

Resource selection by New York City deer reveals the effective interface between wildlife, zoonotic hazards, and humans

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October 31, 2022

Abstract

Although the role of host movement in shaping infectious disease dynamics is widely acknowledged, methodological separation between animal movement and disease ecology has prevented researchers from leveraging empirical insights from movement data to advance landscape-scale understanding of infectious disease risk. To address this knowledge gap, we examine how movement behavior and resource utilization by white-tailed deer (*Odocoileus virginianus*) determine the distribution of blacklegged ticks (*Ixodes scapularis*) which depend on this host for dispersal in a highly fragmented New York City borough. Multi-scale hierarchical resource selection analysis and movement modeling provide insight into how deer's individual movements construct the risk landscape for human exposure to the Lyme disease zoonotic hazard – infected *I. scapularis*. We conclude the distribution of tick-borne disease risk is the result of individual resource selection by deer across spatial scales in response to habitat fragmentation and anthropogenic disturbances.

Introduction

Anthropogenic environmental changes continue to drive the increasing frequency of zoonotic disease emergence – diseases transmitted between wildlife and human populations (Allen *et al.* 2017; Gibb *et al.* 2020). Zoonotic diseases emerge from a suite of processes that require spatio-temporal overlap between humans and infected hosts or vectors for spillover occurrence. Urban ecosystems are a hotbed for emerging zoonoses due to opportunistic species adapted to anthropic landscapes that serve as zoonotic hosts and the existence of interfaces between humans, wildlife, and/or vectors where contact and pathogen spillover can occur (Alirol *et al.* 2011; Hassell *et al.* 2017). Through movement, wildlife hosts influence contact rates between vectors, pathogens, and other hosts, ultimately shaping the distribution of zoonotic hazards in complex multi-host-pathogen systems.

Urban wildlife movement patterns are driven by landscape-dependent and independent fragmentation. Landscape-dependent fragmentation (LDF) alters the physical configuration of habitat patches, preventing species from moving freely across the landscape as patches become increasingly isolated (Magle *et al.* 2014; Berger-Tal & Saltz 2019). As natural land is converted to impervious surface, wildlife hosts aggregate in remaining habitat fragments leading to increased contact rates and spatial hotspots of transmission and spillover (Wilkinson *et al.* 2018). Landscape-independent fragmentation (LIF) results from anthropogenic disturbances which change animals' perception and use of their environment (Berger-Tal & Saltz 2019). For example, resource subsidies lead to LIF whereby fertilized vegetation, gardens, or waste byproducts (Becker

et al. 2015; Langley *et al.* 2021) provide stable, often predictable, resources which influence wildlife host movement (Ossi *et al.* 2020; Ranc *et al.* 2020) and contact patterns at the human interface, where zoonotic hazard becomes risk.

Tick-borne disease emergence is intertwined with land use change and habitat fragmentation (Diuk-Wasser *et al.* 2021) and tick-borne diseases are the most common vector-borne zoonoses in temperate North America, Europe, and Asia. In the United States, Lyme disease (LD), a bacterial infection caused by *Borrelia burgdorferi sensu stricto*, affects 400,000 people annually (Kugeler *et al.* 2021; Schwartz *et al.* 2021). Historically, LD was associated with the incursion of suburban and exurban development into rural areas (Barbour & Fish 1993). More recently, ticks expanded their geographic range with climate change (Sonenshine 2018; Ogden *et al.* 2021) and by occupying diverse and novel landscapes such as cities (VanAcker *et al.* 2019). The urban expansion of LD occurs through two pathways increasing human risk of exposure to the LD hazard: (1) vegetation increases in cities undergoing de-urbanization linked with population decline and land abandonment (Eskew & Olival 2018; Richards & Belcher 2019), or through cities adopting urban greening strategies (Yanget *et al.* 2014; Halsey *et al.* 2022); and (2) expanding urban matrix into surrounding natural habitats. Both pathways increase tick habitat and the prevalence of wildland-urban interfaces where species richness is dominated by synanthropic wildlife species, often tick hosts or pathogen reservoirs (Gibb *et al.* 2020), and human exposure to ticks is high (Diuk-Wasser *et al.* 2021).

In the eastern and midwestern US, the establishment and persistence of the LD vector *Ixodes scapularis* ticks is supported by large mammal hosts. For adult *I. scapularis*, white-tailed deer (*Odocoileus virginianus*, hereafter deer) are the primary reproductive stage host (Barbour & Fish 1993; Rand *et al.* 2004; Ostfeld *et al.* 2018). Importantly, while deer amplify the vector for LD (Carpi *et al.* 2008; Cagnacci *et al.* 2012), deer are not susceptible to *B. burgdorferi* infection and do not support *B. burgdorferi* transmission (Telford III *et al.* 1988). Studies predicting the distribution of *I. scapularis* ticks and LD over large geographic areas typically utilize broad-scale climatic and landcover variables (Estrada-Peña 1998; Diuk-Wasser *et al.* 2006; Soucy *et al.* 2018). This approach, however, lacks power to predict the zoonotic hazard at fine-spatial scales because it ignores local LD ecology and the modulating role of host movement in fragmented environments at different spatial (home range, fine scale movements) and temporal (seasonal, diel) scales.

