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LETTER

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

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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 behaviour and resource utilization by white-tailed deer (*Odocoileus virginianus*) determines blacklegged tick (*Ixodes scapularis*) distribution, which depend on deer for dispersal in a highly fragmented New York City borough. Multi-scale hierarchical resource selection analysis and movement modelling provide insight into how deer's movements contribute to the risk landscape for human exposure to the Lyme disease vector–*I. scapularis*. We find deer select highly vegetated and accessible residential properties which support blacklegged tick survival. We conclude the distribution of tick-borne disease risk results from the individual resource selection by deer across spatial scales in response to habitat fragmentation and anthropogenic disturbances.

KEYWORDS

habitat selection, host movement, integrated step selection analysis, *Ixodes scapularis*, Lyme disease, *Odocoileus virginianus*, spatial disease dynamics, urban tick-borne disease, urbanization, vector amplification

INTRODUCTION

Anthropogenic environmental changes drive the increasing frequency of zoonotic disease emergence—diseases transmitted from wildlife to human populations (Allen et al., 2017; Baker et al., 2022; Carlson et al., 2022; 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

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zoonoses because opportunistic species adapted to anthropic landscapes are often competent zoonotic hosts, and spillover is facilitated by close contact at interfaces between humans, wildlife and/or vectors (Alirol et al., 2011; Hassell et al., 2017). Wildlife host movement influences contact rates between vectors, pathogens and other hosts to shape 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 (Berger-Tal & Saltz, 2019; Magle et al., 2014). 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). Fertilized vegetation, gardens or waste by-products provide stable, often predictable, resource subsides (Becker et al., 2015; Langley et al., 2021) which cause LIF by influencing contact patterns and wildlife host movement (Ossi et al., 2020; Ranc et al., 2020) 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, a bacterial infection caused by *Borrelia burgdorferi* sensu stricto, affects 400,000 people annually (Kugeler et al., 2021; Schwartz et al., 2021). Historically, Lyme disease was associated with the incursion of suburban and exurban development into rural areas (Barbour & Fish, 1993). More recently, ticks have expanded their geographic range with climate change (Ogden et al., 2021; Sonenshine, 2018) and by occupying diverse and novel landscapes, such as cities (VanAcker et al., 2019). The urban expansion of Lyme disease occurs through two pathways that increase human risk of exposure to infected ticks: (1) vegetation increases through cities undergoing de-urbanization linked with population decline and land abandonment (Eskew & Olival, 2018; Richards & Belcher, 2019), or through urban greening strategies (Halsey et al., 2022; Yang et al., 2014); and (2) expanding urban matrix into surrounding natural habitats (Güneralp et al., 2020; van Vliet, 2019). Both pathways increase tick habitat and 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 United States, the establishment and persistence of the Lyme disease vector, *Ixodes scapularis* ticks, is supported by white-tailed deer (*Odocoileus virginianus*, hereafter deer), the primary reproductive stage host for adult *I. scapularis* (Barbour & Fish, 1993; Ostfeld et al., 2018; Rand et al., 2004). While deer amplify *Ixodes* spp. (Cagnacci et al., 2012; Carpi et al., 2008), they 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 Lyme disease over large geographic areas typically utilize broad-scale climatic and landcover variables (Diuk-Wasser et al., 2006; Estrada-Pena, 1998; Soucy et al., 2018). This approach, however, lacks power to predict the zoonotic hazard at fine spatial scales because it ignores local *B. burgdorferi* transmission 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 the movement and resource selection by their wildlife hosts (Ezenwa et al., 2016). Thus, the probability of tick population establishment is affected by the hosts' scale of response to the landscape. 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 behaviour such as foraging close to households (Grund et al., 2002; Kilpatrick et al., 2000; Swihart et al., 1995) and resting in forest patches. If deer habitat selection encompasses anthropogenic resources, residential areas can 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.

This study examines fine scale deer movement in an urban, fragmented borough of New York City (NYC) to determine how deer movement is linked to local distributions of *I. scapularis* ticks. We employ a multi-scale hierarchical resource selection framework to (i) examine deer's scale of response to anthropogenic features when establishing their home range (HR, i.e. responses to LDF in second-order selection), (ii) determine fine scale spatiotemporal effects of the urban landscape on within-HR habitat selection and avoidance (i.e. responses to LIF in third-order selection) and (iii) assess the spatial congruence between deer habitat selection and *I. scapularis* presence. We expect high-intensity development will restrict deer HR 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 HR and to avoid highly anthropic areas during periods of heightened human activity. We further hypothesize that vegetated neighbourhoods nested within areas connected to natural habitats will attract deer to foraging resources and support the microclimate for tick survival, leading to higher tick occupancy compared to neighbourhoods 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 in tick-borne diseases in urban areas globally (Hamer et al., 2012; Hansford et al., 2017, 2021; Heylen et al., 2019; Rizzoli et al., 2014; Simmons et al., 2020; Sormunen et al., 2020; VanAcker et al., 2019), 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 directly links deer movement behaviour to tick distribution across a highly urban landscape. We conclude that resource selection at different spatial scales enables urban deer to navigate fragmented habitats and that sex and individual-based responses to human activity characterize differences in tick distribution capacity.

