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The Effects of Suburbanization on Nest Ectoparasites and Nest Defense Behavior in the Wood Thrush

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THE EFFECTS OF SUBURBANIZATION ON NEST ECTOPARASITES AND NEST DEFENSE BEHAVIOR IN THE WOOD THRUSH

A Thesis Presented

By

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ABSTRACT

THE EFFECTS OF SUBURBANIZATION ON NEST ECTOPARASITES AND NEST DEFENSE BEHAVIOR IN THE WOOD THRUSH

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Many migrant songbird populations have been declining throughout North America due to habitat loss caused by urbanization. As urban development continues to grow, it is important to determine what effects the associated suburban sprawl may have on bird populations. The Wood Thrush (*Hylocichla mustelina*) is declining throughout its range, yet is capable of persisting in both contiguous forests and small forest patches surrounded by human suburban development. Thus, it is an ideal species for gaining insight into the effects of suburbanization on migrant songbirds. I investigated two aspects of Wood Thrush nesting ecology: nest ectoparasites and nest defense behavior in order to determine if suburbanization influences either aspect. Nests from suburban forests had fewer haematophagous mites, though the abundance of haematophagous blowfly larvae did not differ between suburban and contiguous forests. There was no relationship between the abundance of mites and nest site characteristics, though blowfly abundance may be related to nesting substrate species. Parasites had little effect on nestling condition, and the only negative effects detected were in suburban habitats, where parasite abundances were lower. In regard to nest defense, I found that during initial nest visits, suburban Wood Thrushes had shorter flight initiation distances and mount more

active defenses than Wood Thrushes nesting in contiguous forests, suggesting a previously-established sensitization response to human disturbances in suburban birds. I found no consistent shifts in aggression over subsequent nest visits in either habitat type, suggesting that throughout the breeding season, Wood Thrushes neither habituate nor sensitize further to repeated human disturbances. My results suggest that Wood Thrushes nesting in suburban forest patches are subject to fewer nest ectoparasites and defend their nests more aggressively than conspecifics nesting in contiguous forests. These results draw attention to the fact that although Wood Thrushes persist in both rural and suburban habitats, the nesting ecology of the species may be quite different between the two habitat types.

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CHAPTER 1

AN ANALYSIS OF HAEMATOPHAGOUS PARASITES IN THE NESTS OF THE WOOD THRUSH: EVIDENCE FOR PARASITE RELEASE IN SUBURBAN NESTS

Abstract

Ectoparasites often occur in the lining of bird nests. Their detrimental effects on nestlings have been reported, but little is known about their patterns of abundance in relation to urbanization. I compared the abundance of haematophagous parasites in Wood Thrush nests in suburban and contiguous forests and measured nestling size in relation to parasite abundance. Nests from suburban forests had fewer mites, though the abundance of blowflies did not differ between suburban and contiguous forests. There was no relationship between the abundance of mites and nest site characteristics, though blowfly abundance may be related to nesting substrate species. The lack of a relationship between mites and nest site characteristics suggests that differences in parasite life histories can result in certain groups of parasites being more sensitive than others to changes in Wood Thrush nesting sites mediated by changing urban environments. Parasites had little effect on nestling condition, and the only negative effects detected were in suburban habitats, where parasite abundances were lower. Larger nestlings came from contiguous forest nests with higher parasite diversities. My findings highlight the complexity of effects of suburbanization, with suburban Wood Thrush nestlings experiencing lower rates of parasitism by mites and blowflies, but possibly greater impacts when parasitized.

Introduction

Songbirds are parasitized by many invertebrate taxa, the most common of which are blowflies (Protocalliphora); lice (Phtiraptera), and mites and ticks (Acari), which are commonly found in the lining of bird nests (Bennett and Whitworth 1992, Darolova et al. 1997, Proctor and Owens 2000, Roulin et al. 2003). Parasites have been shown to have significant detrimental effects on nestlings (Merino and Potti 1995) but their effects are often overlooked in studies of nesting ecology. Heavy parasite loads have been linked to slower fledgling growth rates and lower fledging mass across several avian taxa (Merino and Potti 1995, Morrison and Johnson 2002, Roulin et al. 2003). Although fledgling mass was not found to be related to survivorship (Anders et al. 1997), it is possible that parasites may reduce fledgling fitness by transmitting disease or by affecting their ability to evade predators (Streby et al. 2009).

Studies that have compared parasite loads on adult birds from urban and rural areas have found a decrease in parasite numbers and diversity in urban habitats (Gregoire et al. 2002, Fokidis et al. 2008, Geue and Partecke 2008, Evans et al. 2009). This presents the intriguing possibility that release from parasitism may contribute to the success of some bird species in colonizing or persisting in urbanizing areas.

Several factors may play a role in parasite reduction in urban areas. Eeva and Klemola (2013) found that blowflies are sensitive to air pollution in the vicinity of Pied Flycatcher (*Ficedula hypoleuca*) nests. Exposure to anthropogenic chemicals is expected to be high in urban areas (Pickett et al. 2011), but may also occur near agricultural land, where many farmers utilize pesticides that are deadly to many avian ectoparasites. Daoust et al. (2012) found that blowfly prevalence was disproportionately reduced with agricultural intensification compared to its host species the Tree Swallow (*Tachycineta bicolor*). It has also been suggested that ectoparasites are sensitive to both nest height and the habitat immediately surrounding the nest (Le Gros et al. 2011). Thus, factors associated with nest site availability, which can vary along urbanization gradients (Reale & Blair, 2005), may also influence nest ectoparasite communities.

The aforementioned studies provide insight into urban ectoparasite patterns; however, they do not address the parasite communities found in forest fragments surrounded by low density development (hereafter, suburban).

I compared abundances of ectoparasites in the nests of Wood Thrushes (*Hylocichila mustelina*) in patches of forest surrounded by human development with nests in larger, contiguously forested areas. I also investigated what factors influence parasite loads at the individual nest level, as well as the impacts these parasites have on fledgling condition. I predicted that: a) suburban nests would have lower abundances of ectoparasites, as seen in previous urban studies; b) that parasitism rates would be associated with particular nest site characteristics; and c) that higher abundances of parasites would result in decreased condition of nestling birds.

Methods

Study Sites

I identified eleven forested sites within 25km of Amherst, Massachusetts, six of which were suburban forest fragments. These forest patches are surrounded by human development, either low-density housing, roads or small-scale agriculture (‘suburban forests' hereafter). The suburban forests' relatively small sizes (<20 hectares) resulted in all of the Wood Thrush nests occurring within 150m of human development. The five other sites (in Montague, Pelham, New Salem and Petersham, MA) are comparatively large (>1000 hectares), and embedded in >12 km^2 blocks of contiguous forest ('contiguously forested sites' hereafter).

Nestling Condition and Parasite Loads

Five research technicians and I performed nest searches in all areas throughout the breeding season (May 10 to August 30, 2012) and monitored nests every other day. We measured nestling condition at twelve days old ± 1 day (just prior to fledging). We measured tarsus length for all nestlings in 29 nests from contiguous forests and 12 nests from suburban forests, and both tarsus and weight for nestlings in 28 nests from contiguous forests and 11 nests from suburban forests. We averaged mass and tarsus length for each brood. We also examined nestlings for the following signs of ectoparasites: mite eggs in the barbs of flight feathers, signs of mites in the ear canals and any visible parasites under the feathers of the flanks, belly and head. Because it was not feasible to count parasites in the field, we calculated an index of parasite abundance as the total number of these five body areas showing evidence of parasites.

Extracting parasites from nests

We collected empty nests within one day after fledging and placed them in clear plastic bags for transport for extraction of parasites. Wood Thrushes do not reuse nests (Roth et al. 1996), so removal of the nest did not impact further potential breeding efforts.