Available niches for parasites are shaped by movement and resource selection of wildlife hosts (Ezenwa *et al.* 2016). Thus, the probability of tick population establishment is affected by the hosts' scale of response to the landscape – for example, the scale at which deer select and establish their home range. Wildlife resource selection spans multiple spatial scales and is hierarchically nested (Johnson 1980), where broad-scale selection constrains fine-scale selection (Senft *et al.* 1987). Multi-scale selection is integral to consider in urban landscapes where deer often display urban-adapted behavior such as foraging close to households (Swihart *et al.* 1995; Kilpatrick *et al.* 2000; Grund *et al.* 2002) while resting in forest patches. If deer habitat selection encompasses anthropogenic resources, residential areas may experience enhanced exposure to infected ticks. Because ticks passively fall from hosts upon engorgement, host movement speed and directionality through varying landcovers affect tick spatial clustering and ticks' likelihood of survival post-feeding. Further, the burden of *I. scapularis*' life stages on deer varies with tick phenology such that seasonal movement patterns exhibited by deer may differentially affect which life stages are dispersed, when, and to where.

This study examines fine-scale deer movement in an urban, fragmented borough of New York City (NYC) to determine how deer movement links to local distributions of *I. scapularis* ticks and heightened LD hazard. We employ a multi-scale hierarchical resource selection framework to (i) examine deer's scale of response to anthropogenic landscape features when establishing their home-range (i.e., responses to LDF in 2nd order selection), (ii) determine fine-scale spatiotemporal effects of the urban landscape on within-home range habitat selection and avoidance (i.e., responses to LIF in 3rd order selection), and (iii) assess the spatial congruence between deer seasonal habitat selection and LD hazard. We expect high intensity development will restrict deer home range selection at fine-spatial scales through limiting available natural habitat and creating movement barriers. We expect deer to exhibit diel variation when selecting for features within the home range and to avoid highly anthropic areas during periods of heightened human activity. We further hypothesize

that vegetated neighborhoods nested within areas connected to natural habitats will attract deer to fine-scale foraging resources and support the microclimate for tick survival, leading to higher tick occupancy compared to neighborhoods that are less accessible to deer and/or present more hostile microclimates for *I. scapularis*.

With the majority of the human population residing in cities (United Nations, Department of Economic and Social Affairs 2018) and the recent increase of tick-borne diseases in urban areas globally (Hamer *et al.* 2012; Rizzoli *et al.* 2014; Hansford *et al.* 2017, 2021; Heylen *et al.* 2019; VanAcker *et al.* 2019; Simmonset *et al.* 2020; Sormunen *et al.* 2020), there is an urgent need to understand the urban ecology of tick-borne disease emergence and the determinants of heterogeneity in tick-borne disease hazard. Here, we pair deer movement and tick surveillance data to provide the first study that links deer movement behavior to tick distribution across a highly urban landscape. We conclude that resource selection at different spatial scales enables urban deer to navigate fragmented habitat and that sex and individual-based responses to human activity characterize differences in tick distribution capacity.

Material and methods

Study area

Staten Island (SI), NYC, USA, has a population of 474,893 with a density of 3,132 people/km² (World Population Review 2022) and the highest tree canopy cover of all NYC boroughs (Nowak *et al.* 2018, 73% development, 27% natural landcover with 12% tree cover; Figure 1). Increasing rates of LD cases on SI from 4 to 25 per 100,000 between 2000 and 2016 (NYC DOHMH 2020) motivated this research. Prior work shows metapopulation dynamics structure tick population persistence in SI parks where park's centrality – its level of connectivity for deer – predicts nymphal tick density and infection prevalence (VanAcker *et al.* 2019). Thus, SI offers an ideal landscape to examine deer movement responses to LDF and LIF and their consequences on tick-borne disease.

Animal collaring

We captured deer during the 2016 – 2019 winters (Supporting Information); 177 yearling and adult males were ear-tagged and fitted with GPS collars (G2110E Iridium, ATS; GPS/GSM ES400, CTT) following non-lethal surgical vasectomies to sterilize male deer for population reduction (Supporting Information: reduced 2,053 to 1,616 deer throughout the study period). Ten female deer were fitted with GPS/GSM (ES400, CTT) collars to complement the male location data during the 2019 winter.

GPS data standardization and segmentation

All location data were screened for outliers using the R (Team 2020, version 4.0.5) package *ctmm* (Calabrese *et al.* 2016) and filtered through multiple inclusion criteria, resulting in a sample size of 50 males and 9 female deer (Supporting Information). We used the R package *AdeHabitatLT* (Calenge 2006) to regularize trajectory segments from male deer to a 2-hour fix schedule and to a 1-hour fix schedule for females, and discretized data to constant time lags. Data were segmented into three seasons according to deer and *I. scapularis* life histories: deer pre-breeding (June 1 – August 31, larval and nymphal *I. scapularis* feeding), breeding (September 1 – December 31, adult *I. scapularis* feeding), and post-breeding (January 1 – May 31, adult *I. scapularis* feeding) (Etter *et al.* 2002; Ogden *et al.* 2007; Schaubert *et al.* 2015). The data spanned from breeding 2016 to the post-breeding 2021 season (excluding data during the pre-breeding 2017 season, Figure S1).

Covariate processing

We reclassified the NLCD 2016 (U.S. Geological Survey 2019) raster layer from 15 original landcovers to four landcover types representing important habitat types for deer or for human exposure to the LD hazard: water/wetland/herbaceous (wetland-herb), open and low-intensity development (low-dev), medium-high intensity development (med-hi-dev), and forested landcover. To explicitly investigate how deer habitat selection can influence human encounters with the LD hazard, we classified residential blocks based on their attractiveness to deer and suitability for tick survival. We selected the block level to match the spatial scale of