MATERIALS AND METHODS

Study area

Staten Island, NYC, USA, has a population of 474,893 with a density of 3132 people/km^2 (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, Supporting Information). Increasing rates of Lyme disease cases on Staten Island from 4 to 25 per 100,000 between 2000 and 2016 (New York City Department of Health and Mental Hygiene, 2020) motivated this research. Prior work shows metapopulation dynamics structure tick population persistence in Staten Island parks where parks' centrality—its level of connectivity for deer—predicts nymphal tick density and infection prevalence (VanAcker et al., 2019) and households' proximity to parks is a risk factor for *I. scapularis* presence in yards (Gregory et al., 2022). Thus, Staten Island offers an ideal landscape to examine deer movement responses to LDF and LIF and their consequences for tick-borne disease.

Animal collaring and tick collection

We captured deer during the 2016–2019 winters; 177 yearling and adult males were ear-tagged and fitted with GPS collars (G2110E Iridium, ATS; GPS/GSM ES400, CTT) following surgical vasectomies to sterilize male deer for population reduction (Supporting Information: reduced 2053 to 1616 deer throughout the study period).

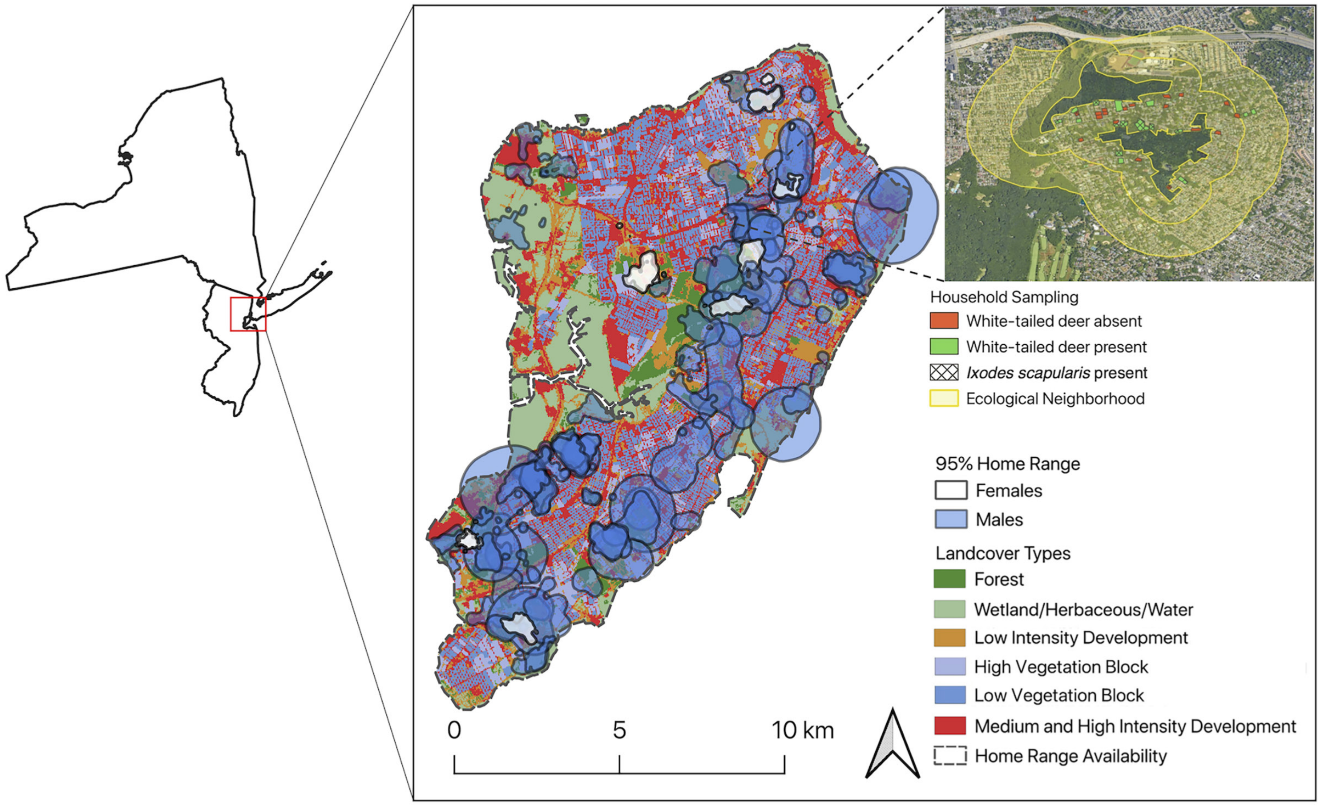

FIGURE 1 Staten Island, NYC: Fine thematic resolution landcover layer used for second- and third-order habitat selection inset within the New York and New Jersey state boundaries, USA. The reclassified landcover types are detailed in the legend and the 95% home range areas are shown in solid lines (blue: males and white: females). The household sampling design is shown in the upper right box where an ecological neighbourhood is indicated with a 500 m buffer surrounding the park where households were primarily sampled. Household parcels are shown in green if deer intersected the property, red if deer did not intersect the property and hashed if *I. scapularis* were present in the household yard.

Ten female deer were fitted with GPS/GSM (ES400, CTT) collars during the 2019 winter.

