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Hidden space use behaviors of a nonbreeding migratory bird: the role of environment and social context

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Abstract

Background Movement behavior strongly mediates species and environment interactions, yet our understanding is constrained by challenges tracking space use at fine spatiotemporal resolutions.

Methods Using an automated telemetry array, we quantified variation in and drivers of space use for a nonbreeding population of migratory bird, the American redstart *Setophaga ruticilla*.

Results We identified two distinct and common behaviors – territoriality and floating,– that were governed primarily by NDVI as a proxy of resource availability. Within seasons, declines in weekly resources increased the prevalence of forays and the area of space utilized. Floaters were less likely to maintain body condition throughout the nonbreeding season, which is expected to negatively influence fitness and survival.

Conclusions Our study demonstrates that nonbreeding migratory birds exhibit a high degree of plasticity in space use that is driven primarily by resource availability but influenced by the dominance hierarchy within an individual's environment which are expected to have important implications on migratory populations.

Keywords Animal movement, Automated telemetry, Non-breeding Season, Dominance, Intraspecific variation, Migratory, Territoriality

Background

How individuals move across space and time governs their species and environment interactions across multiple scales and as such influences everything from global nutrient cycling [1] and disease dynamics [2] to population dynamics and individual behavior [3–7]. Identifying both the patterns and mechanisms underlying intraspecific variability in movement and space use and their ultimate consequences is required to fully understand the ecology of a species and the potential consequences of global change.

Space use, or the manner in which an individual uses its environment, ultimately shapes how it interacts with the entire ecological community. Rather than being fixed, space use behaviors can vary substantially across space and time as environmental (e.g., food availability, habitat quality, mate availability) or social (e.g., social status, mating status) conditions change [4, 8–13]. Even stationary strategies like territoriality [11, 14–16] vary substantially with a range of behaviors that might include everything from defending multiple territories to showing varying degrees of site fidelity [17–19]. In fact, some territorial individuals may defend multiple disjunct territories [10, 20], regularly use but not defend a larger area deemed a home range or overlap home ranges substantially [4, 8,



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21, 22], occasional undergo exploratory movement outside the territory and home range (hereafter foray), or even abandonment entirely [17, 23–29]. Likewise, other individuals that use space more nomadically (e.g., floaters), may forgo defending territories altogether while moving over larger spatial scales, often while prospecting for available territory or mate [4, 30–32]. Here too, spatial scale and site fidelity can vary tremendously with some floaters consistently using areas that encompass a few conspecifics' territories and others moving more nomadically across much larger areas [10, 31–34]. Given this intra and interindividual variability, space use within a given population is therefore best described by a continuous scale rather than being categorically defined (Fig. 1). Understanding the patterns in, mechanisms driving, and consequences of space use require study of intraspecific variability in subtle and difficult to observe movements [24, 35].

Our current understanding of space use has been hindered by our inability to track animals at fine spatiotemporal resolution across seasons or years. This challenge has typically led to a bias towards common or easily detected behaviors over more nomadic and ephemeral movement strategies. As a result, our understanding of



Fig. 1 A conceptual diagram of the underlying variability between space use tactics and the proposed effect of resource availability on the distribution of space use behaviors. The top figure represents the space use distribution of a hypothetical population that consists of three space use tactics (territorial, floater, transient). Each of these behaviors are distinct but overlap substantially in the amount of space utilized. The composition of the population therefore reflects the overall distribution of space use behaviors. Resource availability (bottom figure) can directly influence the distribution by either changing the number of space use tactics expressed and/or by influencing the variability in movements exhibited within each tactic such that resource scarcity (yellow arrow) results in increased variability in space use strategy and overall larger overall space utilized while resource abundance (green arrow) results in less variability in space use behaviors and overall smaller amount of space utilized

space use is insufficient to characterize the true variability in space use at the population-level which may bias estimates of survival and population density [20, 36–40] and directly influence our conservation approaches [9].