deer relocations (average step length, for males: 146m/2hours; for females: 84m/1hour). To construct this landcover layer, we estimated total yard area, canopy height, landcover type proportions within each block, and landscape connectivity for deer within 100m surrounding each block. We standardized the block-level variables and used K-means clustering to define the block types (Supporting Information, Figure S2). Block-1 characterized blocks with high vegetation, low impervious cover, high connectivity for deer, and large yard areas. Block-2 described blocks with low vegetation, high impervious cover, low connectivity for deer, and small yards. We merged block assignments with the reclassified landcover layer to use in the second and third order selection models (Figure 1). We validated the association between block types and tick habitat suitability using a dataset from our prior work assessing tick presence in residential yards bordering urban green spaces from May-June 2018 and 2019 on SI (Gregory *et al.* 2022, Supporting Information). Of 245 household samples around urban forests, 92.41% of yards where ticks were collected were in block-1 ($n = 223$ households) and 7.59% ($n = 22$ households) in block-2. Further, 90% of yards where *I. scapularis* were collected were in block-1. This confirmed that block assignment successfully identified residences that were accessible to deer and support *I. scapularis* survival. Lastly, due to low representation of deer use across all six landcover types, we created a second landcover layer of coarser thematic resolution where the six landcover types were re-classified into either ‘natural’ (forest and wetland-herb) or ‘urban’ (low-dev, med-hi-dev, block-1, and block-2).

Home range estimation and analysis

We estimated home range (HR) size using Epanechnikov kernels to construct probability densities for each animal with the *adehabitatHR* package (Calenge & Fortmann-Roe 2013). We used the reference bandwidth (h_{ref}) as the smoothing parameter and estimated the 95% (Figure 1) and 50% HRs. We estimated the proportion of the HR comprised of each landcover type using the fine thematic resolution layer. From this, we assessed HR habitat richness and evenness by estimating Simpson’s alpha-diversity index.

Second order selection

To understand scale dependence in deer’s response to anthropogenic features during second order selection, we ran resource selection function (RSFs) models with scale optimization. We considered all of SI available for deer and drew nine random locations anywhere on SI for each used location. We then estimated the area of med-hi-dev within buffers (varying from 100m-800m at 100m increments, thus applying a multi-grain assessment (McGarigal *et al.* 2016)) surrounding each used and available location. We applied logistic regression generalized linear models (GLMs) to assess the dependence of used/available locations on the area of med-hi-dev. We selected the model with the minimum Akaike Information Criterion (AIC) score (Burnham & Anderson 2002) as the most predictive radii for individual deer.

Third order selection

We ran integrated Step Selection Analysis (iSSA; Avgar *et al.* 2016) to determine drivers of within-home range fine-scale resource selection while accounting for individual movement using the broad and fine thematic resolution landcover layers. The movement from 59 deer was modeled using broad thematic resolution. Additionally, the movement from a subset of deer ($n = 27$) whose location data spanned all six landcover types was modeled using the fine thematic resolution layer during the deer breeding/adult *I. scapularis* feeding seasons (2016 – 2020).

To prepare the data for iSSA, we used the *amt* (Signer *et al.* 2019) R package to estimate step lengths and turning angles between successive steps to fit tentative gamma and von Mises distributions, respectively. From these distributions, ten random steps were generated for each observed step (Supporting Information). Habitat attributes were extracted at the beginning and end of observed and random steps using the two landcover layers. We fit four iSSA models to data from each deer using the ‘fit_issf’ function in *amt* which uses a conditional logistic regression stratified by start step ID. We included three covariates expected to influence the movement process in the core model and modeled habitat selection for all deer using broad thematic resolution and the subset of 27 deer using fine thematic resolution (Table 1, model 1). We expected time-of-day to vary deer’s strength of selection for features within their HR, thus we included day or night

as an interactive term with habitat selection (model 2). Movement differences driven by the starting habitat were assessed through an interaction between starting step habitat and movement covariates (model 3). To assess whether deer moved differently depending on habitat and time-of-day, we included interactions between the ending step landcover, movement covariates, and time-of-day (model 4).

We assessed model fit for 160 deer-season models by bootstrapping each individual's four models independently ($n = 1000$) to acquire mean coefficient estimates with a 95% confidence interval and used the ΔAIC (Burnham & Anderson 2002) to determine the individual's best fit model between the null model and model 1 and between models 1 - 4 (Table 1). We tallied how many deer showed the strongest support for each model by season and sex to determine the top model (Table 2). The coefficient estimates from the best fit model for each sex were bootstrapped ($n = 1000$) for each individual and the coefficients' standard errors were estimated. We used individual movement parameter estimates from model 4 (where habitat selection was accounted for) to update the tentative gamma and von Mises distributions and estimated movement rates and directionality for individual deer over natural and urban landcovers. These were summarized using boxplots to show deer's average and individual movement rates by sex and landcover, faceted by season.

Lastly, to showcase how individual variation in movement and resource use affects the future probability of vector dispersal, we simulated spatially-explicit dispersal kernels informed by movement and selection coefficients estimated from fitted iSSA models for three individuals that varied in the habitat diversity within their HR and their strength of selection for fine resolution landcover types using *amt* (Signer *et al.* 2017). We utilized the same initialization points for the simulations across individuals in an area of SI that exemplifies the juxtaposition of habitat types in residential areas, but where no individuals were observed occupying. The simulation was informed by the movement and habitat selection coefficients from model 4 that used a fine resolution landcover. Rasterized dispersal kernels were constructed for the first 100 locations for three individuals. The individual dispersal kernels were mosaicked using the maximum cell value from overlapping kernel layers to create a single raster mosaic per deer (Supplemental Information). Because hosts' movement characteristics may translate to vector distribution patterns; simulating deer space use informed by observed movement and habitat selection over a landscape provides a visualization of this connection.

