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RESEARCH ARTICLE

Mismatch between diurnal home ranges and roosting areas in the Wood Thrush (*Hylocichla mustelina*): Possible role of habitat and breeding stage

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ABSTRACT

The behavior of roosting birds has received little attention from ornithologists, despite its importance for understanding the complete avian circadian cycle. We examined the spatial arrangement of roosts in relation to diurnal home ranges for the declining Wood Thrush (*Hylocichla mustelina*) on its breeding grounds in coastal Virginia, USA. To our knowledge, this is the first broad description of roosting ecology for a North American migratory passerine during the breeding season. The primary objective of this study was to determine whether roost sites and diurnal use areas overlapped. Secondly, using LiDAR, we tested the hypothesis that birds roosted at sites with higher local vegetation density than random points. Lastly, we explored the effect of nest status on the roosting patterns of pairs. We tracked 37 radio-tagged males to construct 95% kernel diurnal home ranges. In 10 home ranges we also tagged the female mates. Both sexes were tracked at night to roosting locations. Of 74 male roosts, 31% were located outside diurnal home ranges. LiDAR-derived vegetation density was ~7% higher at roost sites than at random points within diurnal home ranges, and young birds roosted farther from peak diurnal use areas than older birds, suggesting a role of roosting habitat quality. Nest status had a significant effect on pair roosting patterns, as females with active nests roosted exclusively in nest cups, whereas males roosted an average of 121.8 m (95% CI = 72.6–204.2, $n = 11$) away on equivalent nights. Once nests fledged or failed, males roosted within diurnal home ranges while appearing to guard females. We propose that the observed mismatch in male diurnal home ranges and nocturnal roost sites may be based on optimal roosting conditions at those sites; however, male solicitation of extrapair copulations from fertile neighboring females during the morning and evening insemination windows should also be considered.

Keywords: roost, roosting behavior, Wood Thrush, *Hylocichla mustelina*, LiDAR, home range, habitat use

Desacople entre los ámbitos de hogar diurnos y las áreas de descanso en *Hylocichla mustelina*: posible función del hábitat y la etapa reproductiva

RESUMEN

El comportamiento de las aves al descansar ha recibido poca atención por parte de los ornitólogos a pesar de su importancia para entender el ciclo circadiano completo de las aves. Examinamos la disposición espacial de los dormideros en relación con los ámbitos de hogar diurnos de *Hylocichla mustelina* en sus territorios reproductivos en la costa de Virginia. Hasta donde tenemos conocimiento, esta es la primera descripción amplia de la ecología del descanso de un ave paserina migratoria norteamericana durante la temporada reproductiva. El objetivo principal de este estudio fue determinar si hay superposición entre las áreas de descanso y las áreas de uso diurno. Segundo, pusimos a prueba la hipótesis de que las aves duermen en sitios con mayor densidad local de vegetación usando LiDAR. Finalmente, exploramos los efectos del estado de los nidos en los patrones de descanso de parejas de aves. Rastreamos 37 machos marcados con transmisores de radio para construir ámbitos de hogar diurnos con núcleo de 95%. En 10 ámbitos de hogar marcamos a las hembras. Ambos sexos fueron rastreados en la noche hacia sus dormideros. De 74 dormideros de machos, 31% se localizaron por fuera de los ámbitos de hogar diurnos. La densidad de la vegetación derivada de LiDAR fue aproximadamente 7% mayor en los dormideros que en sitios al azar dentro de los ámbitos de hogar diurnos. Las aves jóvenes descansaron más lejos de las áreas de máximo uso diurno que las aves mayores, lo que sugiere una influencia de la calidad del hábitat de descanso. El estado de los nidos tuvo un efecto significativo en los patrones de descanso de las parejas, ya que las hembras con nidos activos descansaron exclusivamente en sus nidos mientras que los machos descansaron en promedio a 121.8 m (IC = 72.6 – 204.2, $n = 11$) del nido en las noches equivalentes. Una vez que los polluelos abandonaron los nidos o que los nidos fracasaron, los machos descansaron dentro de los ámbitos de hogar diurnos mientras que parecían custodiar a las hembras. Proponemos que el desacople observado en el ámbito de hogar diurno de los machos y sus dormideros puede estar basado en las condiciones óptimas para el descanso en tales sitios, aunque la solicitud a los machos de cópulas extra

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pareja por parte de hembras fértiles vecinas durante las ventanas de inseminación en las mañanas y tardes podrían también ser consideradas.

Palabras clave: ámbito de hogar, comportamiento de descanso, dormidero, *Hylocichla mustelina*, LiDAR, uso de hábitat

INTRODUCTION

All animals sleep, yet it is one of the least-studied behaviors (Lima et al. 2005). In forest birds, sleep has been examined primarily in the context of activity at communal roosting sites (Marzluff et al. 1996, McGowan et al. 2006) and the behavior of cavity-utilizing species (Wang and Weathers 2009, Steinmeyer et al. 2010). However, many aspects of roosting ecology are of great interest to biologists. For example, zoonotic disease transmission potential has been linked to roost characteristics of American Robins (*Turdus migratorius*), where West Nile virus vectors preferentially feed on individuals higher in the forest canopy, but the risk of infection decreases for birds roosting in groups (Janousek et al. 2014). In Jamaican coffee farms, nearby forest appears to provision the delivery of an economically substantial ecosystem service by Black-throated Blue Warblers (*Setophaga caerulescens*), as birds forage on coffee pests during the day (Kellermann et al. 2008) after commuting from nocturnal roosts in the woods and large shade trees (Jirinec et al. 2011). A roost, defined in this paper as the nocturnal location of a bird—often a solitary one—has an important function in avian ecology.