Ticks were sampled from yards of park-adjacent residences from April to July during 2018, 2019 and 2021 for a concurrent study (Gregory et al., 2022) that used random cluster sampling within ecological neighbourhoods that encompassed a core park (Figure 1, Supporting Information). All ticks encountered at 10 m intervals were quantified, identified to species and preserved in 70% ethanol.

GPS data standardization and segmentation

All location data were screened for outliers using the R (R Team, 2022, v4.0.5) package *ctmm* (Calabrese et al., 2016) and filtered through multiple inclusion criteria, resulting in a sample size of 50 male and nine female deer (Supporting Information). We used the R package *AdeHabitatLT* (Calenge, 2006) to regularize male trajectory segments to a 2-h fix schedule and female trajectories to a 1-h fix schedule, and rediscretized data to constant time lags. The fix frequencies differed by sex due to study design variation during the data collection period. 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; Schauber et al., 2015). The deer location data spanned from breeding 2016 through post-breeding 2021 (excluding the pre-breeding 2017 season, Figure S2).

Landcover processing for *I. scapularis* exposure risk

We reclassified the NLCD 2016 (U.S. Geological Survey, 2019) raster layer to four landcover types representing important habitat for deer or for human exposure to *I. scapularis*: water/wetland/herbaceous (wetland-herb), open and low-intensity development (low-dev), medium and high-intensity development (med-high-dev), or forested landcover, and merged this with two constructed residential landcover types. We classified residential blocks by their attractiveness to deer and suitability for tick survival to explicitly investigate how deer habitat selection influences human encounters with *I. scapularis*. We estimated total yard area, canopy height, landcover type proportions within blocks and landscape connectivity for deer (VanAcker et al., 2019) within 100 m surrounding each block. We used K-means clustering to define block types (Figure S3). The first block type was characterized by high vegetation, low impervious cover, high connectivity for deer and large yard areas (high-veg-blocks). The second type described blocks with low vegetation, high impervious cover, low connectivity for deer and small yards (low-veg-blocks). We merged block assignments with the reclassified NLCD landcover layer to use in second- and third-order selection models (Figure 1). 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 reclassified into either 'natural' (forest and wetland-herb) or 'urban' (low-dev, med-high-dev, high-veg-block and low-veg-block).

Landcover analysis to assess deer visitation and *I. scapularis* presence

We validated the association between block types and tick habitat suitability using the tick data from park adjacent yards (Gregory et al., 2022, Supporting Information). Of 451 yards surveyed, 408 fell within classified blocks. Block typology successfully identified blocks that could support *I. scapularis* survival, as 94% of yards where *I. scapularis* were collected were from high-veg-blocks ($n = 53$ households). The household sampling design shows select households surrounding a park where deer visits occurred and *I. scapularis* were present in yards.

To assess deer visitation to yards, we examined the intersection between deer GPS points and household tax lot polygons (New York City Department of City Planning, 2020) where ticks were sampled across years using the R package *sf* (Pebesma, 2018). We used the households visited by deer and the households' block type in binomial Generalized Linear Models (GLMs) to predict the presence of *I. scapularis* ticks in residential yards and compared model fit using the Akaike Information Criterion (AIC) score (Burnham & Anderson, 2002).

Home range estimation and analysis

We pooled location data across seasons to estimate the 95% (Figure 1) and 50% HR and compared HR size for females when using a 1-h fix schedule and a 2-h fix schedule (Supporting Information). We estimated the proportion of landcover types within the 95% HRs using the fine thematic resolution layer and estimated HR habitat richness and evenness with Simpson's alpha-diversity index. We ran GLMs to assess whether sex or the percent urban landcover within-HRs predicted the log HR size.

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 Staten Island available for deer and drew nine random locations anywhere on Staten Island for each used location. We then estimated the area of med-high-dev within buffers (varying from 100 to 800 m at 100 m increments, thus applying a multi-grain assessment (McGarigal et al., 2016)) surrounding each used and available location. We applied binomial GLMs to assess the dependence of used/available locations on the area of med-high-dev. We selected the model with the minimum AIC score 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-HR resource selection while accounting for individual movement. To prepare for iSSA, we estimated step lengths and turning angles between successive steps (where 'step' defines a straight line connecting consecutive locations) to fit tentative gamma and von Mises distributions, respectively, using the *amt* (Signer et al., 2019) R package. From these distributions, 10 random steps were generated for each observed step (Supporting Information). Habitat attributes from the two landcover layers were extracted at the beginning and end of observed and random steps. We fit four iSSA models to data from each deer using conditional logistic regression stratified by start step ID in *amt*. Each model included three covariates to account for movement speed and directionality: step length (SL), natural log transformed step length (ln(SL)) and the cosine of the turning angle (Cos(TA)).

We modelled movement behaviour and habitat selection for all deer using broad thematic resolution (two levels) and modelled a subset of 27 deer (female $n=2$, male $n=25$) whose location data spanned all landcover types using the fine thematic resolution layer (six levels) during the deer breeding/adult *I. scapularis* feeding seasons (2016–2020; Table 1, model 1). We expected deer's selection strength for features within their HR to vary temporally, thus we included time-of-day as an interactive term with habitat selection (model 2). Movement differences driven by the starting habitat were assessed through an interaction between the starting step landcover 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 and 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 to update the tentative gamma and von Mises distributions and estimated habitat selection-free mean dispersal distance per step (speed) and directionality for individual deer over natural and urban landcovers. These were summarized using boxplots to show deer's average and individual speed and directional persistence by sex, landcover and season. We assessed speed differences by landcover and season through fitting Gaussian GLMs to the bootstrapped mean speed beta coefficients from individual iSSA models. We included season and landcover (urban/natural) as fixed and interactive predictors and used the inverse variance of the response coefficient as a model weight to reduce the contribution of less certain estimates (Beardsworth et al., 2021).

