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# Background

The Louisiana Waterthrush (Parkesia motacilla), is a neotropical migratory songbird that breeds throughout the central and eastern United States, from Texas and Georgia up through Minnesota, Ontario, and central New England (Prosser & Brooks, 1998). Geographically positioned towards the southwestern periphery of the Louisiana Waterthrush's (LOWA) breeding range, the West Gulf Coastal Plain and Ouchitas bird conservation region (WGCPO) supports roughly five percent of the LOWA breeding population. While not considered a species of concern at the continental scale, within the WGCPO data from the Breeding Bird Survey suggest an overall decline in LOWA detections since 1966 (Sauer et al. 2014). As an interior forest species dependent on high-quality headwater streams, the LOWA is particularly vulnerable to land use changes that characterize the WGCPO region, such as conversion of forest for shale gas development, silviculture, and agriculture. This type of anthropogenic activity not only decreases the availability of large, contiguous tracts of forest but also may alter hydrologic characteristics and functions having potential impacts on the guality of LOWA breeding habitat. With a foraging strategy that is largely dependent on pollution-sensitive aquatic macroinvertebrates, the LOWA is subsequently vulnerable to environmental factors affecting the availability of this resource. As such, the LOWA is an important indicator of stream quality and overall riparian ecosystem health.

Given the documented decline within the WGCPO region, along with its utility as a bioindicator of riparian ecosystem health, the LOWA is considered a conservation priority by the Lower Mississippi Valley Joint Venture (LMVJV). At the forefront of conservation planning and management is the prioritization of areas of optimal breeding habitat that may be critical to sustaining long-term viable populations. The ability to successfully target optimal LOWA breeding habitat requires an understanding of the key habitat features that influence reproductive success. Some habitat associations for the LOWA have been well known for decades, such as the dependence on first and second order headwater streams and large patches of contiguous forest (Bent 1963, S. C. Robbins et al. 1989, Hamel 1992). Over the last two decades, however, researchers have begun to look more closely at the relationship between LOWA reproductive success and both fine-scale habitat features and adjacent land use activity. Most of this research was conducted at a local scale in a few states including Pennsylvania (Mattsson and Cooper 2007, Mulvihill et al. 2008, 2009, Mattsson et al. 2011), West Virginia (Wood et al. 2016, Frantz et al. 2018b), Missouri (Peak et al. 2006) Minnesota (Stucker and Cuthbert 2000), Arkansas (Marshall 2012, Latta et al. 2015), Tennessee (Bryant et al. 2020), and others. With the exception of Tirpak et al. (2009), there is little literature pertaining to LOWA breeding

habitat associations within the WGCPO region. Regardless, the existing body of research regarding this important component of natural history provides crucial information that can be incorporated into management strategies despite the lack of region-specific research.

The following is a synthesis of scientific research, reviews, and literature relating to the LOWA breeding habitat features that are key to sustaining long-term, viable populations. A literature search conducted on Google Scholar using the search terms "Louisiana Waterthrush" and "breeding habitat" yielded 501 results (excluding citations). The first 100 most relevant results were visually scanned to filter out articles that did not include the LOWA in a study relating to or tangentially relating to any breeding habitat feature. Duplicate articles and conference publications were also excluded. The application of filter criteria resulted in 51 results relevant to breeding habitat features for the LOWA. The following pages contain a summary of the key breeding habitat features extracted from this body of literature.

# SUMMARY OF KEY BREEDING HABITAT CHARACTERISTICS

Key breeding habitat characteristics of the LOWA are categorized as components of either overall vegetative cover (e.g., percent canopy cover) and/or foraging habitat (e.g., stream substrate).

