Determining Space Use of Breeding Wood Thrush (Hylocichla mustelina) Pairs in Southeastern Virginia

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Determining space use of breeding Wood Thrush (*Hylocichla mustelina*) pairs in southeastern Virginia

An honors thesis submitted in partial fulfillment of the requirements for the degree of Bachelors of Science in Biology from the College of William & Mary

by

Akshay Deverakonda

__Dr. Matthias Leu, Committee Chair__

__Dr. Rowan Lockwood__

__Dr. John Swaddle__

Williamsburg, Virginia
July 1st, 2015
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**ABSTRACT**

Historically, studies of avian space use, which is critical to fitness, have largely focused on males, just recently on females, and least on pairs. Here, we studied space use and movement patterns of breeding Wood Thrush (*Hylocichla mustelina*) pairs. Our objectives were to estimate male-female space use overlap and how movement around nests related to breeding stage. We tracked 11 pairs using radiotelemetry while keeping track of their nesting activity. We were able to create kernel density estimates from six pairs, and used these estimates to determine space use overlap (the overlap of utilization distributions), delineate home ranges (95% isopleths), and assess proximity of shared space (at 5%, 25%, 50%, 75%, and 95% isopleths). We also calculated the average distance of six males and females from their nests during each nest stage. Space use overlap ranged between 0.45 and 0.81 and was significantly higher in pairs that had fledged at least one nest (henceforth successful) than pairs that did not fledge any nest (henceforth unsuccessful). Shared space in successful pairs showed similar increasing overlap with decreasing space-use intensity, whereas in unsuccessful pairs, shared space of males was always larger than those of females at any space use intensity level. Additionally, males and females ventured furthest from the nest during the incubating and failed nest stages. In tracking pair movements after nest failure, we observed that females generally made the largest
movements and often changed territories. Our findings complement previous studies that show that male nest attendance is linked to reproductive success.

**INTRODUCTION**

How birds use space has ramifications for how they obtain resources and mates, two indicators of fitness (Whitaker and Warkentin 2010). In the past 20 years, the advent of radio-telemetry and other tracking technologies has aided researchers in investigating how birds use space (Whitaker and Warkentin 2010). Understanding space use of Neotropical migrants is of particular interest as many species show population declines due to habitat fragmentation (Rodewald et al. 2013).

Until recently, most spatial ecology studies focused solely on male avian space use (Whitaker and Warkentin 2010). While there is a growing research on female space use, it is still dwarfed by the number of male studies. However, although most Neotropical migrants form socially monogamous pairs with biparental investment into reproduction, both sexes invest differently into fitness and therefore space use should differ among sexes as well (Gwiazda and Ledwoñ 2015). Typically for passerine species, males defend nestlings from predators and resources from inter and intraspecific competitors, and provide food for nestlings and the female while she is incubating, whereas females incubate, brood, and also provide food for young (Reichard and Ketterson 2012).

In recent years, researchers have studied animal space ecology by focusing on home ranges as a more accurate measure of space use (Whitaker and Warkentin 2010). The home range is distinct from the territory as the latter represents areas over which the animal has exclusive or priority use (Whitaker and Warkentin 2010). The home range, however, consists of
areas that an animal may use or travel through but that is not defended (Anich et al. 2012). Additionally, the home range extent by definition always dwarfs the territory extent (Anich et al. 2010).

The most recommended geospatial technique to delineate home ranges is the kernel density estimate (KDE) method (Marzluff et al. 2004). The KDE is a raster in which each cell’s numerical value relates to the density of points around it. Thus, areas in the KDE with a higher density of points will have higher values in the cells nearest those points. From the KDE, one can create a utilization distribution (UD), which is a way of normalizing the KDE so that each raster cell’s value is relative to all others. This standardization shows the probability of an animal occurring at a particular cell. Both the KDE and UD delineate high-use versus low-use areas within an animal’s home range, thereby overcoming the limitations of previous methods that assumed homogenous use throughout the home range. Isopleths are designations of quantiles of values in the KDE, of which the 95% isopleth area, delineating where there is a 95% chance of finding the animal within that area, is typically accepted as the home range (Marzluff et al. 2004).

