**	**Class**	**Order**	**Family**	**Genus**
Chordata	Vertebrata	Amphibia	Caudata	Plethodontidae	*Eurycea*
Arthropoda	Chelicerata	Arachnida	Acari	*	*
Arthropoda	Chelicerata	Arachnida	Araneae	*	*
Arthropoda	Myriapoda	Diplopoda	*	*	*
Arthropoda	Crustacea	Maxillopoda	Harpacticoida	*	*
Arthropoda	Crustacea	Malacostraca	Isopoda	Asellidae	*Lirceus*
Arthropoda	Hexapoda	Insecta	Coleoptera	Carabidae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Curculionidae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Dryopidae	*Helichus*
Arthropoda	Hexapoda	Insecta	Coleoptera	Dytiscidae	*Copelatus*
Arthropoda	Hexapoda	Insecta	Coleoptera	Dytiscidae	*Laccophilus*
Arthropoda	Hexapoda	Insecta	Coleoptera	Elmidae	*Stenelmis*
Arthropoda	Hexapoda	Insecta	Coleoptera	Hydrophilidae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Lampyridae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Noteridae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Psephenidae	*Ectopria*
Arthropoda	Hexapoda	Insecta	Coleoptera	Ptiliidae	*
Arthropoda	Hexapoda	Insecta	Coleoptera	Scirtidae	*Scirtes*
Arthropoda	Hexapoda	Insecta	Coleoptera	Staphylinidae	*Helichus*
Arthropoda	Hexapoda	Insecta	Collembola	Sminthuridae	*
Arthropoda	Hexapoda	Insecta	Collembola	Entomobryidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Ceratopogonidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Chaoboridae	*
Arthropoda	Hexapoda	Insecta	Diptera	Chironomidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Cyclorrhaphous-Brachycera	*
Arthropoda	Hexapoda	Insecta	Diptera	Dixidae	*Dixa*
Arthropoda	Hexapoda	Insecta	Diptera	Dolichopodidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Empididae	*
Arthropoda	Hexapoda	Insecta	Diptera	NematoceraPupae	*
Arthropoda	Hexapoda	Insecta	Diptera	Phychodidae	*Phychoda*
Arthropoda	Hexapoda	Insecta	Diptera	Psychodidae	*Pericoma*
Arthropoda	Hexapoda	Insecta	Diptera	Sciomyzidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Simuliidae	*Simulium*
Arthropoda	Hexapoda	Insecta	Diptera	Stratiomyidae	*Caloparyphus*
Arthropoda	Hexapoda	Insecta	Diptera	Stratiomyidae	*Nemotelus*
Arthropoda	Hexapoda	Insecta	Diptera	Stratiomyidae	*Stratiomys*
Arthropoda	Hexapoda	Insecta	Diptera	Thaumaleidae	*
Arthropoda	Hexapoda	Insecta	Diptera	Tipulidae	*Tipula*
Arthropoda	Hexapoda	Insecta	Diptera	*	*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Ameletidae	*Ameletus*

Phylum	Subphylum	Class	Order	Family	Genus
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Baetidae	*Acentrella*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Baetidae	*Baetis*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Baetidae	*Heterocloeon*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Caenidae	*Caenis*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Ephemerellidae	*Eurylophella*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Ephemerellidae	*Ephemerella*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Heptageniidae	*Maccaffertium*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Heptageniidae	*Ephorus*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Heptageniidae	*Leucrocuta*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Leptophlebiidae	*Choroterpes*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Leptophlebiidae	*Leptophlebia*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Leptophlebiidae	*Paraleptophlebia*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Siphlonuridae	*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	Tricorythidae	*
Arthropoda	Hexapoda	Insecta	Ephemeroptera	*	*
Arthropoda	Hexapoda	Insecta	Hemiptera	Aphididae	*
Arthropoda	Hexapoda	Insecta	Hemiptera	Gerridae	*Aquarius*
Arthropoda	Hexapoda	Insecta	Hemiptera	Gerridae	*Trepobates*
Arthropoda	Hexapoda	Insecta	Hemiptera	Herbridae	*
Arthropoda	Hexapoda	Insecta	Hemiptera	Veliidae	*Microvelia*
Arthropoda	Hexapoda	Insecta	Hymenoptera	Braconidae	*
Arthropoda	Hexapoda	Insecta	Hymenoptera	Formicidae	*
Arthropoda	Hexapoda	Insecta	Hymenoptera	Ichneumonidae	*
Arthropoda	Hexapoda	Insecta	Lepidoptera	Cosmopterigidae	*
Arthropoda	Hexapoda	Insecta	Lepidoptera	Pyralidae	*
Arthropoda	Hexapoda	Insecta	Lepidoptera	Noctuidae	*
Arthropoda	Hexapoda	Insecta	Odonata	Coenagrionidae	*Argia*
Arthropoda	Hexapoda	Insecta	Plecoptera	Chloroperlidae	*Haploperla*
Arthropoda	Hexapoda	Insecta	Plecoptera	Chloroperlidae	*Alloperla*
Arthropoda	Hexapoda	Insecta	Plecoptera	Leuctridae	*Zealeuctra*
Arthropoda	Hexapoda	Insecta	Plecoptera	Nemouridae	*Amphinemura*
Arthropoda	Hexapoda	Insecta	Plecoptera	Nemouridae	*Leuctridae*
Arthropoda	Hexapoda	Insecta	Plecoptera	Perlidae	*Agnetina*
Arthropoda	Hexapoda	Insecta	Plecoptera	Perlidae	*Paragnetina*
Arthropoda	Hexapoda	Insecta	Plecoptera	Perlidae	*Perlesta*
Arthropoda	Hexapoda	Insecta	Plecoptera	Perlodidae	*Clioperla*
Arthropoda	Hexapoda	Insecta	Plecoptera	Perlodidae	*Isoperla*
Arthropoda	Hexapoda	Insecta	Plecoptera	Pteronarcyidae	*
Arthropoda	Hexapoda	Insecta	Plecoptera	Taeniopterygidae	*Strophopteryx*

Phylum	**Subphylum**	**Class**	**Order**	**Family**	**Genus**
Arthropoda	Hexapoda	Insecta	Plecoptera	*	*
Arthropoda	Hexapoda	Insecta	Trichoptera	Beraeidae	*
Arthropoda	Hexapoda	Insecta	Trichoptera	Glossosomatidae	*Agapetus*
Arthropoda	Hexapoda	Insecta	Trichoptera	Helicopsychidae	*Helicopsyche*
Arthropoda	Hexapoda	Insecta	Trichoptera	Hydropsychidae	*Hydropsyche*
Arthropoda	Hexapoda	Insecta	Trichoptera	Hydroptilidae	*
Arthropoda	Hexapoda	Insecta	Trichoptera	Lepidostomatidae	*Lepidostoma*
Arthropoda	Hexapoda	Insecta	Trichoptera	Limnephilidae	*Pycnopsyche*
Arthropoda	Hexapoda	Insecta	Trichoptera	Philopotamidae	*Wormaldia*
Arthropoda	Hexapoda	Insecta	Trichoptera	Phryganeidae	*
Arthropoda	Hexapoda	Insecta	Trichoptera	Polycentropodidae	*
Arthropoda	Hexapoda	Insecta	Trichoptera	Rhyacophilidae	*Rhyacophila*
Phylum	**Class**	**Subclass**	**Order**	**Family**	**Genus**
Annelida	Clitellata	Oligochaeta	Haplotaxida	Enchytraeidae	*
Annelida	Clitellata	Oligochaeta	Lumbriculida	Lumbriculidae	*
Annelida	Clitellata	Oligochaeta	Haplotaxida	Naididae	*
Annelida	Clitellata	Oligochaeta	Haplotaxida	Tubificidae	*
Annelida	Clitellata	Oligochaeta	Haplotaxida	Lumbricidae	*
Mollusca	Gastropoda	Pulmonata	Basommatophora	Physidae	*Physa*
Mollusca	Gastropoda	Pulmonata	Neotaenioglossa	Pleuroceridae	*Elimia*
Mollusca	Gastropoda	Pulmonata	Basommatophora	Lymnaeidae	*
Mollusca	Bivalvia	Heterodonta	Veneroida	Sphaeriidae	*
Nematoda	*	*	*	*	*

Chapter 5:

Louisiana Waterthrush (*Parkesia motacilla*) of the Buffalo National River Watershed and their relationship to a changing riparian habitat

Abstract

The Louisiana Waterthrush is a migratory wood-warbler that maintains linear breeding territories along gravel-bottomed, fast-flowing streams. It has evolved ecological relationships with riparian habitat and aquatic invertebrate prey, allowing the possibility of its utility in assessment of stream ecological integrity. My objectives were to monitor territories on three watershed streams of the Buffalo National River with legally protected and unprotected reaches and determine if differences existed in stream and habitat bioassessment metrics, territory size, fecundity and site fidelity, and to determine if functional relationships existed between lengths of territories and measures of riparian habitat quality. Birds were federally and color-banded and territory boundaries mapped. Perimeters and bank-full widths of stream in each territory were measured and an adjoining riffle and pool was sampled for aquatic invertebrates by duplicating the foraging maneuver of leaf-pulling. Male site fidelity to territories was generally high and, where males returned year after year, boundaries remained similar. Lower-order streams were sometimes incorporated into main territories on perennial streams or were occupied solely by new recruits. Nest success was similar for all males. Significant differences among territories on protected and unprotected reaches of streams were found comparing bioassessment metrics indicative of organic pollution and comparing pollution-tolerant and pollution-intolerant taxa. Significant functional relationships were found between lengths of territories, canopy cover and pollution-tolerant and intolerant aquatic invertebrate taxa indicating Louisiana Waterthrushes could be incorporated into bioassessment metrics as indicators of stream ecological integrity in the watershed of the Buffalo National River.

Keywords: Louisiana Waterthrush*, Parkesia motacilla,* stream ecological assessment, obligate riparian songbird, aquatic invertebrate prey, bioassessment

Introduction

Throughout the world there are estimated to be only 60 bird species that may be classified as riverine specialists. A riverine specialist is defined by Buckton and Ormerod (2002) as those species that occur exclusively along stream or river channels and within stream corridors during significant periods of their life-cycle and take their food primarily from the aquatic ecosystem. The ecological relationships of these obligate riparian species with their habitat provide information pertaining to ecological integrity and health of the stream environment (Ormerod and Tyler 1993). Twenty-nine of 60 riverine specialists derive from eight families of passerines, and of those, only the Louisiana Waterthrush, *Parkesia motacilla*, occurs in the eastern United States (Robinson 1995, Buckton and Ormerod 2002, Mattsson et al. 2009).

This Nearctic-Neotropical migratory wood-warbler establishes and defends linear breeding territories along gravel-bottomed, fast-flowing, forested streams (Robinson 1990, 1995, Prosser and Brooks 1998, Mulvihill et al. 2008). As a riverine specialist and obligate riparian species it feeds almost entirely upon aquatic invertebrates, including benthic macroinvertebrates, taken from shallow areas of riffles and edges of streams (Craig 1984, 1987, Robinson 1995, Mattsson et al. 2009). Nests are built in cavities within stream banks and birds are rarely seen more than 20 m outside the stream’s corridor (Robinson 1995). Their predator-prey relationship with aquatic invertebrates and the bird’s habit of nesting within stream banks make them vulnerable to changes in stream water quality and riparian land use (Prosser and Brooks 1998, Stucker 2000, Mattsson and Cooper 2006, Mulvihill et al. 2008).

Benthic macroinvertebrates, the prey of Louisiana Waterthrushes, have been used effectively as bioindicators for 4 decades (Hellawell 1986, Cairns Jr and Pratt 1993, Bonada et al. 2006, Carter et al. 2006) and they continue to be the most commonly studied indicators of stream ecological integrity (Rosenberg and Resh 1993). Bioassessment using macroinvertebrates is labor intensive and requires knowledge and expertise in identifying taxa. As a result, scientists must focus upon a smaller percentage of the many imperiled stream systems (Mattsson and Cooper 2006). Louisiana Waterthrushes are easily recognized and observed and there exists a large contingent of citizen scientists interested in the study of birds. As a result, Louisiana Waterthrushes may provide the opportunity to integrate an avian species into stream ecological assessment (Mattsson and Cooper 2006).

Presence and absence and relationships of Louisiana Waterthrushes to stream ecological integrity have been studied in southeastern Minnesota. There, territories (n = 46) averaged 460 m in length, with Louisiana Waterthrushes present on streams with a greater abundance of pollution-intolerant benthic macroinvertebrates, Plecoptera and Trichoptera, compared to streams where they were not detected (Stucker 2000). In a study of Louisiana Waterthrushes on headwater streams in the Georgia Piedmont, Mattsson (Mattsson 2006, Mattsson and Cooper 2006) found populations to be more predictably present upon headwater streams with higher percentages of pollution-intolerant taxa, particularly Ephemeroptera, Plecoptera, and Trichoptera, (hereafter % EPT), a lower Family-level biotic index of organic pollution (hereafter FBI), and greater macrobenthos biomass. Where Louisiana Waterthrushes were present, territories averaged 520 m and ranged from 90-1440 m in length. A decline in nestling survival occurred as territory length increased and fewer riffles existed within a territory (Mattsson 2006).

In an ongoing and long-running study on acidified and circumneutral streams in southwestern Pennsylvania, Louisiana Waterthrush territories on acidified streams were nearly twice the length of those on circumneutral streams (Mulvihill et al. 2008). Breeding birds on acidified streams had smaller clutches and decreased site fidelity to those territories. In addition, young, inexperienced birds were found more often occupying acidified streams and tended to move to circumneutral streams opportunistically.

Aquatic invertebrates, particularly Ephemeroptera, are intolerant of stream acidity and Ephemeroptera were almost entirely absent from acidified streams. There, they were replaced by acid-tolerant Plecoptera genera. A significant relationship was found between breeding density and % EPT when those two genera were excluded from analysis (Mulvihill et al. 2008). On both acidified and circumneutral streams territories were as small as 250 m, but only on acidified streams were territories greater than 700 m, 630 ± 50 m (n = 32), with gaps occurring in occupancy along the streams. In contrast, territory lengths averaged 370 ± 10 m (n = 88) on circumneutral streams (Mulvihill et al. 2008).

Territory sizes have previously been suggested to be related to availability of prey. Food value theory (Stenger 1958, Wilson 1975) proposes that the function of territoriality is to ensure enough space for an adequate food supply to rear young. Territorial individuals may monitor prey abundance directly and adjust territory size to available resources or they may adjust territory size based upon the perception of prey availability through structural cues within habitat (Smith and Shugart 1987, Marshall and Cooper 2004). Density and sizes of territories may also be affected by population density. Areas of greater prey density may increase intraspecific competition and result in smaller territory sizes (Smith and Shugart 1987, Marshall and Cooper 2004). This situation may occur more frequently among terrestrial species that are surrounded at all boundaries with multiple neighbors than of riparian species where territories are linear and fewer neighbors are present to compete (Mattsson 2006). Territory sizes have been found to increase as prey density and abundance decreases or as habitat structure results in an expected decrease in density and abundance. This phenomenon was found and first proposed in a neighboring genera, the Ovenbird (Stenger 1958, Smith and Shugart 1987) and has been reported in avian taxa with similarity in their stream habitat and diet: the Dipper (Ormerod and Tyler 1993, Feck and Hall 2004) and Belted Kingfisher (Davis 1982) in shorebirds, Dunlin (Holmes 1970) and Sanderlings (Myers et al. 1979) and in diverse taxa such as Red-eyed Vireos (Marshall and Cooper 2004) and White-tailed Kites (Dunk and Cooper 1994).

In northwest Arkansas, Louisiana Waterthrushes breed on watershed streams of the Buffalo National River, which is imperiled by the rapid conversion of the watershed from forested land to pasture land and a consequent increase in fecal coliform bacteria, nitrification, and sedimentation (Dale et al. 1978, Braun 1986, Weeks 1987, Mott and Steele 1991, Scott and Hofer 1995, Mott and Laurans 2004). This river is one of only five free-flowing rivers that have been federally protected through special acts of Congress (Benke 1990). Headwaters form in the Boston Mountains, and the Buffalo River winds 150 miles east through the Ozark Uplands of northwestern and central Arkansas. National Rivers, unlike Wild and Scenic Rivers, generally have wide segments along riparian corridors included in their protection (Benke 1990). The Buffalo River does not. Of its length, 135 miles are protected as National River, but widths of only one-half to four miles are included in this protection for a total of 11% of the watershed. Another 29% is under State or United States Forest Service protection, leaving 60% of the watershed privately owned. Only 392 km^2 out of 3,465 km^2 of watershed is federally protected (Sagers and Lyon 1996, Mott and Laurans 2004, Brown et al. 2005). Without federal jurisdiction, with poor relationships between the National Park Service and private property owners (Mott and Laurans 2004), and with the lack of implementation of federal protections available to authorities (Pers. Comm.), the health of the watershed and the Buffalo National River itself continues its decline (Scott and Hofer 1995, Mott and Laurans 2004). This decline affects suitability of stream habitat for aquatic invertebrates (Wood and Armitage 1997, Roy et al. 2003, Suberkropp et al. 2010) and, likely, those organisms that rely upon their presence and the presence of suitable riparian environment, such as the Louisiana Waterthrush.

My first objective was to map and monitor Louisiana Waterthrush territories on three streams with legally protected and unprotected reaches and anthropogenic change occurring along their lengths such that comparisons could be made of stream ecological integrity based upon common stream and habitat bioassessment techniques and territory size, fecundity and site fidelity of Louisiana Waterthrushes. My second objective was to determine if functional relationships exist between the length of Louisiana Waterthrush territories and measures of riparian habitat quality that would allow the use of the Louisiana Waterthrush as a measure of stream ecological integrity in the Buffalo National River and its watershed.

Study Site

The majority of the Buffalo National River lies within the Boston Mountain Region and Springfield Plateau and, near its confluence with the White River, it passes briefly through the Salem Plateau (Rafferty 1980). Its adjoining protected riparian corridor is a narrow strip of land encompassing 392 km^2 (Sagers and Lyon 1997, Sagers et al. 1999, Mott and Laurans 2004) while the entire watershed encompasses 3,465 km^2 (Fig. 5.1). Approximately 64% of the river basin is underlain with shale, limestone, chert and dolomite (Scott and Smith 1994). The region is highly erosional. Its topography is characterized by Karst geology with caves, sinkholes, and a complicated groundwater system (Sagers and Lyon 1997, Sagers et al. 1999, Mott and Laurans 2004, Brown et al. 2005). Steep slopes result in extreme rises and falls in the hydrograph of watershed streams and the water is highly alkaline (Mott and Laurans 2004, Brown et al. 2005).

Vegetation includes 377 species (Sagers and Lyon 1996, 1997). Watershed streams of the upper Buffalo National River begin on hillsides of oak-hickory forests and descend through riparian corridors with north-facing slopes characterized by Carolina beech (*Fagus grandifola*), mockernut hickory (*Carya tomentosa*), and sweet gum (*Liquidambar stryaciflua*) and south-facing slopes of post oak (*Quercus stellata*) and black hickory (*Carya texana*). White oak (*Quercus alba*), shagbark hickory (*Carya ovata*), and sugar maple (*Acer saccharum*) occur on both slopes (Smith 1977, Sagers and Lyon 1996).

Reaches of three watershed streams with varying degrees of their length within federally protected and unprotected privately-owned lands were chosen for study within the upper Buffalo National River watershed (Fig. 5.2) in Newton County, near Ponca, Arkansas: Adds Creek (Fig. 5.3), Leatherwood Creek (Fig. 5.4), and Steele Creek (Fig. 5.5). All streams are 1st and 2nd order with adjoining intermittent streams. All are similar in that they tend to dry to pools in late summer conditions and their substrate consists of coarse, predominately chert, cobble interspersed with areas of exposed bedrock (Brown et al. 2005). Adds Creek and Leatherwood Creek empty into the Buffalo National River at the Ponca low-water bridge. Leatherwood Creek runs north and Adds Creek south. Steele Creek empties from the north into the Buffalo River downstream of the Steele Creek campground. Vertical relief differs among the studied reaches of the streams. Steele Creek descends from an elevation of 342 m to 298 m over a distance of 3.1 km, Adds Creek descends from 428 m to 308 m over a distance of 4.1 km, and Leatherwood Creek descends 490 m to 310 m over a distance of 3 km. Upstream 1.9 km from its confluence with the Buffalo National River and at an elevation of 420 m, Leatherwood Creek becomes ephemeral stream over a distance of approximately 345 m to an elevation of 463 m.

Methods

Two hundred and nineteen birds were banded and twenty-three territories monitored from 2006 to 2008 with a preliminary banding season in 2005. Each male was mist-netted and banded with color and federal bands, and territories were mapped by observing frequent aggressive interactions between territorial males at territory boundaries and by mapping song perches. Females were banded in the first season, but females banded before nesting often left the territory (Pers. Obs.). In 2007 and 2008 females were not banded until after they had begun brooding and only banded if they were involved in a study involving fledgling and parental behavior to avoid any influence on pair-bonding and nesting. Nests were found and monitored every three days. Nestlings were banded prior to fledging. Distance of nests from the water was measured weekly and after pronounced rises and flood events.