# COVER

### Forest area

At the landscape scale, one of the most critical breeding habitat features is forest area or patch size. Perhaps the first real systematic study quantifying optimal forest patch size for the LOWA was conducted by Robbins et al. (1989) in Maryland and the adjacent Mid-Atlantic region. In this study, researchers identified forest area as a significant predictor of LOWA relative abundance, showing that maximum probability of occurrence was associated with forest patches greater than 3,000 hectares (ha). Probability of occurrence was at 50% for forest patches as small as 350 ha, although, LOWA were detected at least twice in forest patches ranging from 24.7 ha to 184 ha (Robbins et al. 1989). Prosser and Brooks (1998) and Tirpak et al. (2009) referenced this study in their validated Habitat Suitability Index (HSI) models for the LOWA, where Suitability Index (SI) values for forest patch size included 0 (patches under 42.2 ha from Hayden et al. 1985), 0.5 (patches between 350 and 3,200 ha), and 1.0 (patches greater than 3,200 ha). These estimates of optimal forest area for the LOWA are accepted by the research community and have been frequently reinforced in the literature. For instance, Conner and Dickson (1997), examined the general relationship of the LOWA and forest fragmentation, patch size, edge effects and land use patterns. Based on the work from Robbins et al. (1989), Conner and Dickson suggested that LOWA only become moderately abundant (probability of occurrence = 0.2) in forest patches over 1,000 ha in the WGCPO (Conner and Dickson 1997). In their report on management objectives for breeding birds in the Mississippi Alluvial Valley

(MAV), Mueller et al. (1995) calculated that an area of 7,200 ha is required to support 500 breeding pairs of LOWA.

The relationship of riparian buffer width and LOWA occupancy has received a fair amount of attention in the literature, particularly given that LOWA is a stream-obligate species. Peak and Thompson (2006) investigated LOWA densities in riparian forest patches ranging from narrow (55 to 95 meters) to wide (400 to 530 meters) and found significantly higher densities in riparian forest patches classified as wide. Similarly, Mason et al. (2007) only detected LOWA in forested "greenways" greater than 300 meters wide in North Carolina, further highlighting this species' dependence on large tracts of forest.

There are a few examples in the literature, however, that provide some evidence to suggest that LOWA may have a wider niche breadth with regards to forest area requirements. For instance, in a report establishing resource priorities for the Silvio O. Conte National Fish and Wildlife Refuge (Massachusetts), Thompson (n.d.) suggested that LOWA require a minimum of 250 acres (101 ha) of contiguous forested area, which is smaller than previously mentioned estimates of minimum area requirements. Furthermore, in a study conducted by the U.S. Department of Defense, Nott et al. (2003) found that, while LOWA were associated with areas consisting of 50 - 90% forest cover, population trends decreased with increasing total forest cover. This finding, coupled with the positive relationship found with LOWA abundance and the total amount of forest edge, suggests that this species may tolerate some degree of fragmentation, although this threshold was not identified in this study (Nott et al. 2003).

Interestingly, in a study comparing avian abundance in bottomland-hardwood forest stands of varying widths in South Carolina, Kilgo et al., (2018) found that LOWA had the highest probability of detection in stands less than 25 meters wide. In Indiana, Chapman et al. (2015) detected a higher proportion of LOWA within avian communities within medium-width riparian buffers (26-75 meters, "m") than those over 75 m. It is crucial to note, however, that none of these examples considered breeding success, and therefore do not provide evidence that these smaller patches and narrow riparian buffers provide suitable LOWA breeding habitat.

### Forest overstory structure and composition

Many studies address, to some degree, the preference of the LOWA for a particular forest type. One early study investigating habitat relationships of warblers in North Carolina showed that LOWA selected both beech forest and floodplain forest (Parnell 1969), over pine forest, oak-hickory forest, and mixed pine-hardwood forests. Later, using data from the Breeding Bird Survey (BBS), Hamel (1992) found that, in the Southeast region of the United States, the LOWA was most often associated with mature woody wetlands (i.e., oak-gum-cypress bottomland forests; average of five detections per survey). In Ohio, LOWA were frequently associated with study plots characterized as floodplain (Means and Medley 2010). In the Midwest region, however, researchers found a higher relative abundance of LOWA in upland forests dominated by oak-hickory (relative abundance = 0.56) than in floodplain forests of two major types including elm-ash-cottonwood and oak-gum-cypress (relative abundance = 0.38) (Knutson et al. 1995). LOWA were absent