Invertebrates were extracted from each nest using a Tullgren funnel, running for 48 hours. I focused analyses on mites, ticks and blowfly larvae, since they were the most abundant taxa that could have impacted nestling condition. Other taxa included: springtails (Collembola), ants (Hymenoptera), beetles (Coleoptera), millipedes (Diplopoda) and small spiders (araneae). Mites and blowflies were analyzed separately because they differ in their modes of parasitism (Fig. 1.6) Mites are brought to the nest by adult birds, while blowflies emerge from eggs laid in the nest by adult flies.

Nest substrate

We recorded nest height and the species in which all nests were found. For analyses comparing parasites among nesting substrates, I included plant species that were substrates for two or more nests.

Statistical analyses

I log transformed number of mites and fly larvae per nest prior to statistical tests in order to fit a normal distribution. I excluded data from any nests that waited longer than 11 hours between collection and parasite extraction ($n = 6$). Mean abundance of both mites and fly larvae as well as nestling mass and tarsus length were compared between suburban and contiguous forests using Student's *t*-tests as variances were similar in the two groups. I used linear regression to test for relationships between parasite abundances and Julian date. I used a one-way analysis of variance to detect differences in parasite abundances among nesting substrates. For all tests, I used a significance level of $\alpha = 0.05$.

Results

Forest type and parasite load

All but two of the 55 nests I examined contained mites; both nests without mites were from suburban forest habitats. Mites were significantly more abundant in nests from contiguous forest sites (Fig. 1.1; $t_{53} = 2.58$, $p = 0.01$). The mean number of mites per nest was 91.65 ± 120.22 (n=31) in contiguously forested areas and 30.04 ± 28.50 (n=24) in suburban forest patches.

No significant difference was found in the number of blowfly larvae per nest between contiguous and suburban forests ($t_{53} = 1.10$, $p = 0.28$), but the trends for both overall abundance and presence of fly larvae were in the same direction as for mites, greater in contiguous forests. Mean fly abundances (per nest) were 9.94 ± 16.60 (n=31) in contiguous and 5.92 ± 13.26 (n=24) in suburban areas. The percentages of nests parasitized by fly larvae (51.6% contiguous, 37.5% suburban) also did not differ significantly, ($x^2_{55} = 1.09$, $p = 0.30$).

Nesting substrate and parasite load

Wood Thrush nests were found in a variety of tree and shrub species. The only species that were used as nesting substrates for more than one nest were: white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), witch hazel (*Hamamelis virginiana*) and honeysuckle (*Lonicera sp*.) (n =14, 10, 4, and 2, respectively), and these species accounted for one half of all nest substrates. The frequency of the four most common tree species used as nesting sites differs significantly between forested and suburban sites (Pearson's Chi-squared test: $x^2_{30} = 12.49$, $p < 0.01$). Percentages of nesting substrate species used in contiguous forests were: white pine 44%, hemlock 40%, and witch hazel 16%. Percentages of nesting substrate species used in suburban forests were: White Pine 60% and Honeysuckle 40%. Witch hazel and hemlock were only used as nesting sites in contiguous forests. We found Wood Thrushes nesting in honeysuckle only in suburban forest patches. All honeysuckle shrubs used as nesting sites were exotic invasive species. I found no significant differences in mite or blowfly abundances in relation to nesting substrate species (mites: ANOVA $f_{3, 30} = 0.55$, $p = 0.65$; blowflies: ANOVA $f_{3, 30} = 2.79$, $p = 0.06$, Fig. 1.2).

Nest height and parasite load

Mean nest height differed significantly between contiguous and suburban sites (2.94 ± 1.08, n = 34 and 2.41 ± 0.54, n = 17 respectively; $t_{50} = 2.36$, $p = 0.02$). Fly larvae abundances across both habitat types appeared to peak in nests at around 3 meters above the ground although there was no significant linear or polynomial relationship (Fig. 1.3).

Seasonal variation in parasite load

In nests from contiguous forests, mite abundances exhibited a significant curvilinear relationship with Julian date (Fig. 1.4; $r = 0.69$, $p < 0.001$), peaking around June 27, midway through the nesting cycle. Suburban nests showed a nearly significant negative relationship with Julian date (Fig 1.4; $r = -0.40$, $p = 0.06$, n=20).

Fly larvae abundance increased monotonically through the nesting cycle in nests from contiguous forests (Fig. 1.4; $r = 0.52$, $p < 0.01$, n=30). I found no significant relationship between Julian date and fly abundance in nests from suburban forests (Fig 1.4; $r = 0.35$, $p = 0.11$, n=21).

Impacts of parasite load on nestlings

All nests from which nestlings were examined for parasites contained mites (n=17). Each of these nests contained at least one nestling with evidence of mite parasitism and 87% of all nestlings observed showed evidence of mite parasitism. In addition we frequently observed nestlings with bloody sores on the feet and tarsi, which likely reflect blowfly parasitism.

Mean nestling weight was not statistically different between contiguous forest (35.1 g. ± 2.22, n = 28) and suburban (35.0 g. ± 2.45, n = 11) nestlings. In contiguous forests, however, tarsus length averaged shorter (31.24 mm ± 1.19, n = 29) than nestlings from suburban areas (33.04mm ± 2.29, n = 12; $t_{39} = 3.31$, $p < 0.01$). This difference could have been due to observer effects; researchers measuring nestlings at forested sites were not the same as those working at suburban sites. Because of this site level difference, I analyzed site types separately when comparing nestling condition between nests with and without fly larvae.

Of the nests for which we had data on both nestling size and parasite abundances, all contained mites, while fly larvae were present in 56% of nests from contiguous forests and 50% of suburban forest nests. Average nestling mass and tarsus length were both significantly larger when fly larvae were present in nests from contiguous forests (Fig. 1.5; $t_{16} = 2.85$, $p = 0.01$ mass; $t_{16} = 2.92$, $p = 0.01$ tarsus length). In suburban forests, nestlings tended to be smaller in the presence of fly larvae, though this difference was not significant (Fig. 1.5; $t_5 = 0.51$, $p = 0.63$ mass; $t_6 = 1.49$, $p = 0.19$ tarsus).

Discussion

I found lower abundances of mites and blowflies in Wood Thrush nests in suburban forest patches in Western Massachusetts (Fig. 1.1), a finding that is consistent with other studies in more urban settings (Gregoire et al. 2002, Fokidis et al. 2008, Geue and Partecke 2008). Taken together, these studies suggest that more urban-adaptable species may encounter a release from certain parasites under urban conditions.

The two main groups of parasites I found in this study differ in their life histories and modes of transmission, and this may account for some of the differences I saw in the relationships of the different types of parasitism to suburbanization (Fig.1.6). Compared to blowflies, adult mites are not highly mobile, so it is most likely that the mites we found in nests are the offspring of mites that arrived on parent birds or nesting material (Darolova et al. 1997). Thus, abundances of mites in a nest probably reflect either higher concentrations of mites in areas where the adults have been foraging (within 50 meters from the nest, (Roth et al. 1996) or higher numbers of mites on adult birds at the time of nesting. By contrast, adult blowflies are mobile and must seek out and lay their eggs in bird nests (Bennett and Whitworth 1991). Thus, the number of blowfly larvae found in a nest is likely related to the degree to which that nest is concealed from adult blowflies.

Because of life history differences, I predicted blowfly abundances to be more affected by small-scale differences in nest sites, such as their height and substrate. This prediction was only partially supported. Despite differences in nesting substrate and nest height between suburban and contiguously forested sites, there were no significant relationships between parasite abundance and nest height or substrate. However, blowfly abundance tended to be higher in hemlock and witch hazel, which were more common nesting substrates in contiguous forests (Fig. 1.2). This difference may play a role in the reduction of blowfly parasitism in Wood Thrush nests in suburban forest patches. Thus, it is possible that patterns in blowfly abundance may reflect the influence of plant architecture on the ability of adult blowflies to successfully find Wood Thrush nests. Further investigation into the sensory systems and nest finding methods employed by adult female blowflies is necessary to better understand how small-scale Wood Thrush nesting site characteristics influence blowfly parasitism rates.