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 habitat selection coefficients estimated from fitted iSSA model 4 for three

TABLE 1 ISSA models were used to address two interacting processes, deer movement and habitat selection.

Model	Aim	Movement	Selection
Null	Movement only	SL + ln(SL) + 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) + Cos(TA)	LC(end)
2	Movement + temporal variability in habitat selection	SL + ln(SL) + Cos(TA)	LC(end): TOD
Is deer movement faster or more directional while in, or travelling to, urban or natural habitats? Does this vary with time of day?			
3	Movement differences with starting habitat + habitat selection	SL + ln(SL) + Cos(TA) + LC (start): (SL + ln(SL) + Cos(TA))	LC(end)
4	Movement differences with habitat selection and time of day	SL + ln(SL) + Cos(TA)	LC(end): (SL + ln(SL) + Cos(TA) + TOD)

Note: Data from each individual deer were modelled separately for models 1–4. To model the movement process in each model we included step length (SL), the natural log of step length (ln(SL)) and the cosine of the turning angle between successive steps (Cos(TA)). LC (start) and LC (end) describe the landcover type overlapping the beginning or end of observed and random steps and TOD signifies time-of-day (day/night). Colons indicate term interactions.

TABLE 2 The strength of support for models assessing movement and selection by sex and season.

Season	*n*	Model	Model structure	Minimum AIC tally
Female white-tailed deer				
Pre-Breeding	9	1	SL+ln(SL)+Cos(TA)+LC(end)	0
Breeding	17			1
Post-Breeding	14			0
Pre-Breeding	9	2	SL+ln(SL)+Cos(TA)+LC(end): TOD	4
Breeding	17			7
Post-Breeding	14			7
Pre-Breeding	9	3	SL+ln(SL)+Cos(TA)+LC (start): (SL+ln(SL)+Cos(TA))+LC(end)	4
Breeding	17			5
Post-Breeding	14			6
Pre-Breeding	9	4	SL+ln(SL)+Cos(TA)+LC(end): (SL+ln(SL)+Cos(TA)+TOD)	1
Breeding	17			4
Post-Breeding	14			1
Male white-tailed deer				
Pre-Breeding	18	1	SL+ln(SL)+Cos(TA)+LC(end)	2
Breeding	51			5
Post-Breeding	47			7
Pre-Breeding	18	2	SL+ln(SL)+Cos(TA)+LC(end): TOD	5
Breeding	51			8
Post-Breeding	47			17
Pre-Breeding	18	3	SL+ln(SL)+Cos(TA)+LC (start): (SL+ln(SL)+Cos(TA))+LC(end)	4
Breeding	51			4
Post-Breeding	47			5
Pre-Breeding	18	4	SL+ln(SL)+Cos(TA)+LC(end): (SL+ln(SL)+Cos(TA)+TOD)	7
Breeding	51			34
Post-Breeding	47			18

Note: 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). One male deer had over 95% of its observed steps in high-veg-blocks, this animal was removed from models because the extreme habitat specialization did not support convergence.

deer that varied in their HR habitat diversity and selection strength for fine resolution landcover types using *amt* (Signer et al., 2017). We utilized the same initialization points across deer for the simulations in an area of Staten Island that exemplifies the juxtaposition of habitat types in residential areas, but where no individuals were observed occupying (Supporting Information). For a glossary box defining abbreviated terms, please refer to the supporting information (Table S1).

RESULTS

Residential yard tick surveys and deer visitation

A total of 451 unique yards were surveyed for ticks one-three times totalling 529 sampling events; *I. scapularis* ticks were present in 14% of yards surveyed ($n=65$) over the three-year period. Deer locations were within 72/451 tick-surveyed yards from 1 to 43 times per house by 25/59 deer. We found 26% of yard revisits took place under 10 h, 22% within 72 h, 28% within 2 weeks, and 23% between 2 weeks and 10 months. We examined whether deer visits or households' block type predicts *I. scapularis* presence in residential yards and found the best fit model included deer presence (ß=1.0188, $p=0.002$) and block type (ß=−1.4076, $p=0.02$), where low-veg-blocks had a negative effect on *I. scapularis* presence (Table S2).