altogether from floodplains during a case study in Minnesota and Wisconsin (Knutson et al. 1995). Researchers suggest that a potential explanation for the absence of LOWA in floodplain forests in this region could be that water levels vary greatly, frequently flooding the ground substrate and compromising nest survival rates (Knutson et al. 1995). Skinner (2003) reports LOWA breeding in both upland and floodplain habitats in Ohio. Twedt et al. (2010) report a negative association with LOWA abundance and the proportion of hardwood forest with bottomland hardwood species in a study assessing the relationship between avian abundance and forest condition derived from the Forest Inventory Analysis (FIA) throughout the southeast. Most of the literature pertaining to the LOWA in the southeast, however, supports a preference for, or at least presence in, bottomland hardwood forests (Parnell 1969, Hamel 1992, Mueller et al. 1995).

Evidence in the literature also supports a strong preference for either deciduous, coniferous, or mixed forest habitat in other parts of the LOWA breeding range. In the Central Appalachians, Murray and Stauffer (1995) investigated non-game bird habitat use and found that LOWA were more abundant in riparian areas dominated by deciduous species than those dominated by coniferous hemlock. In their 1998 HSI model, Prosser and Brooks defined optimal forest composition for LOWA breeding habitat in the Mid-Atlantic as mixed deciduous / coniferous forests (Prosser and Brooks 1998). This HSI characterized optimal forest breeding habitat as large forest patches consisting of 30-69% deciduous species, with the coniferous species making up the remaining percentage (SI = 1.0). Forests characterized as mostly coniferous (0-29% deciduous) or mostly deciduous (70-100% deciduous) were each assigned an SI value of 0.5 (Prosser and Brooks 1998). Based on Hamel (1992), Tirpak et al. (2009) modified these SI values pertaining to forest composition in the Southeast region, specifically the WGCPO. Tirpak et al. (2009) combined landform (floodplain-valley, terrace-mesic, and xeric-ridge), landcover type (low-density residential, transitional-shrubland, deciduous forest, evergreen forest, orchard-vineyard, and woody wetlands) and successional age class (grass-forb, shrub-seedling, sapling, pole, and saw timber) to assign SI values to LOWA breeding habitat in the WGCPO. In contrast to Prosser and Brooks (1998) this HSI suggested deciduous and woody wetlands (mature sawtimber) represented optimal LOWA breeding habitat in the WGCPO within floodplain-valley and terrace-mesic landforms (SI = 1.0). Suitability decreased, however, for deciduous and woody wetland stands in both floodplain-valley and terrace-mesic landforms as stand maturity decreased (i.e., pole timber stands; SI = 0.5). Maximum SI for mixed forest in both floodplain-valley and terrace-mesic landforms within the WGCPO region was only 0.33 (mature, saw timber). Maximum suitability within the xeric-ridge landform was represented by latesuccessional (saw timber) woody wetlands (SI = 0.667) and deciduous forest (SI = 0.5). Low quality or suboptimal habitats included mixed, pole timber stands in floodplain-valley and terrace mesic landforms (SI = 0.167), deciduous, pole timber stands in xeric-ridge (SI = 0.25), woody wetland, pole timber stands in xeric ridge (SI = 0.334), and mixed, pole timber stands in xeric-ridge (SI = 0.167). Suitability of forest habitats characterized as early succession (i.e., grass-forb, shrub-seedling, and sapling) was equal to zero for all landforms and landcover types (Tirpak et al. 2009).

In a more recent study assessing the performance of landscape capability models, Loman et al. (2018) found that most LOWA point-count occurrences were in northern hardwood-conifer and central oak-pine forest types across the northeastern United States.

The variation in LOWA forest type preferences reported in the previous studies may be an artifact of geographic variation in habitat availability and quality. With regards to the WGCPO, however, most studies suggest a preference for deciduous bottomland and floodplain forest and woody wetlands (Parnell 1969, Hamel 1992, Mueller et al. 1999, Tirpak 2009).