Characterizing the true distribution of space use behaviors and identifying the underlying drivers requires study designs and technologies that allow movement to be monitored at sufficiently fine spatiotemporal scales to capture variation within and among individuals. Until recently, such high-throughput approaches and technologies were unavailable, especially for small-bodied animals (< 20 g) like most migratory songbirds [41–43]. Therefore, automated telemetry [44-46] and comparable reverse-GPS systems [47], especially small local networks, remain the most practical approach towards capturing fine-scale variability in space use dynamics at the population-level [17]. In this study, we used an automated telemetry array coupled with conventional radio-tracking to more holistically capture the patterns and identify the drivers of population variability in nonbreeding space use behavior of a population of Nearctic-Neotropical migratory bird - the American Redstart (Setophaga ruticilla) - on its tropical nonbreeding grounds in Jamaica.

Understanding the implications of space use behavior on the ecology of a species is likely especially relevant for migratory species that despite spending most of the year on their nonbreeding grounds are relatively understudied during this period of the annual cycle [48]. In addition to local scale variation described earlier (territoriality, floaters, forays, etc.), space use behaviors may also include larger-scale intraseasonal movements that reflect relatively low site fidelity due to relocations of nonbreeding season (i.e., intra-tropical or post migratory nonbreeding movements) [10, 49]. While these post-migratory nonbreeding movements are important [49, 50], for this study, we focus on the more local scale variation exhibited in space use for a species that typically exhibits high winter site fidelity. Regardless of the scale of these movements, previous work has demonstrated links to resource availability and habitat quality [4, 8, 13, 25, 33, 49], diet and foraging behavior [16, 21, 51, 52], and social status [11, 33, 53, 54]. As such, we hypothesized that space use behaviors at the population-level represent behaviors that are shaped by the interplay between individual internal states (i.e., age, sex, body condition), social context (i.e., dominance status), and environmental conditions (i.e., habitat quality, resource availability). As such, we predict that resource availability is likely to drive the distribution of space use behavior exhibited at the population level in one of two ways (Fig. 1). Resource scarcity is expected to promote (1) diversity of space use strategies (i.e., floating, transients, territoriality) as the number of individuals that can be territorial declines and (2)

variability within-space use strategies by influencing how individuals employ a given space use tactic (e.g., increasing territory/home range, increasing prevalence of forays). Further, we predicted that internal states and social status will mediate behavioral plasticity in response to shifts in resource availability. Specifically, dominant individuals (adult males in this system) are expected to be territorial, occupy smaller ranges, and use higher quality habitat – all of which should buffer them from worsening conditions and resulting in more consistent patterns of space use behavior. Finally, we used body condition as an indicator to assess the consequences of space use behavior to nonbreeding season performance and predicted that sedentary birds with reliable access to resources would be in better condition than floaters.

Methods

Study system

This study was conducted January-May of 2016–2019 on a nonbreeding population of American redstarts at the Font Hill Nature Preserve on the southwest coast of, St. Elizabeth Parish, Jamaica (18° 02' N, 77° 57' W, <5 m above sea level). Redstarts are relatively easy to capture, tag, and monitor, allowing us to not only track their changes in space use within and between seasons but also to investigate the consequences of these behaviors. Resource availability in our Jamaican system can vary widely within and between nonbreeding seasons. Further, though most redstarts are territorial in this population [54], redstarts have been shown to exhibit a diverse mix of space use behaviors that range from territoriality, occupation of home ranges, mixed species flocking, and floating [54–57].

To quantify the movement behavior of individuals, we employed two tracking methodologies: one based on *manual hand tracking* and another *automated telemetry* using a network of 5 automated receivers (*sensorgnomes*). Hand tracking allowed us to follow individuals at a coarse temporal resolution (hourly-daily) but at a precise spatial resolution (<5 m). The network of automated receivers provided a very fine temporal resolution (detections every ~ 10 s) but the coarse spatial resolution (~ 300 m detection range of each station; presence/absence). Coupling both approaches allowed us to gather a more complete understanding of both the spatial and temporal variability in movement behavior.