Seasonality of parasitism

Blow fly larvae abundances increased monotonically through the nesting season. Our results suggest that an earlier arrival (and subsequent first brood) would be advantageous from the perspective of minimizing parasitism by blowflies.

In contiguously forested sites, mite abundances show a peak midway through the nesting cycle. Although mean mite abundance was lower in suburban birds' nests, mite abundances in suburban Wood Thrush nests are relatively consistent throughout the nesting season (Fig. 1.4). Urbanization in the temperate United States leads to retention of greater warmth throughout the year in a heat island effect (Pickett et al. 2011). A previous study found higher winter temperatures that potentially facilitate the survival of Virginia opossums (*Didelphis virginiana*) in suburban Amherst (Kanda et al. 2005). Warmer temperatures in suburban forest patches may also facilitate earlier post-winter activity of mites and prolong the period of mite activity through the Wood Thrush nesting season.

Another possible explanation for low parasite abundance in suburban sites is the potential for greater exposure of nesting material to agricultural and household pesticides or other man-made chemicals at these sites. Agriculture is common in our study area and no suburban forest patch was farther than 100 meters from an agricultural area or golf course. Any pesticides used on these properties might pass into nearby suburban forest patches, thereby reducing abundances of nest parasites. In addition, it has been shown that blowfly larvae are sensitive to air pollution (Eeva and Klemola 2013), another factor likely elevated with suburbanization (Pickett et al. 2011). Further study is needed to determine whether nest ectoparasites are exposed to greater amounts of agricultural pesticides and air pollution in suburban forest patches.

We noted that Wood Thrushes commonly used human garbage in suburban nests. Wood Thrushes incorporated newspaper, plastic bags, cellophane, balloons and other miscellaneous pieces of paper that mimic the pale leaves they more typically use as nesting material. Sixty-two percent of suburban nests contained trash, compared to only 5% of contiguous forested nests ($x^2 = 28.22$, $N = 68$, $p < 0.0001$). Wood Thrushes' use of human-made materials has been observed since at least the 1930's (Pearson, 1936). Urban House Sparrow (*Passer domesticus*) and House Finch (*Carpodacus mexicanus*) nests containing cigarette butts contained fewer parasites (Suarez-Rodriguez et al. 2013). However, we found no significant relationship between parasite abundance and the presence of trash in Wood Thrush nests.

Impacts of parasite load on nestlings

Although there are fewer parasites on suburban sites, our data suggest that the impacts of parasites on nestling Wood Thrushes may actually be greater at these sites. We found that nests with more diverse parasite communities (those with both mites and blowfly larvae) had significantly larger nestlings in contiguous forest habitats a pattern that was reversed (though not significant) in nests from suburban fragments (Fig. 1.5). In cavity-nesting Pied Flycatchers, simultaneous large quantities of blowflies and mites reduce the negative impacts of mites on nestlings (Merino and Potti 1995), perhaps as a result of competition over available feeding sites on the nestlings. In cases of heavy parasitism, mites have also been observed feeding on blowfly larvae (Marshall, 1981). Regardless, the data suggest that the effects of multiple parasite types on Wood Thrush nestlings is not simply additive.

There are a few important caveats to consider about our data on nestling condition. We did not record parental feeding rates or food composition. It is possible that the differences in effects of parasitism we observed between contiguous and suburban birds are due to differential food availability between habitat types or due to interactions between food resources and parasitism. If food is more abundant and/or nutrient-rich in contiguous forested sites, chicks may grow faster despite heavier parasitism.

Conclusions

As predicted from previous studies, we found fewer parasites in nests in suburban forest patches. The mechanisms for this difference are unclear, but one possibility is that the significant reduction in mites might be due to increased exposure to chemicals, either from surrounding agriculture or anthropogenic development. While our prediction about nest site characteristics and parasitism rates was not upheld, it remains possible that novel nesting substrates and heights as a result of habitat changes associated with suburbanization may aid Wood Thrushes in escaping blowfly parasitism in suburban areas. Although there are lower rates of parasitism in suburban Wood Thrush nests, only nestlings in suburban nests appeared to be negatively impacted by this parasitism, particularly that of blowfly larvae. Our findings highlight the complexity of effects of suburbanization, with suburban Wood Thrush nestlings experiencing lower rates of parasitism by mites and blowflies, but possibly greater impacts when parasitized. The presence of differential parasitism rates and the effects of parasitism on nestling condition suggests that our findings have implications for the health of Wood Thrush populations nesting in suburban forest patches.

FIGURES

Figure 1.1

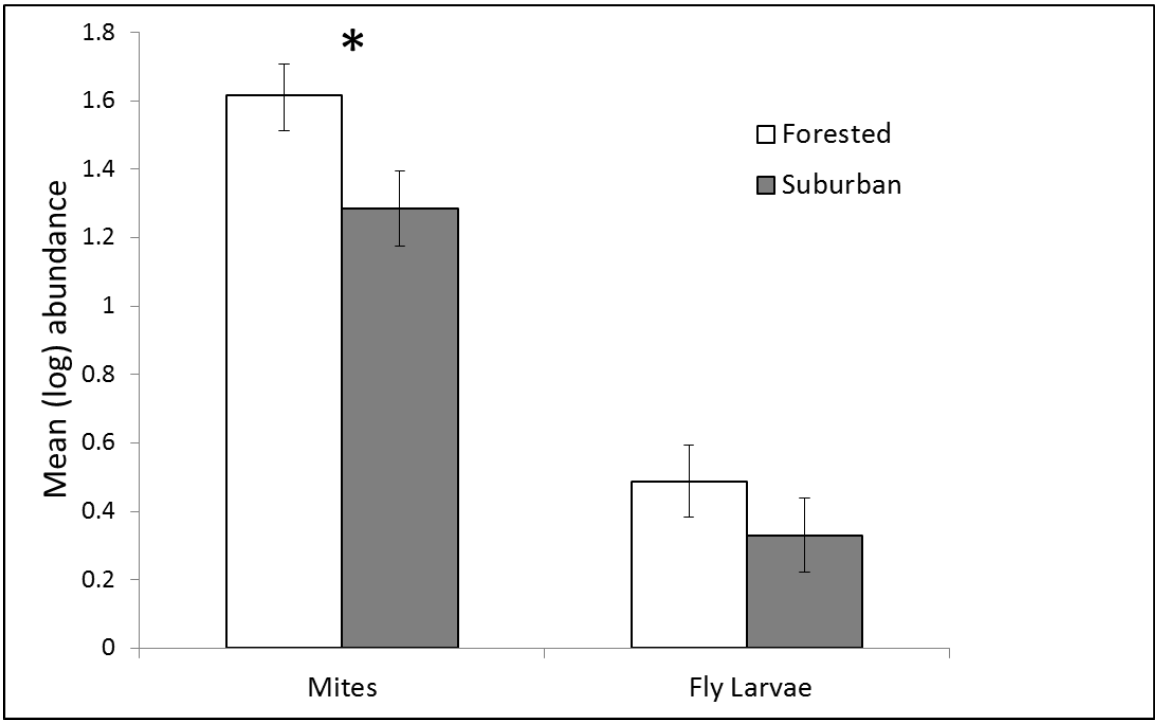

Figure 1.1. Log abundance (mean ± SE) of mites and blowfly larvae found in contiguous (n=31) and suburban (n=24) Wood Thrush nests. * denotes $p < 0.05$