Previous research on avian breeding pair space use is based on select shorebird species, but also on the Rock Ptarmigan (Lagopus muta), and Mallard (Anas platyrhynchos). These studies have documented that shorebirds have larger home ranges before and after their breeding period as compared to during the breeding period itself (Plissner et al. 2000, Haig et al. 2002, Demers et al. 2008). However, the period with the largest home range varied depending on the species. For example, female Piping Plovers (Charadrius melodus) that were unsuccessful in fledging chicks had larger home ranges than successful females (Haffner et al. 2009). This was corroborated by findings where Rock Ptarmigans had larger home ranges when they were
unsuccessful in fledging chicks than successful parents; this result was consistent across both sexes (Favaron et al. 2006). Mack and Clark (2006) related smaller home ranges to reproductive success in female Mallards (Anas platyrhynchos). Roth et al. (2004) pointed out that these smaller home ranges could be due to easier access to areas high in food and other resources.

A collective limitation to the previous studies is that while they do reveal valuable knowledge about space use and breeding ecology, they are based on one sex. Other studies have marked members of both sexes that were not necessarily in breeding pairs (Rivera et al. 2003). Evans and Stutchbury (2012) described various modes of indirect care that males provide to females, including mate guarding when females forage and incubate, that affect a female’s parental and movement behavior. Schmidt and Whelan (2005) quantified this indirect care through visual observations of nest attendance and found that nests attended by males had higher success rates. Evans and Stutchbury (2012) built upon this study and further established that male attendance is correlated to nest success in Wood Thrushes.

Along with a need to investigate pair space use, much of female space use during the breeding season remains unknown. Whitaker and Warkentin (2010) point out that most of the literature surrounding female space use has been focused on space use during the fertile period, while little is known about space use during the non-fertile periods of a female’s nest cycle. Reichard and Ketterson (2012) explored this question by researching how female home ranges decreased in size during the first half of the nestling stage. However, they only compared their findings to Dark-eyed Junco (Junco hyemalis) home ranges during the fertile period from a previous study (Neudorf et al. 2002, Reichard and Ketterson 2012).

Additionally, most of the literature regarding breeding ecology of Neotropical migrants has focused around extra-pair copulations (EPC) (Whitaker and Warkentin 2010). While recent
studies have shown that females in breeding pairs take part in EPCs just as much as males do, the distances that a female is willing to venture away from her nest/territory/home range are largely unknown. More studies of female space use during her non-fertile period are needed, as well as more direct comparisons of female activity during fertile/non-fertile stages. Additionally, each sex’s respective space use and the interactions between the two should be compared across the entire nesting cycle. Finally, additional aspects of space use, such as home range size, should be compared to nesting success to see if there is any relation between the two. This would allow for more nuanced examinations of space use beyond distances or ranges from the nest.

Using the UD, one can look at the overlap of two home ranges by determining the probability that two birds will be in the same area (Marzluff et al. 2004). Previous studies have applied this method only to adjacent male birds (Roth and Johnson 1993, Scarpignato and George 2013). Webb et al. (2012) calculated the proportion of overlap between Common Raven (Corvus corax) pairs, but did not relate it to nest status or stage. Another understudied aspect of pair space use is that even if studies did examine space use of breeding pairs, researchers usually compared only home range sizes between pair members, not overlap (Plissner et al. 2000, Haig et al. 2002, Roth et al. 2004, Bluso-Demers et al. 2008). Even though male and female birds may have similar home range sizes, space use within a home range may not be homogeneous (Anich et al. 2012). Birds emphasize different areas within the home range for different purposes, for example nest care, visiting food sources, deterring predators, which vary by sex as well (Roth et al. 2004, Anich et al. 2012). As the nest is a center of activity in the home range, examining each pair member’s proximity to the nest, in tandem with home range boundaries, can further explain sex differences in space use (Roth et al. 2004).
To explore avian sex differences in space use, we used radio telemetry to simultaneously track male and female Wood Thrush movements during their breeding season. The Wood Thrush is a Neotropical migrant that breeds in deciduous forests east of the Mississippi River in the United States and in southeastern Canada (Evans et al. 2011). Its populations have declined across wide regional scales [−2.12% yr$^{-1}$ from 1966 to 2012, (Sauer et al. 2014)]. These demographic losses, combined with its aesthetic appeal, make it an appropriate case study in pair space use in the face of habitat fragmentation and urbanization (Evans et al. 2011).