Over the course of the study, we equipped a total of 141 redstarts ($N_{2016}=23$, $N_{2017}=66$, $N_{2018}=15$, $N_{2019}=37$) with a 0.29 g digitally coded VHF radio transmitters (NTQB1-1 & NTQB2-1, Lotek Wireless Inc., Newmarket, ON, Canada) using a modified legloop harness [58]. Transmitters operated continuously at a ~ 10.3-s cycle, which resulted in a battery lifespan of

approximately ~ 30-45 days. Individuals were captured randomly across the study sites using a passive netting approach to avoid potentially biasing our tagged sample towards territorial individuals that are more susceptible to capture using playback. Further, to avoid the effects of the migratory preparation on individual movement behavior, we only included individuals tagged before April 1 of each year, which is about 4–5 weeks before May 5, the average date of departure for this population [59, 60]. Of the 141 redstarts radio-tagged, after excluded 11 transients, we were left with a final sample of 63 individuals (33 males, 30 females) were ultimately included in this study. Upon capture, we classified individuals into age and sex classes using plumage and feather characteristics [61] and then uniquely marked them with a combination of USGS aluminum band and two-color bands. We measured standard morphometrics, including body mass (g), fat score, pectoral muscle size [62], and tarsus length (mm). We estimated body condition using the scaled mass index following [63], where body mass was scaled by tarsus size and reported as standardized grams. To investigate the potential role that dominance status plays in influencing space use behaviors (territorial vs. floater), we relied on age and sex as well-established proxies of dominance since adult males have been demonstrated to be dominant over females and young males [64, 65]. Further, to investigate the potential consequences of space use behaviors on the maintenance of individual condition across the nonbreeding season - an important contributor to an individual's fitness [25, 60, 66, 67] - we attempted to recapture as many individuals as possible throughout the season (Mean Capture Window = 30.68 ± 14 days) to quantify changes in body condition.

Movement behaviors are often tied to changes in resource availability, and to explore the plasticity in space use behaviors, we attempted to link changes in the distribution in individual movement behavior to changing resource availability both between years and within a season at weekly intervals. In this system, changes in food availability mirror changes in habitat quality driven by rainfall [60, 68, 69] because drought negatively impacts leaf biomass and subsequently arthropod biomass declines [69]. As such, we utilized normalized difference vegetation index (NDVI) as a proxy for resource availability that provided both a seasonal metric of resource availability to facilitate comparisons across years but also captured changes in resource availability within season. We extracted NDVI across the study site from weekly Sentinel-2 multispectral imagery (10 m resolution) sourced using Google Earth Engine [70].

Manual hand tracking

Following the initial capture and tagging, we used a standardized protocol of localizing each individual daily through a mix of triangulation and homing localization techniques using an SRX-800 (Lotek Wireless Inc., Newmarket, ON, Canada) and a 3-element yagi. Each day, we searched for every active tag (once per round) for approximately 5–10 min near the capture location or the last location the individual was detected. Upon detection, individuals were either localized via homing (identified visually via color bands), and a GPS location taken (<1 m) or triangulated by a single observer taking multiple bearings to the tag within a 3-min period. Because of the close distances (<50 m), triangulated positions were relatively precise (±5 m; LOAS software, Ecological Software Solutions). If an individual was not detected during the initial 5-10 min search of that round, nor opportunistically while traversing the study site between tag detections, we expanded our search to include all areas of the study site that were not originally traversed for approximately 60 min. Because the nanotags are digitally encoded and transmitted on a single frequency, we were able to scan the 166.380 mHz continuously while tracking, enabling us to locate individuals as we moved through the study site. Therefore, this protocol allowed us to confidently assess whether an individual was still alive, died, or departed the study site (~200 ha). Of the 74, 11 individuals were likely *transients* as they were only tracked a few times before ultimately relocating away from the study site and were excluded from further analysis. Following this protocol each season daily from ~6 am—1 pm, which resulted in an average of 26.5 locations per individual (range=5-108) for the 63 individuals included in subsequent analyses.

We quantified space use and the variability in movement behavior in two complimentary ways using this temporally coarse but spatially precise hand-tracking data. First, to quantify an individual's space use area, each individual's 'home range' size was calculated as the area of the minimum convex polygon. While any estimate of home-range area is sensitive to sample size [71], our aims with this approach was to identify large deviations in home range area that amounted from individuals utilizing different space use tactics and not in relatively minute differences between individuals employing the same tactic. Further, as opposed to alternative home range estimators such as KDEs, MCPs typically underestimate home ranges at smaller sample sizes thus only likely underestimating home range estimates for floaters that already occupy areas that are orders of magnitude larger than average territory size. As such, MCP approach allowed us to compare the scale of space use in a continuous way across all individuals irrespective of their space use