Rough measurements of territories were taken in 2006 with GPS coordinates. This proved difficult in the deep stream corridor of Leatherwood Creek, and GPS coordinates were often inaccurate on other streams as well. In 2007 lengths of territories were measured incorrectly by an undergraduate researcher. As a result, 2007 territories were measured again when territories were measured in 2008. Fortunately, high return rates of males of previous years resulted in territory boundaries remaining essentially the same throughout the three years of study.

Territories were measured with a hip chain and cotton (biodegradable) string on one side of the stream. The string was tied and then laid loosely along the stream's perimeter, where water and stream bank met, from one end of a territory to the other. Both perennial reaches and intermittent stream reaches known to be used by a territorial male were included in measurement so that comparisons could be made with and without inclusions of the intermittent reaches.

Intermittent streams were measured as far upstream as a territorial male was observed foraging. Bank-full width was measured at 4 regular intervals within territories on the perennial reach and at two intervals along intermittent reaches. Length and bank-full width were then used to calculate the area of stream within each territory. Where a territory included a stream impoundment and birds were observed foraging along the impoundment's banks, the amount of foraging area along its perimeter was measured as above. The cotton string was collected after measuring each territory to avoid any harm to wildlife (Loegering 1997).

Within each Louisiana Waterthrush territory three blocks of equal size were placed equidistant from one another. Within each of those blocks a 20 m transect was placed randomly at a right angle to the stream with sample points every meter. Canopy cover was measured at each sample point. An ocular sighting tube was made with cross hairs placed at the distal end of the tube and a weight attached at the proximal end (Winkworth and Goodall 1962). The ocular tube was sighted directly over-head and the presence or absence of canopy cover at each point was noted. The total number of times canopy cover was present was multiplied by 100 and divided by the total number of sightings to give percentage canopy cover (James and Shugart 1970).

In order to determine aquatic invertebrates available to Louisiana Waterthrushes and as part of a complementary study of foraging behavior, I duplicated the foraging maneuver of leaf-pulling. One corresponding riffle-pool complex was randomly chosen and sampled within each territory (Marshall 2012). Sampling began on 12 April 2007 and extended through 24 April 2007. This timing precluded any high-water events that would have swept the stream free of isolated leaves and leaf packs. Twenty isolated leaves and five leaves from the top of five packs were removed from the edge of riffle, the edge of a pool, and the center of a riffle, from water no deeper than 2 cm. An aquarium dip-net (12.5 cm width, 9.5 cm length, depth 11 cm, mesh size 0.2 mm) was held slightly downstream from the leaves removed to capture any potential prey that were dislodged by the movement. Upon removal, leaves and their associated taxa were placed in cylinders and a 70 % ethanol solution was added. The samples were transported to the laboratory where leaves were rinsed and handpicked. A total of 1,725 samples were taken from 23 territories. From those, invertebrates were found associated with 704 samples. The number of insects within each of these samples was counted.

Two samples were then randomly chosen from each territory, position, and configuration of leaves; i.e., invertebrates, associated with isolated leaves from edges of riffles, edges of pools, and the center of riffles and with five leaves from leaf packs at edges of riffles, edges of pools, and the center of riffles. Invertebrates were identified to the lowest taxon possible (Merritt and Cummins 1996). Overall abundance and mass of aquatic invertebrates taken from each territory was determined. The following metrics were calculated: Family Biotic Index (FBI) (Hilsenhoff 1988), Family Richness (Resh and McElravy 1993, Lenat and Barbour 1994), EPT Richness as the total number of families within the generally pollution-sensitive orders -Ephemeroptera, Plecoptera, and Trichoptera families (Resh and Jackson 1993, Lenat and Penrose 1996), and % dominant taxons of Ephemeroptera-Plecoptera-Trichoptera, Gastropoda and Chironomidae were calculated as their ratio to total macrobenthos abundance (Barbour et al. 1992). Tolerance values were taken from Hilsenhoff (1988), Lenat (1993), and Bode (1988).

On March 4th and 18th, 2008, the Buffalo National River experienced two “100-year” floods. In the weeks following the 18th birds were seen more often foraging on intermittent streams adjoining their main territories on perennial streams. On April 18th, two territories with an adjoining intermittent stream were chosen from each of the three study streams. Five leaves from the tops of six packs were randomly taken from the center of riffles in the perennial stream and from the center of the adjoining stream to determine what prey were available during periods of high water. Upon removal, leaves were placed in cylinders and a 70% ethanol solution was added to preserve invertebrates. They were then treated as those samples discussed above.

Statistical Analysis

Territories that had their greatest percentage of length upon perennial reaches of study streams were included in analysis. One territory, almost entirely upon an inaccessible adjoining perennial stream on private property to which I had no access, was excluded from analysis. Two territories on the upper perennial reach of Adds Creek were very small and maintained by two unmated males in 2007. Both territories were abandoned in 2008, and they were also excluded from statistical analysis.

A two-factor factorial design was used to compare streams and protected vs. unprotected reaches with both factors treated as fixed effects. Variables having normal distributions were subjected to Analysis of Variance (ANOVA) and those having binomial and binary distributions were analyzed using Logit analysis. Those with a Poisson distribution were analyzed using Poisson regression. Least-squares means were used to determine differences when appropriate. Mayfield logistic regression was used to model nest survival (Mayfield 1961, 1975) and to test for significant differences among streams, protected and unprotected reaches, and years (Aebischer 1993, Hazler 2004). Analysis of nest success and annual fidelity of males to home territories ignored the repeated measure of returns of males to territories in multiple years. In the comparison of fidelity, insufficient sample sizes did not allow testing of interactions. Multiple regression techniques, including calculations of measures of influence and plots of studentized residuals, were used to determine if significant relationships existed between size of territory and prey abundance and mass, bioassessment metrics, and canopy cover. Because the nature of the bioassessment metrics introduced the possibility of collinearity, I calculated variance inflation factors (*VIF*), condition indices (*K*) and variance decomposition proportions. All analysis was performed using SAS software, Version 9.2 (SAS Institute Inc., Cary, NC, USA). Differences were considered significant at $p = 0.05$ or less and marginally significant at $p = 0.10$.

Results

Territories: Adds Creek (n = 8)

The most downstream reach of Adds Creek moves into National Park protection for only 500 m before entering the Buffalo National River (Fig. 5.3). A waterthrush territory was maintained on this reach for three consecutive years by a series of new recruits to the territory. It was bordered above by a 45-m power-line corridor. The males on this first territory rarely crossed the corridor to interact with the next upstream territorial male. Upstream of the power-line corridor is a broken impoundment structure that remains partially intact. It continues to collect a large amount of sediment, cobble and debris above it during high-water events. Previous to this study, the area was used for gravel mining. As a result of impoundment and gravel-mining the stream bed is significantly wider here than at any other reach upon the stream. At present, the area adjacent to what was once the impoundment is leased by Arkansas Game & Fish Commission as an education center. At the beginning of the study, management had begun to reestablish the riparian border. One waterthrush territory was established upon this reach and an adjacent intermittent stream. The territorial male returned to the territory three consecutive years.

Above this territory, the stream is associated with the community of Ponca, AR, with homes, small businesses, and horses, goats, and poultry in confinement on the banks of the stream. A rock quarry is active above the town and stream northeast approximately 100 m. In high-water events Adds Creek carries heavy loads of sediment, cobble, and debris. Stream banks are deeply undercut and in some places homes are beginning to fall into the stream. A single waterthrush territory runs along the length of the town until reaching a second impoundment. This impoundment remains intact and is filling with sediment. The territorial male above the impoundment foraged along its banks and at the impoundment itself where it interacted with its downstream neighbor until late in the final year of study when it was killed by a property owner's cat.

Upstream and out of town boundaries, Adds Creek moves through an area of shrubby second-growth vegetation and into remnants of beech forest. A gravel-road, three homes, two power-line corridors, and pasture adjoin the stream before it enters into an old-growth beech forest. One very long territory included reaches with the first two home sites. The territorial male returned to the territory for two consecutive years and was replaced by a new recruit in the following year of study. Upstream, passing through power-line corridor, past another home and pasture another two territories of only 250 m in length each were maintained by two unmated males one year and then the area was abandoned, and waterthrushes were not seen again along the 500 m reach. The uppermost territory on Adds Creek begins as the stream enters into the old-growth beech forest. The territorial male residing on this reach and an adjoining intermittent stream maintained the territory three consecutive years and attempted to double brood in 2007.

Territories: Leatherwood Creek (n = 6)

Five territories were studied on Leatherwood Creek within National Park boundaries and below the stretch of ephemeral stream and large boulder and bedrock channel (Fig. 5.4). Two had adjoining intermittent streams. Another territory was studied outside National Park boundaries and above the stretch of ephemeral stream. Its channel, unlike other territories, was characterized by large boulders and bedrock. In addition, multiple vehicles and storage buildings sat immediately adjacent to the stream in this territory. This territory was occupied by the same territorial male for two consecutive years and replaced by a new recruit in the third year of my study.

The first five territories had the same territorial males return three consecutive years. Clear-cutting and application of herbicide to a power-line corridor (approx. 20 m) altered the territory nearest the river previous to the breeding season of 2008. Though that territory's male returned spring 2008, he abandoned the main perennial section for the adjoining intermittent stream. After three unsuccessful nesting attempts on that stream, he was not seen again. The male on the second territory upstream began moving down into the still forested section of the first territory as the season progressed. This left a gap between him and the third territorial male. Late in the breeding season a new recruit was seen engaged in disputes with territorial males above and below the newly opened space.

Territories: Steele Creek (n = 8)

Four territories were studied on Steele Creek within National Park boundaries (Fig. 5.5). Another four were studied above National Park boundaries. In 2005 and 2006 the first territory incorporated both a portion of Steele Creek and the Buffalo National River. After 2007, that male was not seen again, and the male on the next territory upstream began to move downstream over the period of a breeding season. The four territories below National Park boundaries were occupied by the same males for three consecutive years and territory boundaries remained essentially the same. All territories were adjoined by intermittent streams. Among years, three new recruits defended a territory almost entirely on an intermittent stream and were sometimes seen where it and Steele Creek joined. However, none of these three were seen in consecutive years. Little change occurred in this area or with the length of territories except for clear-cutting and herbicide spraying of power-line right-of-way (37 m) at the boundary between the second and third territorial males which shortened their territories the following spring.

Upon leaving National Park boundaries and entering private property, the next 2,213 m of Steele Creek's riparian area is characterized by pasture-lands and small intermittent streams adjoining Steele Creek from pastures and wooded areas. Though birds were banded along this area in the first year of study, only the territory adjoining the park boundary was mapped. The entire area was mapped and included for study in 2007 and 2008 with the landowner's approval.

In 2006 the reach above and nearest Park boundaries contained one full territory with a small adjoining intermittent stream and further up two adjoining intermittent streams appeared to support one territorial male each. Moving further upstream, wooded areas were converted to multiple pastures. In 2006, above the first of these pastures, the stream entered an area (37 m) of succession dominated by willows, shrubs, and young trees. Late in the summer of 2006 banding in this area indicated the presence of adult and juvenile Louisiana Waterthrushes. In winter 2007 all shrub vegetation and trees were cut and burned in the stream. Tree limbs, stumps, and vegetation that did not burn entirely, were left to wash downstream. In breeding seasons 2007 and 2008 Louisiana Waterthrushes were no longer found in this area or on the two intermittent streams located just downstream.

The riparian area upstream of the area where vegetation and trees were cut was bordered with oak-hickory forest on one side and with a single line of large trees on the other beyond which was a pasture, roads, barns, and the home of the property owner. In 2007, a total of five consecutive territories on the main perennial stream and the adjoining intermittent streams, were mapped. Between the breeding season of 2007 and 2008, cattle were fenced and pastured such that they created a watering hole in the first territory past the area that had been cut and burned the previous year. Subsequently, this area was also abandoned by Louisiana Waterthrushes. In addition, another territory downstream of the burned area was abandoned. Males on the three remaining territories returned to their territories two consecutive years. Owners of these private lands managed wildlife populations for hunting turkey and deer and protected chickens and domestic ducks from predation. Traps were set along the length of the stream and owners checked traps daily, killing any possible predators caught in traps or seen along the stream.

Length of Territories

The lengths of territories on perennial reaches of streams (Table 5.1) were marginally significantly different in comparisons of protected and unprotected reaches and streams (F = 3.78, df = 1 and 20, P = 0.07). Territories on unprotected reaches (LSM = 512.1 m, SE = 50.3 m) tended to be longer compared to those on protected reaches (LSM = 373.9 m, SE = 50.3 m). In addition, significant differences were found among streams (F = 3.78, df = 2 and 20, P = 0.05) with territories on Adds Creek (LSM = 588.0 m, SE = 68.6 m) significantly longer than those on Steele Creek (LSM = 379.2 m, SE = 44.3 m) or Leatherwood Creek (LSM = 361.8 m, SE = 68.6 m). Relative to the length of both the perennial reaches and adjoining intermittent streams within territories (Table 5.1), marginal differences were found among protected and unprotected reaches (F = 3.47, df = 1 and 20, P = 0.08) and streams (F = 2.83, df = 1 and 20, P = 0.09) . Territories on unprotected reaches (LSM = 608.9 m, SE = 54.7 m) tended to be longer than those located on protected reaches (LSM = 464.7 m, SE = 54.7 m). There were no interactions between streams and status in either comparison of lengths of territories.

Bank-full Width and Area of Territories

No significant differences were found in bank-full widths of territories (Table 5.1) among streams ($F = 0.22$, df = 2 and 20, $P = 0.8$) or in bank-full widths of territories on protected and unprotected reaches of streams ($F = 0.03$, df = 1 and 20, $P = 0.9$). Calculated from average bank-full widths and lengths, a marginal difference ($F = 3.25$, df = 2 and 21, $P = 0.07$) was observed in the amount of territory area including perennial and intermittent stream reaches (Table 5.1). Territories on Adds Creek included the greatest amount of stream area (LSM = 5148.5 m^2, SE = 656.2 m^2) and those on Leatherwood Creek included the least (LSM = 2788.6 m^2, SE = 656.2 m^2). The lack of significance of comparisons of bank-full width suggests that length is likely the most contributing factor of the two calculations to this marginal significance. Comparisons of the area of territories on main perennial reaches were not significantly different among streams ($F = 2.61$, df = 2 and 21, $P = 0.11$) or protected and unprotected reaches ($F = 2.61$, df = 1.7 and 21, $P = 0.21$).

Canopy Cover of Perennial Reaches of Territories

Canopy cover varied widely among territories on Adds Creek (34.4% - 98.9% shaded) and Steele Creek (59.2% - 99.2% shaded). Leatherwood territories were more uniformly shaded (85.1% - 99.2% shaded). When comparing territories on unprotected reaches (34.4% - 98.9 shaded) to protected reaches (88.3% - 99.2% shaded) the range in values was greater for the unprotected reaches. However, no significant differences were found when comparing average canopy cover

(Table 5.1) of territories among streams (*F* = 0.26, df = 2 and 15, *P* = 0.77) or comparing canopy cover on protected and unprotected reaches of streams (*F* = 0.42, df = 1 and 15, *P* = 0.53).

Measures of Stream Ecological Integrity:

Comparing the density of potential prey, there was a significant interaction (F = 38.54, df = 2 and 15, P = <0.0001) among territories according to which stream they were located on and if that reach of stream was protected or unprotected. The single most downstream and unprotected territory on Adds Creek had significantly more aquatic invertebrates (LSM = 311, SE = 17.6) than all other combinations of streams and protected and unprotected reaches. Territories on the unprotected reaches of Steele Creek also had a higher density of potential prey (LSM = 236, SE = 7.7) than territories on its protected reaches, unprotected reaches of Adds Creek, and territories on protected and unprotected reaches of Leatherwood Creek. Density in these two areas was driven by increased numbers of Diptera and pulmonate gastropods. No significant differences were found comparing biomass, however, excluding the mass of gastropods, a significant interaction was evident among streams and their status as protected or unprotected (*F* = 3.80, df = 2 and 20, *P* = 0.05) with the difference attributable primarily to the presence of 2 Tipulid larvae, 5.5 mg, found within the single most upstream and unprotected territory on Leatherwood Creek.

Comparing FBI also resulted in a significant interaction (*F* = 6.89, df = 2 and 20, *P* = 0.01) between territories on different streams and protected and unprotected reaches. Territories with the highest FBI, and thus those more likely to have organic pollution, were the single unprotected and most upstream territory on Leatherwood Creek and the single protected and most downstream territory on Adds Creek (Fig. 5.6). According to Hilsenhoff's (1988) evaluation of water-quality from the FBI, these waters would be rated as fairly poor with substantial pollution likely. The first territory on Adds Creek suffers from its downstream association with the length of unprotected stream above it. The lack of Ephemeroptera in the most upstream territory on Leatherwood resulted in its high FBI scoring. This is likely a result of its mostly boulder and bedrock channel structure. In addition, a large number of discarded automobiles are within the riparian area. Two storage buildings and automotive parts are within meters of the stream and inundated during periods of high flow. Territories on unprotected reaches of Adds Creek and Steele Creek had FBI scores indicating that organic pollution was significantly more likely compared to protected reaches of Leatherwood Creek and Steele Creek which had scores indicating organic pollution as unlikely.

Average family-level taxa richness, a measure of community structure through overall variety in the macroinvertebrate assemblage, showed a near significant difference ($F = 3.79$, df =1 and 20, $P = 0.07$) comparing territories on protected and unprotected reaches of streams. Territories on protected reaches averaged marginally more Family taxa (LSM = 19, SE = 1.2) than unprotected reaches (LSM = 16, SE = 1.2).

The EPT as a proportion of pollution-intolerant aquatic invertebrates to total assemblage of aquatic invertebrates showed a significant interaction ($F = 23.86$, df = 2 and 15, $P = <0.0001$) among territories according to which stream they were located on and if that reach of stream was protected or unprotected. The % EPT was found to be significantly higher in territories on the protected reaches of Steele Creek compared to all others (Fig 5.7). Territories on unprotected reaches of Steele Creek averaged a significantly higher % EPT than those on unprotected reaches of Adds Creek and protected reaches of Leatherwood Creek. The most downstream and only protected territory on Adds Creek had only 4 Ephemeroptera and 11 Plecoptera within its sample, while the uppermost and only unprotected territory on Leatherwood Creek was low as well with only Plecoptera and Trichoptera present, likely as a result of its boulder and bedrock channel structure.

The greatest number of all EPT taxa belonged within the Order Plecoptera. Comparisons of percentages of Plecoptera taxa resulted in a significant interaction ($F = 29.56$, df = 2 and 15, $P = <0.0001$) among territories according to which stream they were located on and if that reach of stream was protected or unprotected. Territories on protected reaches of Steele Creek had a significantly greater percentage of Plecoptera compared to others (Fig. 5.8). Plecoptera in this area were distributed within 6 taxonomic families (Fig. 5.9). Territories on protected reaches of Leatherwood and unprotected reaches of Adds Creek were similar and had significantly higher percentages of Plecoptera taxa compared to the unprotected reach of Steele Creek. The single most upstream and unprotected territory on Leatherwood and territories on unprotected reaches of Adds Creek averaged 18 and 19% Plecoptera within 6 and 4 families, respectively. The territories upstream and within unprotected reaches of Steele Creek averaged only 15% of taxa in the Order Plecoptera within 4 families. Leatherwood Creek territories were the only ones which had aquatic invertebrates in the two Family taxa with lowest pollution-tolerance values. The only protected and most downstream territory on Adds Creek averaged only 6% Plecoptera.

The percentage of Ephemeroptera was significantly different according to the different streams where territories were located ($F = 22.05$, df = 2 and 15, $P = <0.0001$). Steele Creek averaged a significantly greater percentage of Ephemeroptera than both Adds Creek and Leatherwood Creek. Baetidae, a Family that consists of several species that are moderately tolerant of nutrients (Justus et al. 2010), made up the greatest percentage of Ephemeroptera (Fig. 5.10) within territories on Adds Creek (52.8%) and Leatherwood Creek (39.5%), compared to Steele Creek (36%). Leptophlebiidae made up 51% of Ephemeroptera on Steele Creek.

There were not large numbers of Trichoptera where Trichoptera were found, and Adds Creek almost entirely lacked the Order, thus sample sizes were small and comparisons could only be made among streams or among status with no testing for interaction. Marginal significant differences were found in the percentage of Trichopterans among territories on the different streams (*F* = 3.25, df = 2 and 15, *P* = 0.06) or those on reaches of protected and unprotected status (*F* = 2.61, df = 1 and 15, *P* = 0.12). The differences in the distributions of Trichoptera families are interesting to note. Leatherwood Creek had 1.9 % of its taxa within the Order Trichoptera with 10 Families represented (Fig. 5.11). Steele Creek had 1.1% of its taxa within the Order Trichoptera with 6 Families represented, while territories on Adds Creek had only two individual Trichoptera found which belonged within the Families Philopotamidae and Hydroptilidae.