Figure 1.2

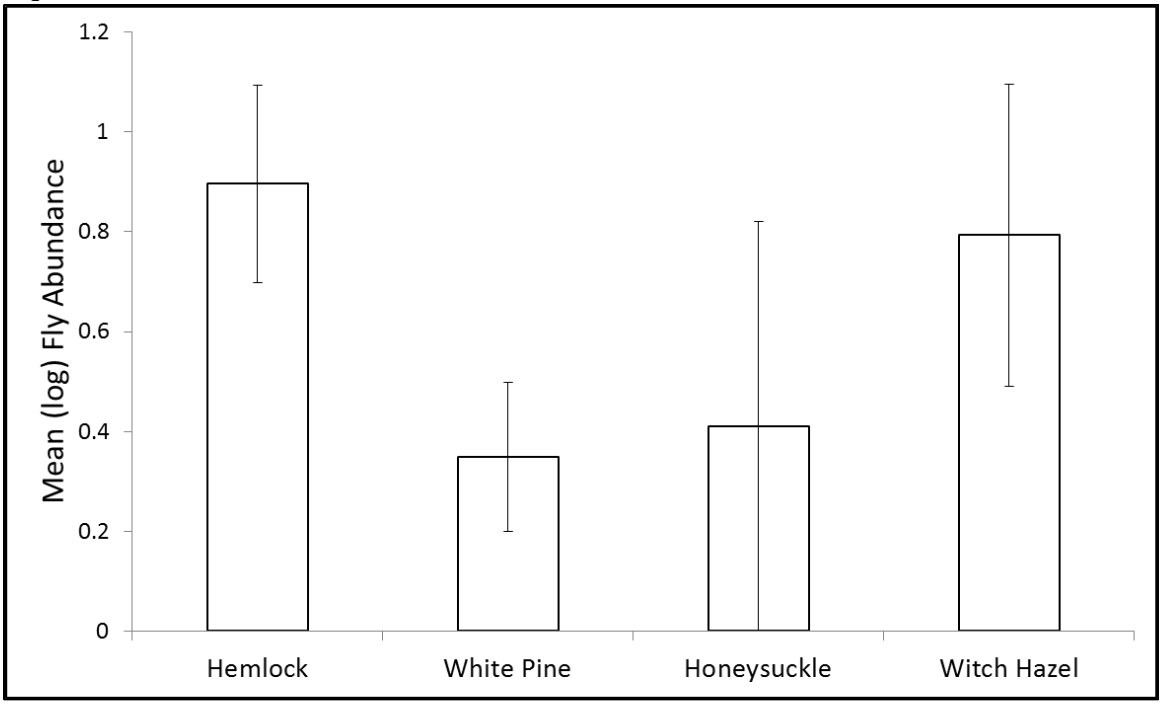

Figure 1.2. Log abundance (mean ± SE) of fly larvae found in the three most common nesting substrate species: Hemlock, White Pine, Honeysuckle and Witch Hazel (n=10, 14, 2, 4, respectively).

Figure 1.3

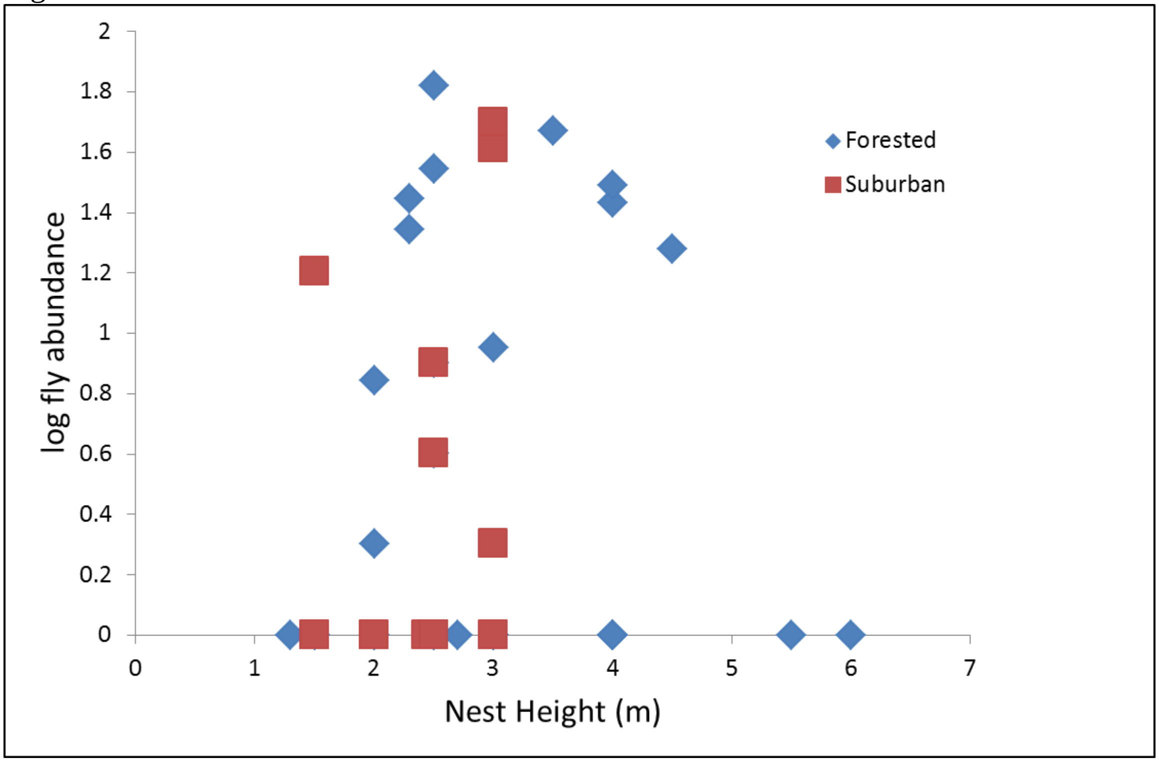

Figure 1.3. Log abundance of blowfly larvae in relation to nest height (meters). Contiguous n=31; suburban n=24.