Comprehensive knowledge of habitat requirements might be considered the major reason to study bird roosting. Declines of Neotropical migratory songbirds indicate the need to consider the habitat requirements of individual species, and highlight the need for understanding habitat use over the entire annual cycle. Migratory songbird declines have been connected with events occurring on the breeding grounds (Rodenhouse and Holmes 1992), in wintering regions (Robbins et al. 1989, Holmes and Sherry 2001, Norris et al. 2004), and at migratory stopover areas (Leu and Thompson 2002, Packett and Dunning 2009), and are ultimately associated with local habitat quality. Information about bird ecology, such as habitat requirements, is commonly inferred from habitat associations derived from daytime observations in one or more of the above areas. This approach would be satisfactory only if daytime and nocturnal use regions were to overlap. Wintering Ovenbirds (*Seiurus aurocapilla*) appear to roost in their core diurnal activity area (Brown and Sherry 2008), which suggests that roosting is correlated with daytime use patterns in some species. However, mounting evidence indicates that many forest migrants roost away from their daytime activity ranges. To our knowledge, this phenomenon has been specifically documented on the wintering grounds for the Prothonotary Warbler (*Protonotaria citrea*; Warkentin and Morton 1995), Northern Waterthrush (*Parkesia noveboracensis*; Smith et al. 2008), Black-throated Blue Warbler (Jirinec et al. 2011), and Bicknell's Thrush (*Catharus bicknelli*; Townsend et al. 2009). Additionally, a recent report provides some evidence for disjunct roosting areas in the Yellow-rumped Warbler (*Setophaga coronata*) during the migratory stopover period (Slager and Rodewald 2015). Furthermore, anecdotal observations suggest that many more Nearctic–Neotropical migrants conduct off-home range commutes to roost sites (see Smith et al. 2008 for a review).

Movements to quality roosting habitat may explain commutes to disjunct roost sites. Predation risk is elevated for sleeping birds, as roosting birds are relatively unresponsive to cues alerting them to predator presence (Lima et al. 2005, Amo et al. 2011). Areas offering optimal foraging opportunities, where vigilance is sufficient to reduce predation, may be too dangerous for sleeping birds, and natural selection should thus favor a change in habitat use (Clark and Shutler 1999). Townsend et al. (2009) documented 9% mortality over ~30 days by introduced rats (*Rattus* spp.) at roosts of Bicknell's Thrushes on the wintering grounds. Although thrushes appeared never to use pine forest during the day, 68% of roosts were in pine, where relative rat abundance was significantly lower. Although nighttime predation risk studies are limited for birds (Lima et al. 2005), research on primates suggests that safety is important in sleeping-site selection (Ramakrishnan and Coss 2001, Qihai et al. 2009). Regardless of the ultimate selection pressure driving divergent temporal habitat use, understanding nighttime habitat demands is essential for bird conservation, as population status is inextricably linked with the quality of such habitat across the annual cycle. This raises the need for research that quantifies the space use of individually marked birds during the entire 24-hr period. Increased logistical difficulties and personnel demands likely contribute to the inadequate number of such studies. Nevertheless, understanding whether diurnal and nocturnal use areas overlap is a first step toward determining whether roosting habitat should be considered independently.

In this study, we considered the physical space utilized by birds both at night and during the day. We defined the daytime area as the "diurnal home range" (DHR). Although a home range has been described as all areas used (Burt 1943), nighttime habitat use patterns of diurnal bird species are largely unknown, rendering this definition potentially misleading without knowledge of roosting areas. We outlined DHRs by the 95% kernel boundary, which included an actively defended territory as well as adjacent areas used opportunistically during the day. In contrast to the DHR, we defined a "roost" as the location where a bird spent its nighttime hours, regardless of whether it was alone or near conspecifics. Our assumption was that within-night roost locations did not change unless a bird was disturbed.

We delineated DHRs and roosts for the Wood Thrush (*Hylocichla mustelina*) during the breeding season. Populations of this migratory songbird show significant, long-term, range-wide declines (–2% yr^{-1} from 1966 to 2012; Sauer et al. 2014), which have been partly attributed to decreased nest success in smaller forest fragments (e.g., Lloyd et al. 2005). On the breeding grounds, areas with frequent daytime Wood Thrush detections have been related to upland deciduous and mixed forests with a moderate subcanopy, a semi-open forest floor with decaying litter, and a wide variety of tall deciduous tree species (Evans et al. 2011). Although the breeding ecology of this species is well studied, knowledge of Wood Thrush nocturnal behavior is limited to anecdotal observations of nesting females (Evans et al. 2011).

The primary objective of this study was to determine whether the Wood Thrush roosts within its diurnal home range. We also had two secondary objectives: to test the hypothesis that local vegetation density differed between roost sites and random sites within diurnal home ranges, and to compare the roosting locations of males and females during times when nests were active and inactive. In analyses of Wood Thrush pairs, we examined the effect of nest status on both intrapair roost distances and mate roosting positions within diurnal home ranges.

METHODS

Study Area

For broader land-cover representation of this wide-ranging species, we captured individual birds in 8 parks and 1 military base located on the coastal plain of southeastern Virginia (centroid: 37.25°N, 76.67°W). Birds were tracked on property managed by the National Park Service, College of William and Mary, Colonial Williamsburg, City of Newport News, City of Williamsburg, York County, James City County, Kingsmill Resort, York River State Park, and the U.S. Navy. The region was moderately covered with eastern deciduous and mixed forest (Monette and Ware 1983), but encroaching urbanization had fragmented many of the wooded study sites.

Bird Capture and Marking

Using radio-telemetry, we tracked 47 birds over 2 breeding seasons (2013 and 2014). Males ($n = 37$) were captured from May 15 to June 3 in both years using mist nets (30 mm mesh) in conjunction with conspecific song playback (Angelier et al. 2010). Targeted netting allowed us to capture individuals with established territories and to avoid floaters, which could quickly depart the study area. To meet the objectives of a parallel study, we trapped birds near existing point count stations such that no more than 1 male was captured within 200 m of each station. Point count stations were randomly placed in forest patches within each study area using a Geographic Information System (GIS), with stratification according to forest land cover (coniferous, upland, and riparian) and a rural-to-urban land use gradient. The female mates ($n = 9$) of a subset of study males were captured in 2014, and we also included observations of 1 banded (but not radio-tagged) female from 2013. Females were captured throughout the breeding season using passive netting near newly discovered nests of radio-tagged males in order to ensure correct pair assignment. We never observed nest abandonment due to such disturbance. Sex was determined by the presence of a brood patch or cloacal protuberance (Pyle 1997). We subsequently monitored the nests of radio-tagged pairs every ~3 days to determine nest status for analyses involving nest stage. We estimated nesting stage (incubation or nestling) based on observations of parental behavior and known stage intervals summarized by Evans et al. (2011). Increased personnel in 2014 allowed for age determination of birds based on molt limits in wing coverts (Pyle 1997) without excessive bird handling. Birds with evidence of a molt limit in the greater coverts were classified as second-year (SY; i.e. the bird was in its first breeding season), whereas birds without a visible molt limit were classified as after-second-year (ASY; i.e. the bird was in at least its second breeding season). Because some SY Wood Thrushes lack a molt limit in the greater coverts (Pyle 1997), a few individuals in the ASY category could have been SY birds, resulting in potential dilution and hence increased variation in the ASY group. Lastly, for each bird, we affixed a U.S. Geological Survey (USGS) aluminum band along with a unique set of 3 color bands for identification in case of premature transmitter detachment.