Significant differences were found among proportions of pollution tolerant taxa, Class Gastropoda and Order Diptera. Territories on the unprotected reach of Leatherwood contained no gastropods and only two individuals were collected in territories on its protected reaches. Comparing protected and unprotected reaches on Adds Creek and Steele Creek, a significant interaction was found (*F* = 50.94, df = 2 and 15, *P* = <0.0001). The single protected and most downstream territory of Adds Creek had a significantly greater proportion of gastropods. It was followed by territories on the unprotected reaches of Steele Creek and Adds Creek. Near significant differences were found comparing the number of gastropods within territories on protected and unprotected reaches of Steele Creek with unprotected reaches supporting greater numbers of Gastropod taxa. The majority of gastropods were classified within Family Physidae and found in the territories of Steele Creek with decreased canopy cover and increased nutrient enrichment and in the single most downstream and unprotected territory of Adds Creek.

There was a significant interaction (*F* = 18.95, df = 2 and15, *P* = < 0.0001) among territories according to which stream they were located on and if the reach of stream was protected or unprotected when comparing proportions of Diptera. Family Chironomidae were most common within the order (Fig. 5.12). Thus differences found comparing Diptera were mirrored when comparing percentages of that Chironomidae with a significant interaction found among territories on the different streams and protected and unprotected reaches of those streams (*F* = 22.17, df = 2 and 15, *P* = < 0.0001). Territories on unprotected reaches of Adds Creek and the single most downstream and protected territory on Adds Creek had significantly greater percentages of Chironomid taxa followed by the unprotected reaches of Steele Creek (Fig. 5.13). Territories on the protected reach of Steele Creek and the single, most upstream territory on Leatherwood Creek had significantly fewer Chironomidae than all others.

Nest Success

I monitored a total of 14 nests on Adds Creek, 15 on Leatherwood, and 23 on Steele Creek from 2006 through 2008 for a total of 52 nests and 649 nest days. No significant differences in nest success were found for streams (χ 2 = 0.83, df = 2, *P* = 0.66) and years (χ 2 = 3.0, df = 2, *P* = 0.22) or protected and unprotected reaches (χ 2 = 0.83, df = 2, *P* = 0.66) and years (χ 2 = .0,45 df = 2, *P* = 0.50). The overall estimate of daily nest survival was 0.9538 (95% CI = 0.9347 – 0.9347) with a probability of success throughout the nesting period of 0.3367 (95% CI = 0.2113 – 0.4676).

Territory Fidelity:

I monitored a total of 9 territories on Adds Creek, 6 on Leatherwood, and 10 on Steele Creek from 2006 through 2008. As a result of the loss of territories in 2007 a total of 47 observations were made overall. In 2007, with the possibility of 24 territorial males returning to their original territories of the previous year, 83.3 %, SE = 7.6 %, returned. In comparison 74%, SE = 9.2 %, of territory holders returned in 2008. Of males that returned, 100% reoccupied the territory they held the previous year. There was not a significant difference (*F* = 0.61, df = 1 and 45, *P* = 0.45) in return rate in 2007. Of the four territories that did not have the original territory holders returning to them in 2007, two were occupied by new recruits to the population and two were never reoccupied. Of the 6 territories that did not have males returning to them in 2008, 3 were occupied by new recruits and 3 were never reoccupied. Thus, a total of 5 territories were lost from the population in 2007 and 2008. Ignoring the effect of year, no significant differences in territory fidelity were found between territories on protected and unprotected reaches of streams (*F* = 1.08, df = 1 and 45, *P* = 0.31). Eighty-six percent (SE = 7.6 %) of males returned to territories on protected reaches compared to 73 % (SE = 8.7 %) on unprotected reaches. However, of the 10 instances when males did not return to their territory, 7 had their territories on unprotected reaches, and, of those, 4 territories were lost entirely from the population. There were also no significant differences among streams (*F* = 1.55, df = 2 and 44, *P* = 0.22), though Least Squares Means showed a marginal significant difference between returns to Leatherwood Creek (LSM = 91.7 % SE = 7.98%) and both Adds Creek (LSM = 64.7 % SE = 11.6 %) and Steele Creek (LSM = 83.3 % SE = 8.78%). Of those territories lost entirely from the population 2 were lost Adds Creek and 3 were lost from Steele Creek

Functional Relationships in Length of Territories and Ecological Integrity

Significant functional relationships were observed modeling length of Louisiana Waterthrush territories on perennial stream reaches with variables indicative of stream biotic integrity and habitat quality (Table 5.3). The model that best explained variation in territory length predicted that, on average, length changed with percentage of pollution intolerant taxa (Plecoptera and Trichoptera) and canopy cover. As ratios of Plecoptera and Trichoptera to total macrobenthos abundance along with the percentage of shading by canopy cover decreased, the length of territory on the perennial reach was predicted to increase (Fig 5.14).

A second model, similar in its explanation of variation (Table 5.3), showed a similar, though inverse, relationship between the length of territories and the percentage of pollution-tolerant taxa and canopy cover. As the ratio of Chironomid taxa to total macrobenthos abundance increased and the percentage of shading by canopy cover decreased, Louisiana Waterthrush territories were predicted to be longer (Fig. 5.15). A single model could not support both the partial regression coefficients of pollution tolerant taxa (Plecoptera and Trichoptera) and pollution intolerant taxa (Chironomidae) because of their inverse relationship and collinearity between the two variables.

The third and fourth models included common bioassessment metrics, Family Biotic Index and % EPT, along with percentage canopy cover (Table 5.3). Including Ephemeroptera into the ratio of Plecoptera and Trichoptera to total macroinvertebrate taxa did not improve the fit of the model (Fig 5.16), but did result in a similar significant relationship predicting decrease in the length of territories with increase of % EPT taxa and decreased canopy cover. Family Biotic Index assesses the degree of organic pollution found within streams based upon the macroinvertebrate taxa found there (Hilsenhoff 1988). As the metric increases it signifies a decrease in water quality as a result of organic pollution. The method of calculating this metric results in a high potential for its collinearity with other variables of ratios of macrobenthos abundance, % EPT, % Chironomid taxa, and separate calculations of ratios of Ephemeroptera, Plecoptera, and Trichoptera taxa. Though this model did not explain as much variation as the others (Table 5.3), increases in Family Biotic Index, and thus increases in the amount of organic pollution along with decreases in canopy cover predicted increasingly longer reaches of perennial stream within Louisiana Waterthrush territories (Fig 5.17) in a way similar to that of percentage taxa intolerant and tolerant to organic pollution.

A significant functional relationship was not found between the total lengths of territories (including adjacent intermittent streams) with variables indicative of stream biotic integrity and habitat quality. In addition, a simple linear relationship was not found between the length of territory on the perennial stream and the length of the length of the adjoining intermittent stream of that same territory (Fig 5.18). Comparisons of prey availability on the main perennial stream and adjacent intermittent streams during periods of high water and increased flow showed a significant differences in density (F = 14.36, df = 2 and 139, P = <0.001) as a result of a large number of small Diptera larvae within Adds Creek and no significant differences in mass (F = 1.63, df = 5 and 72, P = 0.17).

Discussion

Attributes of stream ecological integrity, as measured by bioassessment metrics calculated from aquatic invertebrate prey available to Louisiana Waterthrushes through leaf-pulling, differed among Louisiana Waterthrush territories according to their location on three streams in the watershed of the upper Buffalo National River and according to the location of the territories on legally protected and unprotected reaches of those streams. Territories on unprotected reaches exhibited significantly greater degrees of organic pollution according to Hilsenhoff's FBI, significantly higher percentages of pollution-tolerant taxa, significantly lower percentages of some pollution-intolerant taxa, and were marginally lower in taxa richness. It was also on unprotected reaches that, as anthropogenic activities continued unchecked across years, Louisiana Waterthrush territories disappeared entirely along their lengths.

Louisiana Waterthrush territories were significantly longer on the stream with the least protection, and territories on unprotected reaches tended to be marginally longer than those on protected reaches. No significant differences were found comparing nest success and site fidelity of males on the three streams and protected and unprotected reaches. The lack of significant differences in nest success among birds on different streams and reaches, along with the longer territories being found in more degraded areas, suggests that Louisiana Waterthrushes may be compensating or adjusting to stream habitat and quality and availability of food resources by increasing lengths of territories so that fitness is not strongly affected (Fretwell and Lucas 1970, Feck and Hall 2004, Mulvihill et al. 2008). Strong territory fidelity is common in male passerines which establish and defend breeding territories annually (Greenwood 1980). Knowledge of the previous year's territory and previous establishment of boundaries among neighbors reduces the energy required for initial breeding territory establishment (Godard 1991). Thus, economically, males may be better served if they return to a territory previously established if reproductive success is possible there.

Multiple regression models, associating Louisiana Waterthrush territory length to bioassessment metrics, resulted in predictions of increasingly longer territories as stream ecological integrity decreased. Bioassessment metrics retained in these models included percentage pollution-tolerant taxa, percentage pollution-intolerant taxa, FBI, and percentage canopy cover. Bioassessment metrics tended to be collinear, thus multiple models were created including only those metrics that could be fitted without collinearity.

Canopy cover was a significant factor in all models and predicted longer territories as the percentage of shading by canopy cover decreased. This was expected based upon knowledge of importance of forest to the bird's presence (Robinson 1995, Prosser and Brooks 1998). The most parsimonious models for explanation of Louisiana Waterthrush territory lengths were percentages of pollution-tolerant Chironomidae larvae and percentages of pollution-intolerant Plecoptera and Trichoptera to total macrobenthos abundance. These variables, indicative of degraded and undegraded water-quality conditions, had a strong inverse relationship with one another, and thus could not be modeled together. Modeling them separately along with % canopy cover, I found that when the % Chironomidae taxa increased and % canopy cover decreased, territories were predictably longer. Modeling the percentage of pollution-intolerant taxa, % Plecoptera and % Trichoptera, along with % canopy cover predicted a decreasing length of territories as the pollution-intolerant taxa and canopy cover increased.

Modeling % EPT, i.e. including % Ephemeroptera, resulted in a similar functional relationship to that found in the model using % Plecoptera and % Trichoptera as independent factors. However, there was a decrease in this model's ability to predict variation in territory length. The applicability of the EPT index to the tributaries of the Buffalo National River has been debated (Mathis 2001, Bowles et al. 2007, Pers. Comm. Bacon 2011). Water resource managers from the National Park Service, Buffalo National River, have chosen to exclude Ephemeroptera from their bioassessment metrics (Bowles et al. 2007). Their argument for this exclusion is that the greatest proportions of Ephemeroptera found in the region are relatively pollution intolerant, and that calculation of EPT indices are misleading. Instead, calculations of the most pollution sensitive taxa, the Trichoptera, along with Plecoptera, are better indicators of water quality within the geographical area. Modeling FBI values, useful for detecting organic pollution and based upon ascribing pollution tolerance scores to different aquatic invertebrate taxa, along with % canopy cover, explained a similar amount of variation as the model with % EPT and also predicted increasing lengths of territories as organic pollution increased and canopy cover decreased.

Studies comparing populations of Louisiana Waterthrushes on acidified and circumneutral streams in southeastern Pennsylvania, found that territories on streams degraded by acidification were twice the length of those on circumneutral streams (Mulvihill et al. 2008). They also found no significant differences in reproductive success or daily nest survival, though birds breeding on acidified streams tended to have smaller clutches. In the Georgia Piedmont, Louisiana Waterthrush nest survival was predicted to be greatest during periods of intermediate rainfall within a season and nestling survival rate was predicted to be lowest in large territories with fewer riffles (Mattsson 2006).

My findings on territory fidelity were also similar to those of Mulvihill et al. (2008) in that degraded streams had gaps in occupancy along their length, while less degraded areas had a greater density, and territories abutted one another. However, in their study, males and females exhibited marginal differences in site fidelity with decreased fidelity to acidified streams. I did not find significant differences in male territory fidelity, though the greatest percentage of territories where males were replaced by new recruits and where territories were lost entirely from the population were on unprotected reaches. After the first year of study, I felt that banding of females might be affecting their fidelity to territories chosen on spring arrival, and, thus, I did not band and follow females as closely across years as I did males, thus, there may have been undocumented differences in fidelity among females in my study area.

Measures of riparian habitat quality have previously been found to be correlated to the presence or absence of Louisiana Waterthrushes. Biotic indices predictive of presence and absence have included % of Plecoptera and Trichoptera taxa and % riffle habitat in southeastern Minnesota (Stucker 2000), and % EPT, FBI, and biomass of macrobenthos in conjunction with riffle and other habitat variables in the Georgia Piedmont (Mattsson and Cooper 2006, Mattsson et al. 2009b). My results are most similar to those of Mulvihill et al. (2008) in studies of Louisiana Waterthrushes in southwestern Pennsylvania where a significant relationship was found between breeding density and % EPT when two genera of Plecoptera with high tolerances to acidity were excluded from analysis (Mulvihill et al. 2008). My results are similar to those of Stucker (2000) in that the more important of the EPT taxa were the Plecoptera and Trichoptera, but differ from Mulvihill et al. (2008) in the theoretical importance of Ephemeroptera to the diet of Louisiana Waterthrushes. This may be a result of differences in location, taxa, and the stressor on water quality being acidity in the Pennsylvania region while organic pollution and sedimentation was the major stressor in the Buffalo National River watershed.

Louisiana Waterthrushes may develop a preference for certain taxa based upon abundance and/or nutritional quality of the available prey. The effect of prey quality and its effect upon sizes of territories has been less often studied than food abundance (Maher and Lott 2000). Presence, absence, and size of American Dipper territories have been shown to be affected by relative abundances of preferred prey rather than bioassessment variables such as % EPT and total invertebrate abundance. Territory area decreased as the abundance of preferred prey, Trichoptera, *Drunella* and Heptageniidae, increased (Feck and Hall 2004). Craig (1984, 1987) reported that Louisiana Waterthrushes in Connecticut preferred ephemeropterans, trichopterans, and dipterans although they maintained a wide range of diet.

In my study, more degraded and thus marginally longer territories contained greater percentages of chironomid taxa. Chironomid larvae are small, but when found, they are often numerous. This can be true of EPT taxa as well, if they are found in earlier instars, however, they have greater potential to be larger prey items than Chironomids. Optimal foraging theory (Schoener 1971, Pyke et al. 1977) predicts that an optimal diet will maximize the net rate energy intake of the forager and thus increase its fitness. Choice of what an animal eats depends upon the energy available within a prey item and the energy it takes to handle (pursue, subdue, and consume) that prey type. Thus the food value of each prey is a ratio of calories consumed to calories spent (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). Prey items are ranked according to their profitability and when calories are unknown, they are ranked according to size so that an optimum diet can be calculated. A predator should have a broader diet in a less productive environment (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977).

Ranking Louisiana Waterthrush prey by size would place the Chironomidae into the category of least productive prey type because of their small size, while Tipulidae and Trichoptera would likely be the more profitable prey. Additionally, foraging upon multiple small chironomids would result in an increased number of foraging maneuvers, while taking larger prey, such as Tipulidae or Trichoptera, would result in devotion of more time to prey handling. In my study degraded territories characterized by greater percentages of Chironomidae were longer. This may be a result of increasing territory size to increase the probability of finding preferred prey, such as EPT taxa and perhaps Tipulidae larvae. Longer territories would be more costly in terms of handling time in that birds must spend more time traveling to find sufficient prey and, if nesting, must travel further to and from the nest. This may affect a bird’s fitness and the fitness of their offspring in ways that were unmeasured in my study (MacArthur and Pianka

1966, Schoener 1971, Pyke et al. 1977). It should also be considered that prey switching may occur with changes in abundances of prey types (Murdoch 1969). Predators tend to eat a larger percentage of a common prey type and as they do they increase their efficiency at doing so. This may be a result of the development of a search image for that type prey (Tinbergen 1960).

My study concentrated on prey available to the Louisiana Waterthrush as a result of a unique foraging maneuver, leaf-pulling, during the early part of the breeding season when birds have been shown to more often employ the maneuver (Craig 1984, Robinson 1990). Yet, they also use other foraging maneuvers, of which picking is the most common. Therefore, the samples that I took are biased to prey associated with leaves and leaf packs. They may differ somewhat from prey found directly within the benthic substrate with leaves likely supporting greater numbers of shredding macroinvertebrate taxa along with macroinvertebrates seeking refugia within the leaves. In addition shredding macroinvertebrate taxa tend to show a preference for certain leaf species (Finni 1973, Reice 1978, Cummins et al. 1980, Peckarsky 1980, Reice 1980, Murphy et al. 1998). In addition to this, my methods of weighing macroinvertebrates for comparisons of biomass may be biased as a result of my using a 70% ethanol solution to store the samples previous to drying and weighing. Alcohol preservation affects mass by dissolving fats**.** Additionally, different taxa lose mass in this way to different degrees (Howmiller 1972, Stanford 1972, Dermott and Patterson 1974, Donald and Patterson 1977, Leuven et al. 1985, Wetzel et al. 2005). Correction factors for this loss of mass do not exist for many taxa and thus, I made no effort to correct for only a percentage of the collection. Lastly, because of small sample size and the many differences that occur within and among streams in different ecological regions, results should be interpreted with caution.

In my models, the presence of pollution tolerant and intolerant taxa and the amount of shading within territories did not explain all variability in lengths of territories. Sizes of territories and other spacing mechanisms are generally determined by multiple factors with no one accounting for all variance (Maher and Lott 2000). Ecological variables are often considered separately from behavioral variables. Behavioral characteristics of territory owners can also be an important component in the spacing systems. In order to incorporate behavioral mechanisms measurements, as suggested by Pyke et al. (1996), the degree of aggression used by individuals in territorial behavior should be measured, along with the sharpness of maintained boundaries between territory holders, and the exclusivity of the use of resources within a territory.

Additional ecological variables used to explain variability in lengths of territories include channel structure, number of riffles present within each territory (Stucker 2000, Mattsson 2006), propensity of headwater streams to become increasingly intermittent as the breeding season progresses, the amount and structure of vegetation found adjoining the stream corridor and characteristics of its substrate (Eaton 1958, Smith 1977, Craig 1981, 1984, Robinson 1990).

Differences in channel structure (Brussock et al. 1985) were likely the most important factor in differences in biota and bioassessment metrics found comparing the single most upstream and unprotected territory in my study to all others. In the most upstream territory on Leatherwood Creek boulders were very large, and pools developed as a result of location of boulders and the location of associated accumulations of inorganic and organic debris similar to descriptions by Leopold et al. (1964) and Richards (1982). As a result pools and riffles were not consistently spaced. All other territories in the study had a channel structure with well-developed riffles and pools and abundant gravel, such that there was more variation in habitat and thus greater diversity in community structure (Brown and Brown 1984, Brussock et al. 1985).

Also, differences may have existed in the degree of intermittency in upstream territories as compared to downstream territories, and this may have resulted in differences in biota that could influence lengths of territories. Intermittent reaches have been reported to have lower densities and diversities of aquatic invertebrates (Brown and Brussock 1991), and a study in the headwaters of the Buffalo National River showed a distinct difference in community structure of perennial and intermittent streams (Dick 1998). Additionally, timing and degree of intermittency differ from year to year with precipitation, temperature, and evapotranspiration (Delucchi 1988, Feminella 1996, Dick 1998, Magoulick 2000). Intermittency appeared to be similar within territories along all the reaches of the study streams except for the territory that was located within the boulder and bedrock channel structure. Additionally, Louisiana Waterthrushes arrive prior to leaf-out and breeding activities occur during periods of high-water levels. In most cases, breeding pairs have fledged young prior to June and after fledging territory boundaries essentially disappear with birds wandering over larger areas and foraging more frequently within multiple habitats in addition to water. This suggests that additional measures of the riparian habitat such as herbaceous coverage, shrub density, and type of substrate could provide more insight into lengths of territories.

Other researchers have found number of riffles within a territory to be correlated to presence of Louisiana Waterthrushes as well as to their reproductive success (Stucker 2000, Mattsson 2006, Mulvihill et al. 2008). Additionally, Stucker (2000) found Louisiana Waterthrushes were more likely to be found in streams that were rockier and with more riffles. Such shallow streams would be important in increasing the number of foraging areas for Louisiana Waterthrushes. The amount of shallow or rocky habitat within streams has previously been incorporated into indices pertaining to accessibility of foraging microhabitat for Louisiana

Waterthrushes relative to water surface, depth of the water, and exposed submerged rocks and large woody debris (Master et al. 2005). Additionally, riffles are important to the relative abundances of Ephemeroptera, Plecoptera, and Trichoptera that are more commonly found within healthy stream reaches and riffle habitats (Brussock et al. 1985, Smith 1986, Brown and Brussock 1991, Kobayashi and Kagaya 2002, Roy et al. 2003). As a result, riffles may serve as important structural cues (Marshall and Cooper 2004) to Louisiana Waterthrushes whereby the structure of the habitat reflects potential prey availability (Smith and Shugart 1987).