# Canopy cover

Many studies and references exist in the literature that associate optimal LOWA breeding habitat with a heavily forested, closed-canopy landscape (Schulz et al. 1992, Prosser and Brooks 1998, Nott et al. 2003, Peak and Thompson 2006, Tirpak et al. 2009, Latta 2009, Marshall 2012, McClure and Hill 2012, etc.). The Prosser and Brooks 1998 HSI characterized optimal percent canopy cover for LOWA breeding habitat as greater than 80% (SI = 1.0), followed by 60-80% (SI = 0.7). Sub-optimal habitats were characterized by 40-59% canopy cover (SI = 0.2). LOWA were not associated with forest patches with less than 40% canopy cover (SI = 0). In a 2002 study conducted in the Georgia Piedmont region, researchers found a negative correlation with LOWA abundance and percent canopy cover, although the relationship was not significant (Hyder 2002). In northeastern Missouri, Peak and Thompson (2006) found that LOWA densities were highest in forest areas characterized by a dense canopy (88.04% canopy cover). Tirpak et al. (2009) modified Prosser and Brooks SI scores for canopy cover in their HSI for the WGCPO, restricting maximum optimality (SI = 1.0) to forest areas with greater than 90% canopy cover (60-89%, SI = 0.7; 40-59%, SI = 0.2, < 40%, SI = 0).

There are several studies linking canopy cover with habitat quality and nesting success. Canopy cover was positively correlated with LOWA nesting success (as measured by successfully fledged fledglings) in a 2009 study conducted in western Pennsylvania (Latta 2009). In the Buffalo National River watershed of northern Arkansas, researchers found a significant inverse relationship between canopy cover and LOWA linear territory length (Marshall 2012). Given that LOWA territory size has been shown to increase with decreasing habitat quality (Mulvihill et al. 2008, Mattsson and Cooper 2009), the relationship found by Marshall (2012) effectively suggests a positive relationship between canopy cover and habitat suitability.

Other studies provide further evidence that the LOWA require a closed canopy forest structure, even though they did not measure nesting success directly. For instance, in a study investigating the effects of herbicides on breeding birds in central Oklahoma, researchers found that LOWA had significantly higher densities on closed-canopy control sites relative to treatment plots (Schulz et al. 1992). McClure and Hill (2012) found that LOWA were significantly more likely to colonize areas with high canopy cover in Alabama, although no percentages were reported. In a study investigating the relationship between reproductive rate and minimum area breeding requirements in central and eastern United States, researchers estimated that the LOWA required a minimum of 99% forest cover to

reach 50% probability of presence (Vance et al. 2003). It is important to note, however, that this study relied on BBS data, and therefore LOWA may have had lower detection rates, given their close association with riparian habitats.

As part of a greater study assessing the relationship between avian demographic trends and landscape patterns on Department of Defense (DoD) installations, Nott et al. (2003) showed that LOWA were associated with areas characterized by 50-90% forest cover. Interestingly, however, this study showed a negative association with adult LOWA abundance and percent forest cover and a positive association with total amount of agricultural edge. Despite the findings reported in Nott et al. (2003), the literature reliably supports a preference of the LOWA for closed canopy, heavily forested landscape.

# Successional stage

There are several examples in the literature associating LOWA with the successional stage of the forest. In a 1979 study investigating the effects of silviculture on the forest bird community in Virginia's pine-oak forests, Conner et al. only detected LOWA in mature forest stands over 30 years old. Likewise, LOWA were absent from stands characterized by saplings and pole-timber in both oak-hickory and Loblolly-shortleaf pine forests, and only associated with mature stands greater than 60 years old in central and southeastern forests (Dickson et al. 1992). Skinner, in a breeding bird survey in 2003 in Ohio, found LOWA were only present in forest stands classified as mature. A 2011 study in Ohio assessing habitat composition and structure found a positive correlation with LOWA detections and canopy height, suggesting a preference for mature forest (Pennington and Blair 2011). To our knowledge there are no studies contradicting the LOWA's dependence on old-growth and mature forest stands.