Figure 1.4

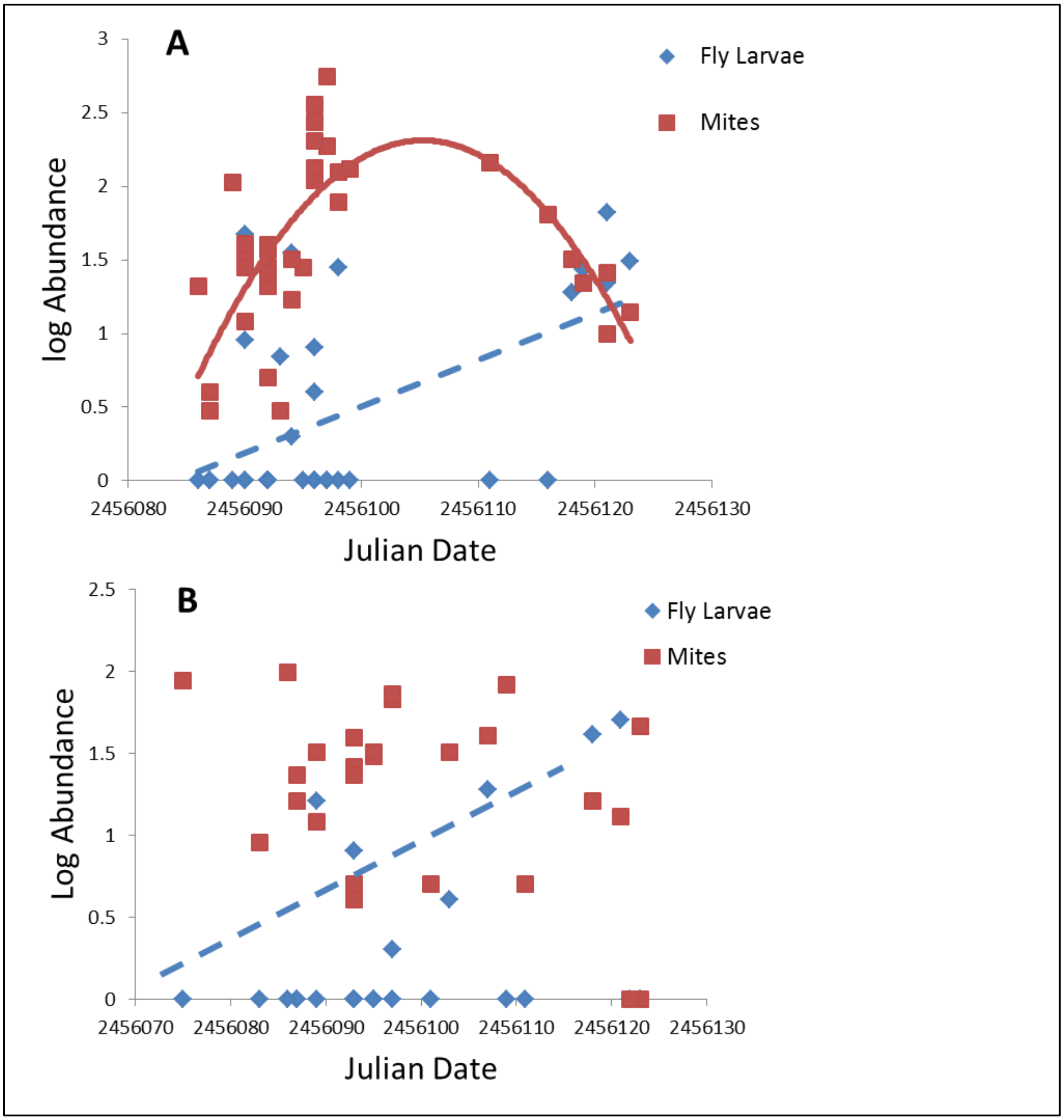

Figure 1.4. Log abundance of mites and blowfly larvae in relation to Julian date in contiguous (a) and suburban (b) nests. Solid line represents a quadratic fit of forested mite abundances (r^2 = 0.47, p < .0001). Dashed lines represent linear relationships for contiguous and suburban mite abundances (r^2 = 0.27, p < 0.01 and r^2 = 0.12, p = 0.11, respectively).

Figure 1.5

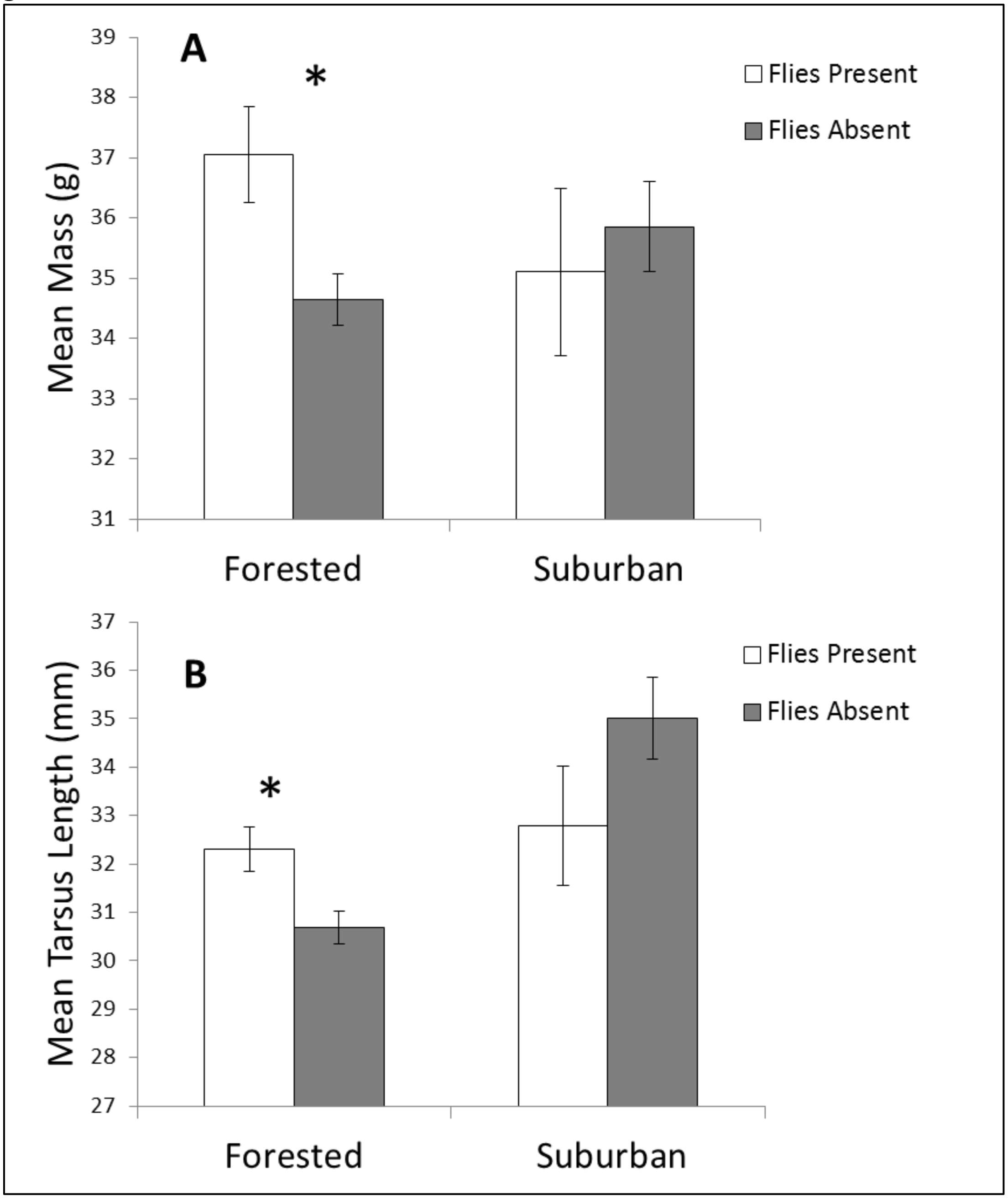

Figure 1.5. Mean ± SE nestling mass (a) and tarsus length (b) in the presence and absence of blowfly larvae. * denotes $p < 0.05$.

Figure 1.6

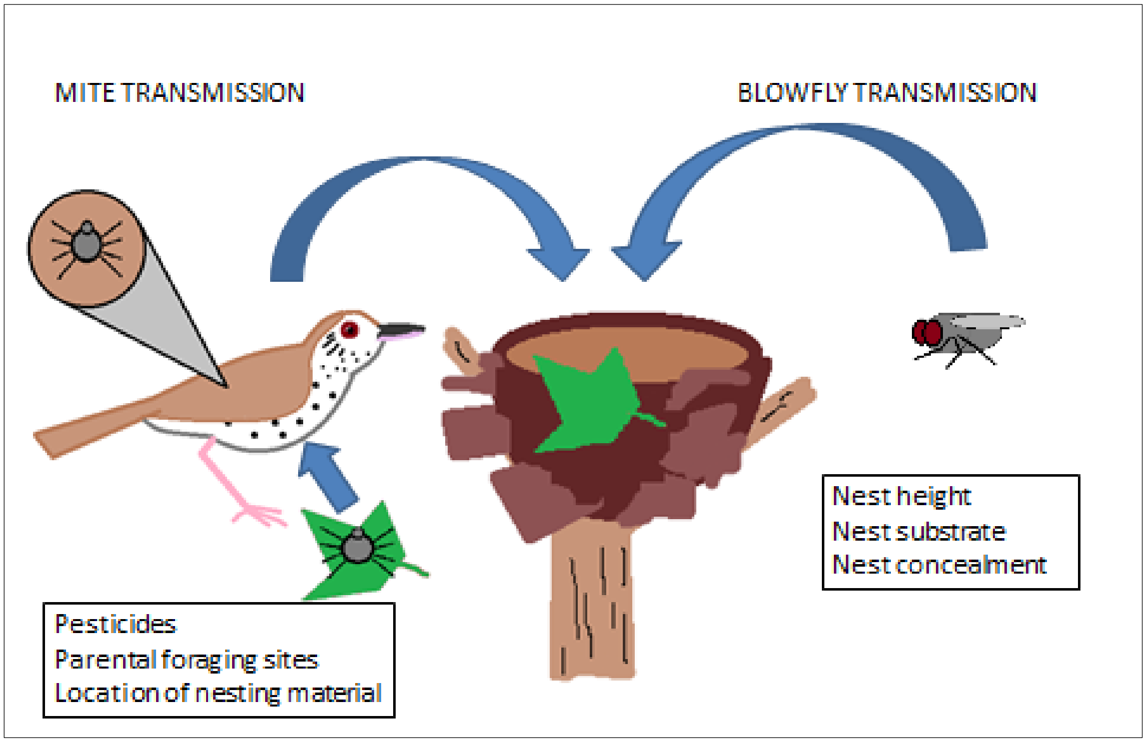

Figure 1.6. Modes of transmission for mites and blowflies. Text boxes represent potential factors that may influence the rates of parasitism in Wood Thrush Nests.