Though I studied only three streams, 9 km of stream reach, and began with a population of 24 territories, the destructive activities within the unprotected reaches of those streams were consistent with reports of other researchers studying the Buffalo National River watershed across decades (Dale et al. 1978, Weeks 1987, Mathis 1990, Mott and Steele 1991, Scott and Smith 1994, Scott and Hofer 1995, Mott and Laurans 2004). Yet, little has been accomplished to end the continued degradation of the watershed (Mott and Laurans 2004).

Protected may be a misnomer for reaches of streams lying downstream of unprotected reaches. The most degraded territory in my study was the single protected and most downstream territory on Adds Creek, immediately adjacent the Buffalo National River. The entire length of Adds Creek above this protected territory is unprotected and territories there were also significantly degraded (higher FBI scores, higher ratios of pollution-tolerant taxa, and nearly totally lacking the most sensitive taxa in the EPT index, the Trichoptera). Contributions of pollution from unprotected reaches of Adds Creek collect as water moves downstream, driving the more substantial degradation of the territory most downstream, then, these waters move immediately into the Buffalo National River. This is indicative of contributions of other, similarly partially protected, reaches of streams throughout the watershed of the Buffalo National River.

The upper and unprotected reaches of Steele Creek were similar to the unprotected reaches of Adds Creek in having bioassessment values indicative of significantly higher levels of organic pollution. Adds Creek and Steele Creek differ from one another in the types of degradation they suffer and in the historical record of the degradation. The town of Ponca, Arkansas, whose homes and animal enclosures literally abut the very edge of Adds Creek's undercut stream banks, was established in the 1890s when zinc and lead ore was found and mined along its length (Liles 2006). Since then and today human habitation has subjected the stream to influxes of organic wastes from people and animals and increases in sedimentation as a result of gravel-mining above and within the stream. Residents continue to build up undercut banks with fill, usually clay, but do not maintain a planted riparian border. Thus, fill continues to be washed downstream during periods of high water. I had the opportunity to watch the effects of stream degradation across years on the upper reaches of Steele Creek as land was increasingly converted to pasture and cattle pastured within the stream.

The most important difference between Steele Creek and Adds Creek is the amount of protection afforded their length by the National Park Service. Adds Creek is only protected for 500 m before it joins the Buffalo National River. Steele Creek is protected for 1,234 m of its length prior to joining the Buffalo National River. Beginning in the upstream and unprotected territories of Steele Creek and moving progressively downstream, Family Biotic Index values continue to indicate significantly higher levels of organic pollution within the first protected territory and decrease further entering into the protected reaches of Steele Creek indicating significantly lower levels of organic pollution. Moving downstream, ratios of pollution-tolerant taxa, gastropods, dipterans, and Chironomidae became lower while percentages of pollution sensitive EPT taxa increased.

As Steele Creek moves into National Park Protection six small streams adjoin it before it reaches the Buffalo River. These streams originate from springs and tend to have some flow throughout the year with highest flow in winter and spring. All are within protected area and they may have a buffering effect upon the lower reaches and Louisiana Waterthrush territories of protected Steele Creek, which had significantly higher percentages of pollution-sensitive taxa than all other streams and reaches both including and disregarding the Ephemeroptera, which, in this geographic area, are ubiquitous and less sensitive to organic pollution compared to other pollution-intolerant taxa. These results are indicative of the importance of protecting greater percentages of watershed streams such that waters flowing into the Buffalo National River may be less polluted than when watershed streams are granted proportionally shorter lengths within National Park protection.

In the last year of study, the Buffalo National River experienced two “100-year” floods and another important attribute of these adjacent intermittent streams came to light. During the weeks following flooding and with continued high-water levels, birds were difficult to find within their territories along the main perennial streams. It became increasingly apparent that birds were foraging more often in the adjoining streams. This allowed the opportunity to take a relatively small sample of aquatic invertebrates from these streams and compare them to samples taken from the perennial stream they adjoined. The lack of differences between aquatic invertebrate biomass, density, and a similarity in taxa (Brown et al. 1997) between the main perennial streams and adjacent intermittent streams incorporated into territories during periods of high water suggest that adjoining streams can serve as an important source of prey availability during periods of high flow. These adjacent streams are poorly studied (Brown et al. 1997) in both the disciplines of stream ecology and in studies of Louisiana Waterthrushes, however, future study should not neglect to take into consideration their importance to the behavioral ecology of the Louisiana Waterthrush and the biota on which they depend.

Functional relationships between measures of stream ecological integrity and lengths of Louisiana Waterthrush territories suggest that Louisiana Waterthrush populations may be successfully incorporated into measures of stream ecological integrity in the Buffalo National River and its watershed. Multiple regression analysis does not establish causal relationships, but it does provide an exploratory tool for gaining insight into causal relationships and sets the stage for further research that can expand upon the original collection of data (Norris and Georges 1993), thus providing more information on the reasons for variation in an ecological variable such as the length of territories. Increasing the number of streams studied within the Buffalo National River watershed would decrease error and increase the power of the model to predict territory lengths and provide more in-depth information on the status of the many, largely unprotected, watershed streams. The models I have created also present a foundation for future manipulation of variables within the models through experimentation to establish and support causal relationships (Norris and Georges 1993). Additional studies of prey choice and diet width of Louisiana Waterthrushes would allow better explanations of how changes in abundances of pollution tolerant taxa (ex. Chironomids) and pollution intolerant taxa (ex. Plecoptera, Trichoptera, and Ephemeroptera) that occur with changes in water quality are reflected in Louisiana Waterthrush behavioral ecology.

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Table 5.1. Characteristics of Louisiana Waterthrush territories on protected and unprotected reaches of 3 streams within the Upper Buffalo National River Watershed

	Protected n = 10		Unprotected n = 10	
Territory	Mean	SE	Mean	SE
Length on Perennial Stream (m)	302.7	37.3	536.1	47.8
Total Stream Length$_a$ (m)	420.1	39.6	665.1	54.3
Intermittent Stream Width (m)	2.6	0.5	2.6	0.3
Perennial Stream Width (m)	8.6	0.6	8.5	1.2
Total Stream Area$_b$ (m^2)	3079.0	381.5	4853.8	501.8
Area of Perennial Stream (m^2)	2730.8	356.1	4439.3	1608.5
% Canopy Cover	89.6	1.6	72.2	6.8

a = Total length of territory including perennial and intermittent stream

b = Calculation from total length of territory and average bank-full widths of perennial and intermittent streams within a territory

Table 5.2. Characteristics of Louisiana Waterthrush territories on 3 streams within the Upper Buffalo National River Watershed

	Adds Creek n = 6		Leatherwood Creek n = 6		Steele Creek n = 8	
Territory	Mean	SE	Mean	SE	Mean	SE
Length on Perennial Stream (m)	597.5	61.3	294.9	52.8	379.2	47.5
Total Stream Length$_a$ (m)	704.2	64.3	365.0	97.5	554.6	55.4
Intermittent Stream Width (m)	2.5	0.6	2.5	1.1	2.8	0.1
Perennial Stream Width (m)	9.1	2.0	7.5	0.5	8.9	0.8
Total Stream Area$_b$ (m^2)	5432.4	688.3	2337.7	325.4	4088.4	304.6
Area of Perennial Stream (m^2)	5063.5	685.2	2145.9	364.3	3555.8	901.0
% Canopy Cover	67.8	9.6	92.6	1.9	81.8	4.5

a = Total length of territory including perennial and intermittent stream reaches

b = Calculation from total length of territory and average bank-full widths of perennial and intermittent streams within a territory

Table 5.3. Significant functional relationships modeling the length of Louisiana Waterthrush territories on perennial stream reaches with variables indicative of stream biotic integrity and habitat quality

	Model 1			Model 2			Model 3			Model 4		
Main Length	Coefficient	SE	P	Coefficient	SE	P	Coefficient	SE	P	Coefficient	SE	P
Intercept	990.0	176.6	<.0001	769.6	172.1	0.0004	1139.8	202.1	<.0001	568.0	210.6	0.0165
% Cc_a	-409.7	205.1	0.0656	-641.9	205.0	0.0069	-621.9	222.6	0.0136	-637.0	223.9	0.0123
% P_b	-573.1	202.9	0.0135	*	*	*	*	*	*	*	*	*
% T_c	-9089.6	3005.3	0.0091	*	*	*	*	*	*	*	*	*
% C_d	*	*	*	569.4	149.9	0.0018	*	*	*	*	*	*
% EPT_e	*	*	*	*	*	*	-534.3	170.2	0.0068	*	*	*
FBI_f	*	*	*	*	*	*	*	*	*	97.4	31.3	0.0071
	MSE = 12204			*MSE = 13756*			*MSE = 16283*			*MSE = 16377*		
	P =0.0014			*P = 0.0013*			*P = 0.0045*			*P = 0.0047*		
	Adj R2 = 0.5861			*Adj R2 = 0.5335*			*Adj R2 = 0.4478*			*Adj R2 = 0.4446*		

a = % canopy cover within territory

b = % Plecoptera within territory

c = % Trichoptera within territory

d = % Chironomid within territory

e = % Ephemeroptera, Plecoptera, and Trichoptera within territory

f = Family Biotic Index for territory

Figure 5.1. Map of the Buffalo National River and its watershed (Center for Advanced Spatial Technologies 2006; www.arkansaswater.com Accessed on 10/12/2011)

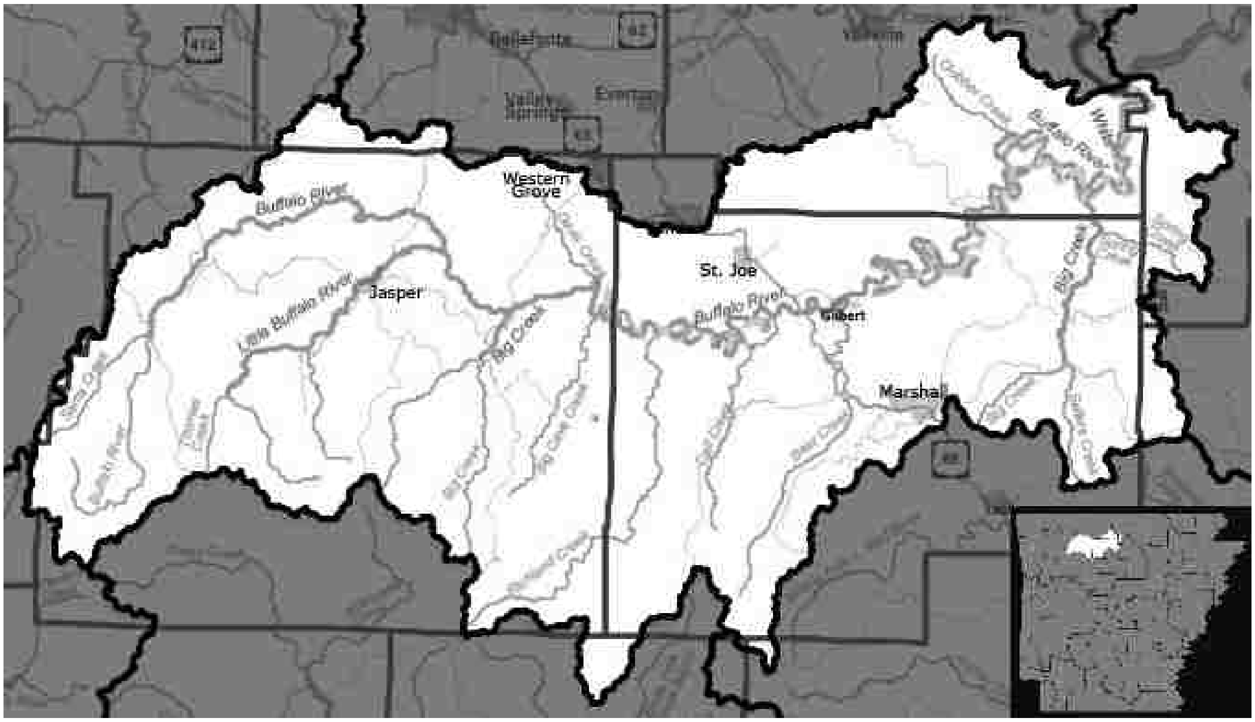


Figure 5.2. Map of the headwaters of the Buffalo National River with study area circled (Nominal Scale: 1:240,000; Center for Advanced Spatial Technologies 2006; www.arkansaswater.com Accessed on 10/12/2011)

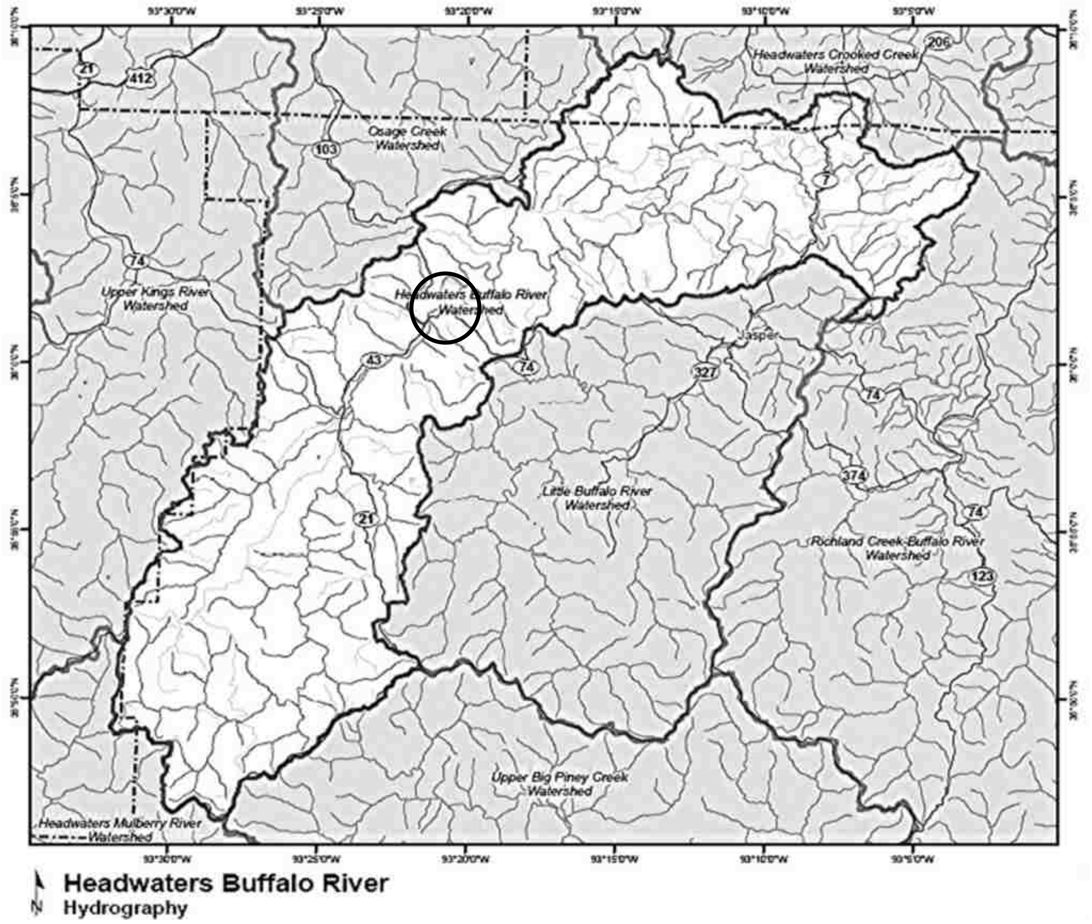


Figure 5.3. Adds Creek with Louisiana Waterthrush territories and territory boundaries. Numbering of territories begins with lowest numeral nearest confluence with the Buffalo National River. Circles illustrate placement of homes, livestock enclosures, and businesses that have their boundaries upon the riparian corridor. The National Park Boundary is marked with an arrow and lower territory numbers are within federally protected areas. GPS map detail = 500 m (Garmin Map Source 1999-2010, Version 6.15.11, Garmin LTD)

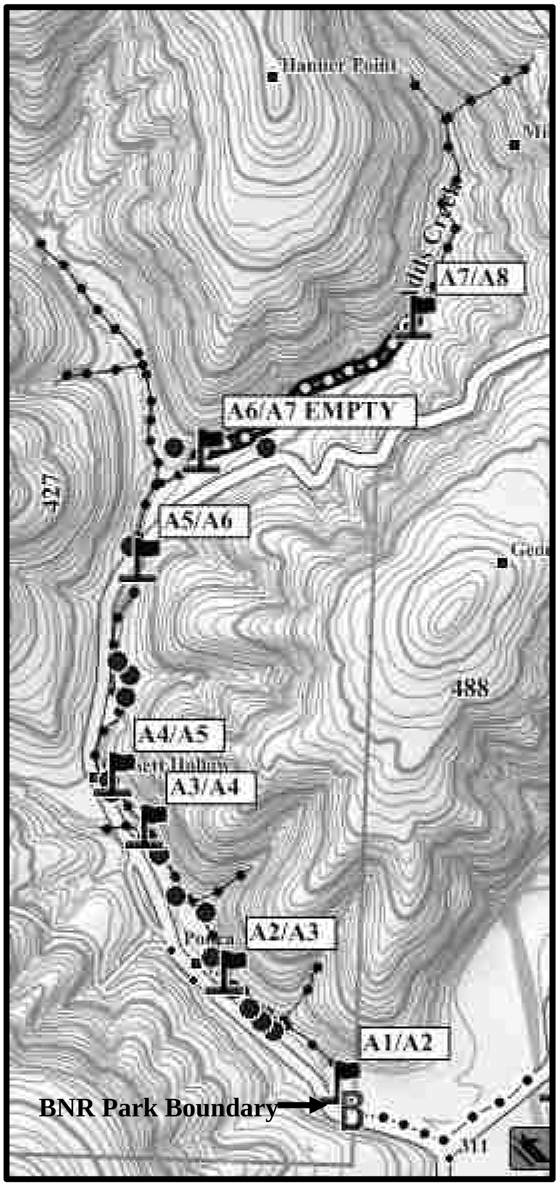


Figure 5.4. Leatherwood Creek with Louisiana Waterthrush territories and territory boundaries. Numbering of territories begins with lowest numeral nearest confluence with the Buffalo National River. Circles illustrate placement of automotive shop and storage buildings. The National Park Boundary is marked with an arrow and lower territory numbers are within federally protected areas. GPS map detail = 500 m (Garmin Map Source 1999-2010, Version 6.15.11, Garmin LTD)

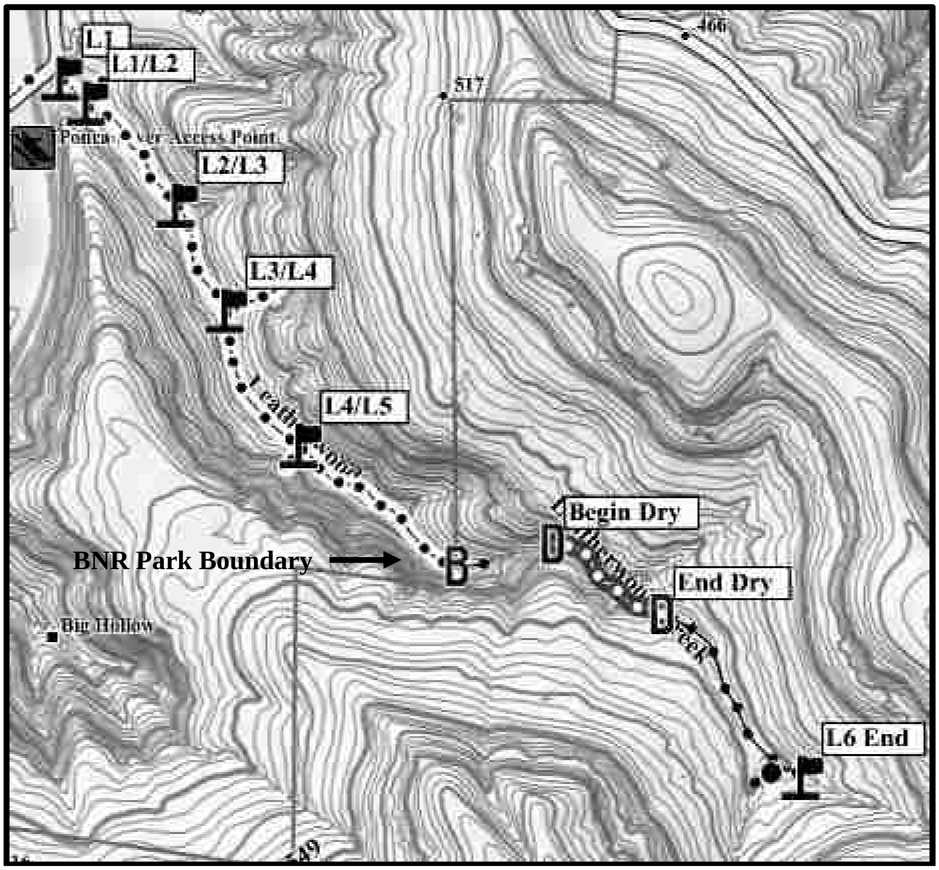


Figure 5.5. Steele Creek with Louisiana Waterthrush territories and territory boundaries. Numbering of territories begins with lowest numeral nearest confluence with the Buffalo National River. Circles illustrate placement of homes, barns, feedlots, and storage buildings. The National Park Boundary is marked with an arrow and lower territory numbers are within federally protected areas. GPS map detail = 500 m (Garmin Map Source 1999-2010, Version 6.15.11, Garmin LTD)