# Riparian vegetative structure and understory composition

At a smaller scale, vegetation characteristics of the immediate riparian habitat may be crucial to LOWA breeding success, although there are only a few studies that directly address this relationship. Prosser and Brooks (1998) assigned maximum HSI scores to riparian habitats characterized by understory shrub cover over 1.5 meters in height in moderate densities (SI = 1), followed by sparsely distributed shrub cover over 1.5 meters (SI = 0.8). Habitats with dense shrub cover over 1.5 meters (SI = 0.4), as well as shrub cover less than 1.5 meters high at high, moderate, and sparse densities (SI = 0.1, 0.3, and 0.5, respectively) represent sub-optimal habitat. Regarding herbaceous cover, habitat suitability was dependent on height and density of herbaceous cover, where most suitable habitat was associated with moderate to sparsely distributed low cover (< 5 cm; SI = 1). However, optimal suitability was also associated with sparsely distributed, tall (> 20 cm; SI =1) herbaceous cover. Areas characterized by low, but densely distributed herbaceous cover received an SI of 0.7, suggesting high suitability as did areas where herbaceous cover ranged from 5 - 20 cm and was present in moderate densities. A suboptimal SI of 0.3 was assigned to areas with tall herbaceous cover present in moderate densities as well as dense cover ranging from 5 - 20 cm in height. Dense herbaceous cover over 20 cm high resulted in unsuitable breeding habitat (SI = 0). Findings from Schulz et al. (1992) also suggested that the LOWA was associated with forest areas

containing lower proportions of herbaceous ground cover, although this study was not restricted to riparian zones, but rather characterized whole forest stands.

One study conducted in the Great Smokey Mountains in the southern Appalachians linked breeding success, as measured by daily survival rate (DSR), with understory composition (Bryant et al. 2020). In this study, DSR decreased with the proportion of deciduous understory, suggesting higher DSR in habitats with an understory dominated by conifers. Collectively, there appears to be a lack of empirical studies linking breeding success to surrounding understory woody and herbaceous cover and more work is necessary to fully understand how the immediate riparian understory impacts LOWA nesting success across the entirety of its range.

# **Foraging and Nesting Habitat**

# Stream morphology and in-stream habitat

The association of LOWA with headwater streams, first order (small streams with no tributaries) and second order (small streams fed by only one tributary) is well established in the literature (Eaton 1958, Thompson 1996, Mulvihill et al. 2009, Prosser and Brooks 2011, Frantz et al. 2018*b*). In addition to stream order, stream regime is an important factor associated with LOWA presence and breeding success, as demonstrated by Latta (2009) who found a significant positive relationship between unsuccessful nests and the proportion of intermittent streams, highlighting LOWA dependence on perennial streams (Latta 2009).

Stream morphology was also shown to influence LOWA density, productivity, and nest survivorship (Barnes et al. 2018). In this study focusing on hemlock dominated streams in northern Pennsylvania, researchers found that LOWA had higher densities and breeding success in bench streams (e.g., braided streams flowing throughout a fairly wide, flat floodplain) when compared to ravines (e.g., fast flowing, high gradient streams with steep, V-shaped banks) (Barnes et al. 2018). The authors propose that predation rates may have been higher in ravines, therefore rendering these habitats less suitable for LOWA breeding.

In-stream habitat is also influential to LOWA presence and breeding success, including stream microtopography, stream substrate, and proportion of exposed rock (Prosser and Brooks 1998, Stucker and Cuthbert 2000, Hyder 2002, Latta 2009, Mattsson and Cooper 2009, Barnes et al. 2018). Prosser and Brooks (1998) suggested maximum suitability for first and second order streams with riffles (i.e., shallow, fast moving parts of the stream with rocks breeching the surface) and pools (i.e., deep, slower moving parts of the stream; SI = 1). Streams of first and second order with a higher topographic gradient and faster moving water over riffles were still largely suitable (SI = 0.7). Habitat suitability decreases with  $3^{rd}$  order streams, although the presence of riffles can provide sub-optimal habitat (SI = 0.5). Third order streams consisting of mostly runs provide poor habitat for LOWA (SI = 0.2).