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CHAPTER 2

WOOD THRUSH NEST DEFENSE INCREASES WITH SUBURBANIZATION

Abstract

Many migrant songbird populations have been declining throughout North America due to habitat loss caused by urbanization. As urban development continues to grow, it is important to determine what effects the associated suburban sprawl may have on bird populations. The Wood Thrush (*Hylocichla mustelina*) is declining throughout its range, yet is capable of persisting in both contiguous forests and small forest patches surrounded by human suburban development. Thus, it is an ideal species for gaining insight into the effects of suburbanization on migrant songbirds. One aspect of Wood Thrush ecology that may be influenced by increased suburbanization is nest defense. We compared Wood Thrush nest defense behaviors between contiguous and suburban forests to examine whether Wood Thrushes exhibit a habituation response to human intrusion. We found that during initial nest visits, suburban Wood Thrushes had shorter flight initiation distances and mount more active defenses than conspecifics nesting in contiguous forests, suggesting a previously-established sensitization response to human disturbances in suburban birds. We found no consistent shifts in aggression over subsequent nest visits in either habitat type, suggesting that throughout the breeding season, Wood Thrushes neither habituate nor sensitize further to repeated human disturbances. Our results suggest that Wood Thrushes in suburban habitats display more aggressive behavior. This increased aggressiveness may allow them to cope with the elevated human disturbance and higher predator densities found in suburban environments.

Introduction

Breeding bird surveys and banding station data show that many bird populations throughout North America are declining, including the Wood Thrush (*Hylocichla mustelina*) (King et al. 2006). These declines are often attributed to anthropogenic factors such as habitat loss from human development (Ballard et al. 2003, Lloyd-Evans and Atwood 2004). For many songbird species, urban development has led to a severe loss of suitable habitat, smaller patch sizes and increasing fragmentation of existing breeding habitat. Some species, such as American Robins (*Turdus migratorius*) and Carolina Wren (*Thryothorus ludovicianus*) have shown their ability to exist in the presence of heavy human influence by thriving in the midst of intensive urbanization (Minor and Urban 2010). Other species seem to be able to exist in areas of less extreme human influence, such as areas of low density suburban development (Chace and Walsh 2006, Cardilini et al. 2013) or wildland-urban interface (Boren et al. 1997).

Throughout its range, the Neotropical migrant Wood Thrush breeds in heavily forested areas as well as suburban forest fragments (Roth et al. 1996). Given its ability to breed in both areas prone to anthropogenic factors and areas largely isolated from disturbance, the Wood Thrush is an ideal model species for investigating the influences of suburban development and human disturbances on songbird nesting ecology.

Aggressive nest defense has been associated with increased nest success in thrushes (Weidinger 2002, Schmidt and Whelan 2005, Halupka and Greeney 2009). Thus, habitat-level differences in Wood Thrush nest defense behavior may lead to decreased nest success in certain habitats.

Many organisms behave differently in more urban environments, relative to more native conditions. One such response, known as habituation, occurs when an organism acclimates to human or other disturbances and reacts less often or intensely to such disturbances (Petrinov.L and Peeke 1973, Samuni et al. 2014). It has been proposed that habituation to anthropogenic disturbances may facilitate colonization of novel environments, such as those found in cities and suburbs (Scales et al. 2011). Although habituation has been observed in many bird species, including, Savannah Sparrows (Fernandez-Juricic et al. 2009), Song Sparrows (Evans et al. 2010), Great Blue Herons (Vennesland 2010), Ferruginous Hawks (Keeley and Bechard 2011), and Choughs (Jiménez et al. 2011), studies of habituation in nest defense responses are few (Smith-Castro and Rodewald 2010).

There are at least two possible responses of Wood Thrushes to increased urbanization in the context of nest defense. Nesting Wood Thrushes may habituate to human disturbances in moderately urbanized (hereafter, “suburban”) habitats. Habituation in the context of nest defense in Wood Thrushes could include but is not limited to: increased flight initiation distance (FID) and decreased aggressive behavior at the nest. Shorter FIDs are usually associated with habituation in perching birds (Smith-Castro and Rodewald 2010), but in the case of nesting birds, a shortened FID represents more vigorous nest defense (Cooper and Blumstein 2014). Another possible response to frequent disturbance is sensitization (Petrinovich and Patterson 1981) – in this case reflected in shorter FIDs and an increase in aggressive behavior at the nest. The effect of urbanization on nest defense behaviors is unknown and difficult to predict a priori, but either response has the potential to be adaptive with respect to the persistence of the species in suburban forest patches.

We tested whether Wood Thrushes show signs of habituation or sensitization to human disturbances by comparing the nest defense behavior of Wood Thrushes in two conditions: forest patches within a suburban matrix and rural, contiguously forested areas. We collected data over repeated nest visits through the nesting season, which allowed us to detect baseline differences in behavior during initial nest visits as well as short-term changes in defensive behavior in response to repeated human disturbances at the nest. Differences in behavior between habitat types during initial visits may indicate prior, long-term habituation or sensitization to human intrusion has taken place in response to suburbanization. Changes in behavior over repeated visits to nests by humans would further indicate whether Wood Thrushes continue to modify their behavior based on exposure versus exhibiting a more stable population-level difference in behavior.

Methods

Study Sites

I identified eleven forested patches within 25km of Amherst, MA. Six study areas are suburban forest fragments located in Amherst, MA ('suburban forests' hereafter). These suburban forest patches are surrounded by human development. The suburban forests' smaller sizes (<20 hectares) resulted in all of the Wood Thrush nests being within 150m of human development, such as houses, roads or agriculture. In addition to the high degree of surrounding human development, frequently used public walking trails were present in each suburban forest patch resulting in high levels of exposure to human activities. The other study areas are large (>1000 hectares), contiguously forested, and undeveloped forests (‘contiguous forests’ hereafter) in Montague, Pelham, New Salem and Petersham, MA. Nesting Wood Thrushes in contiguous forests are not near walking trails or other access points and experience little to no exposure to humans.

Parental Behavior

We searched for Wood Thrushes in all areas throughout the breeding season (May 10 to August 30, 2012) and monitored nests every other day until fledging. Higher nests required the used of mirrors to examine nest contents. During nest checks, 5 field technicians and I recorded two measures of parental nest defense. In order to limit sampling biases, all field technicians were trained on protocols for approaching nests and recording parental responses. First, for each regular visit to check on nest status, we recorded flight initiation distance (FID), the distance at which the researcher caused the bird to flush off the nest. Nests were approached from the same direction from a point where the observer could see a bird on the nest. We did not record FID if a bird was not actively sitting on the nest at the start of the observer’s approach. We also compiled a “defensive behavior index” from parental responses while we checked the nest. We categorized responses, from least to most defensive, as: leaves the area; is flushed but stays in the area; stays in the area and vocalizes; stays in the area and attacks the researcher or the mirror; or both parents stay in the area and attack the researcher or mirror (ordinal variable, ranging from 0-4). Defensive behavior indices were still recorded for nest checks in which FID was not recorded due to the absence of a bird sitting on the nest. During nest checks we recorded the contents of each nest: number of eggs/young and estimated age of nest contents.