The primary objective of this study was to investigate the spatial breeding ecology of the Wood Thrush. We tested the hypothesis that space use differs between successful pairs and unsuccessful pairs. We predicted that space use extent is larger in unsuccessful pairs as they have more extended movements and therefore space use (Schmidt and Whelan 2005, Evans 2012). As a secondary hypothesis, we tested whether males and females have similar movement patterns across the breeding season. We predicted that movement, as measured by distance from the nest, is larger for males than females, as females tend to be closer to their nests than males (Evans et al. 2012).

**METHODS**

**Study area** — Our study was conducted in forest patches located between Williamsburg and Yorktown in southeastern Virginia (37° 15’ N, 76° 40’ W) at randomly selected bird point count locations related to a concurrent study. Study sites overlapped with eastern deciduous forest embedded in a matrix of rural to low-density housing development. Deciduous forests in southeastern Virginia are dominated by American Beech (*Fagus grandifolia*), White Oak (*Quercus alba*), Tuliptree (*Liriodendron tulipifera*) and Sweetgum (*Liquidambar styraciflua*). Red Maple (*Acer rubrum*), American Holly (*Ilex opaca*), and Dogwood (*Cornus florida*) occur
in the understory. Coniferous forests typically are managed and planted with Loblolly Pine (*Pinus taeda*) and Virginia Pine (*P. virginiana*; Monette and Ware 1983).

**Bird capture** — We caught 11 male Wood Thrushes from May 25th to June 3rd in 2014 using playbacks to lure them into 30 mm mist nets (10 m long). For each male, we captured the female to which he was currently paired. Our strategy for capturing females was to first see if captured males flew near a nest or were seen flying with another Wood Thrush, upon which further tracking led to a nest. Once we confirmed that the male was associated with a nest, we set up mist nets around or as close to the nest as possible to catch the female while she happened to fly to or from the nest. This method was a more passive form of capture, as females did not respond to male Wood Thrush song playback.

Once caught, each individual was sexed using brood patch presence and cloacal protuberance (Pyle 1997), weighed, measured, tagged with a 1.3 g (2.6-3.3 % of the Wood Thrush’s range of body mass) VHF transmitter (BD-2, Holohil Systems Ltd, Carp, ON, Canada) with a unique frequency. We attached transmitters to individuals using a harness made of 0.7 mm Stretch Magic jewelry cord (intra-loop distance = 57 mm). Following release, individuals were tracked the following day to confirm status to the transmitter. We obtained all necessary federal, state, and local permits, and the College of William & Mary Animal Use and Care Committee (IACUC-2013-02-15-8462-mleu) approved the project.

**Tracking protocol** — Individuals were tracked from May 16th - August 12th using three-element Yagi antennas and Wildlife Materials receivers (TRX-1000S, TRX-3000S). Each Wood Thrush was followed at a distance of 40-50 m until their location could be confirmed, either through visual sighting, or through biangulation/triangulation. Locations of sighted Wood Thrushes were georeferenced using a GPS unit (Garmin GPSmap 62). When we could not get close enough to a
Wood Thrush without disturbing it, we projected the points using GPS coordinates, compasses (Silva Ranger CL Sighting Compass), and laser range finders (Opti-Logic Insight 400 LH). We refrained from tracking birds in inclement weather. Each bird was usually tracked for 4-5 hours each week; the emphasis on tracking particular birds during any given week changed depending on which bird was closest to its transmitter’s predicted expiration date and the status of that bird’s nest. We sampled individuals until either the transmitter ran out of battery (60-70 days) or the individual went missing.

To account for temporal variation in behavior and space use across the time of day, we took at least one spatial location every hour from 8 AM to 8 PM, and took points at least 20 minutes apart to ensure independence among spatial locations and to influence each bird as little as possible. Along with each spatial location, qualitative aspects of each Wood Thrush’s behavior were recorded as well, including pairing status (paired, unpaired), vocalizing behavior between three distinct sets of song/alarm calls (singing, mild warning, and intense warning), and visual sighting.

We also monitored nest status when females were monitored. Nest monitoring began either when a female was captured near her current nest, or when she established a new nest. We recorded status (active, failed, or fledged) of nests for each observation, and if available, the number of days the nest was observed in each stage. We used existing observations to retrospectively determine lengths of other stages. Nests were determined to have failed if we observed no activity for at least one hour by either by nestlings or parents. For this study, nests were deemed successful if at least one nestling fledged.