Results

Home range estimation and analysis

Deer utilized wetland-herb, block-1, and low-dev in similar proportions to the amount these habitats were available in the study area. In contrast, deer used forests in higher proportion to the amount available and used med-hi-development and block-2 in lower proportions to the habitat available (Figure 2a). Deer more frequently used urban landcovers at night and occupied wetland-herb and forested landcovers with higher frequency during the day (Figure 2a). The 95% male HRs ranged from 30 hectares (ha) to 1,049 ha with an average size of 170 ha. Female HRs varied from 24 ha to 79 ha with an average of 50 ha. As HR size increased, the percent natural (forest and wetland-herb) landcover decreased while the percent urban (low-dev, block-1, med-high-dev, and block-2) landcover within the HR increased with habitat diversity (Figure S4). Male HRs on average were comprised of 33% natural landcover and 66% urban landcover whereas female HRs averaged 43% natural and 56% urban landcover. Across deer, we observed HRs with high landcover diversity as well as HRs dominated by few landcover types (Figures 2b, S5).

Second order selection

For second-order selection of HRs, all male and female deer responded strongest to med-hi-development at fine-spatial scales of 100m radius ($n = 59$), indicated by the low AIC score for this spatial scale during model comparison (Table S2 and Figure S6). The relative strength of selection varied within the population, although all coefficients were negative and statistically significant (Table S2, Figure S7).

Third order selection

We first examined whether movement alone could predict third order selection (null model), the selection of resources within the HR, or if including habitat selection strengthened the model fit (model 1). We found

habitat selection significantly improved the model fits for most individuals across seasons, except for 17 unique deer represented in 23 deer-seasons (23 models/160 total models showed the null model with lowest ΔAIC). For these 17 deer, model 1 which incorporated habitat selection, was $<2 \Delta AIC$ from the movement only models indicating that both models adequately fit the data.

The top model describing movement and habitat selection within the HR for male deer across pre-breeding, breeding, and post-breeding seasons was model 4 (Tables 2, S3) providing support for speed and directionality differences by time-of-day and habitat selected. The top model for female deer was model 2 for breeding and post-breeding seasons providing support for a time-of-day effect on habitat selection (Tables 2, S3). During the pre-breeding seasons, the numbers of female deer showing model 2 and 3 as the best fit were equal. One male deer had over 95% of its observed steps in residential block-1, this animal was removed from models because the extreme habitat specialization did not support convergence. Deer selected natural over urban habitats most frequently (124/160 models per deer-season), six models showed positive selection of urban landcover in reference to natural habitat, and 30 models resulted in a neutral response to urban landcover indicated by a non-significant coefficient for urban landcover selection in reference to forest.

A subset of individuals ($n = 27$) was used to model resource selection during breeding seasons (2016 – 2020) using fine thematic resolution; most deer significantly avoided residential block-2 and med-hi intensity development relative to forested habitat and individuals showed high variation in selection strength (Figure 3b). Deer showed stronger avoidance of increasingly developed landcover (Figure 3b). Wetland-herb was significantly selected for in 10.34% of models, selected against relative to forest in 41.38% of models, and deer showed a neutral response in 48.42% of models. Low-dev was selected for in 3.45% of models, selected against relative to forest in 55.17% of models, and 41.38% of models showed a neutral response. Residential block-1 was selected for in 3.57% of models, selected against in 64.29% of models, and 32.14% of models showed a neutral response. Importantly, residential block-2 was never selected for relative to forest, was selected against in 96.30% of models, and 3.70% of models showed a neutral response. Lastly, med-hi-dev was selected against in 96.55% of models relative to forest and 3.45% of deer showed a neutral response.

The simulations based on parameters from the animal with the largest proportion of residential block-1 and low-dev within its HR (1151, Figure 3a top) and the highest relative selection strength for block-1 (Figure 3b), showed high dispersal probability over block-1 and low-dev and low dispersal probability over block-2 (Figure 3c left). Deer 1150's HR was mostly comprised of block-1 and forest (Figure 3a middle) and its selection strength for non-forested landcover types were low or neutral compared to forest (Figure 3b). The highest dispersal probability for deer 1150 is centered at forested landcover and block-1 (Figure 3c middle). Lastly, the animal with high wetland-herb landcover and the highest proportion of block-2 in their HR (1093, Figure 3a bottom) showed a neutral response to block-2 (Figure 3b) and high dispersal tendency over block-2 (Figure 3c, right) with less contrast in dispersal probability between block types when compared to deer 1151. Variation in the simulation kernels' size and shape results from individual variation in step length and turning angle distributions conditioned by land use type.

Males and females moved faster through natural than urban landcovers across seasons, although the speed differences were greater for male deer (Figures 4 and S8). Movement speeds for male individuals ranged from 8m/2 hours over urban landcover to 541m/2 hours over natural landcover while female speeds ranged from 46m/1 hour over urban landcover to 142m/1 hour over natural landcover. The fastest average speed was during the breeding season in natural habitats for males (586m/2 hours) and females (156m/1 hour). Males moved an average of 175m/2 hours in natural areas with a maximum speed of 586m/2 hours and a mean of 133m/2 hours in urban landcover with maximum movement of 252m/2 hours. Males moved slowest during the pre-breeding season through urban landcovers. Females moved an average of 92m/1 hour and a maximum movement of 156m/1 hour in natural landcovers and 82m/1 hour with a maximum movement of 129m/1 hour in urban landcovers. Females moved slowest during the breeding season through urban development.

Discussion

Host movement is a missing component in predicting vector-borne disease emergence, spread, and transmission (Hartemink *et al.* 2015; Dougherty *et al.* 2018) and has mainly been explored through mathematical models (Hartfield *et al.* 2011; Sumner *et al.* 2017; Tardy *et al.* 2021). However, individual movement is often not accounted for when modeling the transmission process (Fofana & Hurford 2017). Our results demonstrate individual resource selection of development intensity is modified by deer’s sex, tendency to utilize habitat at the human interface, and their location in the urban matrix. This finding suggests modeling individual-scale movement is essential when assessing hosts’ distribution of ticks and tick-borne pathogens into residential areas.