A 2000 study in Minnesota found that there was a significantly higher proportion of riffles on streams occupied by LOWA (Stucker and Cuthbert 2000). This study found that stream reaches occupied by LOWA have, on average, roughly 40% riffle versus 20% in unoccupied reaches. Another study conducted in Georgia found a positive, yet nonsignificant association of LOWA presence with increasing percent riffle (Hyder 2002). Along with the presence of riffles, the amount of exposed rock within a particular stream reach is important to LOWA foraging. In a Minnesota study aimed at understanding LOWA reproductive success and breeding habitat characteristics, percent of exposed rock in LOWA-occupied reaches was, on average, roughly 15% versus 7% in unoccupied stream reaches (Stucker 2000). Bryant et al. (2020) more recently found that percent of exposed in-stream rock was the top predictor for LOWA forage habitat selection, along with exposed woody debris.

In addition to stream order, percent riffle and exposed rock, stream substrate and clarity are critical to LOWA foraging. Prosser and Brooks (1998) showed that optimal habitat consisted of a coarse or sandy stream substrate and high clarity (SI = 1). Stream reaches characterized as clear with fine substrate or turbid with coarse or sandy substrate were suboptimal (SI = 0.5). LOWA were very unlikely to be found breeding along turbid stream reaches with fine substrate (SI = 0, Prosser and Brooks 2011).

The literature collectively and consistently shows that LOWA require healthy first or second order headwater streams with a moderate to high proportion of riffles and exposed rock.

# Proximity to anthropogenic disturbance

Given that the LOWA is an area-sensitive, forest interior species, it is rarely associated with anthropogenic habitats. However, there is a substantial body of work investigating the impacts of human activity on LOWA habitat and breeding success (Hyder 2002, Mulvihill et al. 2008, Mattsson and Cooper 2009, Marshall 2012, Latta et al. 2015, Frantz et al. 2018*a*, 2019, Farwell et al. 2019).

In Georgia, Hyder (2002) found that LOWA were more abundant in large riparian buffers surrounded by non-hostile adjacent habitat (e.g., rotation loblolly pine forest) than in buffers surrounded by hostile adjacent habitats (e.g., clear-cuts). In another Georgia study, nestling survival was low when territories in wide riparian buffers (at least 160 meters) were within 1.75 km of agriculture (Mattsson and Cooper 2009).

Cowbird parasitism is generally higher in more fragmented forests as the amount of edge habitat adjacent to hostile habitats including clear-cuts and agriculture increases. Where cowbirds are present, researchers have shown a decrease LOWA fledging success (Stucker and Cuthbert, 2000), although there is research to suggest that rates of brood parasitism are low in LOWA, as this species is typically found within the forest interior (Robinson and Wilcove 1999). Lower LOWA productivity found in association with cowbird parasitism, however, has important implications as fragmentation continues to affect the landscape. Another study investigated the relationship of LOWA habitat quality

and anthropogenic land use in northern Arkansas (Marshall 2012). When comparing protected and unprotected stream reaches, this study found that LOWA territories were larger on unprotected streams more heavily impacted by hostile adjacent habitats and land use (Marshall 2012). Territory size can be an important proxy for habitat quality, as LOWA territories have been shown to have an inverse relationship with both habitat quality and breeding productivity (Mulvihill et al. 2008, Mattsson and Cooper 2009, Frantz et al. 2018*b*). Marshall (2012) also showed that the proportion of pollutant intolerant macroinvertebrate taxa, an important food source for LOWA, decreased in unprotected, polluted streams.