At different stages of the study, we lost the signal on different individuals. To locate these birds, we drove along the surrounding roads at night with active telemetry equipment to
locate each missing bird. Where roads did not provide full accessibility, we attempted to relocate missing birds using walking/biking transects in nearby forest patches or aerial transects flown with a fixed-wing aircraft. We determined that premature transmitter failure was not a cause for losing individuals as one male in a concurrent study dropped his transmitter while it was still active, and we recovered both transmitters from two birds that died over the course of the study. We determined the distance that each bird moved as well as an overall search area based on transects done by foot, bike, car, truck, and airplane in ArcMap 10.2 (ESRI, Redlands, California, USA).

**Home range size** — Using Geospatial Modeling Environment (GME; Beyer 2011), we created kernel density estimates (KDE) for each of the 12 Wood Thrushes for which there were sufficient data. The KDE estimates an individual’s space within its home range based on the distribution of observed locations. Locations within a home range with a high density of observations have higher KDE values compared to areas with fewer observations. For breeding pairs, we used temporally overlapping observations only. We created the 95% isopleth, the line designating the top 95% of space most used, in GME from the KDE to delineate the home range size (Beyer 2011). We tested the hypothesis that home range size differs between sexes using a paired t-test. We used a paired t-test because male and female home range sizes in each pair were likely influenced by each other and thus were not independent.

**Space use overlap** — The proportion of space use overlap provides non-spatially explicit insights into how much a male’s and female’s activity patterns overlap. While merely calculating the area of the intersection of a pair’s home ranges gives a two-dimensional representation of where pair members overlap, factoring in probability (and thus intensity of space use) allowed us to determine the likelihood of finding both pair members in the same area. We converted KDEs
into utilization distributions (UD) to standardize probabilities of occurrence within an
individual’s home range among individuals. This conversion was necessary because the number
of observations, and therefore density estimates, differ among individuals. To create the UD$s, we
summed all KDE values within a home range, and then divided that total into each cell within a
KDE to derive a bird’s occurrence for each 1-m cell within a bird’s home range relative to the
cumulative space use (Marzluff et al. 2004). We then used the “minimum-value” algorithm in
ArcGIS 10.2 to extract the minimum value for each cell of paired male and female UD’s and
summed all minimum occurrence values to derive an estimate of the proportion of overlap. If
space use of pair members perfectly overlaps, the UD values would add up to 1. Conversely, a
UD total of 0 would indicate that pair members’ space use never overlaps. We compared the
overlaps of successful pairs and unsuccessful pairs using a t-test.

**Shared space** — Our objective was to determine the spatial juxtaposition of male and female
high-use areas across different levels of space use intensity. We use the shared space between
areas to infer proximity of those areas. This analysis is based on isopleths, which we delineated
from the KDE by designating five different levels of space-use intensity. We created polygons
representing each pair’s member’s 5%, 25%, 50%, 75%, and 95% isopleths. Each percentage
represents the top percent of space most used; the top 5% of space most used would be a high-
priority use area while the 95% of space most used would signify a general-use area. While using
the 95% isopleth as the home range is a widely accepted method in wildlife biology, some
studies have designated the 50% or 55% isopleths as “core areas” (Bluso-Demers et al. 2008,
Demers et al. 2008, Rivera et al. 2003). While these core areas do represent the top half of space
most used, there has been little reasoning to support only examining the top half of space used as
opposed to simultaneously examining space use at multiple levels. We calculated how much
space is shared between each pair member at different levels of space use. We defined the proportion of the female’s area shared with the male’s area as:

\[ P_f = \frac{\text{Intersecting area } \varphi \text{ and } \delta}{\varphi \text{ isopleth area}} \]

Similarly, we defined the proportion of the male’s area shared with the female’s area as:

\[ P_m = \frac{\text{Intersecting overlap } \varphi \text{ and } \delta}{\delta \text{ isopleth area}} \]

In cases where there were multiple polygons for a given isopleth (multiple non-continuous areas that represent a certain intensity of space usage), we divided the intersecting area of the pair by the total area of the other sex’s polygons for that level of space use, not just the intersecting polygon. We compared proportion of overlap at each of the five isopleth levels graphically. If graphs for each sex overlap, then space use between sexes is identical.