Analyses

In order to detect initial patterns of responses, I compared FID and defense indices from first nest visits in response to nest height between habitat types. I plotted the relationship between both responses (FID and defense index) and nest height. I then compared mean responses between habitat types over the first four nest visits because I had the most complete data for that period.

Results

We observed nest defense behavior for 47 Wood Thrush nests; 31 in contiguous forests and 16 in suburban forest patches.

Both FID and defense index varied with nest height (Fig. 2.1 and 2.2). Birds in suburban forests had lower FIDs and higher defense indices on initial nest visits than those nesting in contiguously forested sites when controlling for nest height (Fig. 2.1 and 2.2).

Consistent with our tests of initial visits, we found that over the first four visits, suburban birds had lower mean FIDs and higher mean defense indices (Fig. 2.3 and 2.4). There also appears to be no linear trend in either FID or defense index over the first four visits.

Discussion

By collecting data over repeated nest visits, our methods were designed to detect habitat-level differences in Wood Thrush behavior resulting from exposure to humans through suburbanization as well as short-term changes in defensive behavior in response to repeated human disturbances at the nest. Wood Thrushes nesting in suburban forest patches were consistently more aggressive than birds nesting in contiguous forests (Fig. 2.1 and 2.2), but we found no changes in aggressive responses over repeated nest visits (Fig. 2.3 and 2.4).

Our results are consistent with other studies that have found increased aggressive responses to human disturbances (Cilento and Jones 1999, Keeley and Bechard 2011, Scales et al. 2011, Cardilini et al. 2013).Upon initial nest visits, Wood Thrushes in suburban forest patches displayed higher defense indices than those seen in birds nesting in contiguous forests (Fig. 2.2). Birds nesting in suburban patches also had lower FIDs – they allowed researchers to approach their nests much closer before flushing in contrast to birds nesting in contiguous forests (Fig. 2.1). Both of these results suggest that Wood Thrushes nesting in these two habitat types exhibit long-term, population-level differences in their nest defense behavior in response to human intrusion.

We observed no effects of multiple nest visits on bird behavior. Although between the first and second visits, forested birds appear to be sensitizing to human disturbance (Figures 2.3 and 2.4), we were unable to detect either sensitization or habituation responses in suburban birds. As seen in our analyses of nest defense behaviors during initial visits, Wood Thrushes behave differently between the two habitat types, thus there may be no need for birds to alter their behavior in response to our nest visits. It is also possible that the suburban birds were already at the maximum response level and, due to a ceiling effect, further sensitization was undetectable.

One possible reason for the behavioral differences between habitat types could be differences in the proportions of individuals in each population with particular behavioral syndromes in the continuum from less aggressive to bold (Evans et al. 2010). If suburban birds defend their nests more aggressively than birds nesting in contiguous forests, it could be because bolder individuals are more successful in suburban areas. Urban behavioral syndromes have been observed in multiple avian systems and across several taxa (Lowry et al. 2013). For example, laboratory reared European Blackbirds (*Turdus merula*), close relatives of the Wood Thrush, from both urban and rural habitats show differential corticosteroid responses to stressors (Partecke et al. 2006) as well as different behavioral responses to novel stimuli (Miranda et al. 2013). It is not clear whether these behaviors represent phenotypic plasticity or have a genetic basis.

Our results contradict previous studies that have shown suburban birds readily habituate to human disturbances (Vennesland 2010, Jiménez et al. 2011, Keeley and Bechard 2011) and instead suggest that some species nesting in suburban landscapes may have more aggressive responses to human disturbances. Generally, numbers of potential nest predators are higher in urban habitats than in nearby, more-natural habitats (Sorace 2002, Sorace and Gustin 2009, Fischer et al. 2012, Stracey and Robinson 2012). If aggressive responses deter the predators found in suburban forest fragments, there could be selective pressure for more aggressive nest defense in suburban birds. Conversely, there is some evidence that aggressive nest defense may result in higher risk of predation by attracting 'third-party' (usually corvid) nest predators (Bonnington et al. 2013), leading to increased predation rates. Further study is needed to determine whether the composition of predator communities on our study sites could result in reduced nest success for more aggressive Wood Thrushes.

Historically, Wood Thrushes have been a species known to nest in both forested and suburban landscapes. Although the statewide population is declining (MassAudubon, 2014), Wood Thrushes still occupy both habitat types. Suburban habitats have been shown to contain higher numbers of potential nest predators, yet Wood Thrush nest success in our study area from 2011 to 2013 did not consistently differ between habitat types (M. Klein, unpublished data). Suburban Wood Thrush nests also contained fewer ectoparasites than those from forested sites (see Chapter 1). Although habitat loss due to suburbanization has been deemed a cause for declines in many Neotropical migrants nesting in Massachusetts (MassAudubon, 2014), Wood Thrushes seem to persist in suburban areas as well as in contiguous forests. More aggressive nest defense may be one adaptation to suburbanization that aids the Wood Thrush in persisting in these habitats.

FIGURES

Figure 2.1

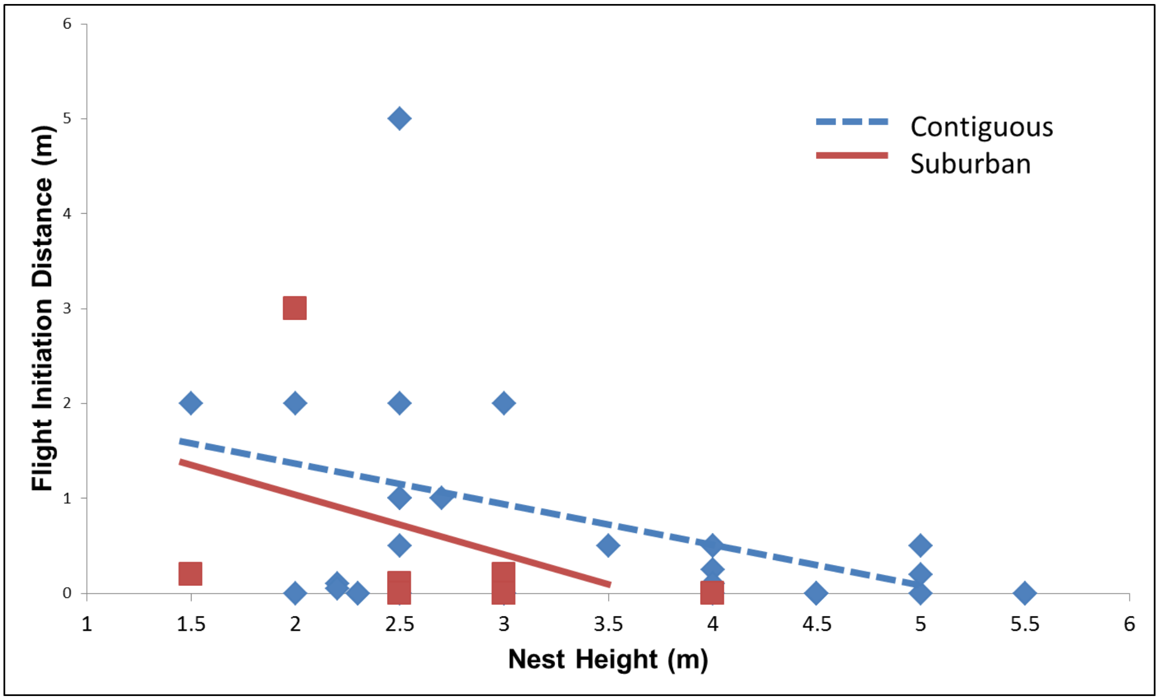

Figure 2.1. Flight initiation distances during initial nest visits were lower for suburban birds. Linear regression: suburban: y = -0.5685x + 1.9654, r^2 = 0.1697; contiguous: y = -0.3479x + 1.7886, r^2 = 0.1466