We used a figure-eight leg harness (Rappole and Tipton 1991) to attach a 1.3-g VHF transmitter (BD-2; Holohil Systems Ltd., Carp, Ontario, Canada) to each bird. We utilized 0.7-mm Stretch Magic (Pepperell Braiding, Pepperell, Massachusetts, USA) jewelry cord for the harnesses (intraloop distance = 57.5 mm), and observed no injurious rubbing on individuals ($n = 6$) recaptured up to 46 days after initial transmitter deployment.

Diurnal Home Range (DHR) Estimation

DHRs were derived from diurnal radio-telemetry locations (Marzluff et al. 2004). Birds were tracked from May 16 through July 25 in both years (mean 11.9 ± 0.8 unique days per bird), between 06:30 and 20:30 EDT, until transmitter battery depletion (average battery life was ~60 days). To account for variation in temporal space use (Anich et al. 2012), each bird was sampled at least once each hour between 08:00 and 20:00 during the tracking period. To ensure biological independence between locations (defined as an interval long enough to reach any point within the DHR; Barg et al. 2005), points were recorded $\geq$20 min apart. This interval was equal to or longer than that used in similar studies of 3 warbler species (Anich et al. 2012), and we believe that it was adequate as birds often moved substantially between relocations, easily traversing their DHRs. We spaced tracking events to maintain similar sampling intervals throughout the transmitter lifespan up to the target sample size of 50 locations per bird, after which birds were tracked only opportunistically. Bird locations were determined by observers equipped with 3-element Yagi antennas and receivers (TRX-1000S and TRX-3000S; Wildlife Materials, Murphysboro, Illinois, USA). To avoid telemetry location bias due to observer disturbance, we found target individuals by homing to within 50 m of each bird and then obtaining signal readings from multiple locations until the bird's position was narrowed down to a small area (~5 m^2). We then acquired projected bird coordinates in GPS units (GPSMAP 62; Garmin, Olathe, Kansas, USA) using a compass bearing and distance established with a laser rangefinder (400LH; Opti-Logic, Tullahoma, Tennessee, USA). Visual observations were obtained in ~16% of cases. In cases in which birds moved beyond the detection radius (Lang et al. 2002), we performed extensive ground searches from vehicles with twin truck-mounted antennas along with aerial telemetry using a fixed-wing aircraft.

We based DHRs on utilization distributions generated from 95% kernel density estimations (Worton 1989, Marzluff et al. 2004, Barg et al. 2005). A utilization distribution is a representation of an individual's space use as a function of telemetry location density, thus portraying the relative use level (hereafter relative percent diurnal use) within each pixel of the individual's activity area (Marzluff et al. 2004, Horne and Garton 2006). We used inverse isopleths (i.e. quantiles of kernel estimates) of the utilization distribution to represent relative percent diurnal use (0–100%; Figure 1). The DHR edge thus corresponds to 5% relative use for a conservative area estimate (Pechacek and Nelson 2004), whereas areas outside the DHR represent 0% relative diurnal use, and the most-used sections within the DHR approach peak relative use (100%). For analyses for which designation of the DHR center was necessary, we considered the uppermost kernel value as the DHR center (peak relative diurnal use). Because males defend territories and a pair's DHRs overlapped highly (A. Deverakonda personal observation), we used male DHR for pair roost analyses. Although the least-squares cross-validation (LSCVh) method is commonly used for kernel bandwidth selection (Gitzen and Millspaugh 2003), we found that this approach did not perform well for individual birds with multiple frequently used areas. An alternative to LSCVh is likelihood cross-validation (CVh), which has generally been shown to yield estimates with better fit and less variability than LSCVh, and to perform better with smaller sample sizes (Horne and Garton 2006). Barg et al. (2005) recommended 50 animal locations as the lower limit for LSCVh kernels. Although we used on average 53.9 ± 1.3 locations (range: 50–80) to construct DHRs, we used the CVh method for kernel bandwidth selection as this approach performed better with our dataset. Kernel density estimation and subsequent utilization distribution isopleths were constructed in Geospatial Modeling Environment (Beyer 2011).

Roost Site Location

The roost sites of each bird were located on separate nights throughout the diurnal tracking period. Nocturnal tracking began at least 1 hr after sunset and continued until no later than 1 hr before sunrise (Jirinec et al. 2011). We ensured that birds were settled in for the night by confirming signal immobility prior to recording roost locations. We located roosts in a similar manner as confirming diurnal locations, by homing in as closely as possible to the signal source and then carefully attempting to locate the roosting bird. We attempted to visually locate birds using headlamps. In cases where we achieved visual confirmation, we recorded roost height, tree species, and whether conspecifics were nearby. To avoid disturbing birds, we projected roost coordinates from a distance (see Diurnal Home Range Estimation) and obtained above-ground roost height using the height function in the rangefinders. In many instances we were unable to see the target bird (61%), particularly if the roost was high up or obscured by foliage, in which case we circled the signal source and considered its strength before estimating roost location and height without disturbing the bird. For males, we obtained 2 roost locations per bird, for a total of 74 roosts. For marked pairs ($n = 10$), we attempted to get 2 roosts per sex, with the location of each member of the pair recorded on the same night. In cases in which females were captured after male roost site data collection was already underway, we detected additional male roost sites to complete same-night pair locations.