**Proximity to nest across nesting stages** — We matched telemetry points of each bird to the pair’s nest stage during which they were taken and then determined the distance of each observation to the active nest. If the nest had failed, we matched points taken at that particular nest status to the most recent active nest. We calculated distances from the nest to each observation in ArcMap 10.2. To test the hypothesis that distance to nest differs between sexes and between nesting stages, we used a Bonferroni-adjusted paired t-test to test for significance between the male and female average distances from the nest across each breeding stage. We did not use a repeated measure ANOVA for multiple comparisons because data could not be collected for each nesting stage from each pair and because nests failed among pairs during different nesting stages which precluded data collection from other nest stages. For example, for some pairs we only collected data during the incubation stage whereas for others we collected data only during the fledgling stage.
RESULTS

DEMOGRAPHY

Female survival — Of the 11 female Wood Thrushes caught, two were killed over the course of the breeding season. One was observed with internal bleeding, a broken left wing, a broken right foot, missing tail feathers, and broken ribs. We inferred from these signs and from observations of her fluttering along the ground that she was hit by a car. This female was found dead two days later, and our examination of the corpse revealed predation by a small mammal. Another female was found dead near her nest tree. The nest itself was overturned nearby and was empty. Post-mortem examination of this bird revealed gripping marks indicative of a bird of prey.

Nesting success — We found a total of 17 nests between 11 nesting pairs of Wood Thrushes (Table 1). Nesting attempts varied between one to three per pair, with 55% of pairs having only one nesting attempt, and 24% having two. Only one pair built three nests. Apparent nesting success was 23.5%. We did not determine the exact cause of failure as many nests were built in inaccessible sections of trees.

SPACE USE

Home range size — We collected an average of 53.2 points (SD = 16.9, range 26-83) from the 12 Wood Thrushes from which we collected substantial data, with an average of 51.3 points (SD = 16.5, range 26-74) from six males and an average of 55.0 points (SD = 18.7, range 38-83) from six females. The average home range size was 10.4 ha (SD = 10.9) for sexes combined (Table 2). There was a trend for average male home range size (15.7 ha ±13.5 SD) to be larger than average female home range size (5.0 ha ±= 3.1 SD), but the difference was only marginally significant (at
In pairs with no successful nests, male home ranges (26.8 ha ± 9.3 SD) were much larger than female home ranges (5.6 ha ± 2.9 SD). Pairs with at least one successful nest had more equal male (4.7 ha ± 2.7 SD) and female (4.5 ± 3.7 SD) home range sizes.

**Space use overlap** — Space-use overlap varied across the six pairs, ranging between 0.45 and 0.81 (Table 3; Fig 1). Average space use overlap was significantly larger (0.74 ± 0.08) in pairs who successfully raised at least one brood compared to unsuccessful pairs (0.47 ± 0.02; t = 4.57, p = 0.02).

**Shared space** — In general, males occupied most of a female’s space. However, in four out of six pairs high-use areas (5% isopleth) had little intersection (Fig. 2). For four pairs (pairs 2, 3, 8, 11), the shared space of the male’s high-use area (5 and/or 25% isopleth) with the female’s high-use area was below 20% overlap in three pairs and 0% in one pair, indicating little overlap of their high-use areas and thus showing that males and females use different areas.

Shared space differed between successful pairs and unsuccessful pairs, largely by the level of female proximity to her male’s space. For successful pairs (pairs 2, 3, and 10), shared space use increased with decreasing intensity of space use whereas for unsuccessful pairs (pairs 6, 8, and 11) shared space was always higher for females than males, regardless of the level of space use intensity (Fig. 2). In unsuccessful pairs, male home ranges completely subsume that of the female, which is small in comparison.

**Proximity to nest across nesting stages** — Males were significantly further away from the nest compared to females during the building + incubating stage (t = -4.31, df = 157, p = 0.00001; Bonferroni adjusted p < 0.05 if test p < 0.0125) and failed stage (t = -3.01, df = 65, p = 0.0038) (Fig. 3). Proximity to the nest did not differ between sexes during the nestling stage (t = -2.25, df = 34, p = 0.0312) or fledgling stage (t = 0.3455, df = 38, p = 0.7316).
MOVEMENT

Wood Thrushes moved after a failed breeding attempt at least once to a new location, with one female moving twice (Table 4). Of pairs with at least one failed nest, 71% of females moved to a new home range. Inter-nest distance was on average 347 m (± 365.9) and ranged between 142 to 988 m (Table 5). Females moved on average 1,234 m (SD = 1094.5 m; range = 419 m to 3,392 m).