Home range estimation and analysis

An equality of proportions test showed no evidence that deer utilized wetland-herb, forest and low-dev more or less than expected based on the amount of each habitat available (Table S3a). In contrast, deer used med-high-dev and low-veg-blocks in significantly lower proportions to the habitat available ($p=0.03$ and $p=0.02$, respectively, Figure 2a; Table S3a), while there was weak evidence that deer used high-veg-blocks more than expected ($p=0.09$, Table S3a). Deer used urban (low-dev, high-veg-block, med-high-dev and low-veg-block) landcovers

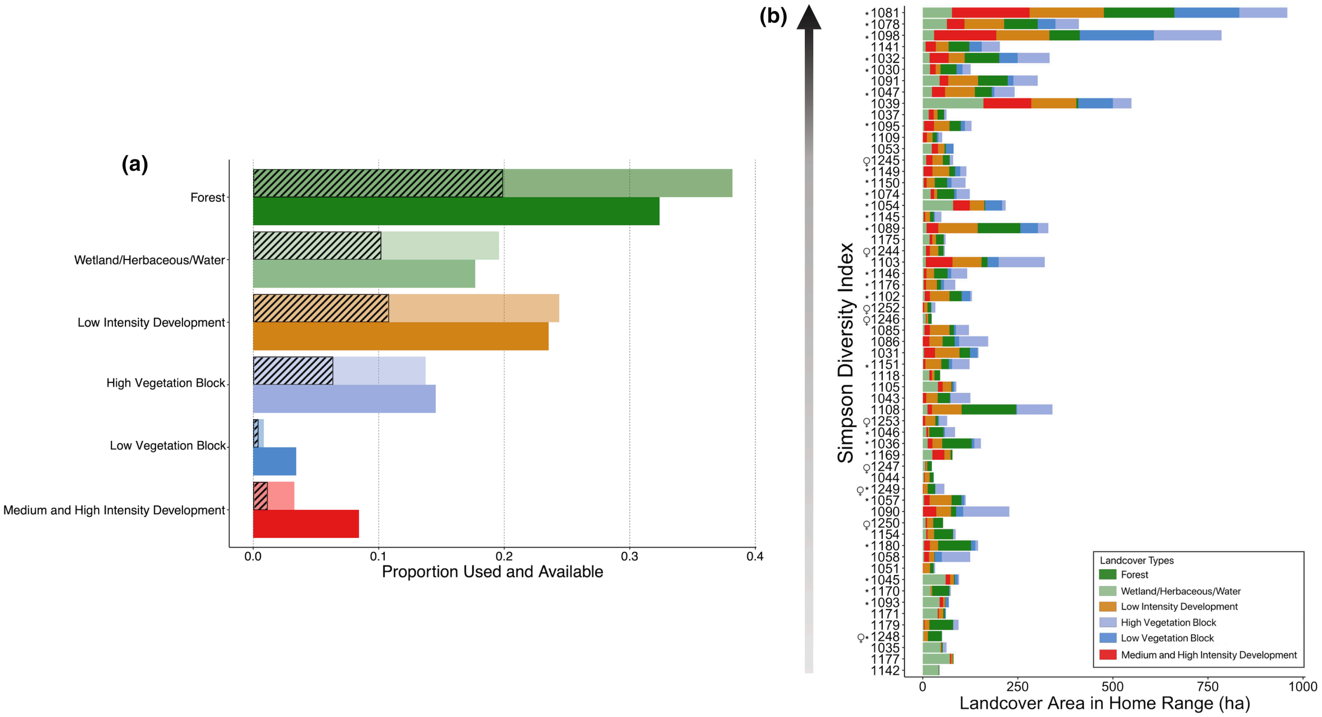

FIGURE 2 (a) The used and available habitats and time-of-day use of landcover types for deer population across sexes. The proportion of habitat types used are shown by the top bars with light colouring and the proportion of habitats available for use are shown by the bottom darker coloured bars. The diagonal lines indicate daytime use for each respective landcover type whereas the solid colour signifies night-time 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.

more frequently at night (>58% of night-time steps) and occupied natural landcovers (forest and wetland-herb) more frequently during the day (>53% of daytime steps, Figure 2a), although there was no statistical difference in these proportions (Table S3b). The 95% male HRs ranged from 30 to 1049 hectares (ha) with a 170 ha average. Female HRs varied from 24 to 79 ha with a 50 ha average (Table S4). There was weak evidence that deer sex affects HR size (male ß: 120.63, $p = 0.07$), however the deer tracked were heavily male biased. This relationship remained when female fix frequencies were standardized to 2-h fix schedule to match males (male ß: 118.47, $p = 0.07$). As HR size increased, the percent natural landcover decreased while the percent urban landcover within the HR increased alongside habitat diversity (Figure 2b). A higher percent urban landcover within the HR was associated with larger HR size (ß: 0.01, $p = 0.005$, Figures S5 and S6). Male HRs on average were comprised of 33% natural and 66% urban landcover whereas female HRs averaged 43% natural and 56% urban landcover.

Second-order selection

For second-order selection of HRs, all male and female deer responded strongest to med-high-development at fine spatial scales of 100 m radius ($n = 59$), indicated by the low AIC score for this spatial scale during model comparison (Figure S7). The relative strength of selection varied within the population, although all individuals negatively selected for med-high-development (Table S5 and Figure S8).

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). Habitat selection significantly improved model fit for most individuals across seasons, except for 17 unique deer represented in 23 deer-seasons for which the movement only models were equally parsimonious to model 1 which incorporated habitat selection.

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; Table S6) indicating speed and directionality differ 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, Table S6). During the pre-breeding seasons, the number of female deer showing model 2 and 3 as the best fit were equal. 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.