Roosting Habitat

We used discrete return Light Detection and Ranging (LiDAR) data to test the hypothesis that Wood Thrush roosts were located in densely vegetated areas. LiDAR has been used to quantify three-dimensional forest structure at

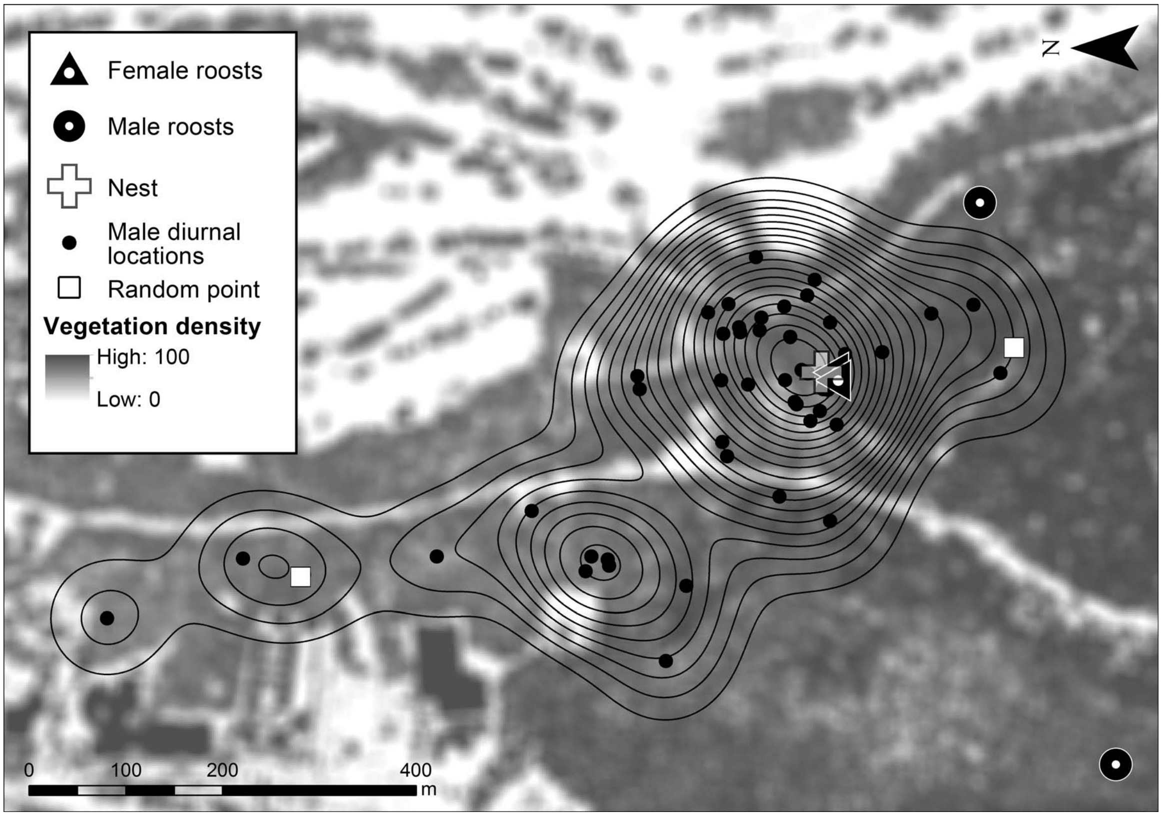

FIGURE 1. Sample diurnal home range (DHR) with corresponding roost locations for a single Wood Thrush (*Hylocichla mustelina*) pair in southeastern Virginia, USA, 2013–2014. DHRs represent 95% kernel density estimations, and employed male diurnal telemetry locations (black dots; $n \geq 50$) to derive relative percent diurnal use (black isopleths; outside = 0% diurnal use, DHR boundary = 5%, DHR center = 100%). Two roosts for each male (circles) were identified on separate nights throughout the diurnal tracking period. For radio-tagged pairs, we located female roosts (triangles) on the same nights that we located male roosts. When nests were in the incubation and nestling stages, females roosted on nests (cross) located near peak relative diurnal use, while males were often outside the DHR boundary. Two random points (squares) in each DHR were used for comparisons of vegetation density.

relatively high resolution (Lefsky et al. 2002), including detailed vertical biomass distribution (Vierling et al. 2008).

LiDAR data were collected from April 22 to May 10, 2010, and from March 21 to 31, 2013. Therefore, data corresponding to ~30% of bird sites were gathered in late March—before the arrival of most birds. The leaf area index is lower in March than in June, when most roosts were identified. However, the leafy parts of trees and shrubs should correlate with the density of woody stems and branches, and our pairwise analysis (see Analysis) controlled for temporal differences in return density.

We computed vegetation density using LAStools software (http://lastools.org). Percent vegetation density was calculated as the number of returns ≥1 m above ground divided by the number of all returns within a 2-m grid cell (Morsdorf et al. 2006). Given the density of the raw LiDAR point cloud, 2-m cell size was the smallest resolution without data gaps in the output density raster. We removed low-lying LiDAR points (<1 m) to avoid understory vegetation that was not used for roosting. To account for the error associated with georeferencing roost locations under thick canopy (GPS maximum error ±10 m), we averaged vegetation density within a 10-m circular neighborhood using focal statistics in GIS (ArcMap 10.1; ESRI, Redlands, California, USA). To assess LiDAR data and density calculations, we ground-checked the density output using known areas of high and low vegetation volume. The density output validated well, with locations associated with abundant foliage (such as sapling stands) yielding higher density values than open forest. Finally, we compared vegetation density at each roost site with a GIS-generated random location within the respective DHR.

Analysis

Unpaired roosts of males were analyzed separately from same-night roosts of pairs. Male unpaired roosts ($n = 74$) were used to determine whether DHR and roosting areas overlapped, and to test the hypothesis that local vegetation