Four female Wood Thrushes went missing over the course of the study after a failed nesting attempt. Of the four missing females, three went missing shortly after we had radio-tagged them. As a result, we were not able to analyze their movements due to lack of sufficient data. However for one female (Pair 9), we were able to collect sufficient data for analyses. This female vacated her nesting area after failure of her first nest (Figure 4). She moved 3,392 meters to a new location, but then moved again 1,261 meters to yet another new location. Her male could not be found after the first nest failed. Based on telemetry observations, we documented both bouts of activity but also stationary periods, suggesting a second nest. Visual sightings also indicated the female foraging with an untagged male without color bands, indicating a potential divorce from first male. In another pair, Pair 4, the male stayed on the territory after nest failure, whereas we could not detect the female again. In a third pair, Pair 5, we could not find the signal of either the male or the female within the search area (Appendix A) of 114 km². Finally, in the fourth pair, Pair 11, we continued to observe the female in the original home range after nest failure before she went missing, well before her transmitter was predicted to have run out of battery.
DISCUSSION

Our study is one of a handful to examine space use in breeding pairs of birds. While previous studies have applied calculations of proportion of overlap, this study is the first to apply them to breeding pairs as opposed to only birds in adjacent territories (Scarpignato and George 2013). While previous studies have focused on delineating male and female breeding ecology only in terms of home range size, examining space-use overlap complements distance studies by showing additional facets of pair investment into reproduction. Additionally, this study examined female movements across the fertile/non-fertile period, building on Reichard and Ketterson (2012)’s research comparing non-fertile female home ranges to previously studied fertile female home ranges (Neudorf et al. 2002). The large variation in movements throughout all six breeding pairs affirms that birds can widely vary their mobility in response to environmental factors, including forest fragmentation, resource needs, and predator pressure, in addition to different priorities of space use at the individual level (Whitaker and Warkentin 2010, Anich et al. 2012).

We found support for our hypothesis that pairs who had at least one successful nest had a higher proportion of space use overlap compared to pairs whose nests failed. A study on nest attendance by Evans et al. (2012) showed that more successful Wood Thrush nests generally had higher male attendance and higher levels of nest defense behavior. The Evans et al. (2012) findings complement those of our study as females’ home ranges, which were centered around nests in all six pairs, showed lower proportions of overlap with males’ home ranges in unsuccessful pairs than in successful pairs. In other words, there was less of a chance of the male and female being relatively close together in unsuccessful pairs, which is what Evans et al. (2012) highlighted as a determinant of nest success.
The larger home range (and thus smaller proportion of overlap) could be indicative that unsuccessful males either not attend the nest as much as in successful pairs or having to travel farther to obtain resources for incubating/brooding females or the nestlings/fledglings in fragmented forest landscapes (Evans et al. 2009). Either way, this would make the female or her nest more vulnerable to predation in addition to potentially shortening provision times if the male has to travel farther between feeding bouts. In smaller home ranges, birds may not have to spend as much time traveling to find resources (Roth et al. 2004).

The proportion of overlap calculations take into account all levels of space use. However, the calculation of high use areas and their proximity to each other’s shared space at different levels of space use intensity shows at which levels pair members are and are not likely to be in the same spaces within home ranges. Assuming that differential space usage implies using space for different functions, the relative lack of shared space at high intensity levels affirms previous conclusions that male and female birds in pairs prioritize space differently (Anich et al. 2012). For successful pairs, the fact that shared space increases with decreasing intensity of space use shows that males and females largely use the same areas for general space use, and more so compared with the unsuccessful pairs. Coupled with the fact that successful male home ranges are smaller than those of unsuccessful males, this could imply that it is easier for successful males to travel back to the nest for nest defense and care (Evans and Stutchbury 2012).

By determining the average distance of the male and the female from their nest during each nesting stage, we were able to shed light on how far pair members usually travel to and from their nest under different conditions. Our research suggests that, on average, both the males and females were closer to the nest during the nestling stage than during the nest building or incubating stages. This trend makes sense as the further along the nest is in its cycle, the more
invested both pair members would be in its success (Roth et al. 2004). Our results do not corroborate previous research which suggests that Wood Thrushes specifically use the non-fertile period (after incubation and onwards) to seek extra pair copulations, if we use distance from the nest to be indicative of EPC-foray behavior. We interpret our results to mean that both sexes stay close to the nest for the purpose of nest defense against predators. The significant difference between male and female average distances during the building + incubating stage could be due to males pursuing EPCs during the incubation period (Evans et al. 2008). As the nest progresses further through its cycle, both pair members may be inclined to defend the nest against predators instead of pursuing EPCs (Evans and Stutchbury 2012). This can take the form of either active nest defense behavior (chasing away or scaring off predators, alarming, etc.) or passive defense behavior being at the nest as a deterrent (Evans and Stutchbury 2012). However, when the nest fails, males and females have their highest recorded distance away from the nest. This could show that individuals might be looking for new nesting locations in order to start a new nest. As stated earlier, this behavior may also be indicative of them leaving an area of high predator density (Powell and Frasch 2000).