behavior because differences in home range area varied by orders of magnitude between territorial (<0.5 ha), floater (>2-10 ha), and transient individuals (>10 ha). Second, to draw comparisons between previous work and evaluate outcomes of space use behavior on individual performance (detailed below), we used net square displacement (NSD) to broadly categorize individuals into sedentary ('territorial') and alternative space use behaviors ('floaters' and 'transients'). NSD is a frequently used movement metric that captures the scale and breadth of an individual's trajectory as it measures the square of the Euclidean distance between subsequent locations. Distinct patterns in NSD time-series are expected from specific movement strategies with asymptotic patterns in NSD associated with a sedentary behavior (territory or home range) and NSD increasing over time representative of nomadic movements (floaters and transients). Although many studies have used non-linear parametric models to assign individuals to discrete movement strategies [72–74], patterns in net square displacement over time were distinct enough to visually classify individuals in this study as territorial or floaters in this study (see Appendix, Figure S2).

Automated telemetry

To track individuals at a fine temporal resolution across the study site, we utilized an automated radio tracking system that consisted of 5 Sensorgnome receivers (Appendix, Figure S1).

All tagged individuals were initially caught within the detection range of any given receiver ensuring that most individuals but because individuals often moved from their point of capture we only included individuals that were detected consistently for at least 5 days to accurately capture space use behaviors. Of the 63 individuals captured as part of this study, 36 were detected frequently enough across the array to include in this foray analysis.

Each receiver was equipped with four horizontally polarized omnidirectional antennas positioned 9 m high on a galvanized steel mast. These receivers continuously collected incoming signals from any nearby transmitter and logged the tag ID, timestamp, signal strength, and antenna port for each detection. Data collected by the automated telemetry system was uploaded to the Motus Wildlife Tracking System network for preliminary processing [46] and we used the R packages *Motus* [75] & *tidyverse* [76] to download, filter, and analyze the data. Although detections occurred approximately every 10 s, we smoothed the detection data at one-minute intervals by calculating the median signal strength from a series of consecutive detections for each receiver and then converted this into a detection history (1 s and 0 s).

Given our array configuration (Appendix, Figure S1), we were able to unambiguously determine that detections across different receivers of the same individual were indicative of relatively long-distance forays. First, these omni-directional antennas have reduced detection range compared to the typical directional yagis conventionally used. Based on the average distance at which an individual with known position was not detected, each receiver had an approximate detection range of ~ 300 m when individuals were moving at or below the canopy level. Further, the spatial configuration of receivers was such that they were distributed over an a large area $(338,561.7 m^2)$ and separated by distances between 299.4 m and 1,147.8 m, which are orders of magnitude larger than the average territory size of a redstart $(1,800 \pm 1,000m^2; [77])$. Taken together, sequential detections across different towers were indicative of exploratory forays outside of the territory or home range of an individual. Conventional hand-tracking approaches do not offer the temporal resolution needed to effectively capture these relatively rare or infrequent movements and therefore underrepresent the diversity of movement behaviors. As such, quantifying median daily forays enabled us to quantify the extent to which individuals (territorial or floaters) explored the study site on a continuous scale which allowed us to estimate the effect that seasonally variable resource availability, such as NDVI, had on the extent and prevalence of these movement behaviors.

Forays can be quantified in two ways using the automated telemetry array: movements between one receiver and another (Transitions) or movements out of range of one receiver and back (Recursions). Transitions are unambiguous because, with this array configuration, departures from one receiver's detection range into another's reflect true, relatively large-scale, movements. Recursions, however, are more ambiguous. They can either represent the movement of individuals temporarily out of range of the receiver but still within its home range or territory, or they can represent forays outside of their respective home range but in areas not covered by our array (Appendix, Figure S1). Given their ambiguity, in this manuscript, we chose to exclude recursions and therefore our quantification of daily forays represents a conservative estimate.