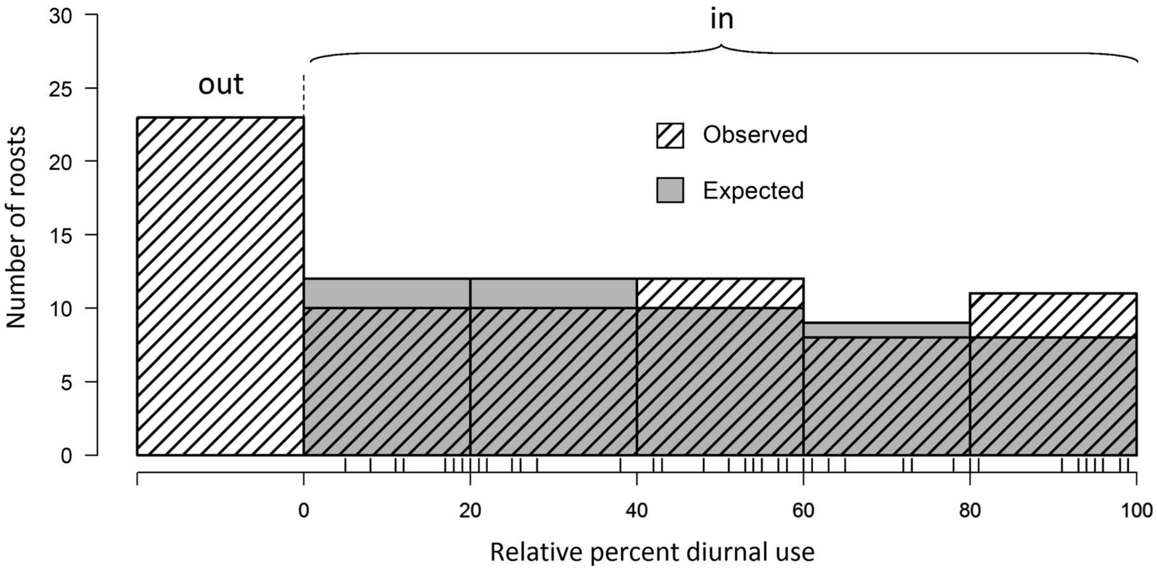

FIGURE 2. Male Wood Thrush roost positions (dashed bins) in relation to their diurnal home ranges (DHR) in southeastern Virginia, USA, 2013–2014. Out of 74 roost locations, 23 (31%) were located outside ("out") the respective diurnal home range (in the 0% diurnal use bin). Roosts within DHRs ($n = 51$) were not positioned in areas of higher relative diurnal use, as the number of observed roosts within the 5 DHR segments (relative use bins) did not significantly differ from corresponding area-based expected roost totals ($\chi^2_4 = 2.5$, $P = 0.64$). Vertical dashes on the x-axis denote the exact relative diurnal use value for each of the 51 within-DHR roosts.

density explained roost site selection. Same-night pair roost locations ($n = 36$) were utilized to explore the effect of nesting status on pair roosting patterns. In cases in which we had >2 roosts per male (in pairs with late-caught females), we used the first 2 roosts to determine DHR overlap and to test the vegetation density hypothesis. Only roosts collected for both sexes on the same night were applied to the analysis of pair roosting patterns.

Spatial relationships between roosting positions and DHRs were determined with GIS and examined with either parametric or nonparametric tests. We chose tests and parameters based on tests of normality (Shapiro and Wilk 1965) and homogeneity of variance (Levene 1960) assumptions after histogram and boxplot evaluation. In cases of nonnormal data, we used natural-log transformation for analyses with parametric tests, or resorted to nonparametric tests if transformations failed to produce normal datasets.

We used a chi-square test to determine whether day and night space use patterns matched. To do this, we assumed that the entire DHR was available for roosting, and then examined the relative percent diurnal use at observed roosting locations. A significant chi-square test would be interpreted as Wood Thrushes roosting in any segment of the DHR out of proportion to its availability, i.e. if we observed more or fewer roosts in a segment than would be expected based on its fraction of the total DHR area. We created DHR segments utilizing the relative diurnal use isopleths and calculated the area for each DHR segment (a relative use "bin") in GIS. We divided DHRs into 5 bins (0–20% relative diurnal use, 20–40%, etc.; Figure 2)—5 bins were chosen to retain a sufficient number of observed roosts per bin (≥5)—and calculated the expected roost number by multiplying the sum of all within-DHR roosts by the proportion of bin area (Isdell et al. 2015). Because each bird's DHR area differed, this proportion was derived from the sum of corresponding bins and DHRs of all 37 male birds.

We used t-tests to examine the effect of male age on roost commute distance and to check for differences in vegetation density between roosts and random sites, whereas a t-test along with a Wilcoxon signed-rank test was utilized to assess the effect of breeding stage on pair roosting patterns. To test the hypothesis that younger males commuted greater distances to roosts, we employed a t-test on log-transformed data. We report back-transformed means and confidence intervals whenever we ran tests on transformed datasets. A paired t-test was employed to check for a mean difference in vegetation density between roost locations and paired random sites (pseudoabsences; Barbet-Massin et al. 2012) within DHRs. Although we used 2 sets of LiDAR data differing in collection dates (early vs. late spring), collection date differences did not bias our analyses, because within-bird vegetation data were derived from the same dataset, and the paired t-test was based on differences between random DHR points and associated roosts. In Wood Thrush pair analyses, we used a t-test to test the hypothesis that roost distance to nest varied by sex, and that mate separation in pairs without active nests

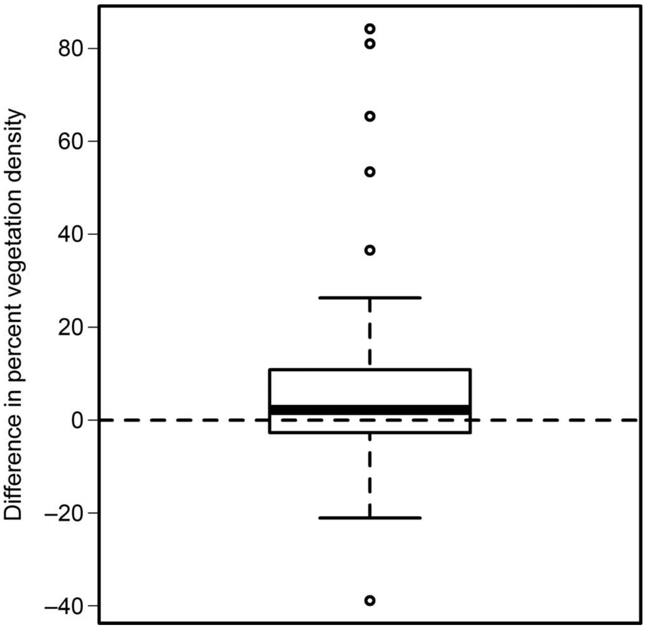

FIGURE 3. Mean difference in vegetation density between roost sites and paired random points within Wood Thrush diurnal home ranges in southeastern Virginia, USA, 2013–2014, derived from LiDAR data. Positive differences indicate higher vegetation density at roost sites. Mean vegetation density within a 10-m neighborhood was significantly higher at roost sites than at random points within diurnal home ranges (mean difference = 7%, 95% CI = 2–11%, $n = 74$; paired t-test: $t_{73} = 2.8$, $P = 0.006$).

differed from that of pairs with females incubating eggs or brooding nestlings. Because the distances of roosting birds to their nests and mates did not convey the relationship of roost positions to relative diurnal use levels, we applied a Wilcoxon signed-rank test to examine whether roosts differed in relative diurnal use by sex and nest stage. All analyses were conducted in R (R Development Core Team 2014), using package 'boot' to generate 95% confidence intervals for medians for the results of Wilcoxon signed-rank tests by resampling datasets with 1,000 bootstrapping iterations. We report 95% confidence intervals (CIs) throughout. To report sensible CIs for results of the analyses of log-transformed data, we present back-transformed CIs corresponding to the antilog of the mean ± 1.96 SE in the transformed, normal dataset. Where appropriate, we report means ± SE. All tests were two-tailed and set to a significance level of $\alpha < 0.05$.