When fine thematic resolution habitat was used for breeding season models (2016–2020; *n*=27 individuals), most deer significantly avoided residential low-veg-block and med-high-dev relative to forested habitat, but with high variation in selection strength. Deer showed stronger avoidance of increasingly developed landcover (Figure 3b). Relative to forest, wetland-herb was significantly selected in 10.34% of models, selected against in 41.38% of models and deer showed a neutral response in 48.42% of models. Low-dev was selected in 3.45% of models, selected against in 55.17% of models and 41.38% of models showed a neutral response relative to forest. Residential high-veg-block was selected in 3.57% of models, selected against in 64.29% of models and 32.14% of models showed a neutral response. Importantly, residential low-veg-block was never selected relative to forest, was selected against in 96.30% of models and 3.70% of models showed a neutral response. Lastly, med-high-dev was selected against in 96.55% of models relative to forest and 3.45% of deer showed a neutral response.

The range of estimated selection-free speeds through natural landcover was 30–541 m/2 h with an average of 181 m/2 h for males and 54–142 m/1 h with an average of 92 m/1 h for females, while in urban landcover male speeds ranged from 44 to 253 m/2 h with an average of 133 m/2 h and 46–129 m/1 h with an average of 82 m/1 h for females. Female speed depended on landcover and season with a negative effect of urban landcover (ß: −7.4, *p*=0.04, Figure 4) and a positive effect of the post-breeding season on speed in reference to the breeding season (ß: 9.4, *p*=0.03) while pre-breeding season speed was not significantly different (Figure S9). Male deer speed depended on season, with post-breeding (ß: 57.74,

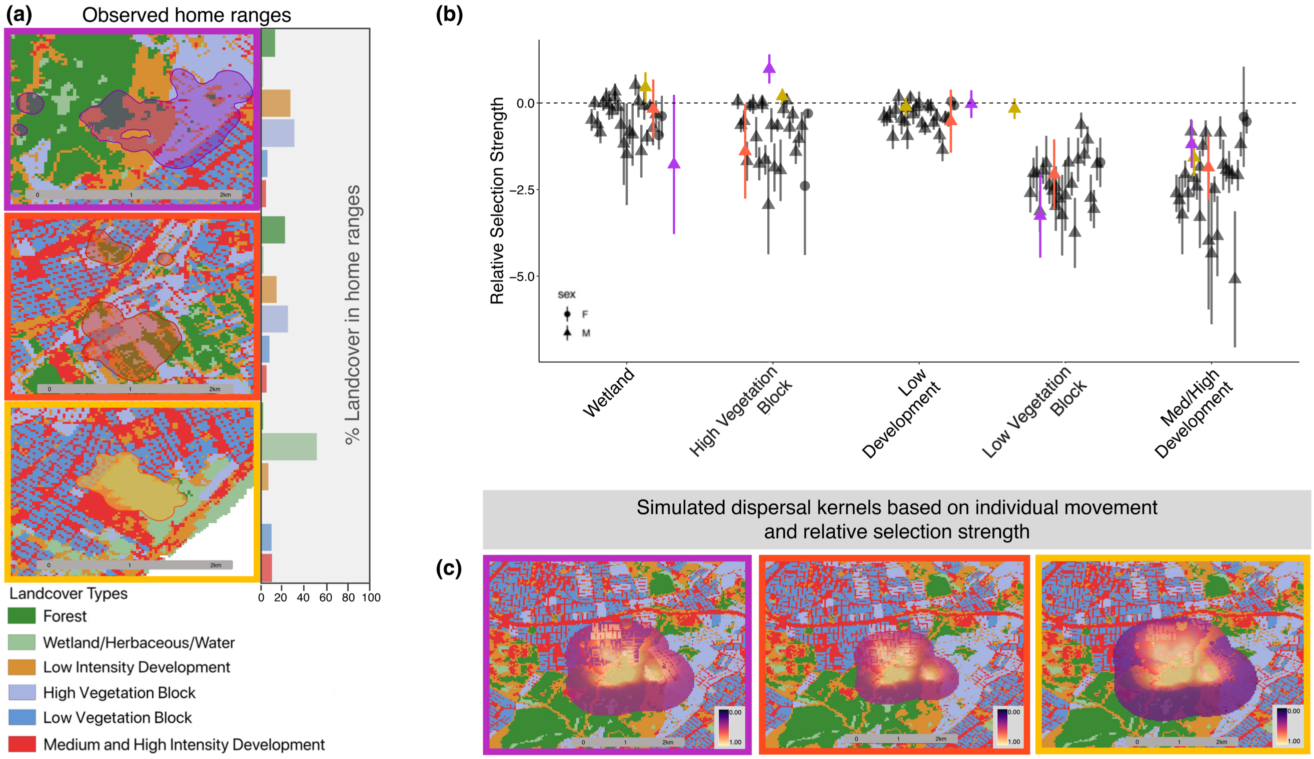

FIGURE 3 A showcase of the relationship between habitat selection and space use across individual deer and simulated dispersal probabilities. (a) Observed home ranges and the proportion of each landcover type within an individual's home range for IDs 1151 (top panel: purple polygon), 1150 (middle panel: red polygon) and 1093 (bottom panel: yellow polygon). The matched-colour triangles highlight the same example individuals in the plot in (b) and the coloured 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 colours represent low probability of future dispersal and light colours indicate high probabilities of future dispersal across the landcover types indicated in the legend.