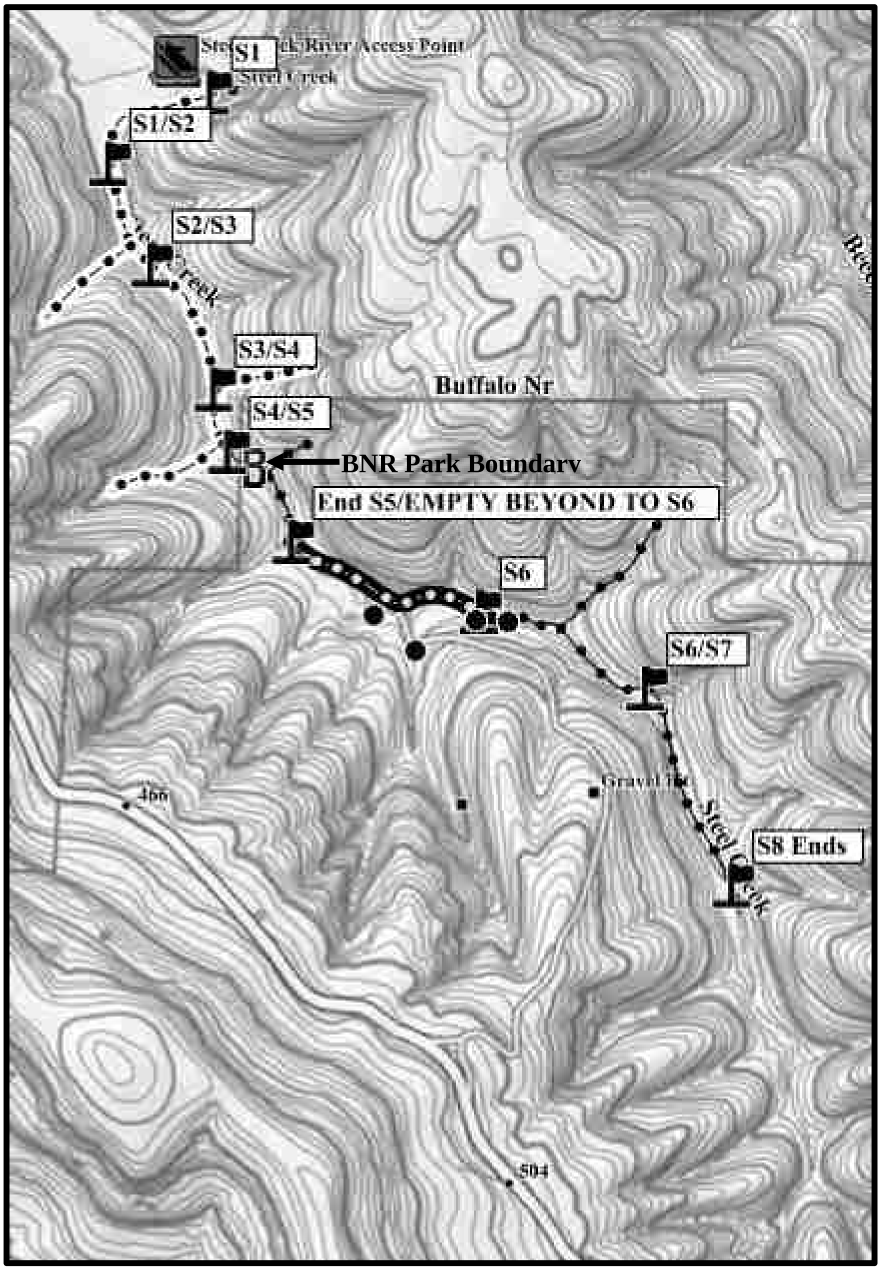


Figure 5.6. Least-squares means and SE of Family Biotic Index (FBI) of territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

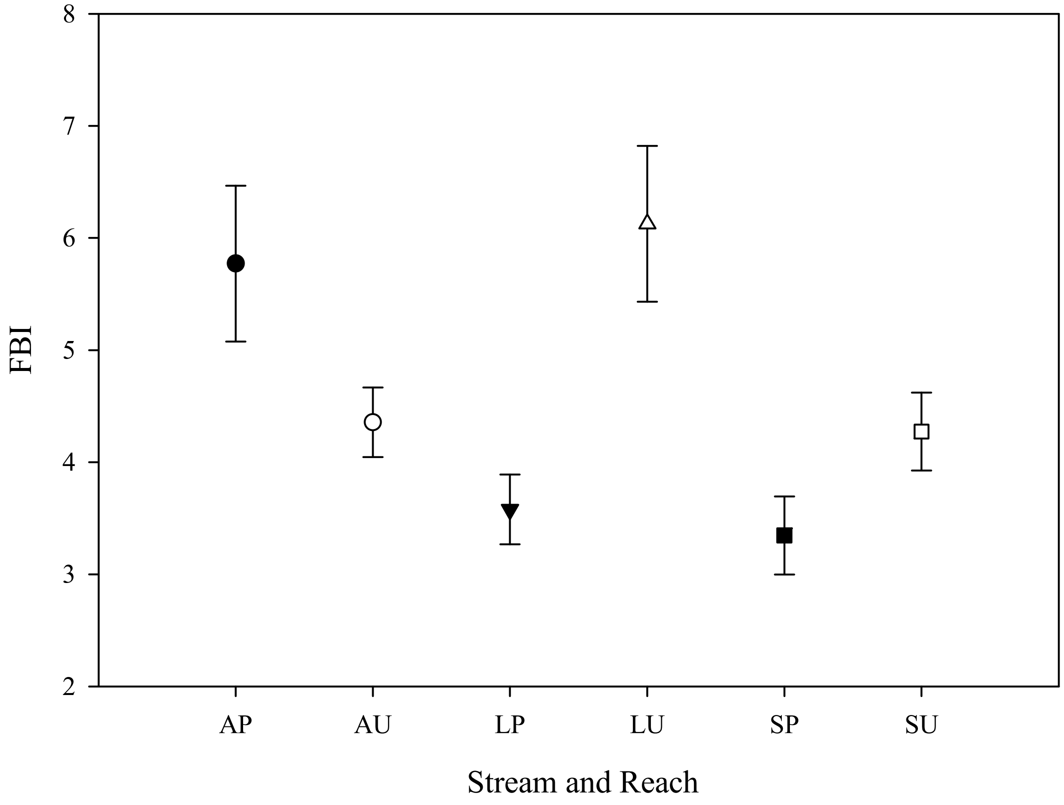


Figure 5.7. Percentage EPT of territories in three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

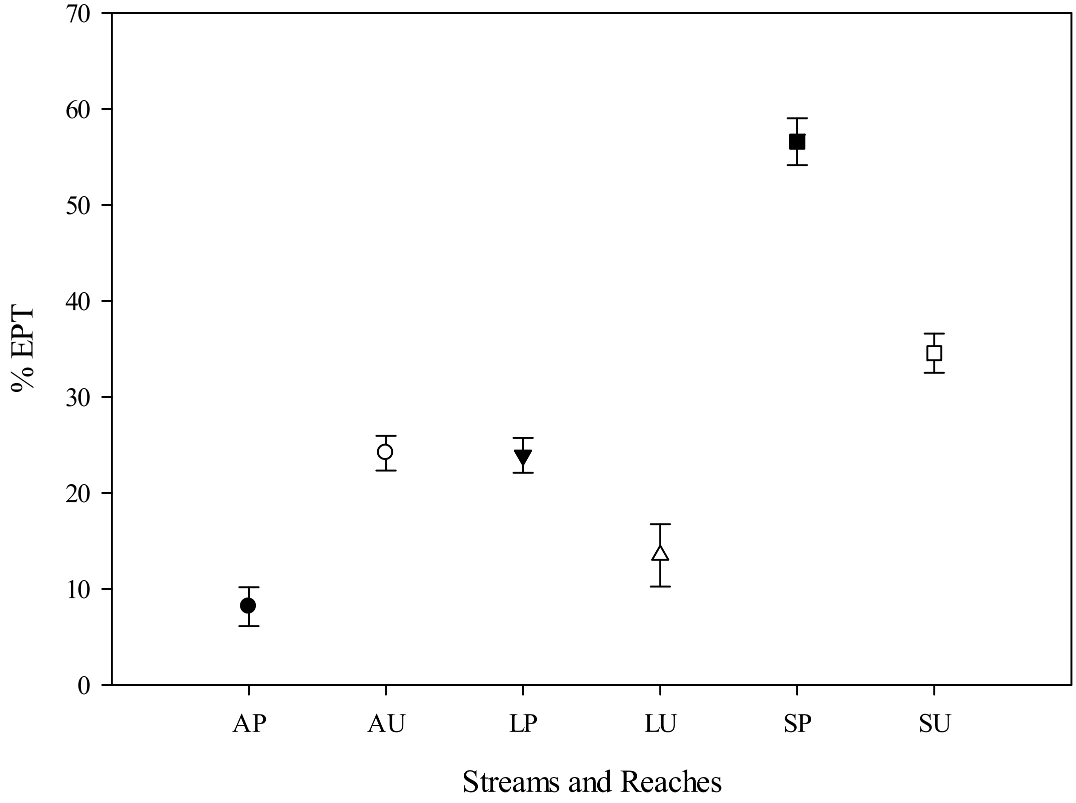


Figure 5.8. Percentage of Plecoptera in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

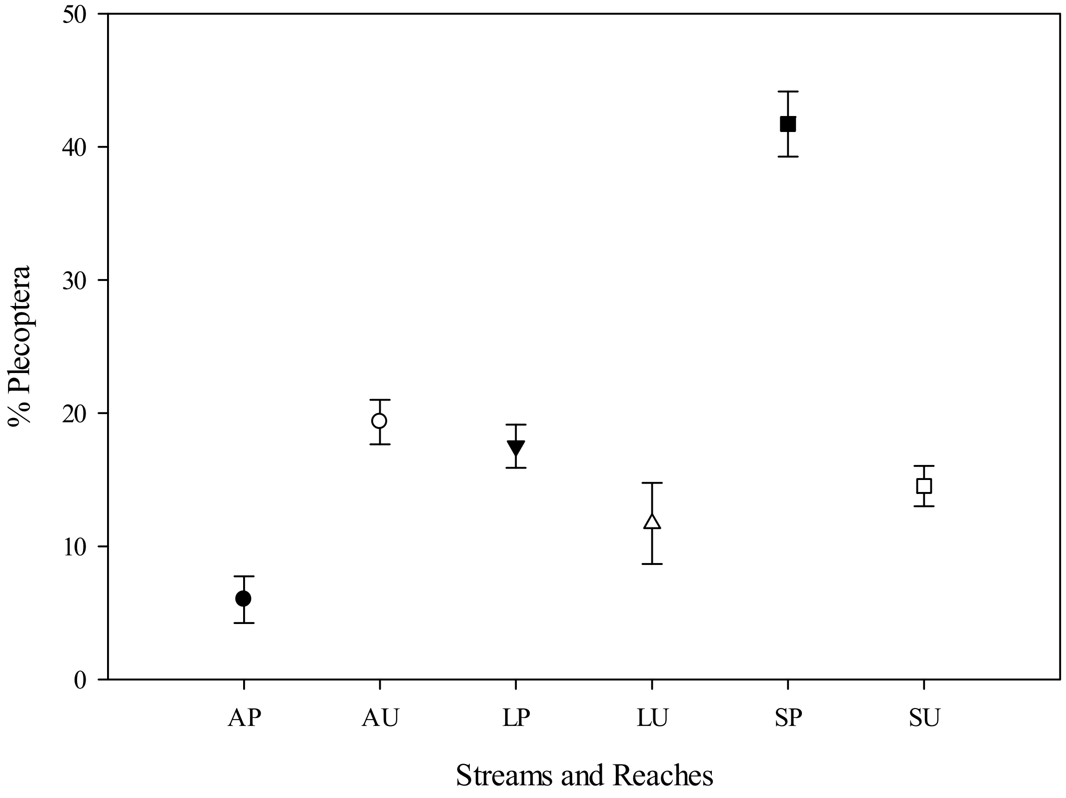


Figure 5.9. Count of individuals collected among Families of Plecoptera in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

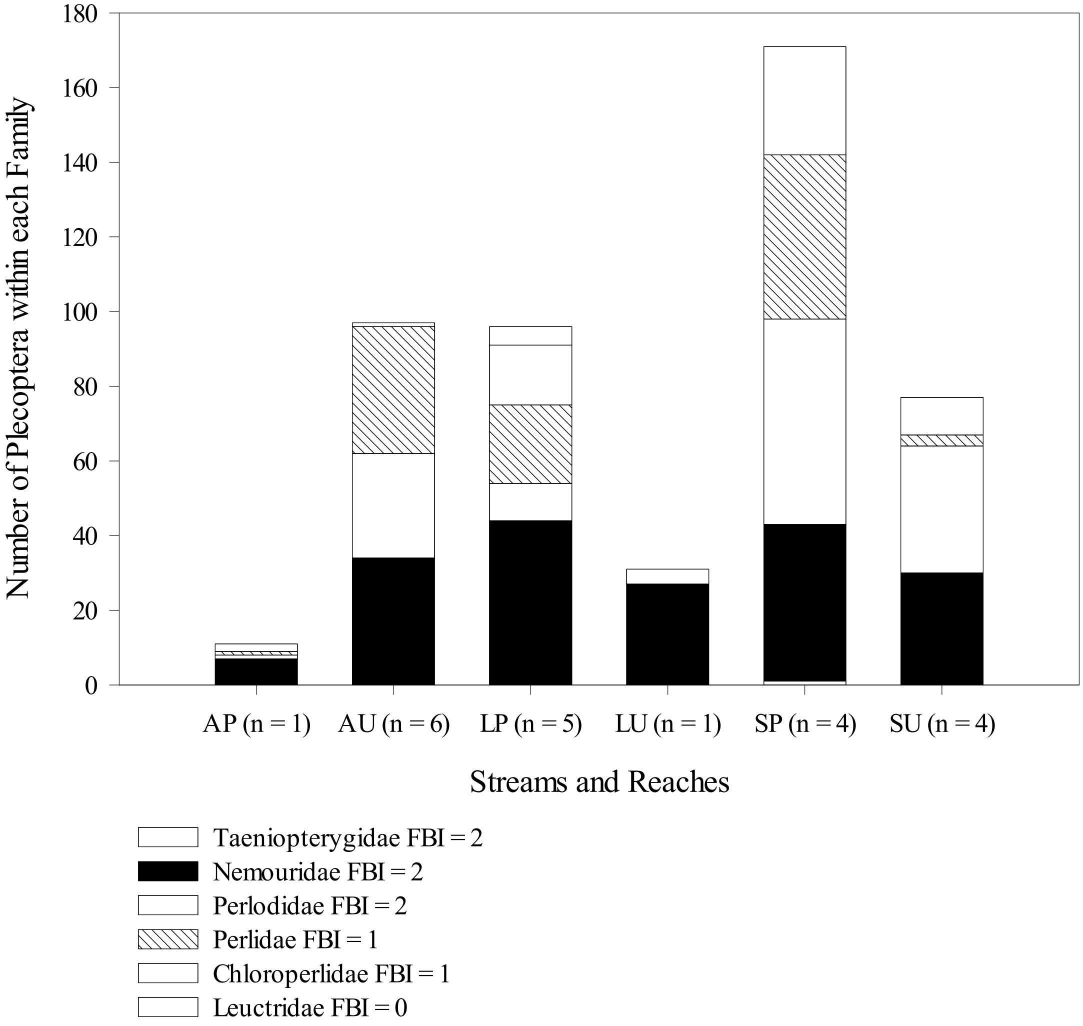


Figure 5.10. Count of individuals collected among Families of Ephemeroptera in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S). Families are illustrated along with family-biotic index values

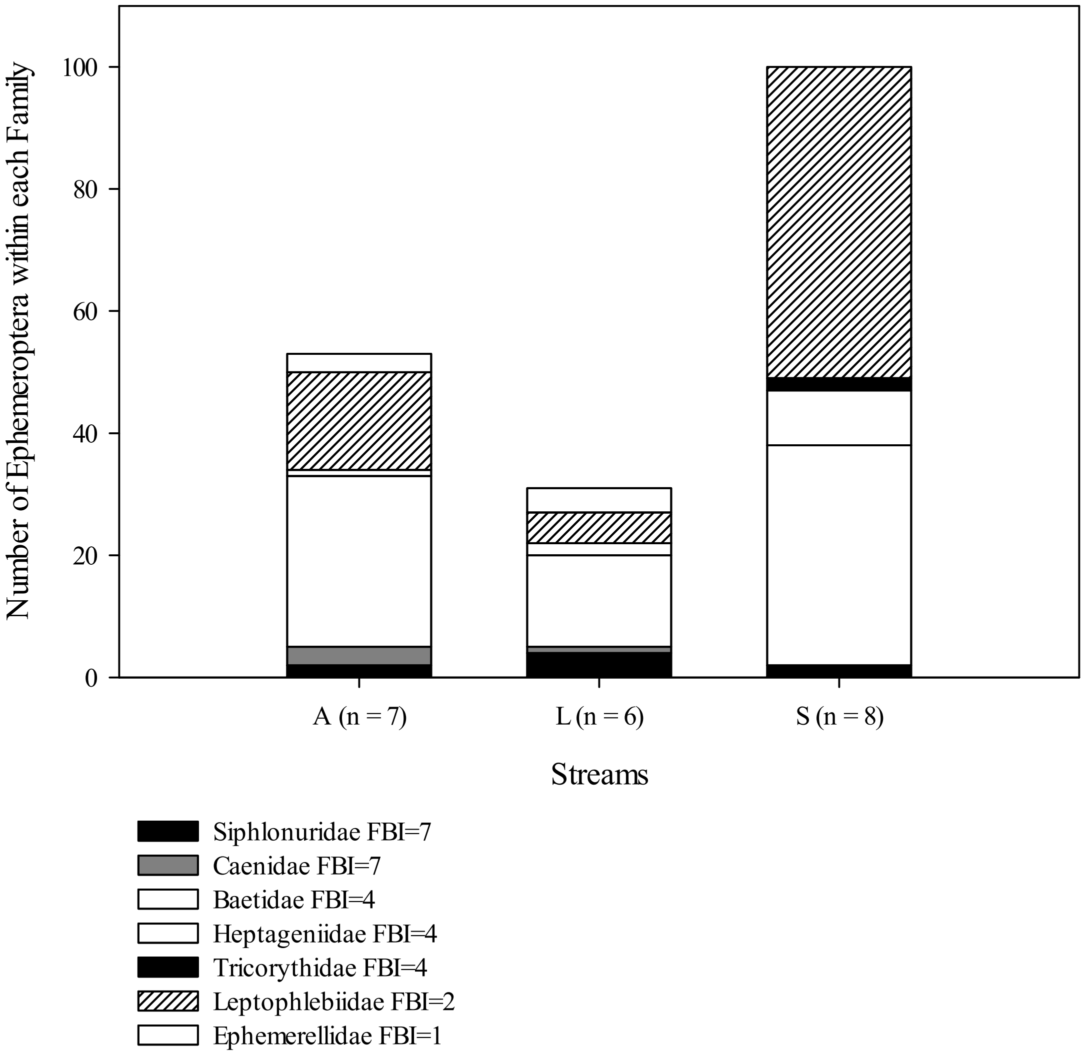


Figure 5.11. Count of individuals collected among Families of Trichoptera in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S)