Several studies highlight the detrimental effects of stream acidification associated with shale gas development on water quality, the benthic macroinvertebrate community, and, subsequently, LOWA habitat quality and breeding success (Mulvihill et al. 2008, Latta et al. 2015, Frantz et al. 2018b, 2019, 2020). Mulvihill et al. (2008) found higher rates of site fidelity on circumneutral (i.e., neutral pH) streams than streams with low pH in southwestern Pennsylvania, suggesting the circumneutral streams represent more suitable habitat. Similarly, Frantz et al. (2019) found that female LOWA had lower site fidelity and lower reproductive success in areas impacted by shale gas in West Virginia. In an earlier study, Frantz et al. found significantly lower DSR, and, ultimately, lower productivity, in LOWA territories impacted by shale gas runoff or falling within 60 m of shale gas development and associated infrastructure (Frantz et al. 2018b). This study also found LOWA were breeding in lower densities along stream reaches impacted by shale gas. Based on these findings, Frantz et al. (2018b) suggested that LOWA breeding along degraded streams impacted by shale gas development serve as "sink" populations due to lower nest survival and productivity. In addition to lower reproductive success, researchers have also found evidence of bioaccumulation of metals (specifically Barium and Strontium) and an associated epigenetic response in LOWA breeding along impacted streams in both Pennsylvania and Arkansas (Latta et al. 2015, Frantz et al. 2020). Although the latter study did not address breeding success, it does provide evidence of an interaction between contaminants associated with shale gas development and the riparian ecosystem. More evidence of a negative association with shale gas development and LOWA habitat suitability comes from Farwell et al. (2019) who found that LOWA abundance was negatively associated with shale gas development in West Virginia.

The evidence presented collectively in the literature suggest that LOWA may be sensitive to surrounding land use practices, and proximity to anthropogenic disturbance may influence the quality of breeding habitat by impacting water quality and food availability.

# Prey availability and abundance

The availability of food resources for the LOWA is associated with several of the factors mentioned above. In-stream habitat (e.g., proportion of riffles), proportion of exposed rock, and stream substrate, for instance, facilitate LOWA foraging success. LOWA focus most of their foraging efforts on aquatic, benthic, macroinvertebrates in first and second order streams (Craig 1984). In a study comparing the foraging ecology of LOWA with the closely related Northern Waterthrush, Craig (1984) observed LOWA consuming isopods (e.g., aquatic pill bugs), gastropods (e.g., freshwater snails), nymphs of Ephemeroptera

(mayflies), Trichoptera (caddisflies) larvae, Culicidae (mosquitos), and Dytiscidae (aquatic beetles).

Many studies that mention LOWA foraging ecology focus on invertebrates representing the orders Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies; EPT taxa). EPT taxa are vulnerable to changes in stream water quality, and there is a substantial body of work supporting the association of LOWA presence and productivity with the abundance of EPT taxa (Stucker and Cuthbert 2000, Mattsson and Cooper 2006, Mulvihill et al. 2008, Trevelline et al. 2016, 2018, Frantz et al. 2018a, 2019). For instance, Stucker and Cuthbert (2000) found a higher proportion of EPT taxa in stream reaches occupied by breeding LOWA than those unoccupied. Mattsson and Cooper (2006) showed that LOWA occupancy was a useful indicator of the proportion of EPT taxa within a stream reach. When investigating the effects of stream-water acidification on the breeding ecology of LOWA, Mulvihill et al. (2008) found that there was a lower proportion of Ephemeroptera taxa in acidic versus circumneutral streams. Frantz et al. (2019) similarly found that EPT richness declined with shale gas activity, and that LOWA were observed to expand their foraging diet along degraded stream reaches. These findings, in addition to higher site fidelity on circumneutral streams, indicate that stream acidification and pollution decrease habitat suitability for the LOWA.