Figure 2.2

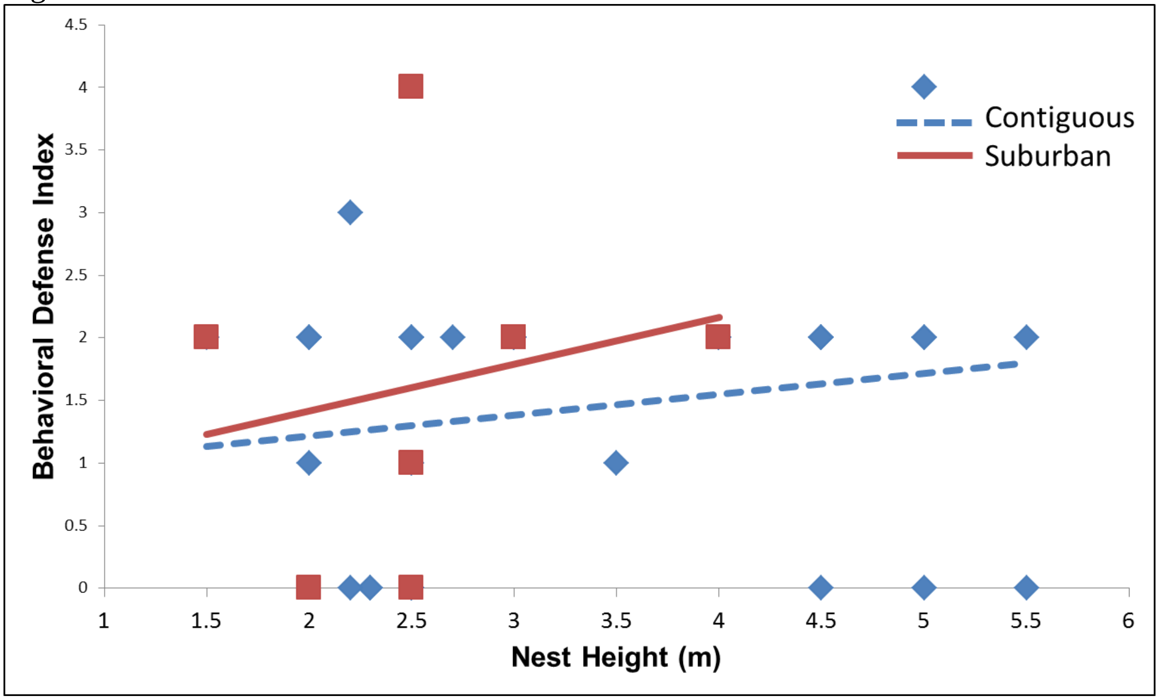

Figure 2.2. Defense index during initial nest visits was higher for suburban birds. Linear regression: suburban: y = 0.375x + 0.6667, r^2 = 0.0469; forested: y = 0.1679x + 0.8793, r^2 = 0.0361

Figure 2.3

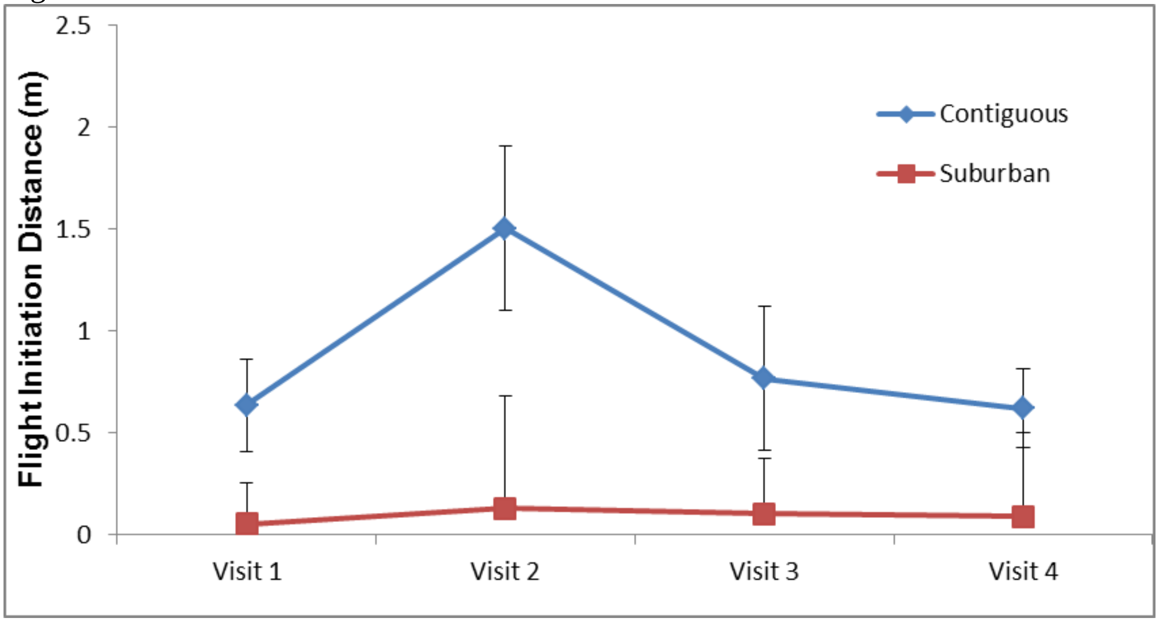

Figure 2.3. Mean flight initiation distance ± SE over the first four nest visits for forested and suburban nests.

Figure 2.4

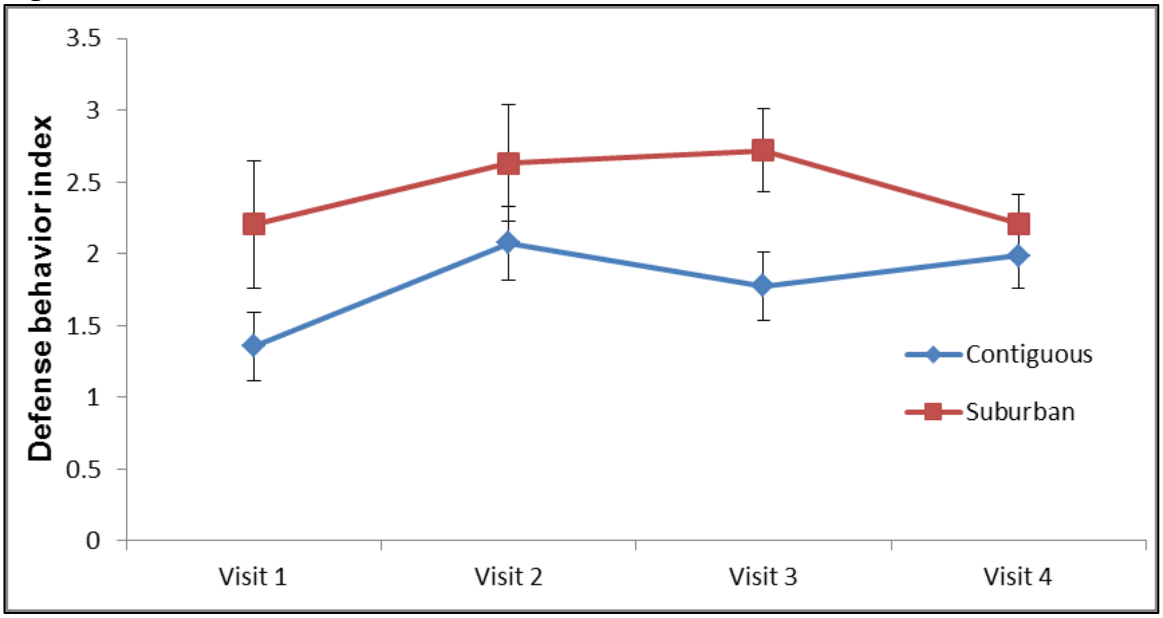

Figure 2.4. Mean defense index ± SE over the first four nest visits for forested and suburban nests.

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