Evaluating the consequences of space use tactics on nonbreeding season condition

Nonbreeding season condition – defined as how well an individual maintains or improves their body condition throughout the nonbreeding season – is a key trait that underlies the overall performance of an individual and is inherently tied to fitness in this species through a seasonal interaction on departure time [60, 68]. However,

body condition is an inherently multifaceted trait that is difficult to measure and rarely captured with single metrics. Because we were primarily interested in the relative mass and muscle an individual accumulates or maintains throughout the season, we keyed in on the change in scaled mass index (~ size corrected mass, g) [63] and change in pectoral muscle size (mm)[62, 78] as response variables in linear models that included space use tactic (territorial vs. floaters) as well as age, sex, and habitat type to account for their confounding effects. Of the 63 individuals tracked in this study, we recaptured 46 at least twice within a season (>10 days apart), which allowed us to assess how space use strategy influenced changes in nonbreeding season condition. Key positive indicators of condition were positive changes in scaled mass index (increases in body mass) and increases in muscle size. Poor performers, on the other hand, would expect to lose or maintain mass throughout the season and decrease in muscle size as expected from a previous food-reduction experiment in this study system [25].

Data analysis

We fit general linear models that included age class (second year and after second year) and sex (male and female) to investigate how home range area of an individual, its space use tactic (territorial vs floater), and its median daily forays was influenced by its dominance status. We also included year as a fixed effect to assess how the average space use behavior of the population differed among years. With the home range area models, we opted to weight the variance by the number of locations used to estimate the MCP to account for the fact that home range area is sensitive to the number of locations used to estimate the MCP. As such observations that included more locations were given more weight than observations with fewer locations. While the home range area and forays were modelled using normal distributions, individual space use tactic was modeled using a logistic distribution. We initially fit all three models (home range area, space use tactic, and forays) with two-way interactions between habitat and age and sex but found that those interactions were non-significant. As such, we dropped those terms and report only results of the additive models.

We explored within-year changes in space use behavior (mean daily forays & mean daily displacement) averaged across a week using linear mixed models that included individual as a random effect and weekly NDVI at the study site level as the predictor. We included age class, sex, and habitat type (dry scrub vs. wet mangrove) along with their respective interactions with NDVI to explore how an individual's space use response to changes in environmental conditions varied by dominance status and habitat type. Because both mean daily forays and mean daily displacement were quite variable and spanned orders of magnitude, we log transformed these variables. In the case of mean daily forays which included 0's, we added 1 to each value. All analyses were run in R and mixed models were fit using the lme4 package [79]. We assessed significance of all parameters at the $\alpha = 0.05$ level and where appropriate used likelihood ratio tests on reduced model varieties for models that included random effects.

Results

Patterns and drivers of space use

The spatial scale of space use behaviors varied widely among individuals (Fligner-Killeen; $\chi^2 = 6.26$, df = 2, P = 0.04) and the median home range (for both territorial and floaters) decreased by 2.97 ha $(\pm 1.87SE)$ from 2016 to 2017, 2.40 ha $(\pm 2.13SE)$ from 2017 to 2018, 1.28 ha (±3.61SE) from 2018 to 2019. Home range area was negatively correlated with median NDVI across the nonbreeding period such that as the nonbreeding seasons became wetter and greener mean home range size decreased (Fig. 2; Weighted Least Squares: $\beta_{NDVI} = -21.54$, T = -4.26, df = 2, P = 0.05). These reductions in space use, prompted by increasing greenness (e.g., NDVI), matched declines in the proportion of floaters in the population (2016: 54%, 2017: 42%, 2018: 33%). Further, floaters had ranges ($MCP_{Floater} = 5.89ha$) that were 9.35 times larger than those used by territorial birds ($\overline{MCP}_{Territory} = 0.63ha$), suggesting that at least part of the population-level decline in the distribution of space use (home range area) could be attributable to the greater proportion of territorial individuals in the population in addition to annual differences in home range sizes. Further no tracked individuals switched space use behaviors during the season.

We found that space use behavior and subsequently home range area was affected by age but not by nor habitat. Sex was not significantly sex related to the size of area used (Fig. **3**a; $\overline{\text{MCP}}_{\text{Territory}}$: $\beta_{Male} = -1.13, t = -0.605, df = 56, P = 0.55$) nor the probability of being a floater(Prob(Floating): $\beta_{Male} = 0.031, t = 0.040, P = 0.968$). Second-year birds were more likely to exhibit floater behaviors (Prob(Floating) : $\beta_{SY} = -1.894, t = -2.085, P = 0.037$) and used larger ranges (Fig. 3b; $MCP_{Territory}\beta_{SY} =$ 3.69, t = 2.08, df = 56, P = 0.04)than older adult birds. Further, habitat had no effect on home-range size $(MCP_{Territory} : \beta_{Mangrove} = 1.23, t = 62, df = 56, P = 0.54).$