We observed seasonal sex-based movement differences important for vector dispersal in urban deer. Males moved faster and selected developed habitats more frequently than females, that instead maintained smaller HRs with more forested habitat than developed landcover. This suggests male deer may disproportionately distribute ticks outside of natural areas while females maintain ‘source’ tick populations in urban green spaces through providing bloodmeals and short-distance dispersal opportunities. Further, because male movement was slowest through urban areas during the pre-breeding and females during the breeding season, male movements could drive the distribution of feeding nymphs, while females could propagate feeding adult ticks to human interfaces.

Our analysis identified predictable responses in deer use of specific landcover classes at the individual scale, highlighting the potential to understand deer response under different urban development scenarios. Deer use of wetland and herbaceous habitats, low-intensity development, and highly vegetated residential areas scaled alongside the availability of these habitats. In contrast, highly developed public and residential landcovers were used less than the amount available, indicating a threshold may exist for urban deer’s tolerance of impervious surfaces and high human activity. This finding is consistent with studies that found deer use declines with increasing housing density (Urbanek & Nielsen 2013). However, larger HRs were associated with increased use of highly developed areas, suggesting development may be more utilized as natural resources become limited. Finally, deer used developed landcovers more at night compared to daytime hours. This diel activity pattern supports global meta-analyses showing increased wildlife nocturnality in response to human activity (Gaynor *et al.* 2018) and provides evidence of anthropogenic-driven alteration of deer space use.

Our results indicate urban deer have an immediate response to landscape-dependent fragmentation and strongly avoid development at the spatial scale of 100m when establishing their HRs. In our study, deer avoided the urban environment and depended on natural habitats when establishing their HR but were more tolerant of urban features within the HR, using those resources according to their availability or, for some individuals, selecting them. Our findings on the spatial scale of second order selection to human impact may differ from other work that observed second order selection over a larger distance (Nagy-Reis *et al.* 2019) because SI’s urban landscape presents extreme spatial heterogeneity over short distances (Band *et al.* 2005), forcing deer to respond to the surrounding environment more imminently than in more natural environments.

We identified block level characteristics important for deer resource use that were associated with tick presence – suggesting residential attributes may increase or decrease the likelihood of tick introduction and survival in ecotones that directly interface with humans. This finding provides evidence to LIF influencing deer’s perception and use of the landscape as observed through their movement. Although our models showed deer overall preferred forested habitat, there was high variation in use of non-forested landcover types and stronger avoidance as development intensity of non-forested habitats increased. While residential block-1 was selected for by few individuals, 30% of models using fine thematic landcover resulted in a neutral response, indicating that some deer may not use residential landcover more or less than expected by chance and that there is not strong aversion of this habitat. In comparison, over 90% of models showed deer select against block-2 and only 3% of models resulted in a neutral response towards block-2. This contrast between the two residential landcover types indicates that deer prioritize more accessible concentrated resources in block-1.

Critically, our findings provide further evidence to support the need for a landscape lens of tick-borne disease (Diuk-Wasser *et al.* 2021). We observed individual movement responses that can directly impact the risk

landscape for urban tick-borne disease. Deer that maintained smaller HRs occupied more natural habitats where they may amplify vectors if habitat is suitable for *I. scapularis* survival (e.g. deciduous forest). The diversity and percentage of more developed landcover types within HRs increased with HR size. Individuals with larger HRs may functionally connect selected habitat types resulting in conduits of movement. The juxtaposition of these patterns of deer space use may jointly contribute to the amplification and dispersal of ticks, two components at the core of increasing tick-borne disease incidence and spread. As observed in models examining the role of landscape connectivity for deer on tick-borne disease risk (VanAcker *et al.* 2019; Tardy *et al.* 2021), higher functional connectivity for deer can enhance the spread of ticks between isolated habitat patches. Home ranges of male (30-1049 ha; average: 170 ha) and female (24-79 ha; average: 50 ha) deer far exceed the spatial extent of most forest patches sampled in studies that laid the foundation for the dilution effect theory (0.3 to 19 ha) (Allan *et al.* 2003; LoGiudice *et al.* 2008), indicating that patches where nymphal tick density and infection prevalence were estimated and treated independent from one another were likely functionally connected through deer (and potentially other host) movement. Thus, we recommend using the scale of the animal's space use to examine the spatial unit of influence that wildlife hosts have on tick-borne disease dynamics (Bolzoni *et al.* 2012). This study addresses this by leveraging tools and analytical approaches from movement and disease ecology to reconcile the hierarchical structure of resource selection with variation in spatial behaviors exhibited by individual animals, rarely attempted before in an urban setting where the outcome of habitat selection impacts zoonotic hazard. With increased attention on translating movement mechanisms to spatial epidemiological modeling (Manlove *et al.* 2022), we hope this work provides a foundation to formalize integrating movement and epidemiological datasets.

The individual based hierarchical approach employed in this study increased our ability to identify movement behaviors that would have otherwise been missed with a single-scale mean-population approach. Examining the response of deer to development across spatial scales provided insight into how urban deer differ from those in more natural landscapes in their response to human activity during second-order selection. By examining space use in a hierarchical manner, we gained a nuanced understanding of how deer both avoid and exploit anthropogenic development and resources in human-dominated environments, effectively shedding light on how ecological relationships emerge at the human-wildlife interface altering the state of zoonotic hazards. The individual-based modeling framework allowed us to see consistency in movement behaviors across individuals (ie. patterns across sexes) and important movement anomalies (ie. high variation in HR size and use of high intensity development). Finally, translating deer's observed movement behaviors to an area with unobserved space-use through simulation revealed how resource selection can determine an animal's use of the human interface, modulating transmission risk. We observed how simulations based on deer that selected highly forested, connected residential blocks resulted in high dispersal probability into the urban matrix than the simulation based on the individual which showed neutral selection to non-forested landcovers. Simulating future space use from individual movement models advances our understanding of how host-environment interactions through movement connects to the spatial spread or concentration of vectors and pathogens across landscapes and at human interfaces and improves the use of static risk-maps to display infectious disease risk.