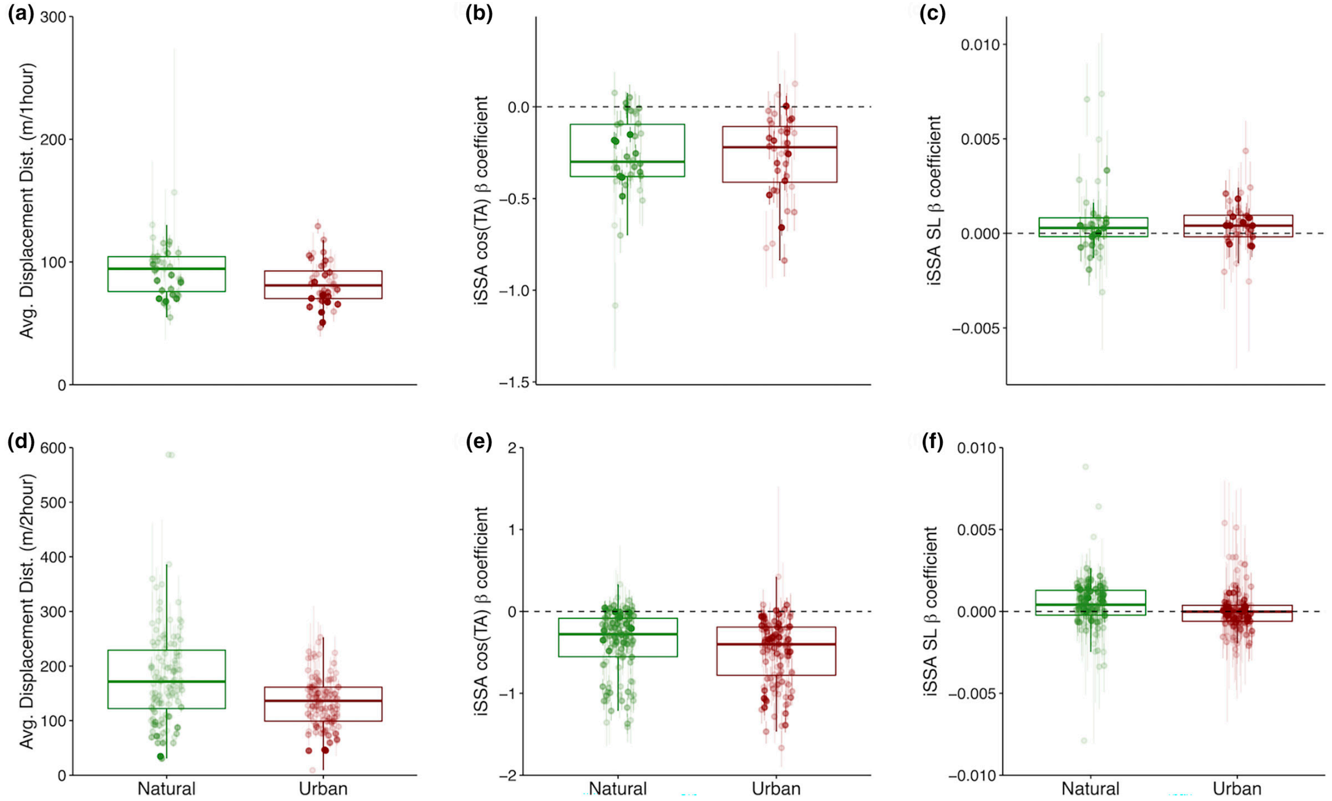

FIGURE 4 Calculated speed (average displacement distance), directionality (cosine (turning angle) β coefficient) and step length (step length β coefficient) for all female (top) and male deer (bottom) across all seasons in natural and urban landcover types. Parameter estimates were derived from model 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.

$p \leq 0.003$) and pre-breeding (ß: 67.67, $p \leq 0.001$) movements being significantly slower than breeding season ones (Figure S9). Male speed did not statistically differ by landcover ($p = 0.31$), although the variable was included in the model with the lowest AIC.

The simulations based on movement parameters from deer 1151 with the largest proportion of residential high-veg-block and low-dev in its HR (Figure 3a top) and the highest relative selection strength for high-veg-block (Figure 3b), showed high dispersal probability over high-veg-block and low-dev and low dispersal probability over low-veg-block (Figure 3c left). Deer 1150's HR was mostly comprised of high-veg-block and forest (Figure 3a middle) and its selection strength for non-forested landcover types was low or neutral compared to forest (Figure 3b). The highest dispersal probability for deer 1150 is centred at forested landcover and high-veg-block (Figure 3c middle). Lastly, deer 1093 had high wetland-herb landcover and the highest proportion of low-veg-block in its HR (Figure 3a bottom) and showed a neutral response and high dispersal tendency over low-veg-block (Figure 3b,c 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 step length and turning angle distributions conditioned by landcover type.

DISCUSSION

Host movement is a missing component in predicting vector-borne disease emergence, spread and transmission (Dougherty et al., 2018; Hartemink et al., 2015), except in select studies described with theoretical mathematical models (Hartfield et al., 2011; Sumner et al., 2017; Tardy et al., 2021). Furthermore, individual movement is often not accounted for when modelling the transmission process (Fofana & Hurford, 2017). Our results demonstrate that the resource selection and movement behaviours of individual deer are modified by sex, tendency to utilize habitat at the human interface and the animal's location in the urban matrix which cascades to influence vector dispersal. These findings suggest integrating individual-scale behavioural responses to the environment is essential to understand and assess hosts' distribution of ticks and tick-borne pathogens into residential areas.