Of the 36 individuals whose movements were tracked continuously, 28 (78%) of them exhibited at least one foray. On average, individuals undertook 0.76 forays per day (range:0–7). We found habitat type did not influence the number of forays taken by individuals



Fig. 2 The distribution of space use behaviors (home range size and median daily forays) varied with nonbreeding season resource availability (NDVI; normalized difference vegetation index). Overall, in wetter years with higher NDVI (darker shades of green), individuals utilized smaller ranges (left figure) and forayed (right figure) more frequently than in drier years (paler shades of yellow; Weighted Least Squares: $\beta_{NDVI} = -21.54$, T = -4.26, df = 2, P = 0.05). Year is noted above by color that corresponds to it seasonal NDVI. Shaded density plots depict the distribution of space use behavior within a given year

 $(\beta_{Habitat} = -0.35, t = -1.23, P = 0.22)$. However, significantly fewer daily forays were made by males than females, (Fig. 3c; $\beta_{male} = -0.58, t = -2.1, P = 0.03$) and marginally less for adults than second-year birds (Fig. 3d; $\beta_{juvenile} = 0.49, t = 1.8, P = 0.08$), which is consistent with juveniles' greater propensity to being floaters.

Within a season, forays declined as environmental conditions (e.g., NDVI) improved ($\beta_{NDVI} = -6.38, t = -3.5$, 95%*CI* = -9.87, -2.91). We found that males are less likely to foray than females ($\beta_{Males} = -0.36, t = -2.5$, 95%*CI* = -0.64, -0.09) and juveniles were more likely to foray than adults ($\beta_{juveniles} = 0.60, t = 3.8, 95\% CI = 0.30, 0.89$). Further, birds in higher quality wet mangrove habitat were less likely to foray than birds occupying habitats in dry scrub ($\beta_{Mangrove} = -4.17, t = -2.9, 95\% CI = -6.84, -1.51$). The best supported model included habitat interaction with NDVI (*LikilihoodRatioTest*; $\chi^2 = 8.86$, df = 2, p = 0.01). The sensitivity in foray behavior to changing NDVI was modified by habitat (Fig. 4; $\beta_{NDVI*Mangrove} = 8.69, t = 2.62$, 95%*CI* = 3.07, 15.13) whereby birds in dry scrub decreased the prevalence of forays within increasing NDVI but not in wet mangrove habitat (Fig. 4).

Consequences of space use strategy

Across the season, body condition generally declined for floaters and was either maintained or improved for territorial individuals (Fig. 5). Floaters on average lost 0.33 g of size corrected mass $(\beta_{Floater} = -0.331, t = -2.579, P = 0.015)$ compared to territorial individuals over a period of 30.6 (± 14 days). This change in mass was likely due to the significant decline in the size of the pectoral muscle (*ChangeinMuscleSize* : $\beta_{Floater} = -0.819, t = -2.566, P = 0.014$). Changes in condition (both muscle size and body mass) were not influenced by age (Change in Mass : $\beta_{SY} =$ 0.161, t = 0.106, P = 0.136, Change in Muscle Size : $\beta_{SY} =$ 0.086, t = 0.301, P = 0.765) or by sex (Δ Mass: $\beta_{Male} = -0.185, t = -1.76, P = 0.0856, \Delta$ Muscle Size : : $\beta_{Male} = -0.460, t = -1.60, P = 0.117).$ However, these physical costs of floating were only fully realized in poor-quality dry scrub habitats. Floaters in wet mangrove habitat maintained their mass (Δ Mass : $\beta_{Floater*Mangrove} = 0.472$, t = 2.115, P = 0.041) and showed only marginal, nonsignificant changes in muscle size (\triangle Muscle Size : $\beta_{Floater*Mangrove} = 1.06, t = 1.751, P = 0.088$).