RESULTS

Unpaired Data

We obtained visual confirmation of 39% of 74 male roosting locations. Males observed roosting were frequently concealed by vegetation from the dorsal and most lateral views, but the feathers of their abdomens were often visible in the headlamp beam. Birds appeared undisturbed by the light and usually did not appear to awaken (feathers fluffed, head tucked in, regularly perching on one leg). At roosts where birds were detected visually ($n = 29$), average roost height was 6.8 ± 1.0 m (range: 2.0–26.5 m). Most (69%) roosting birds were seen in American holly (*Ilex opaca*; 21%), American beech (*Fagus grandifolia*; 17%), red maple (*Acer rubrum*; 17%), and pawpaw (*Asimina triloba*; 14%).

Males were usually detected in different roosting areas on the different nights that we found them. Average temporal separation between consecutive roosting locations was 12 ± 1 days, which yielded a mean distance between the 2 roosts of 158 ± 25 m (range: 2–607 m), excluding an outlier of 1,301 m where a male relocated to a new DHR. Only 8% of males roosted in the same spot, defined as within 20 m of the previous roost, on both nights. Because we recorded roost positions to $\leq$10 m GPS accuracy, 20 m constitutes twice the maximum position error. Accordingly, we designated individual roosts as sampling units, rather than individual birds (Jirinec et al. 2011).

Roost positions did not match diurnal activity patterns and differed with bird age. Roosting locations were distributed throughout DHRs, and 23 (31%) were placed outside DHRs entirely (Figure 2). Mean distance to the respective DHR edge for external roosts was 91 ± 20 m (range: 9–322 m). Roosts within DHRs ($n = 51$) were not positioned in areas of higher relative diurnal use, as the number of observed roosts within the 5 DHR segments (relative use bins) did not significantly differ from corresponding area-based expected roost totals ($\chi^2_4 = 2.5$, $P = 0.64$), indicating a lack of selection of sleeping sites based on diurnal use. The mean distance of roost sites from peak use areas was 100% greater for SY males (140.4 m, 95% CI = 81.4–242.1, $n = 16$) than for ASY males (70.2 m, 95% CI = 49.1–100.5, $n = 18$; two-sample t-test: $t_{32} = 2.1$, $P = 0.04$).

Roosts were located in areas with higher vegetation density than random points (Figure 3). The mean difference in vegetation density within a 10-m neighborhood was ~7% higher at roost sites than at random points within DHRs (95% CI = 2–11%, $n = 74$; paired t-test: $t_{73} = 2.8$, $P = 0.006$).

Pair Data

The distance between mates in roosting pairs differed with nesting status (Figure 4). Females with nests in the incubation and early nestling stages ("active" nests) roosted exclusively in the nest cup, while males were an average of 121.8 m (95% CI = 72.6–204.2, $n = 11$) away on equivalent nights. However, once nests failed or fledged ("inactive" nests), the mean distance between pair members was 91% shorter (10.6 m, 95% CI = 2.2–51.9, $n = 7$; two-sample t-test: $t_{16} = 3.4$, $P = 0.004$). Most of these cases ($n = 5$) were

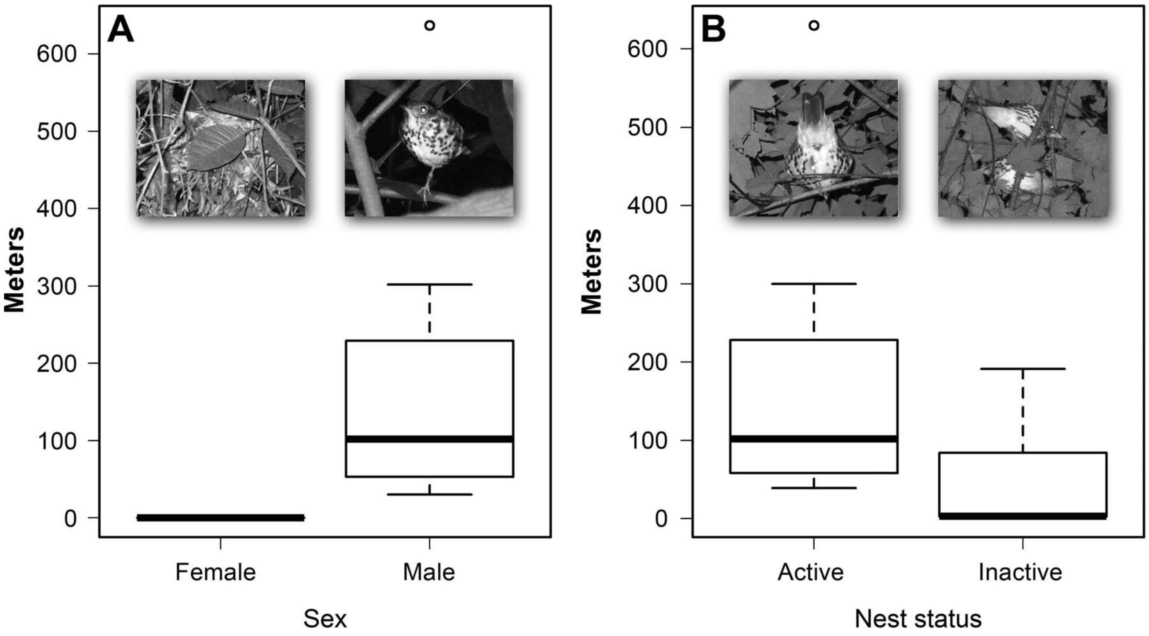

FIGURE 4. (**A**) Distance to active nest, and (**B**) pair separation based on nest status for Wood Thrush pairs in southeastern Virginia, USA, 2013–2014. (**A**) Females with nests in the incubation and early nestling stages ("active" nests) roosted exclusively in the nest cup, with males an average of 121.8 m (95% CI = 72.6–204.2, $n = 11$) away on the same nights. (**B**) The mean separation of male and female roost sites was significantly larger when pairs had an active nest than when their nest was inactive, i.e. failed or fledged (10.6 m, 95% CI = 2.2–51.9, $n = 7$; two-sample t-test: $t_{16} = 3.4$, $P = 0.004$).