We found an apparent nesting success of 23.5%, which is similar to previously documented rates of nesting success in a Wood Thrush population in Pennsylvania (Gow and Stutchbury 2013). Of the Wood Thrush pairs with failed nests, 71% of the females moved to a new location. Of the three successful pairs, two continued breeding activity in the same home range. Failed pairs moved farther than pairs with successful nests, consistent with what previous studies have found (Weinberg and Roth 1998, Rivera et al. 1999, Friesen et al. 2000). Female movements after nest failure were all greater than male movements. If we assume that the birds that we could not find left the study area, then it is likely that female movement dwarfs male
movement. Leaving an area entirely after nest failure could be a mechanism to avoid predators, as birds have been known to disperse following nest failure in order to move well out of the home range of predators (Powell and Frasch 2000).

Our distances between subsequent nests were greater than previously reported averages of 72.6 m between nests and 38 m (Roth et al. 1993, Friesen et al. 2000), regardless of whether the first nest was a success or a failure. MacIntosh et al. (2011) show that Wood Thrushes travel farther in fragmented forest as compared to continuous forest; although their study was focused on ephemeral foray movements, a similar principle could apply in nesting locations as well.

Assuming movement distances are indicators of site fidelity, our data indicate that males are much more likely to stay in an area both after nest success and nest failure than females. Dominance hierarchies could also play a role in site fidelity (Chin et al. 2014). Within bird social systems established during breeding seasons, males are typically dominant. Male Wood Thrushes arrive at breeding grounds first and establish territories that females later join (Evans et al. 2011). The larger female movements could indicate that they are less tied to sites than males. Roth and Johnson (1993) similarly note that female site fidelity between breeding seasons decreases with reproductive failure. Site fidelity has also been shown to be positively correlated with reproductive success (Weinberg and Roth 1998). We found that both pairs that had a successful nest continued breeding activity in the same area. Even though one pair’s second nest failed, the pair still stayed in the same area to establish a third nest. However, in the two pairs that had a failed first nest and stayed in the same area to establish a second nest, their distances between nests were greater than nest distances in the successful pairs.

**Limitations of study** — Clearly the results of this study should be considered a case study because of the small sample size. The biggest difficulty we faced in establishing a larger sample
size was capturing females. Because we could not influence female activity as much as we could male activity with song playback, the time it took to catch each female varied tremendously and unpredictably, ranging from as few as twenty minutes to as long as a week. Another sample size limit was the expensive equipment required to track each tagged bird, especially the transmitters. Compounding the problem is the fact that of the original 11 pairs caught, five females in five of the pairs became invalid for the study as two of them were killed and three went missing. With only six pairs to work with, the utility of many statistical comparisons was diminished, particularly when comparing space use between unsuccessful and successful pairs.

Another issue was the incomplete data gathered on most of the female birds. Because females inherently had to have been already engaged in nesting activity, usually their first brood, for successful capture, we could not obtain valuable complete movement and behavioral data on female Wood Thrushes during their first brood as we missed the building and laying periods, as well as the first part of their incubation periods. As was seen with the missing three birds, there was no guarantee that we would have been able to collect these data on a second brood.

We found an apparent female survival rate of 81.8%. One may call into question the utility of the transmitters that the Wood Thrushes wear and whether it interferes with their behavior, endangers their safety, or disadvantages their brood somehow. However, Gow et al. (2011) point out that radio transmitters do not affect nesting success, parental provisioning rates, nest attendance, or female brooding in Wood Thrushes. Additionally, we observed that many females foraged along road verges where they were more vulnerable to car strikes (Deverakonda unpl. data).

The fledgling time periods used in the distance calculations could be slightly inaccurate as we did not have fledgling Wood Thrushes radiotagged like their parents. Although the
literature gives a 21-day period for fledglings to be with the parents, there was no firm way to
determine when parents with successful nests moved onto their next nest.