We identified residential block characteristics important for deer resource use and tick survival that were associated with tick presence—suggesting block-scale attributes like vegetation cover and height, broader landscape connectivity for the host and yard area may modulate 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 response to anthropogenic land-uses. Highly vegetated neighbourhood blocks and deer presence in yards determined *I. scapularis* presence when compared to more impervious blocks or those not visited by deer. This finding links neighbourhood characteristics that drive deer habitat selection of human interfaces with tick dispersal to peridomestic settings, where the likelihood of humans encountering ticks is high.

We identified predictable responses in deer use of specific landcover classes at the individual scale, highlighting the potential to understand deer responses under different urban development scenarios. Deer use of forest, 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 which found deer use declines with increasing housing density (Urbanek & Nielsen, 2013). However, larger HRs were associated with increased use of highly developed areas, suggesting developed landcover may be more utilized as natural resources become limited (Morellet et al., 2013). Lastly, similar to past work we detected a small signal of deer using developed landcovers more at night compared to daytime hours (Roden-Reynolds et al., 2022). If this pattern holds true beyond this study, this diel activity pattern supports global meta-analyses showing increased wildlife nocturnality in response to human activity (Gaynor et al., 2018, see Bonnot et al., 2020 for deer specific analysis) and provides evidence of anthropogenic-driven alteration of deer space use (Salvatori et al., 2022).

Second-order selection results show urban deer respond to LDF over short distances and strongly avoid med-high-development at the spatial scale of 100 m when establishing their HRs. Our findings on the spatial scale of second-order selection to human impact differ from other work which observed second-order selection over a larger distance (Nagy-Reis et al., 2019). This may be because Staten Island'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.

Third-order selection models showed deer overall preferred forested habitat, although there was high variation in use of non-forested landcover types and stronger avoidance as development intensity of non-forested habitats increased (a dose–response relationship). While residential high-veg-blocks were selected for by few individuals, 30% of models using fine thematic landcover resulted in a neutral response, indicating there is not strong aversion of this habitat. In comparison, over 90% of models showed deer select against low-veg-blocks with 3% of models resulted in a neutral response. This contrast between the two residential landcover types indicates that deer prioritize more accessible concentrated resources in high-veg-blocks. While deer avoided the urban class when establishing their HR during second-order selection, they were more tolerant of urban features within the HR through third-order selection, using those resources according to their availability or, for some individuals, selecting them.

Seasonal movement patterns exhibited by deer may differentially affect the tick life stages that are dispersed because the burden of *I. scapularis*' life stages on deer varies with tick phenology. Male deer moved slowest during the pre-breeding season and females moved slowest during the breeding season suggesting male movements could drive the distribution of feeding nymphs, while females could propagate feeding adult ticks. Male deer had larger HRs and selected urban landcover more frequently than females, that instead maintained smaller HRs which encompassed more equal proportions of natural and urban landcover. This suggests females may maintain 'source' tick populations in urban green spaces through providing bloodmeals and short-distance dispersal opportunities while male deer disproportionately distribute ticks across landcover types to 'sink' habitats.

Critically, our findings provide further evidence to support the need for a landscape lens for tick-borne disease (Diuk-Wasser et al., 2021). 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. Thus, individuals with larger HRs may functionally connect selected habitat types resulting in conduits of movement and vector dispersal. The juxtaposition of these 'small-natural' and 'large-mixed landcover' patterns of deer space use can jointly contribute to the amplification and dispersal of ticks, both drivers of increasing tick-borne pathogen persistence and spread. As observed in models examining the role of landscape connectivity for deer on tick-borne disease risk (Tardy et al., 2021; VanAcker et al., 2019), higher functional connectivity for deer can enhance the spread of ticks between isolated habitat patches. HRs 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 (0.3–19 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 hosts) movement. Thus, we recommend using the scale of the animal's space use as 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 behaviours 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 modelling (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 behaviours 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 modelling framework allowed us to see consistency in movement behaviours across individuals (i.e. patterns across sexes) and important movement anomalies (i.e. high variation in HR size and use of high-intensity development). Finally, translating deer's observed movement behaviours to an area with unobserved space use through simulation revealed how second- and third-order resource selection can determine an animal's use of the human interface, modulating zoonotic risk. We observed how simulations based on parameter values estimated from an individual that selected highly vegetated, connected residential blocks resulted in high dispersal probability into the urban matrix compared to simulations based on those from an individual which showed neutral selection to non-forested landcovers and less contrast in their dispersal probability over heterogenous landcover types. 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 and can significantly improve spatial risk predictions over currently used static risk maps of infectious disease risk.

AUTHOR CONTRIBUTIONS

VLD, AJD, SGA, RS and KLT collected and shared data. MCV collected and cleaned data. MCV and MDW, with support from FC, designed the study. MCV designed the analysis, performed modelling and analysed output, with support from FC and MDW. MCV wrote the first draft of the manuscript and MDW and FC contributed substantially to revisions. All authors provided final manuscript review and revision.

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DATA AVAILABILITY STATEMENT

The data used in the current analysis is deposited to Dryad and is publicly available, excluding human subject data. The data DOI is included at the end of the article: https://doi.org/10.5061/dryad.t76hdr85p

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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