Fig. 3 Patterns of space use behavior (home range size and forays) by sex (orange = males, yellow = females), age class (green = juveniles (second year), red = adults (after-second years)), and habitat (dry scrub, wet mangrove). After accounting for year, sex (*a*), and habitat type (*a*,*b*), age was the only significant predictor of home range size (minimum convex polygon) with juveniles on average occupying home ranges that are 3.7 ha larger than adults (*b*). Considering average territory sizes of 0.18 ha, this difference in home range size is likely due to younger individuals more likely to exhibit floater space use patterns. Median daily forays differed significantly between year, sex (*c*), age (*d*), and habitat (*c*,*d*). Males exhibited less forays than females (*c*), adults forayed less than juveniles (*d*), and birds occupying mangrove tended to foray less than birds occupying dry scrub habitats (*c*,*d*).

Discussion

Coupling automated telemetry system within intensive hand-tracking, we provide three lines of evidence that space use behavior during the nonbreeding season for a migratory bird is highly plastic and driven by environmental conditions and dominance status. First, we observed a decline in the area of space utilized annually and a reduction in the prevalence of non-territorial floaters within the population as annual resource availability increased (as measured by NDVI). Second, we



Fig. 4 Changes in the frequency of forays in response to seasonal changes in resource availability (weekly NDVI) by sex and habitat types (yellow = dry scrub, dark green = wet mangrove). Plasticity in foray behavior was mediated by a habitat interaction, such that birds in dry scrub habitats were more sensitive to increasing NDVI while birds occupying sites in higher-quality mangrove habitat did not respond as strongly ($\beta_{NDVI*Mangrove} = 8.69, t = 2.62, 95\%CI = 3.07, 15.13$)



Fig. 5 Space use tactic significantly influenced the change in body condition and composition of nonbreeding American redstarts (*Setophaga ruticilla*) but were not influenced by sex (orange = males, yellow = females) or age class (SY = second year, ASY = after-second year). Floaters on average lost mass compared to territory owners (top row) likely due to the significant decrease in the size of pectoral muscle (bottom row). Box and whisker plots demonstrate the median (bold line), interquartile range (box), and min and max excluding outliers calculated as Q \mp IQR*1.5. Points have been jittered to accentuate each individual point

found that within-season movements of individuals were linked to changes in resource availability. Specifically, individuals made more forays when resources were scarce. However, the social context played a crucial role in mediating this pattern, such that whether subordinate individuals adjusted their behavior (typically juveniles and females) to changing resource availability depended on the sex-biased habitat they occupied and the competitive pressure they presumably faced. Lastly, our study highlights the physical consequences of movement behaviors, as floaters could not maintain their body condition over the nonbreeding season; a well-document pattern that is mediated by the effect of poor-quality scrub habitat on body condition in redstarts. With longterm trends in seasonal rainfall declining throughout the Caribbean and across much of Neotropics [80, 81], our study suggests that the distribution of space use behaviors within populations are likely undergoing rapid changes, and these could contribute to population-level consequences.

Space use and movement behaviors are increasingly recognized as being highly variable, especially for nonbreeding migratory birds [4, 8, 13, 34, 40, 54, 82]. Yet assessment of the underlying drivers has thus far remained elusive largely due to limitations in the resolution of our tracking technology. By characterizing space use behavior along both a spatial (e.g. home range area) and temporal (e.g., site-fidelity) continuum we could capture the true distribution of space use behaviors within the non-breeding period of a migratory bird population. The high degree of variation in behaviors over time and both within- and among individuals in our system and in others [19, 26, 83, 84] contrasts sharply with the persistent perception that territoriality is a fixed and sedentary space use strategy [15, 85]. In our system nearly every territorial individual adjusted their movements throughout the season by undertaking extensive forays (i.e., varying levels of site fidelity). As resource abundance increased (high NDVI), individuals restricted the area of space used, exhibited a higher degree of site-fidelity (lower prevalence of forays), and the population overall had a lower proportion of floaters. In contrast, when resource abundance decreased, individuals exhibited a higher prevalence of forays, and the population had a higher prevalence of floaters. Taken together, these data suggest that nonbreeding space use behaviors allow individuals to flexibly adjust their movement and space use behaviors to changing environmental conditions [8, 11, 13, 86, 87].