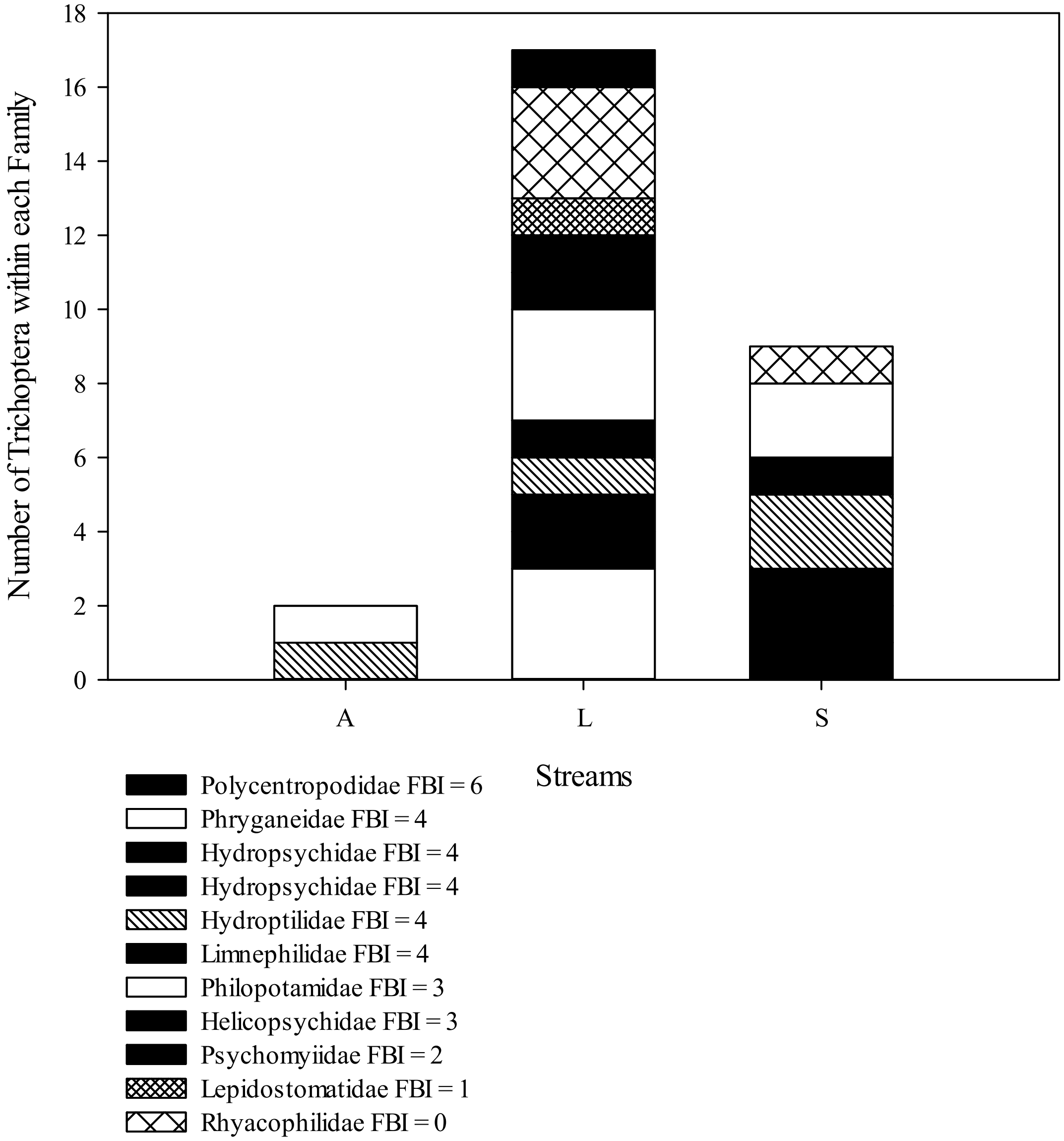


Figure 5.12. Count of individuals collected among Families within Order Diptera in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

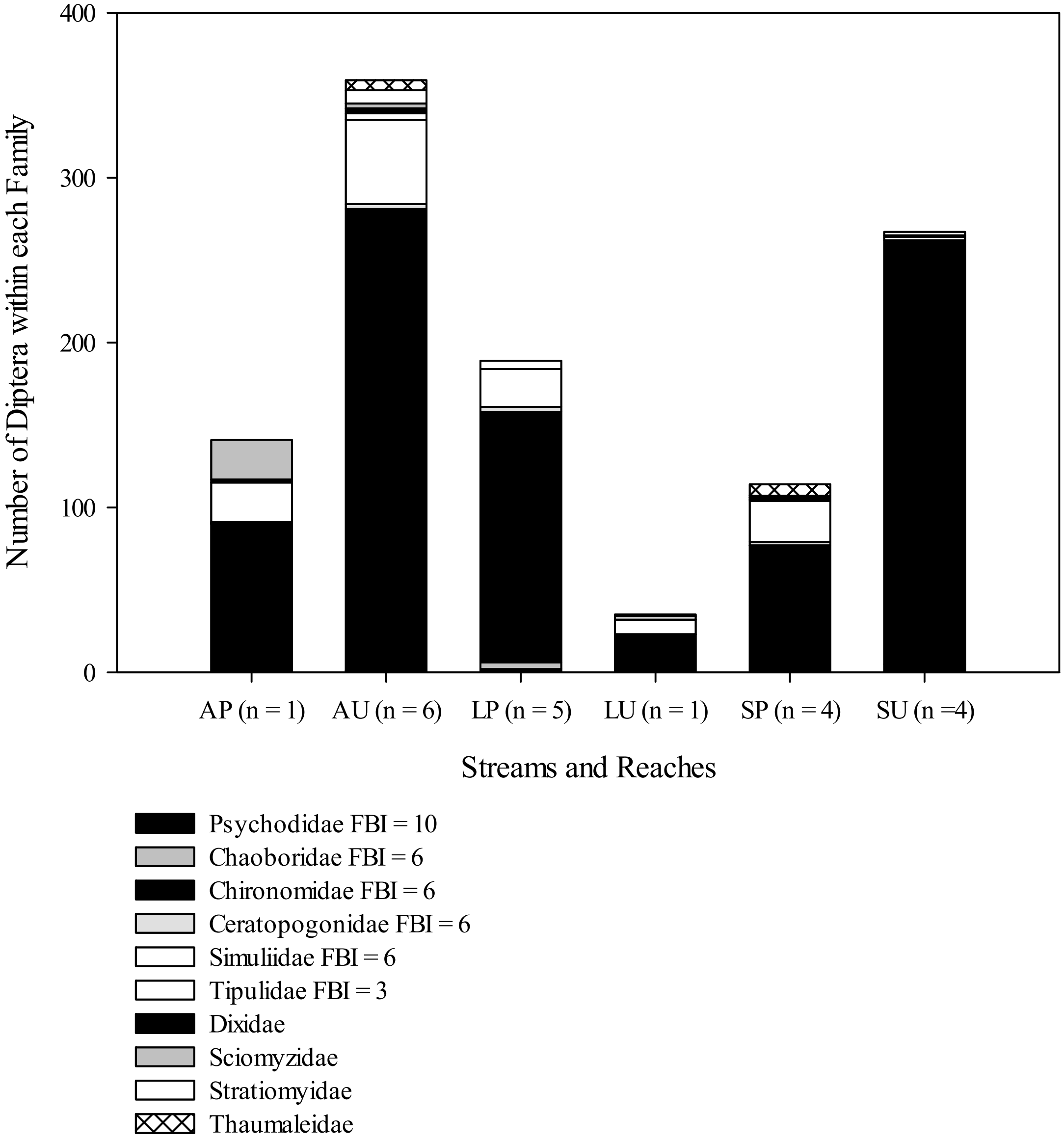


Figure 5.13. Percentages of taxa in the Order Chironomidae found in territories on three streams (Adds Creek = A, Leatherwood Creek = L, and Steele Creek = S) and reaches either within the Buffalo National River's boundaries (P = protected) or outside those boundaries (U = unprotected)

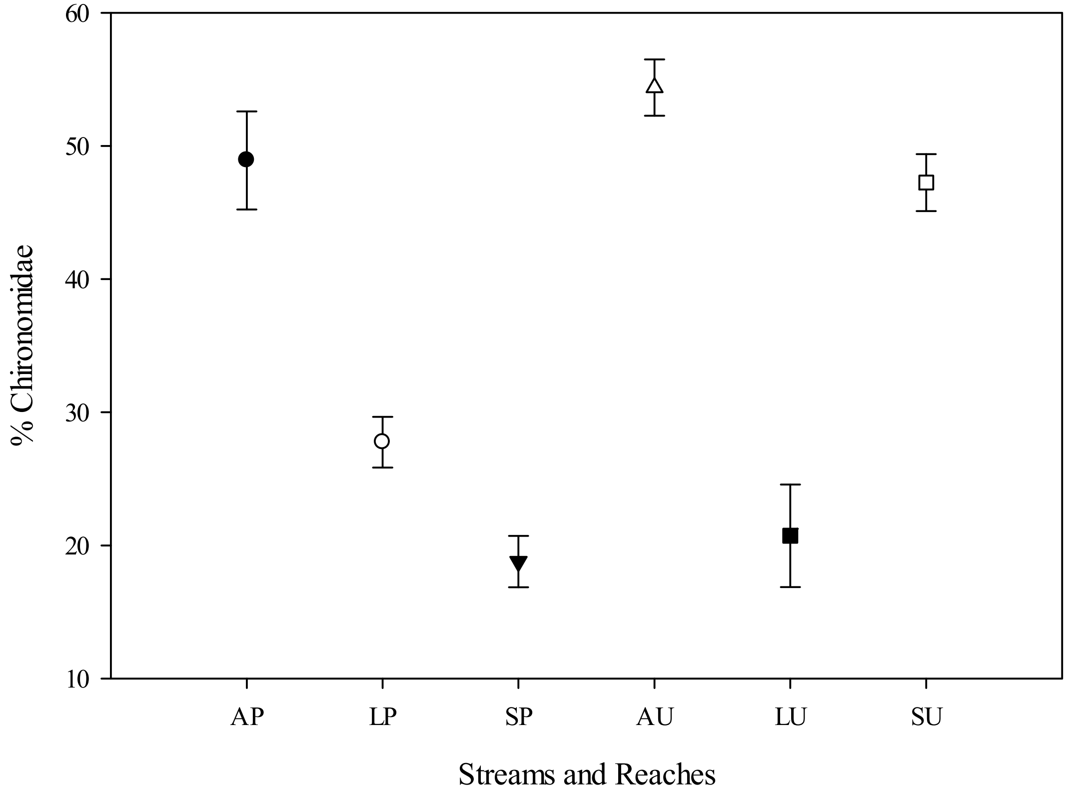


Figure 5.14. Partial regression residual plots for multiple regression: $\hat{Y}$= 1046.6 - 599.5x_1- 8907.9x_2 - 468.2x_3, with $\hat{Y}$ = length of territory on main perennial stream, x_1 = % Plecoptera and x_2 = % Trichoptera, and x_3 = % canopy cover

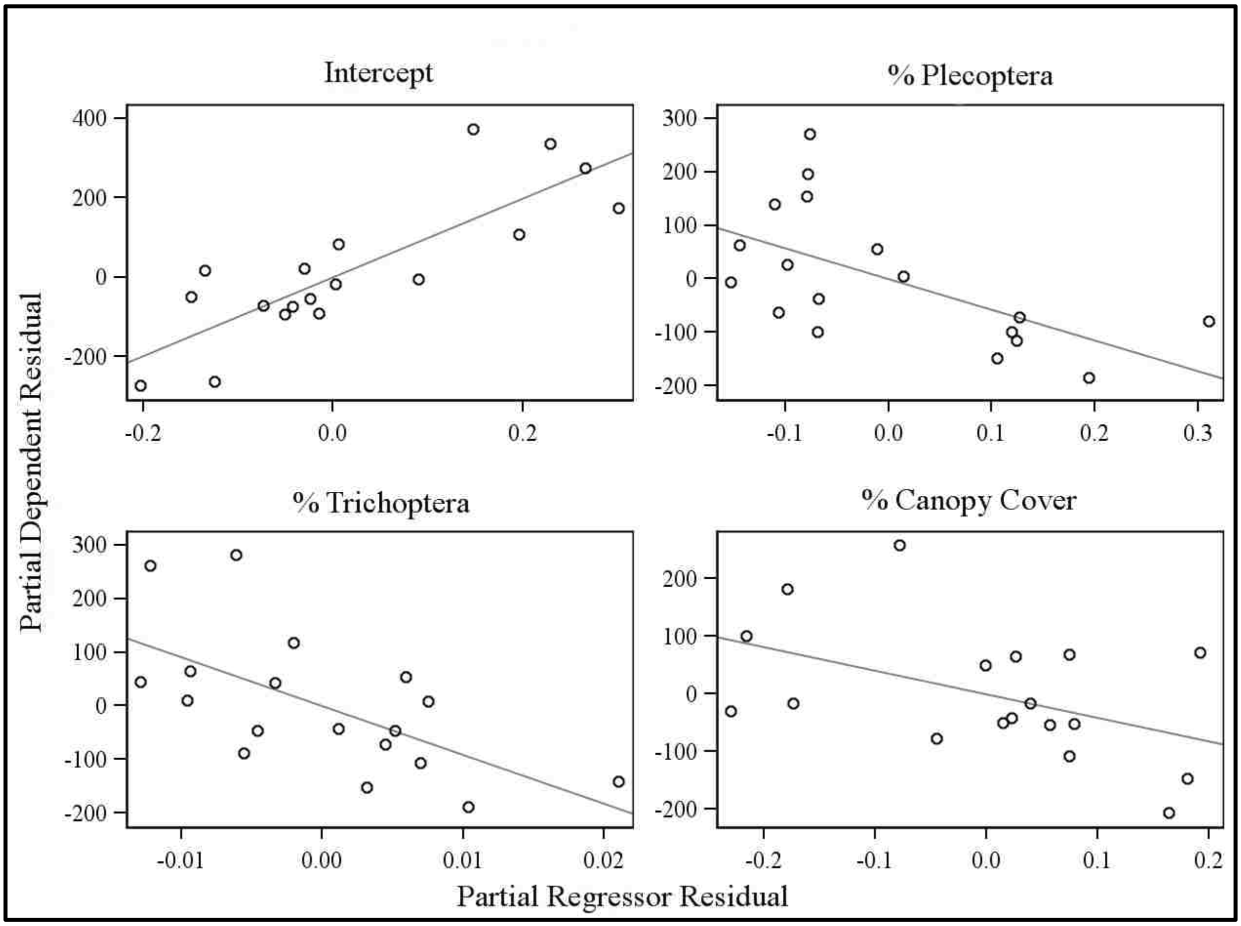


Figure 5.15. Partial regression residual plots for multiple regression: $\hat{Y} = 814.7 + 574.7x_1 - 694.0x_2$, with $\hat{Y}$ = length of territory on main perennial stream, x_1 = % Chironomidae and x_2 = % canopy cover

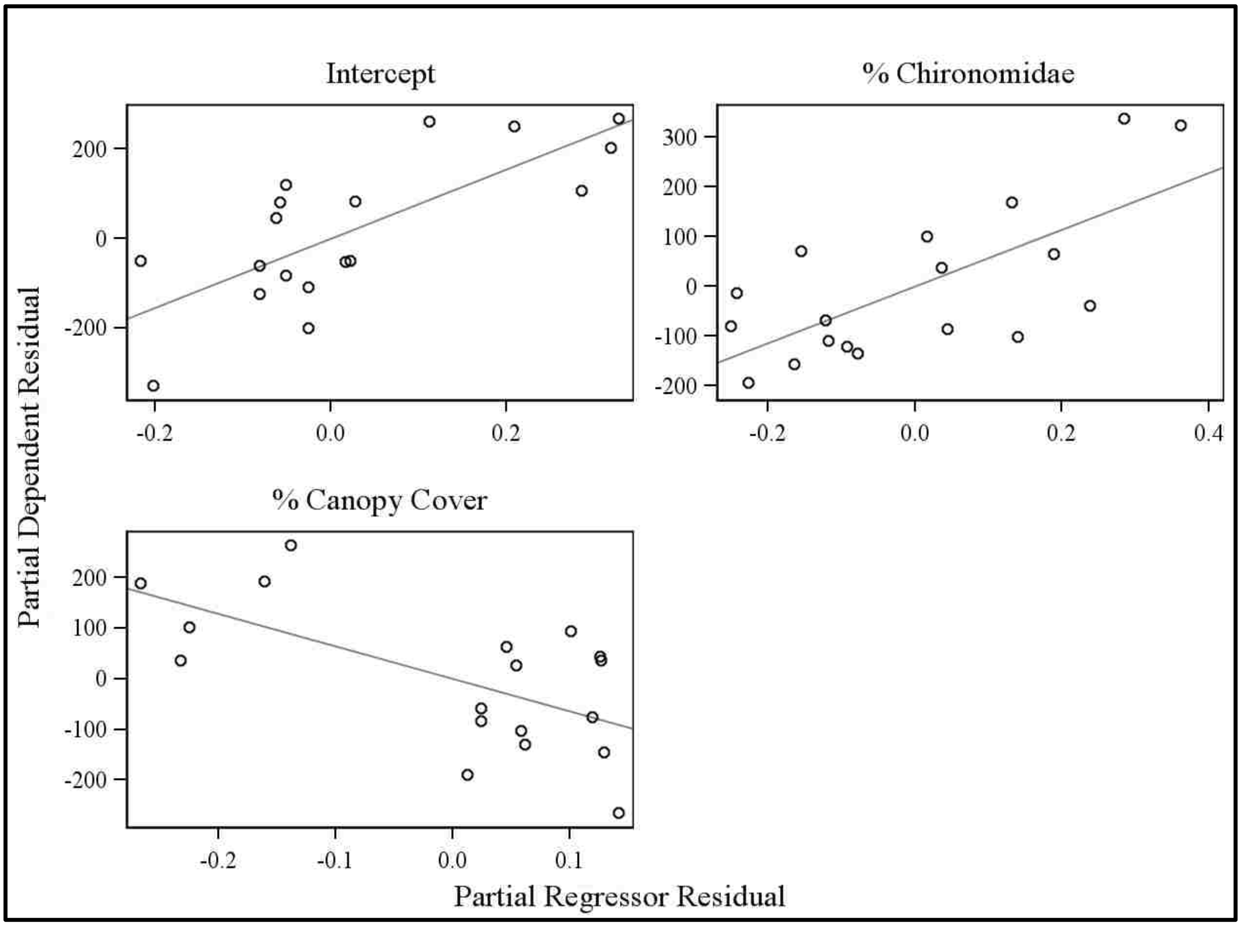


Figure 5.16. Partial regression residual plots for multiple regression: $\hat{Y} = 1139.8 - 534.3x_1 - 621.9x_2$, with $\hat{Y}$ = length of territory on main perennial stream, x_1 = % EPT and x_2 = % canopy cover

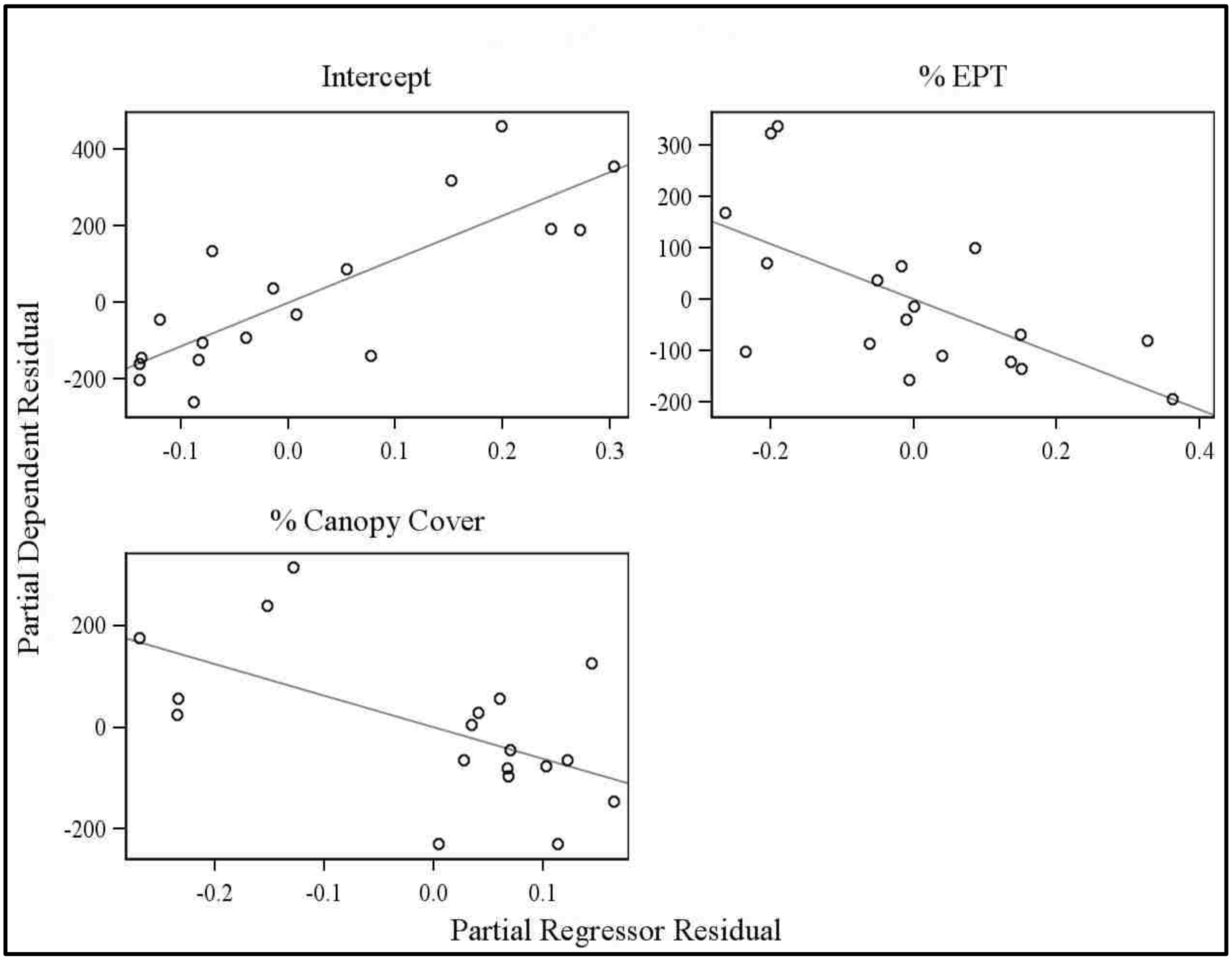


Figure 5.17. Partial regression residual plots for multiple regression: $\hat{Y} = 605.7 + 100.1x_1 - 690.9x_2$, with $\hat{Y}$ = length of territory on main perennial stream, x_1 = FBI and x_2 = % canopy cover