Acknowledgements

We thank the New York City Department of Parks and Recreation and White Buffalo Inc. for making this study possible through data contribution. The authors would especially like to thank Pilar Fernandez and Nichar Gregory for sharing residential tick density data from Staten Island yards and the field assistants who helped in data collection. We also thank Ferdinando Urbano, Johannes Signer, Pallavi Kache, Andrea Corradini, Giole Passoni, and Nathan Ranc for help with data processing and methodological feedback.

Funding information

This publication was supported by the Cooperative Agreement Number U01CK000509-01 between the Centers for Disease Control and Prevention and Northeast Regional Center for Excellence in Vector Borne Diseases, and the National Science Foundation's Coupled Natural Human Systems 2/Dynamics of Integrated Socio-Environmental Systems (CNH2/DISES) program (Award #1924061). Its contents are solely

the responsibility of the authors and do not necessarily represent the official views of the Centers for Disease Control and Prevention, the Department of Health and Human Services or the National Science Foundation.

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Figures and Tables

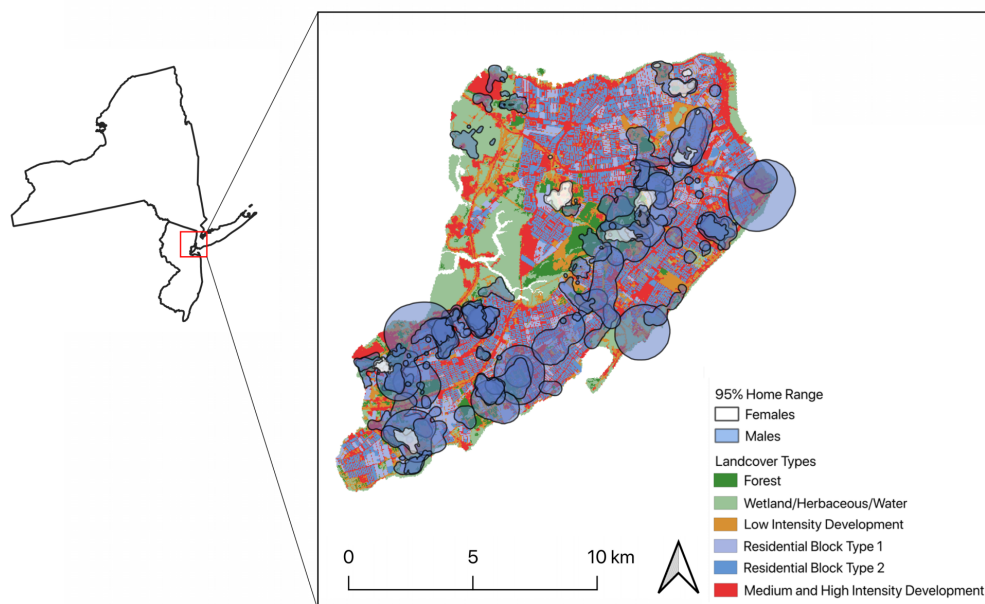


Figure 1: Fine thematic resolution landcover layer used for second and third order habitat selection inset within the New York and New Jersey state boundaries, USA. The reclassified landcover types are detailed in the legend and the 95% home range areas are shown in solid lines (blue: males and white: female).