Individual behavior regarding forays is linked to dominance status and can be affected by social context and habitat quality. During the breeding season, forays are common and facilitate extra-pair copulations [28, 88, 89] and prospecting for future breeding sites [24, 84]. However, the reasons behind nonbreeding season forays remain unclear. It may serve as an opportunity to prospect for supplemental resources outside of the territory in times of scarcity [90-92]. Forays were found to be more common in poor quality scrub habitats and by females, suggesting that they help individuals supplement their resource needs. Furthermore, the prevalence of forays was mediated by social context via a habitat and sex interaction, with females adjusting their behavior in low-quality scrub habitats but not in higher-quality mangrove habitats. Dominance-mediated habitat segregation results in male biased settlement of high-quality mangrove habitats[64], suggesting that this habitat-sex interaction is likely mediated by the relative dominance status of the individual within its given environment. The social environment therefore plays an important role in an individual's ability to adapt to changing environmental conditions, and subsequent consequences of those movement behaviors [93 and references therein].

Our findings provide new insights into how redstarts and other migratory species may respond to changes in climate and land use that affect habitat quality and quantity on the nonbreeding grounds. In the Caribbean specifically, the frequency and severity of droughts are projected to increase [81, 94] which result in drastic reductions of resource availability [$\sim 60\%$; 25,70]. These declines in resource availability will prompt shifts away from territorial and sedentary behaviors towards floater and nomadic movements. In fact, Cooper et al. (2015) demonstrated that some territorial redstarts adopted floater behaviors following experimental reduction of food availability. Interestingly, we found that floaters were more likely to experience significant declines in body condition over the nonbreeding period as compared to territorial individuals. This suggests that more nomadic space use behaviors are likely costly within this system. Drought conditions can negatively impact migrants either directly by negatively influencing body condition and survival or indirectly by negatively influencing reproductive success on the breeding grounds through its effect on migration timing and migratory behavior [59, 60, 68, 95]. Considering the negative consequence of floating on nonbreeding body condition, we anticipate that within this system, shifts towards more nomadic movements and behaviors are likely to result in both indirect and direct fitness consequences through nonbreeding seasonal interactions. Therefore, continued drought in the Caribbean is expected to not only shift the distribution of space use behavior towards more nomadic behaviors but also negatively impact per capita fitness. More importantly, although we are able to directly observe and monitor the impacts of shifting climate on the fitness of territorial individuals; the same isn't true for more difficult to observe nomadic individuals without higher resolution tracking approaches. Unfortunately, our understanding of the impacts of climate and climate change on migratory birds is severely biased towards more sedentary and easy-to-observe individuals.

Conclusion

Our study grows out of increasing interest in understanding how individual decisions about movement and use of space can scale to influence ecological and evolutionary processes [6, 96-99]. However, this relies on our ability to capture the rich variability in space use and movement behaviors. Unfortunately, much of the variability in space use behavior demonstrated here is often missed entirely by conventional low-resolution monitoring approaches (e.g., color band resights, manual telemetry, etc.) that cannot capture these ephemeral movements and more nomadic individuals. Using an automated telemetry array, we demonstrate an important but subtle interaction between environmental conditions and social status on individual behavior and how it ultimately scales up to influence the distribution of space use behaviors at the population level. The application of automated tracking approaches that allow insights into the behavior of individual animals at high spatiotemporal resolution is necessary to understand further the undeniable connection between individual movement and population dynamics. This is especially important given the ongoing climatic changes that are currently affecting the Caribbean and much of the Neotropics [80, 81] and is paramount to our understanding of the ongoing declines of migratory birds [100].

Abbreviations

ASY	After-Second Year Bird (Adult)
IACUC	Institutional Animal Care and Use Committee
MCP	Minimum Convex Polygon
MDD	Mean Daily Displacement
NDVI	Normalized Difference Vegetation Index
NSD	Net Squared Displacement
SY	Second Year Bird (Subadult)

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-024-00523-4.

Additional file1 (DOCX 2089 KB)

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Author contributions

BCD, ADR, and PPM conceived of the idea for the paper. BCD collected the data and conducted analyses; BCD, ADR, and PPM wrote the first draft; all authors contributed to the final manuscript.

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Availability of data and materials

Data are available on Dryad (https://doi.org/10.5061/dryad.gb5mkkwx1).

Declarations

Ethics approval and consent to participate

Field work was conducted in accordance with permits from the United States Geological Survey, the Jamaican National Environment and Protection Agency, Cornell University, and Smithsonian National Zoo IACUC approval 14–03.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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