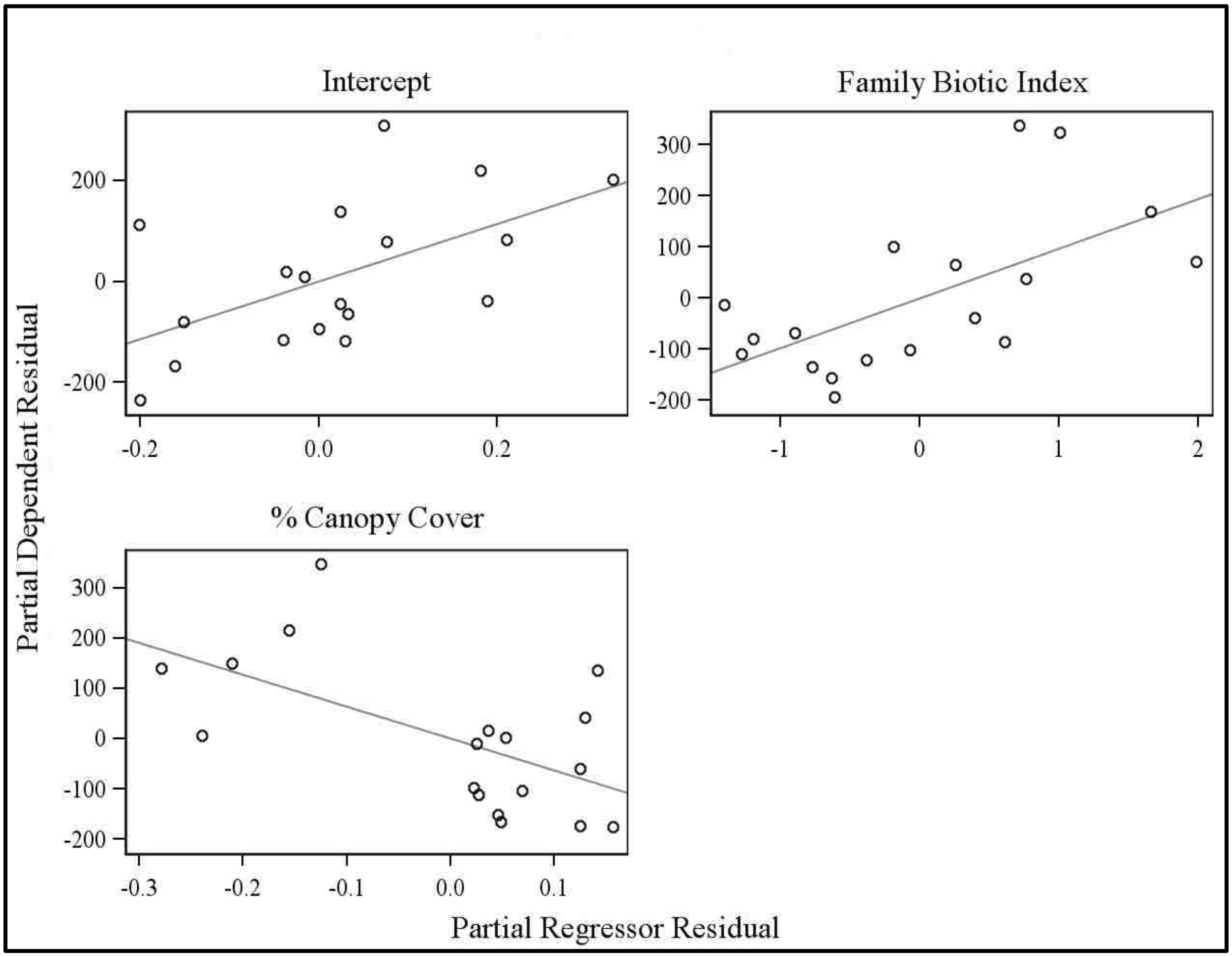
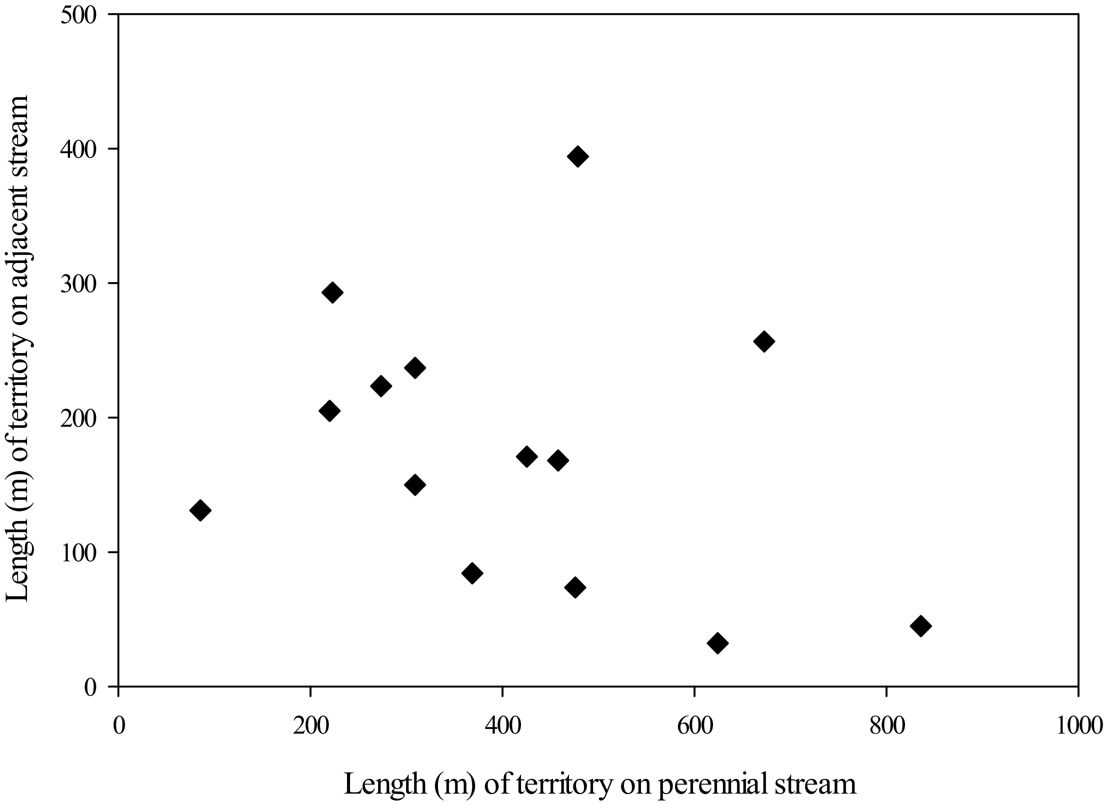


Figure 5.18. Relationship of the length of adjoining streams incorportated in territories to the length of the territory on the main perennial stream



Chapter 6: Conclusion

The Louisiana Waterthrush, *Parkesia motacilla*, exhibits territoriality through aggressive defensive behavior and song to exclude others from its territory. The ecological exclusion of the territory from others is the outcome of the behavior of defense (Maher and Lott 1995).

Chapter II: Behavior, song, and motivation of male Louisiana Waterthrushes, P*arkesia motacilla*, in response to neighbors, strangers, and neighbors at incorrect boundaries

Territorial male Louisiana Waterthrushes were found to exhibit different behaviors in response to songs of strangers, songs of neighbors at correct boundaries, and songs of neighbors present at incorrect boundaries (i.e. the opposite boundary on a linear territory) as predicted by the level of threat each presented to the territorial male. A stranger is predicted to present the greatest threat to a territory holder in that a stranger found singing upon another male's territory more likely intends to usurp the resident male and establish its own territory. Louisiana Waterthrush males responding to a stranger's songs (neighbor-stranger discrimination trials) sang significantly more extended songs and made more flights around the playback speaker in search of a perceived intruder. Also, though not significant at a $p = 0.05$ level, there was an indication that males approached the stranger song stimuli more closely and more rapidly, reacted with extended song more quickly, and took longer to return to foraging when compared to their reactions to a correct neighbor. Additionally, soft song, thought to be the most aggressive of signals, as it is usually given just prior to attack (Nice 1943, Searcy et al. 2006, Hof and Hazlett 2010), was sung more often in response to strangers, except for in the case of the male tested earliest in the season who responded in all trials with soft song.

Differences were more apparent when comparing a territorial male's responses to stranger songs versus correct neighbor's songs than when comparing a territorial male's responses to correct neighbor's songs versus a correct neighbor's song at an incorrect boundary.

Responses of males to neighbor's song sung at the incorrect boundary (neighbor-neighbor or individual discrimination trials) were not significantly different from responses to correct neighbors singing at correct boundaries at the $p = 0.05$ level. However, differences at $p = 0.10$ were found with the territorial male approaching the song stimuli more closely and singing extended song more quickly. A neighbor singing at an incorrect territorial boundary, i.e. the territory on the opposite end of the resident male's territory, presents less threat than a stranger. Unlike a stranger, a neighbor having wandered widely outside its territory may present a threat to the resident male by looking to lengthen its present territory.

Extended song and soft song correlated with more aggressive behavior and approach. Primary song correlated with less aggressive behavior. As aggression decreased throughout a playback trial males lapsed from extended to primary song as predicted by Smith and Smith (1996) who found that Louisiana Waterthrushes sing extended song while searching for an intruder and lapse into primary song when an intruder cannot be found. Soft song was used in response to a stranger's song more often and earlier in the breeding season.

Aggressive responses waned as the breeding season continued through its cycles of arrival, mate attraction and pair bonding, through reproductive states of nesting, feeding of nestlings and fledglings, and in some cases, predation of offspring and a renewed effort at reproduction. More aggressive birds earlier in the season reacted more quickly, more often with soft song, spent more time searching and singing extended song, and took longer to lapse back into primary song.

Chapter III: Motivation-structural code and extended song acoustic structure in territorial male Louisiana Waterthrushes (*Parkesia motacilla*)

Increased levels of aggression in response to songs of strangers, and to a lesser extent to songs of neighbors at incorrect boundaries, were found to correlate with more aggressive behavior and approach. These differences were expressed in the acoustic structure of the extended song type as predicted by Morton's motivation-structural rules of vocalizations (Morton 1977). Comparing songs used in responses to neighbors, strangers, and (to a more limited extent) neighbors at incorrect boundaries, more aggressive interactions resulted in extended song suffixes that were longer as a result of an increased number of harsh, low frequency components. Additionally, lower average low frequencies were found in both the primary segments of the extended song and also in the extended song suffixes.

A territorial male's aggressive responses wane as its breeding season continues (Wingfield and Hahn 1994, Catchpole and Slater 2008, Voigt and Leitner 2008). Higher levels of aggression occurring early in the breeding season resulted in lower low frequency components and longer song suffixes of extended songs. Early in the breeding season less discrimination was shown among neighbors, strangers, and neighbors at incorrect boundaries and resulted in a tendency for similarity in the acoustic structure of extended song during the very early periods of territory establishment. Discrimination, as evidenced by the structure of the extended song, between neighbors and strangers became increasingly more evident as the season continued, and then increasingly less evident as the season was coming to an end. Decreasing levels of aggression with the progression of the breeding season correlated with shorter suffixes and primary segments with higher high frequencies and lower low frequencies.

Differences in frequency of songs could also be attributed to individuality among males. The decline in low frequency of the primary song segment and the extended song suffix with the breeding season was not predicted by Morton's motivation-structural rules (Morton 1977). If focal males were becoming increasingly less aggressive as the season progressed then it would be expected that low frequency would instead increase with days into the season. Frequency differences may have been a result of signal-to-noise ratios and measurements of recordings. I did not use a relative-amplitude criterion in identifying minimum and maximum frequencies. Background noise on any given day on a stream is relatively louder or quieter based upon water levels in the stream. As a result, louder songs on quieter days may have been measured as having lower minimum and higher maximum frequencies. This would explain the lower minimum frequencies and higher maximum frequencies measured within songs as days progressed from early in the season when water and its associated noise was at its highest, to later in the season when water was at its lowest and quietest.

Chapter IV: Leaf-pulling by Louisiana Waterthrushes: prey availability due to a unique foraging maneuver in a stream environment

Simulating the Louisiana Waterthrush foraging maneuver of leaf pulling early in the breeding season indicated that the greatest density of prey in healthy stream reaches of the watershed of the Upper Buffalo National River was found within centers of riffles in packs of leaves compared to edges of riffles and edges of pools. This was true also when comparisons were made between the densities of prey associated with an isolated leaf and that associated with a single leaf taken from a pack. The greatest biomass, not including gastropods and tipulids, was also found associated with packs of leaves in centers of riffles. However, differences were not found with biomass comparing an isolated leaf in the stream environment and a single leaf from a pack. Differences in taxa occurred among different positions of leaves and leaf packs within the stream environment with some taxa found more often associated with centers and edges of riffles and others more often associated with edges of riffles and pools. Overall, my results suggest that an optimally foraging Louisiana Waterthrush (Schoener 1971, Krebs 1973, Pyke et al. 1977) would be more successful pulling leaves to search for prey from packs in centers of shallow riffles in healthy stream reaches within constraints of nutrient availability of prey and the potential of its own predation (Schoener 1971, Curio 1976, Pyke et al. 1977, Werner et al. 1983, Stephens and Krebs 1986).

Differences in assemblage, density, and biomass were also found among Louisiana Waterthrush territories. Those territories suffering from anthropogenic degradation through sedimentation, increased nutrient input, and increased sunlight supported different densities and types of taxa compared to less degraded territories. The physical characteristics and ubiquitous nature of pollution-tolerant taxa in the stream corridor affected biomass estimates for territories such that degraded territories sometimes showed greater biomass and densities. In these territories, both pollution-tolerant taxa, ephemeropterans and plecopterans, and pollution-intolerant taxa, chironomids, were more often found at the edges of the stream corridor than within the center of riffles. Facultative taxa, which can move from riffle habitat to bank habitat for refuge, do so when sedimentation increases and fills the interstices between cobbles in riffles (Roy et al. 2003). Taxa obligate to riffles will initially move to the edges of the stream corridor with reduction or destruction of riffle habitat before being lost to the stream community. Thus, Louisiana Waterthrushes foraging within more degraded habitats may be found foraging more often at the edge of these streams than at their center.

Chapter V. Louisiana Waterthrush (*Parkesia motacilla*) of the Buffalo National River Watershed and Their Relationship to a Changing Riparian Habitat

Attributes of stream ecological integrity, as measured by bioassessment metrics calculated from aquatic invertebrate prey available to Louisiana Waterthrushes through leaf-pulling, differed among Louisiana Waterthrush territories according to their location on three streams in the watershed of the upper Buffalo National River and according to the location of the territories on legally protected and unprotected reaches of those streams. Territories on unprotected reaches showed significantly greater degradation of water quality according to Hilsenhoff’s Family

Biotic Index, percentages of pollution tolerant taxa, and percentages of the most pollution intolerant taxa (Ephemeroptera and Plecoptera), and marginally lower taxa richness. Louisiana Waterthrush territories were significantly longer on the stream with the least protection and greatest degree of anthropogenic change, and territories on unprotected reaches of streams tended to be marginally longer than those on protected reaches. It was also on unprotected reaches that territories disappeared along the length of the stream. The increased lengths of territories within degraded areas suggests that Louisiana Waterthrushes may increase the lengths of their territories to compensate for what resources may be lacking as a result of the degradation of the habitat and water quality in order to maintain their fitness. This is evidenced also by the lack of significant differences in nest success among males holding territories on the different streams and their protected and unprotected reaches. Also, when comparing fidelity to territories, males were not significantly different. Strong site and territory fidelity is a common attribute of male passerines (Fretwell and Lucas 1970, Feck and Hall 2004) as previous establishment and knowledge of territories reduces the energy required for initial breeding territory establishment (Godard 1991). Thus, economically, males may be better served if they return to a territory previously established if it were not so degraded that reproductive success remains possible there.

Multiple regression models resulted in predictions of increasingly longer Louisiana Waterthrush territories as stream ecological integrity decreased. Canopy cover was a significant factor in all models and in all cases predicted longer territories as the percentage of shading by canopy cover decreased. Bioassessment metrics tended to be collinear, thus multiple models were created including only those metrics that could be fitted without collinearity.

The most parsimonious models predicted that as the percentage of pollution tolerant taxa, % Chironomidae, increased and % canopy cover decreased, territories would be longer and that as the percentage of pollution-intolerant taxa, % Plecoptera and % Trichoptera, along with % canopy cover increased territory lengths would decrease. Another two models, including the more common bioassessment metrics, % EPT and Hilsenhoff's Family Biotic Index (Hilsenhoff 1988), with % canopy cover resulted in similar predictions such that as stream ecological integrity decreased territories would lengthen. These functional relationships between measures of stream ecological integrity and lengths of Louisiana Waterthrush territories suggest that Louisiana Waterthrush populations may be successfully incorporated into measures of stream ecological integrity in the Buffalo National River and its imperiled watershed.