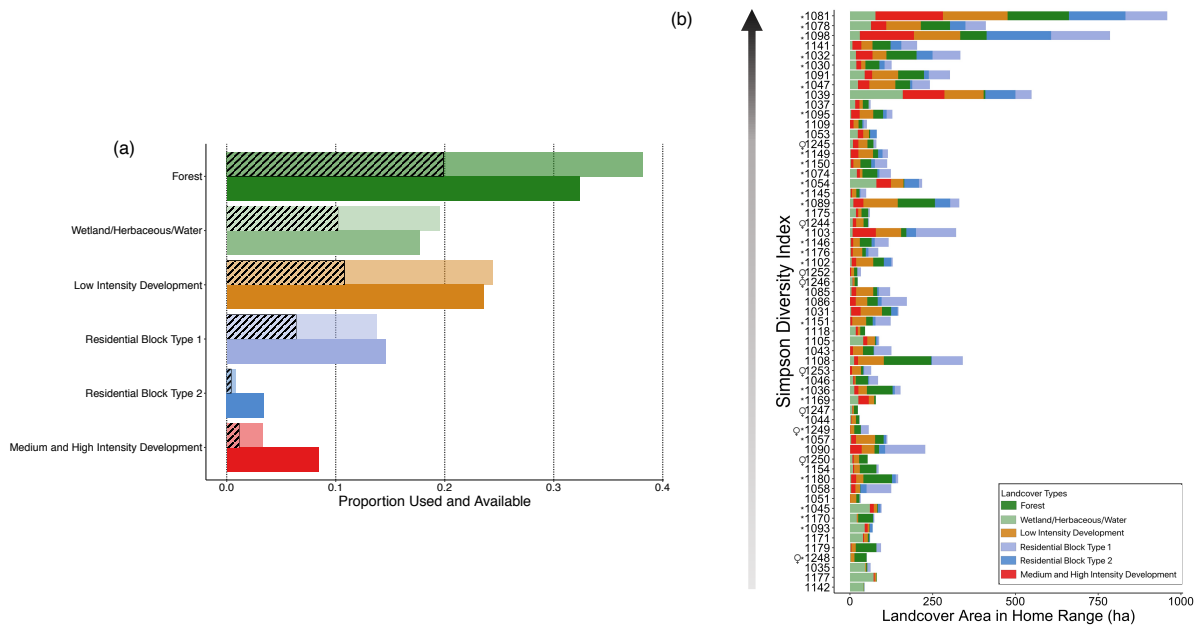


Figure 2: (a) The used and available habitats and time of day use of landcover types for deer population across sexes. The proportion of habitat types used are shown by the top bars with light coloring and the proportion of habitats available for use are shown by the bottom darker colored bars. The diagonal lines indicate daytime use for each respective landcover type whereas the solid color signifies nighttime use. (b) The area and diversity of landcover types within each deer home range. The deer IDs are ordered along the y-axis by increasing habitat diversity within their home range (top IDs have the highest Simpson's diversity index and bottom IDs have the lowest Simpson's diversity index). The asterisks indicate the 27 individuals that were included in the iSSA model using the fine thematic landcover layer and the ♀ symbol indicates female deer.

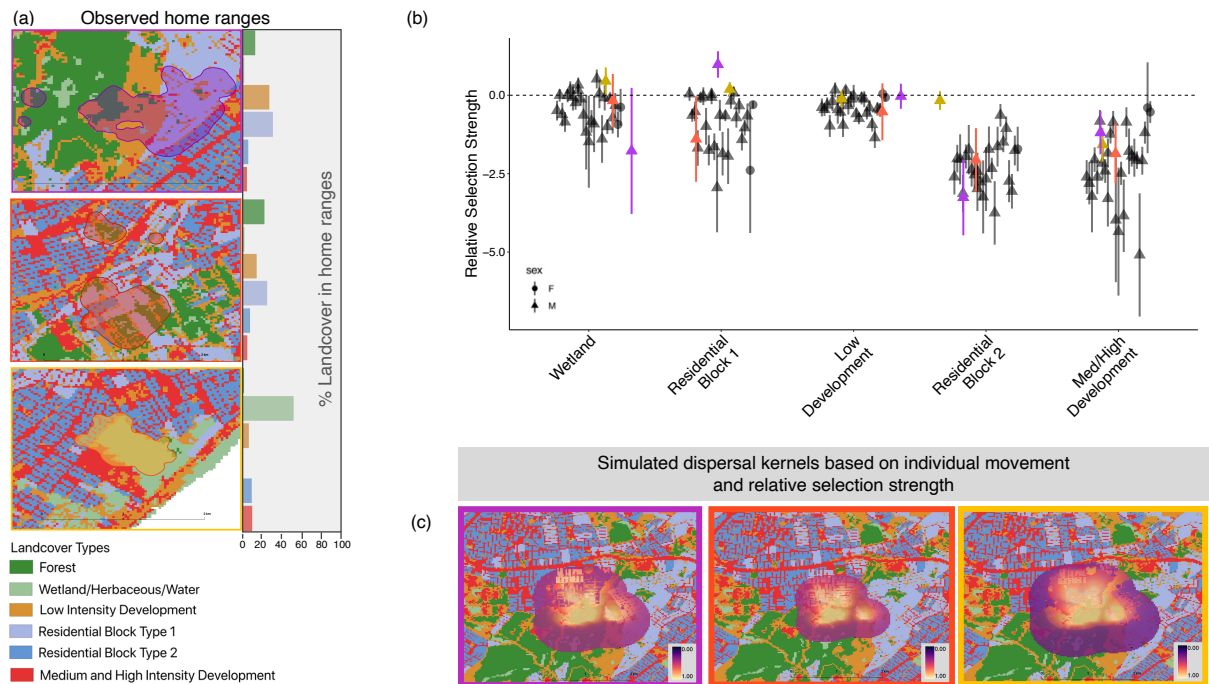


Figure 3: A showcase of the relationship between habitat selection and space use across individual deer and simulated dispersal probabilities. (a) Observed home ranges and the proportion of each landcover type within an individual's home range for IDs 1151 (top panel: purple polygon), 1150 (middle panel: red polygon), and 1093 (bottom panel: yellow polygon). The matched-color triangles highlight the same example individuals in the plot in (b) and the colored box outlines in (c). (b) Relative selection strength of male and female deer ($n = 27$) of fine thematic resolution landcover types during breeding seasons 2016 – 2021. The dashed line indicates a coefficient of 0. Points with confidence intervals above the dashed line signify positive selection in reference to forested landcover and points with intervals below the dashed line show negative selection in reference to forest. Deer sex is shown by symbol shape and vertical lines show 95% confidence intervals around coefficient estimates. (c) Simulated dispersal kernels informed by iSSA movement and habitat selection coefficient values where dark colors represent low probability of future dispersal and light colors indicate high probabilities of future dispersal across the landcover types indicated in the legend.