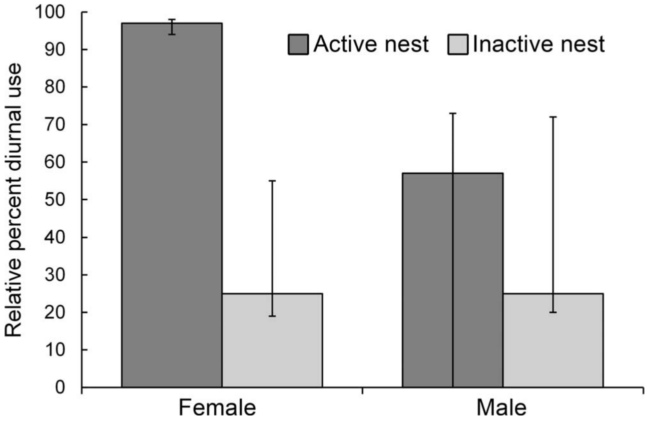

FIGURE 5. Roosts within Wood Thrush diurnal home ranges (relative percent diurnal use) in southeastern Virginia, USA, 2013–2014, by sex and nest status. Females with active nests (dark gray bars) roosted on nests located near peak diurnal activity areas. Median diurnal use (97%, 95% CI = 94–98%, $n = 11$) at roosts by actively nesting females differed significantly from diurnal use by males at same-night roosts (57%, 95% CI = 0–73%, $n = 11$; Wilcoxon signed rank test: $V = 66$, $P = 0.004$). When a nest had failed or fledged (light gray bars), female roosting positions did not differ from those of males in relation to diurnal use ($n = 7$; Wilcoxon signed rank test: $V = 9$, $P = 0.89$). Error bars represent 95% confidence intervals derived from 1,000 bootstrap samples.

"duo-roosts," with the male and female roosting side by side, inside the DHR.

Mate roost positions compared with relative diurnal use differed by sex and nest status (Figure 5). Females with active nests roosted on nests (see above), which were located in peak diurnal use areas. Median relative percent diurnal use (97%, 95% CI = 94–98%, $n = 11$) at roosts of actively nesting females was 70% higher than at same-night male roosts (57%, 95% CI = 0–73%, $n = 11$; Wilcoxon signed-rank test: $V = 66$, $P = 0.004$). After nests failed or fledged, female roosting positions did not differ from male roost sites in relation to relative diurnal use ($n = 7$; Wilcoxon signed-rank test: $V = 9$, $P = 0.89$).

DISCUSSION

Our results suggest frequent disparity between Wood Thrush daytime home ranges and corresponding roost sites. We used telemetry-derived utilization distributions to represent relative percent space use within each DHR. If activity throughout each day is assumed to follow the probability of use represented by the DHR, we would expect thrushes to most likely be located near relative diurnal use peaks immediately before the commencement of roosting. Accordingly, we were surprised to find that the mean distance between peak use areas and male nocturnal roosts was 115.7 m (95% CI = 92.2–145.1, $n = 74$), with the longest distance observed at 702 m. One-third of male roosts were located completely outside their respective DHRs. Some birds therefore traveled substantial distances to roosting sites.

Long commutes to roosts, especially to areas outside DHRs, require an explanation. Breeding is energetically taxing for passerines (Merila and Wiggins 1997), with birds expending much of their energy on mate acquisition, nest building, and feeding of young, as well as territory defense. Energetic costs associated with commutes to nocturnal roosts would be expected to decrease individual reproductive output, however slightly, and therefore should not be favored by natural selection. Moreover, individuals wandering outside their territories risk losing paternity or territory ownership to rival males, as well as agonistic encounters with other males whose territories they pass through.

Roosting and Habitat

We did not reject the hypothesis that birds roost in areas with higher vegetation cover. Roosting in densely vegetated areas may decrease the chances of depredation, as individuals are camouflaged by surrounding vegetation from visual predators such as the Barred Owl (*Strix varia*). Predation pressure has been shown to guide sleeping-site selection in primates (Ramakrishnan and Coss 2001, Qihai et al. 2009). For birds, the preference for roosting in areas with high vegetation cover has been suggested as an antipredation strategy for the Capercaillie (*Tetrao urogallus*; Finne et al. 2000) and the Sichuan Partridge (*Arborophila rufipectus*; Liao et al. 2008). For some species, such as the Black-throated Blue Warbler, long commutes to roosts are necessitated by diurnal use of agricultural habitat likely lacking suitable roost sites (Jirinec et al. 2011). Wood Thrushes, in contrast, appeared to occupy DHRs in continuous forested areas that did not differ dramatically from roosting habitat, yet they often made commutes nonetheless. It was this observation that led to the hypothesis that vegetation cover would be denser at selected roost sites than at random points within DHRs.

Although differences in vegetation density between roost sites and DHRs were statistically significant, they were not biologically large (~7%). Thus, further research will be necessary to understand what Wood Thrushes gain from commuting to nocturnal roosts. One possibility is that an optimal roost microclimate or maximum camouflage requires a rare habitat attribute, and that only the best territories contain such a trait. Our observation that SY males commuted farther to nocturnal roosts than older males is consistent with the idea that the best DHRs, presumably occupied by older males (Holmes et al. 1996), may contain better roost sites within them. An alternative hypothesis is that males roost far from active nests to avoid attracting attention to the nest. This is consistent with our observation that when nests were not active, both pair members often roosted together, inside the DHR. Another alternative hypothesis is that males choose distant roost sites to improve their chances of obtaining extrapair copulations from neighboring females.

Roosting and Extrapair Behavior

The roosting patterns of pairs varied with nest stage. Only female Wood Thrushes incubate eggs, and we were therefore not surprised to find all females with active nests roosting in the nest cup. We were surprised, however, to record so many occasions on which their male mates roosted far away on equivalent nights (Figure 4A). Once a nesting attempt was terminated, either through predation or nestling independence, pairs were found sleeping side by side (Figure 4B), inside the DHR. We observed this phenomenon in 5 of 7 cases in which we obtained pair roost locations for pairs without an active nest. The 7 cases included 2 observations (intrapair distances of 136 and 191 m) for which we suspected a divorce, as these pairs decoupled their diurnal use regions in subsequent tracking days.