When looking at LOWA nestling diet, Trevelline et al. (2016) found that, while the relative abundance of EPT taxa was high across study sites in Pennsylvania and Arkansas, the three most common orders included terrestrial Lepidoptera (butterflies and moths), aquatic Diptera (flies), and Ephemeroptera. Later, in a study comparing nestling diets of LOWA, Acadian Flycatcher, and Wood Thrush, Trevelline et al. (2018) continued to find a high proportion of Lepidopterans. The prevalence of terrestrial Lepidopteran taxa highlights that, in addition to reliance on the aquatic invertebrate community, reproductive success may also rely on the terrestrial invertebrate community later in the breeding season. Plecoptera and Trichoptera were unique to LOWA nestling diet.

That both adults and nestlings are known to consume pollutant intolerant taxa supports the negative association with lower Louisiana Water abundance and productivity and stream degradation resulting from human activity, including shale gas development, mining, and agriculture.

# Nesting habitat

Habitat features important for nesting include the slope and construct of the stream bank as well as surrounding ground characteristics (Prosser and Brooks, 1998, Stucker and Cuthbert 2000, Bryant et al. 2020). The 1998 HSI suggested that the presence of fallen trees within 50 meters of the stream was associated with optimally suitable nesting habitat (SI = 1.0), as LOWA typically construct their nests within the roots of upturned trees (Prosser and Brooks 2011). LOWA also build their nests in depressions along stream banks (Prosser and Brooks 1998). Stream banks consisting of a mix of soil, rocks, and tree roots provide crevices to facilitate nest building and provide optimal habitat (SI = 1.0 for bank slopes over 30°; SI = 0.7 for gentle bank slope less than 30°) (Prosser and Brooks 1998). Stream banks consisting of more than 75% rock or 70% herbaceous cover provide poor habitat, regardless of slope (SI = 0.1) (Prosser and Brooks, 1998). Stucker and Cuthbert (2000) also found that LOWA were nesting along moderately steep stream banks (average slop =  $69^{\circ}$ ). LOWA nests in this Minnesota study site were typically within 1.4 meters of the stream and 1.3 meters above the stream surface (Stucker and Cuthbert, 2000). Maple leaves were prominent nesting material in this study (Stucker and Cuthbert, 2000). In a 2020 study on the indirect effects of an invasive insect on LOWA nest survival, Bryant et al. (2020) found that nest site selection was associated with the interaction of exposed live roots and hemlock condition – if hemlock condition was poor due to infestation, nests were more likely to be constructed in roots. These findings further highlight the potential for exposed roots to facilitate nesting.

# **Other features**

Aside from the components mentioned above (forest area, forest overstory structure and composition, canopy cover, successional stage, riparian vegetation and understory structure, stream morphology, proximity to anthropogenic disturbance, prey availability, and nesting) several other features have been linked to LOWA breeding success and habitat suitability.

Mattsson and Cooper found that rainfall was the main driver of LOWA reproductive success in a 2009 Georgia study. In this study, DSR was highest when rainfall was moderate during the nesting season (3-10 mm day<sup>-1</sup>). Nestling survival, however, was maximized when rainfall was high (>14 mm day<sup>-1</sup>). The researchers suggest that food availability is highest with moderate to high levels of rainfall, potentially leading to higher reproductive success.

Fire, a common land management practice (particularly in the WGCPO and southeastern US), has been linked in LOWA presence in a 2014 study comparing avian communities in burned versus unburned forest stands in Nebraska towards the northwest periphery of the LOWAs range. Jorgensen et al. (2014) only detected LOWA in burned forest stands, with no detections in any of the unburned stands over the three-year study period. These findings suggest that LOWA may be avoiding forest areas with dense, well-developed understories, and may have important implications for the WGCPO, where burns are frequently incorporated in forest management.

# Conclusion

The information provided in this summary is meant to serve as a guide for land managers, or anyone interested in understanding key LOWA breeding habitat characteristics. While every effort was made to ensure the information provided here represents a comprehensive compilation and synthesis of literature relevant to LOWA breeding habitat, it is possible that pertinent information was missed, and therefore unintentionally omitted from this summary. The accompanying annotated bibliography is designed to provide a more in-depth representation of the studies and works cited in this summary; however, the reader may have to refer to the original source to obtain more specific information (e.g., detailed methodology).

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