**Recommendations for future research** — Future studies should focus on catching and tagging
the females not long after they return their breeding grounds and before they begin nesting.
Additionally, indicators of habitat quality should be investigated in future studies to look for any
relationship between home range overlap, nesting success, and habitat quality. A larger sample
size would also enable researchers to look at how the age of the birds relates to nesting success,
which we were not able to investigate. Future studies should also look at vocal activity of Wood
Thrushes to see how it relates to movement. Although distance-from-the-nest data was pooled
for this study, future studies that are able to gather enough data across each breeding stage for
each pair would be able to examine how that particular pair’s distances from their nest relates to
nest success and overlap. It would also be useful to obtain enough data to make an overlap
estimate for just the time period spanning one nest, as opposed to over the entire breeding
season. This would allow for more direct comparisons of overlap to nest success.

**LITERATURE CITED**

Anich, N. M., Benson, T. J., & Bednarz, J. C. 2010. Factors influencing home-range size of
Swainson's Warblers in eastern Arkansas. Condor 112: 149-158.

Anich, N. M., Benson, T. J., & Bednarz, J. C. 2012. What factors explain differential use within


Deverakonda 25


Table 1. Nest fates of 17 nests.

<table>
<thead>
<tr>
<th>Pair</th>
<th>Nest 1</th>
<th>Nest 2</th>
<th>Nest 3</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Fail</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Success</td>
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</tr>
<tr>
<td>8</td>
<td>Fail</td>
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<tr>
<td>9</td>
<td>Fail</td>
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</tr>
<tr>
<td>10</td>
<td>Success</td>
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</tr>
<tr>
<td>11</td>
<td>Fail</td>
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Table 2. Home range sizes for six male and female Wood Thrushes

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<tr>
<th>Pair</th>
<th>Male (ha)</th>
<th>Female (ha)</th>
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<tbody>
<tr>
<td>2</td>
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<tr>
<td>3</td>
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<td>6</td>
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<td>8</td>
<td>36.33</td>
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<tr>
<td>11</td>
<td>26.14</td>
<td>2.84</td>
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Table 3. Space use overlap of Wood Thrush breeding pairs in relation to nesting success

<table>
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<tr>
<th>Pair</th>
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<th>Nest 3</th>
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<tr>
<td>2</td>
<td>0.81</td>
<td>Successful</td>
<td>Failed</td>
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<tr>
<td>3</td>
<td>0.75</td>
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<tr>
<td>11</td>
<td>0.48</td>
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<td></td>
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<tr>
<td>Bird</td>
<td>Movement</td>
<td>Distance (m)</td>
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<tr>
<td>------------</td>
<td>----------</td>
<td>--------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pair 9 male</td>
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<td></td>
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<tr>
<td>Pair 9 female</td>
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<tr>
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<td>2</td>
<td>1261</td>
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<tr>
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<td>2</td>
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<td>Pair 6 female</td>
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<td>928</td>
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Table 5. Distance between nests

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<th>Pair</th>
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<td>6</td>
<td>Nest 1 to Nest 2</td>
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<tr>
<td>6</td>
<td>Nest 2 to Nest 3</td>
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<td>8</td>
<td>Nest 1 to Nest 2</td>
<td>302</td>
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<tr>
<td>10</td>
<td>Nest 1 to Nest 2</td>
<td>142</td>
</tr>
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Figure 1. Overlap (yellow) between home ranges of six Wood Thrush breeding pairs (Male = blue, female = red). Home ranges are based on 95% isopleth. Pairs in left column never fledged young whereas pairs in right column successfully fledged at least one young. Note different scales on each image.
Figures 2. Proximity of high-use areas for six pairs of Wood Thrushes. Red lines represent females (F) and blue lines represent males (M). Graphs on the left show proximity of high-use areas for unsuccessful pairs (pairs 6, 8, and 11), whereas graphs on the right show proximity of high-use for successful pairs (pairs 2, 3, and 10). The x-axis represents space use intensity from high (5% top percent of space used) to low (95% top percent of space used), and the y-axis represents the percent of space that the two pair members shared.
Figure 3. Average distances of male and female Wood Thrushes from their nest in relation to breeding stages. Number of pairs in each breeding stage are given in parentheses. Asterisks above graphs present significant differences in distances between sexes based on Bonferroni adjusted paired t-tests.
Figure 4: Movement in the pair 9 breeding pair.
Appendix A: Search area for missing Wood Thrushes in southeastern Virginia
Appendix B. Locations of breeding Wood Thrush pairs caught and tracked in this study.