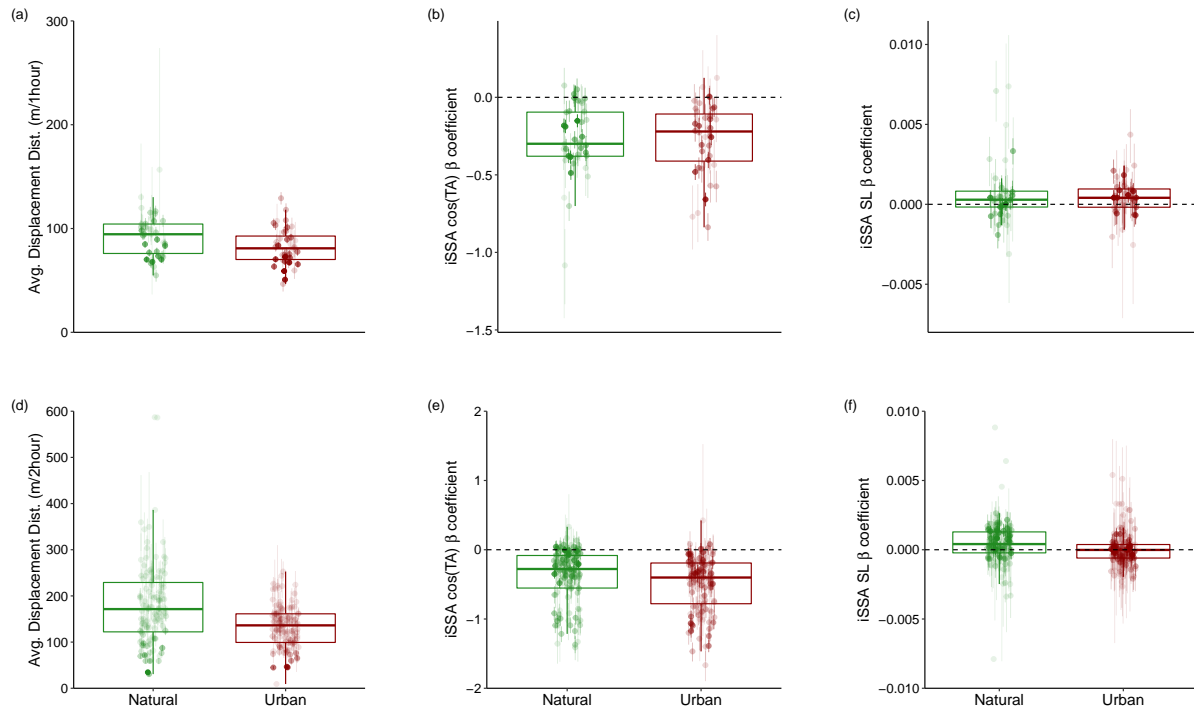


Figure 4: The estimated speed (average displacement distance), directionality (cosine (turning angle) β coefficient), and step length (step length β coefficient) for all female (top) and male deer (bottom) across all seasons in natural and urban landcover types. Parameter estimates were derived from model 4. Boxplots with 95% confidence intervals are shown with the bootstrapped point estimates from each individual model. The transparency of the points and 95% confidence interval lines display the inverse variance values for each coefficient estimate where darker points indicate more certain estimates with higher inverse variance values.

Model	Aim	Movement	Selection
Null	Movement only	$SL + \ln(SL) + \text{Cos}(TA)$	-
How likely are deer to select urban over forested habitat and does this vary with time of day?			
1	Movement + habitat selection	$SL + \ln(SL) + \text{Cos}(TA)$	LC(end)
2	Movement + temporal variability in habitat selection	$SL + \ln(SL) + \text{Cos}(TA)$	LC(end) : TOD
Is deer movement faster or more directional while in, or traveling to, urban or natural habitats? Does this vary with time of day?			
3	Movement differences with starting habitat + habitat selection	$SL + \ln(SL) + \text{Cos}(TA) + \text{LC}(\text{start}) : (SL + \ln(SL) + \text{Cos}(TA))$	LC(end)
4	Movement differences with habitat selection and time of day	$SL + \ln(SL) + \text{Cos}(TA)$	LC(end) : $(SL + \ln(SL) + \text{Cos}(TA) + \text{TOD})$

Table 1 . ISSA models were used to address two interacting processes, deer movement and habitat selection. Data from each individual deer were modeled separately for models 1 - 4. To model movement in each model we included step length (SL), the natural log of step length ($\ln(\text{SL})$), and the cosine of the turning angle between successive steps ($\text{Cos}(\text{TA})$). LC (start) and LC (end) describe the land cover type overlapping the start or end step and TOD signifies time of day (day/night). Colons indicate term interactions.

Female white-tailed deer				
Season	<i>n</i>	Model	Model Structure	Minimum AIC Tally
Pre-Breeding	9	1	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end})$	0
Breeding	17			1
Post-Breeding	14			0
Pre-Breeding	9	2	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end}) : \text{TOD}$	4
Breeding	17			7
Post-Breeding	14			7
Pre-Breeding	9	3	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{start}) : (\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA})) + \text{LC}(\text{end})$	4
Breeding	17			5
Post-Breeding	14			6
Pre-Breeding	9	4	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end}) : (\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{TOD})$	1
Breeding	17			4
Post-Breeding	14			1

Male white-tailed deer				
Season	<i>n</i>	Model	Model Structure	Minimum AIC Tally
Pre-Breeding	18	1	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end})$	2
Breeding	51			5
Post-Breeding	47			7
Pre-Breeding	18	2	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end}) : \text{TOD}$	5
Breeding	51			8
Post-Breeding	47			17
Pre-Breeding	18	3	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{start}) : (\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA})) + \text{LC}(\text{end})$	4
Breeding	51			4
Post-Breeding	47			5
Pre-Breeding	18	4	$\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{LC}(\text{end}) : (\text{SL} + \ln(\text{SL}) + \text{Cos}(\text{TA}) + \text{TOD})$	7
Breeding	51			34
Post-Breeding	47			18

Table 2. The strength of support for models assessing movement and selection by sex and season. Each individual model was bootstrapped ($n = 1000$), the model fit was summarized per deer, the number of deer with data overlapping each season is shown by *n*, and the minimum AIC tally indicates how many individuals showed that corresponding model as the best fit (lowest AIC).