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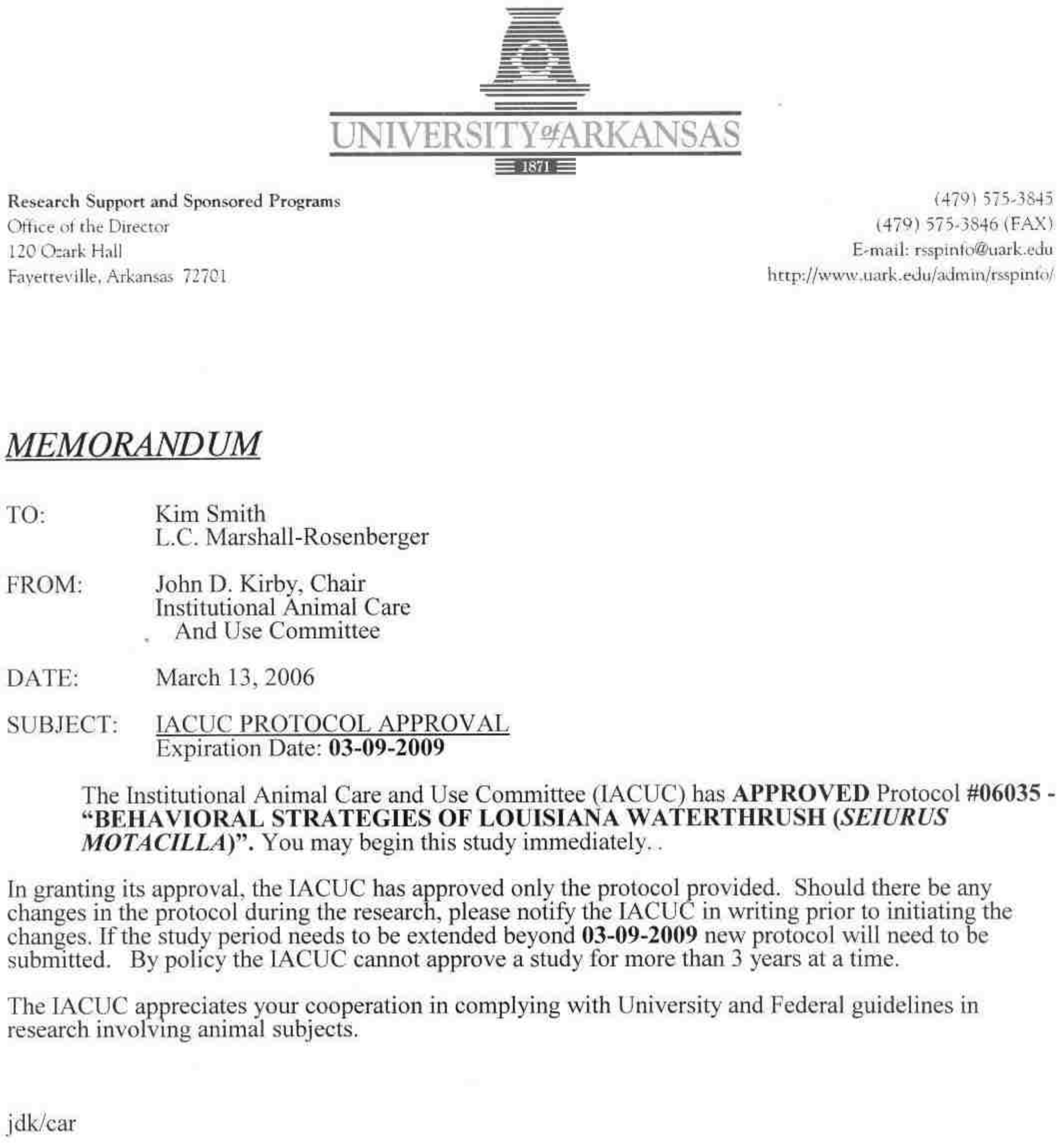
Appendix 1. Institutional Animal Care and Use Committee Protocol Approval # 060305

“Behavioral strategies of Louisiana Waterthrush (*Seiurus Motacilla*)”



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http://www.uark.edu/admin/rsspinfo/

MEMORANDUM

TO: Kim Smith
L.C. Marshall-Rosenberger

FROM: John D. Kirby, Chair
Institutional Animal Care
And Use Committee

DATE: March 13, 2006

SUBJECT: IACUC PROTOCOL APPROVAL
Expiration Date: **03-09-2009**

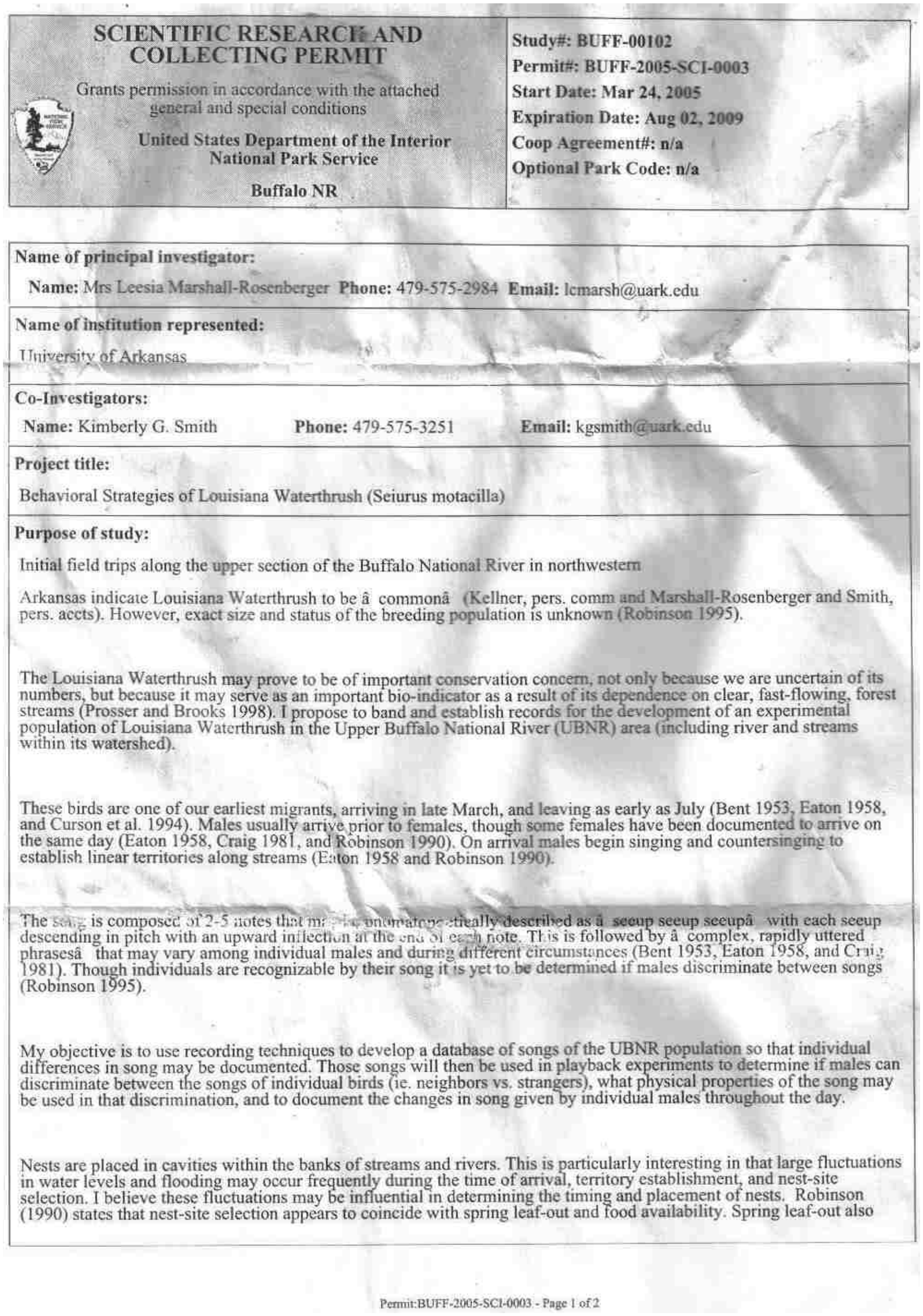
The Institutional Animal Care and Use Committee (IACUC) has **APPROVED** Protocol **#06035 - “BEHAVIORAL STRATEGIES OF LOUISIANA WATERTHRUSH (*SEIURUS MOTACILLA*)”.** You may begin this study immediately. .

In granting its approval, the IACUC has approved only the protocol provided. Should there be any changes in the protocol during the research, please notify the IACUC in writing prior to initiating the changes. If the study period needs to be extended beyond **03-09-2009** new protocol will need to be submitted. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines in research involving animal subjects.

jdk/car

Appendix 2. United States Department of the Interior National Park Service Study # BUFF-00102, Permit # BUFF-2005-SCI-0003



SCIENTIFIC RESEARCH AND COLLECTING PERMIT

Grants permission in accordance with the attached general and special conditions

United States Department of the Interior
National Park Service

Buffalo NR

Study#: BUFF-00102
Permit#: BUFF-2005-SCI-0003
Start Date: Mar 24, 2005
Expiration Date: Aug 02, 2009
Coop Agreement#: n/a
Optional Park Code: n/a

Name of principal investigator:

Name: Mrs Leesia Marshall-Rosenberger **Phone:** 479-575-2984 **Email:** lcmarsh@uark.edu

Name of institution represented:

University of Arkansas

Co-Investigators:

Name: Kimberly G. Smith **Phone:** 479-575-3251 **Email:** kgsmith@uark.edu

Project title:

Behavioral Strategies of Louisiana Waterthrush (Seiurus motacilla)

Purpose of study:

Initial field trips along the upper section of the Buffalo National River in northwestern

Arkansas indicate Louisiana Waterthrush to be â commonâ (Kellner, pers. comm and Marshall-Rosenberger and Smith, pers. accts). However, exact size and status of the breeding population is unknown (Robinson 1995).

The Louisiana Waterthrush may prove to be of important conservation concern, not only because we are uncertain of its numbers, but because it may serve as an important bio-indicator as a result of its dependence on clear, fast-flowing, forest streams (Prosser and Brooks 1998). I propose to band and establish records for the development of an experimental population of Louisiana Waterthrush in the Upper Buffalo National River (UBNR) area (including river and streams within its watershed).

These birds are one of our earliest migrants, arriving in late March, and leaving as early as July (Bent 1953, Eaton 1958, and Curson et al. 1994). Males usually arrive prior to females, though some females have been documented to arrive on the same day (Eaton 1958, Craig 1981, and Robinson 1990). On arrival males begin singing and countersinging to establish linear territories along streams (Eaton 1958 and Robinson 1990).

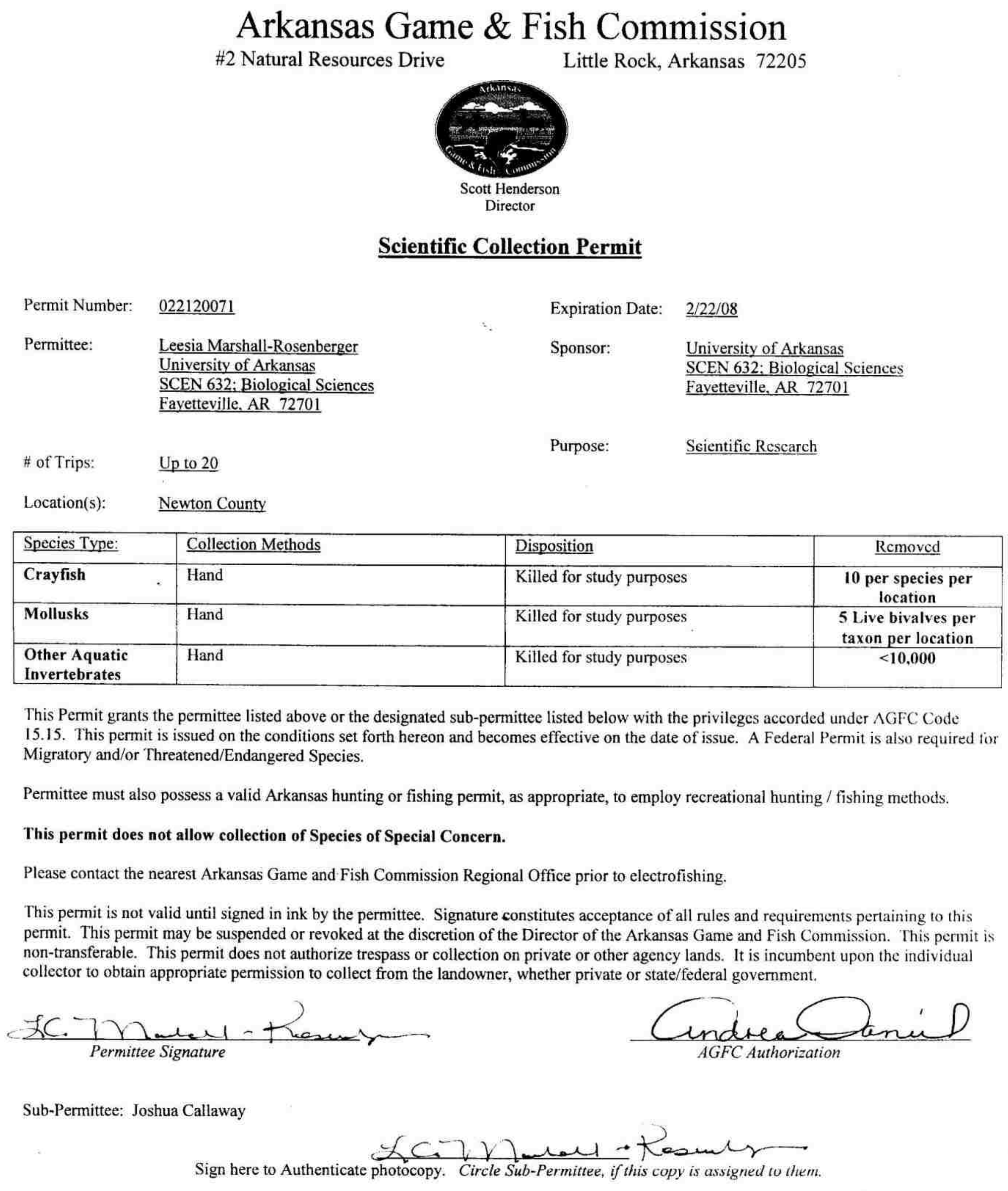
The song is composed of 2-5 notes that may be onomatopoetically described as â seeup seeup seeupâ with each seeup descending in pitch with an upward inflection at the end of each note. This is followed by â complex, rapidly uttered phrasesâ that may vary among individual males and during different circumstances (Bent 1953, Eaton 1958, and Craig 1981). Though individuals are recognizable by their song it is yet to be determined if males discriminate between songs (Robinson 1995).

My objective is to use recording techniques to develop a database of songs of the UBNR population so that individual differences in song may be documented. Those songs will then be used in playback experiments to determine if males can discriminate between the songs of individual birds (ie. neighbors vs. strangers), what physical properties of the song may be used in that discrimination, and to document the changes in song given by individual males throughout the day.

Nests are placed in cavities within the banks of streams and rivers. This is particularly interesting in that large fluctuations in water levels and flooding may occur frequently during the time of arrival, territory establishment, and nest-site selection. I believe these fluctuations may be influential in determining the timing and placement of nests. Robinson (1990) states that nest-site selection appears to coincide with spring leaf-out and food availability. Spring leaf-out also

Permit:BUFF-2005-SCI-0003 - Page 1 of 2

Appendix 3. Arkansas Game and Fish Commission Collection Permit # 022120071



Arkansas Game & Fish Commission

#2 Natural Resources Drive Little Rock, Arkansas 72205

Scott Henderson
Director

Scientific Collection Permit

Permit Number: 022120071

Expiration Date: 2/22/08

Permittee:
Leesia Marshall-Rosenberger
University of Arkansas
SCEN 632; Biological Sciences
Fayetteville, AR 72701

Sponsor:
University of Arkansas
SCEN 632; Biological Sciences
Fayetteville, AR 72701

Purpose: Scientific Research

# of Trips: Up to 20

Location(s): Newton County

Species Type:	Collection Methods	Disposition	Removed
Crayfish	Hand	Killed for study purposes	**10 per species per location**
Mollusks	Hand	Killed for study purposes	**5 Live bivalves per taxon per location**
Other Aquatic Invertebrates	Hand	Killed for study purposes	**<10,000**

This Permit grants the permittee listed above or the designated sub-permittee listed below with the privileges accorded under AGFC Code 15.15. This permit is issued on the conditions set forth hereon and becomes effective on the date of issue. A Federal Permit is also required for Migratory and/or Threatened/Endangered Species.

Permittee must also possess a valid Arkansas hunting or fishing permit, as appropriate, to employ recreational hunting / fishing methods.

This permit does not allow collection of Species of Special Concern.

Please contact the nearest Arkansas Game and Fish Commission Regional Office prior to electrofishing.

This permit is not valid until signed in ink by the permittee. Signature constitutes acceptance of all rules and requirements pertaining to this permit. This permit may be suspended or revoked at the discretion of the Director of the Arkansas Game and Fish Commission. This permit is non-transferable. This permit does not authorize trespass or collection on private or other agency lands. It is incumbent upon the individual collector to obtain appropriate permission to collect from the landowner, whether private or state/federal government.

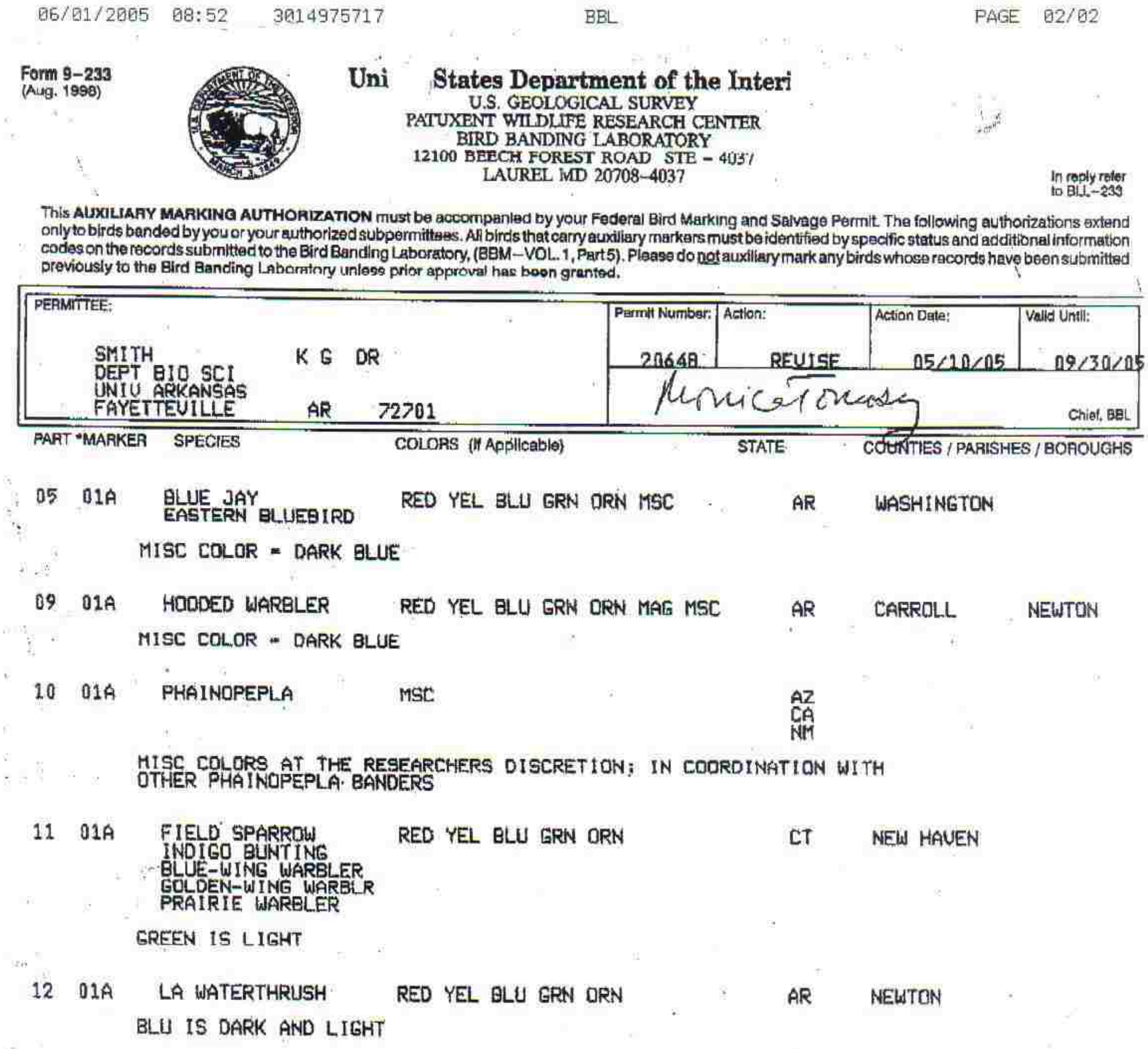
Permittee Signature

Andrea Daniel
AGFC Authorization

Sub-Permittee: Joshua Callaway

Sign here to Authenticate photocopy. *Circle Sub-Permittee, if this copy is assigned to them.*

Appendix 4. United States Department of the Interior, U.S. Geological Survey, Patuxent Wildlife Research Center, Bird Banding Laboratory, Banding Permit



06/01/2005 08:52 3014975717 BBL PAGE 02/02

Form 9–233
(Aug. 1998)

Uni States Department of the Interi
U.S. GEOLOGICAL SURVEY
PATUXENT WILDLIFE RESEARCH CENTER
BIRD BANDING LABORATORY
12100 BEECH FOREST ROAD STE – 4037
LAUREL MD 20708–4037

In reply refer
to BBL–233

This **AUXILIARY MARKING AUTHORIZATION** must be accompanied by your Federal Bird Marking and Salvage Permit. The following authorizations extend only to birds banded by you or your authorized subpermittees. All birds that carry auxiliary markers must be identified by specific status and additional information codes on the records submitted to the Bird Banding Laboratory, (BBM–VOL. 1, Part 5). Please do <u>not</u> auxiliary mark any birds whose records have been submitted previously to the Bird Banding Laboratory unless prior approval has been granted.

PERMITTEE:
SMITH K G DR
DEPT BIO SCI
UNIV ARKANSAS
FAYETTEVILLE AR 72701

Permit Number:	Action:	Action Date:	Valid Until:
20648	REVISE	05/10/05	09/30/05

Chief, BBL

PART	*MARKER	SPECIES	COLORS (If Applicable)	STATE	COUNTIES / PARISHES / BOROUGHS
05	01A	BLUE JAY EASTERN BLUEBIRD	RED YEL BLU GRN ORN MSC	AR	WASHINGTON
		MISC COLOR = DARK BLUE			
09	01A	HOODED WARBLER	RED YEL BLU GRN ORN MAG MSC	AR	CARROLL NEWTON
		MISC COLOR = DARK BLUE			
10	01A	PHAINOPEPLA	MSC	AZ CA NM	
		MISC COLORS AT THE RESEARCHERS DISCRETION; IN COORDINATION WITH OTHER PHAINOPEPLA BANDERS			
11	01A	FIELD SPARROW INDIGO BUNTING BLUE-WING WARBLER GOLDEN-WING WARBLR PRAIRIE WARBLER	RED YEL BLU GRN ORN	CT	NEW HAVEN
		GREEN IS LIGHT			
12	01A	LA WATERTHRUSH	RED YEL BLU GRN ORN	AR	NEWTON
		BLU IS DARK AND LIGHT			