The switch in roosting pattern with a change in nest status was reflected in roost positions within relative diurnal use areas (Figure 5). When pairs had active nests, we observed females on nests (see above), which were located in peak relative diurnal use areas, while male roosts were located at sites where corresponding relative diurnal use values were significantly lower.

We propose that the above pattern is at least partly explained by extrapair sexual behavior of this socially monogamous bird. A well-supported hypothesis for close proximity of pair members is mate guarding conducted by males to ensure paternity during female fertile periods, especially in egg prelaying and laying (Birkhead and Moller 1992). Alatalo et al. (1987) demonstrated a linear relationship between daytime distance between pair members and extrapair copulation rate in the European Pied Flycatcher (*Ficedula hypoleuca*). Furthermore, Birkhead et al. (1987) found that the greatest number (54%) of avian genera examined copulated most frequently in the mornings, followed by 25% of genera with peaks both in the morning and evening. An equally bimodal pattern described by Briskie (1992) closely matched peaks of mate-guarding behavior by males of the Smith's Longspur (*Calcarius pictus*). The existence of corresponding physiologically mediated female "insemination windows" is discussed by Birkhead et al. (1996). Extrapair paternity has been documented in as many as 40% of Wood Thrush nestlings (Evans et al. 2009), whereas Evans et al. (2008) found that social mates were present during 74% of off-territory forays conducted by fertile females, suggesting that mate guarding is a strategy employed by Wood Thrush males to ensure paternity. The roosting period, abutted by at least one insemination window, is thus implicated as a critical period for mate-guarding efforts and for taking advantage of insemination windows in neighboring females.

Solicitation of extrapair copulations (EPCs) is consistent with the roosting patterns observed in this study. Males with females in prelaying and egg laying periods (i.e. without "active" nests), and thus susceptible to EPCs, roosted immediately adjacent to their mates. However, once females were securely incubating or brooding young nestlings, males often roosted far from their mates. A similar pattern was documented in gallinaceous birds that roosted within home ranges (Liao et al. 2008), although the authors proposed this as a nest predation reduction strategy. Our observation of 31% of male roosts outside DHRs could be a consequence of males soliciting EPCs from neighboring females in optimal morning and evening hours, and although this hypothesis was not explicitly tested in this study, it is consistent with our observations. Such a possibility is corroborated by our observation that no female roosts, including roosts alongside males, occurred outside corresponding DHRs. In Pennsylvania, USA, female Wood Thrushes in the fertile period made more frequent off-territory forays accompanied by guarding mates than alone, whereas solo males made frequent forays when females were incubating (Evans et al. 2008). In our study, females either roosted on active nests without males nearby (with males often outside the DHR), or were guarded by males while fertile. Roost commutes for EPC solicitation with guarding males thwarting EPCs might thus be futile for females, making movement uneconomic. However, our observation of younger males roosting farther from peak diurnal use areas does not necessarily follow the hypothesis that movement to roosts is due to EPC solicitation because, in passerines, older males tend to gain more extrapair paternity than young males (Cleasby and Nakagawa 2012). Evidence of more extraterritorial forays and extrapair offspring for older birds has been presented for the socially monogamous Reed Bunting (*Emberiza schoeniclus*; Kleven et al. 2005), indicating that, along with higher extrapair success, the frequency of EPC solicitation might also increase with age. If the Wood Thrush follows such a pattern, it is more likely that commutes to roosting habitat are due to movements to optimal roosting habitat, rather than for seeking EPCs.

Several potentially confounding factors are worth noting. Observers flushed roosting birds from their perches in 12% (9 of 74) of cases, often in densely vegetated areas or when the transmitter antenna position resulted in a weaker-than-expected signal. Disturbed birds generally moved only a short distance before settling back down, and subsequent roosts did not appear to differ from roosts used by birds that were never flushed. Also, we would like to emphasize that our roost observations were not completely independent, as the same birds were sampled repeatedly. Nevertheless, having truly independent observations for our pair analysis would have necessitated impractically large sample sizes, and we found that 92% of 37 males roosted $\geq$20 m from their previous roost, indicating that roost selection occurs nightly (Jirinec et al. 2011).

Lastly, radio-transmitter signal detection was considerably better at night, when the generally ground-dwelling Wood Thrush roosted higher up in the trees of the subcanopy and canopy. As Lang et al. (2002) noted, the species regularly moved long distances between nesting attempts (up to 17,388 m). In our study, we found that 23 (56%) radio-tagged males relocated their DHRs within the tracking period at least once. Except for 4 individuals, missing birds were found again, up to 4.29 km away from their previous known locations. We relocated birds from both aircraft ($n = 3$) and vehicles ($n = 16$), of which the latter was the more effective method, especially when the search was conducted at night.

Conclusion

To our knowledge, here we provide the first broad description of roosting ecology for a Nearctic–Neotropical migratory passerine during the breeding season. Unexpectedly, many male Wood Thrush roosts were located outside their diurnal home ranges. This study found that the species tended to roost in areas with higher canopy density than that of randomly selected points in their daytime range, but we suggest caution before concluding that the roost commute was driven by roosting habitat availability. The observed patterns in both unpaired and same-night pair roosts are also consistent with the notion that opportunities for extrapair copulations may play a role in bird movement to roosting areas. This hypothesis deserves more attention in subsequent research.

Advances in tracking technology and battery life allow for transmitter attachment to ever-smaller birds for longer periods, which stimulates research on avian movement patterns across a broad taxonomic extent. Despite abundant research utilizing individually radio-tagged diurnal birds, few researchers have extended the tracking interval into the nighttime hours. This is a missed opportunity to gain valuable information on avian roosting behavior, which includes an increasing number of reports quantifying commutes to disjunct roosting areas. Such knowledge is critical for a comprehensive understanding of habitat requirements for migratory birds, many of which are declining rapidly.

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Ethics statement: All federal, state, and local permits were secured prior to field work, and the project was approved by the College of William and Mary Animal Use and Care Committee (IACUC-2013-02-15-8462-mleu).

Author contributions: (1) V.J. and M.L. conceived the idea, design, and experiment (supervised research, formulated question and/or hypothesis); (2) V.J., C.P.V., and C.J.S. performed the experiments (collected data, conducted the research); (3) V.J. and M.L. wrote the paper (or substantially edited the paper); (4) V.J. and M.L. developed and/or designed the methods:; (5) V.J. and M.L. analyzed the data; and (6) M.L. contributed substantial materials, resources, and/or funding.

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