RESEARCH ARTICLE



Individuality, diel time, and landscape context shape space-use of an elusive carnivore in a risky environment

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Abstract

Context Individual animal's perception of risk can alter how it navigates a landscape altered by anthropogenic and natural disturbances. As perception depends on experience, we should expect habitat selection to be context dependent and individualistic. *Objectives* We hypothesized that: (i) fine-scale habitat selection of fisher (*Pekania pennanti*) in a human dominated landscape is driven by multiple interacting spatio-temporal factors; and (ii) an individual's response to these factors depend on their exposure to anthropogenic disturbance within their home range (i.e., functional response).

Methods We used fine-scale GPS location data of fisher in step-selection functions to make inference on

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Rhode Island Department of Environmental Management, Fish and Wildlife Division, West Kingston, RI, USA the effects of human development, habitat loss, and road risk on fisher habitat selection.

Results We found fisher habitat selection is individualistic, spatio-temporally dependent and a function of their exposure to anthropogenic disturbance in their home range. Fisher selected areas of lower road risk more frequently relative to availability, particularly during daylight hours. Higher road risk areas were only used more frequently when they were available at night. With a higher human land use in their home ranges fisher selected space near roads at night only, however when the extent of human use in their home range was lower, they selected areas further from roads at all times.

Conclusions Our study shows how individual variability allows fisher to adapt their diel activity to utilize resources in areas of high human land use. This further emphasizes the importance of accounting for individuality and multiple interacting spatio-temporal factors in habitat selection, particularly in highly human modified landscapes.

 $\label{eq:Keywords} \begin{array}{l} Fisher \cdot Habitat \ selection \cdot \\ Individuality \cdot Resource-use \cdot Risk \cdot Roads \cdot Spatio- \\ temporal \ effects \end{array}$

Introduction

How animals choose environmental resources is critical for understanding a wide range of ecological processes. These choices are governed by numerous complex and interacting factors including individual perception of risk and reward, and the quality and quantity of resources (Hutchinson 1957; McLoughlin et al. 2006; Aldridge and Boyce 2007). Such factors can lead to instances in which individuals make vastly different choices due to, for example, their boldness and perception of fitness tradeoffs (Breck et al. 2019; Brehm et al. 2019). This individuality adds complexity to our understanding of animal behavior and resource use (Stuber et al. 2022; Heit et al. 2023). However, untangling this complexity is critical for understanding these processes and applying the results for conservation and management.

Habitat selection is the process by which animals use resources in different proportion than their availability on the landscape (Matthiopoulos et al. 2020) and has important implications for understanding population distribution, abundance, and trophic dynamics, among other ecological processes (Northrup et al. 2022). Individuality, or the degree to which individual habitat selection varies from population-level patterns, is an important and often over-looked aspect of wildlife space-use. In studies of habitat selection, aspects of individuality can be incorporated by simultaneously considering three different sampling and estimation components: (1) changing availability of resources in the context of an individual animal's movement across the landscape (e.g., movement modeling; Matthiopoulos et al. 2020; Northrup et al. 2022), (2) the variation in individual responses to resource availability as a result of uniqueness, such as boldness (e.g., via random effects; Montgomery et al. 2018; Muff et al. 2020), and (3) the variation of resource availability based on where an animal lives (i.e., functional response; Holbrook et al. 2017; Moreau et al. 2012; Mysterud and Ims 1998). For example, the bedding behavior of individual grizzly bears (Ursus arctos horribilis) is context dependent on where they live and how their past experiences influence their movement and what is available to them at a given space and time. This can vary spatially and temporally in response to variation in human intensity, suggesting that the perception of risk during resting bouts were context dependent and may be informed by past experiences and their own risk-reward perceptions (Cristescu et al. 2013).

An animal's perception of risk may present differently across individuals of a species due to variation in exposure to disturbances, with some risky features (e.g., roads) also providing rewards (e.g., scavenging opportunities from vehicle strike; Frid and Dill 2002; Gaynor et al. 2018). In areas with high human activity, roads, residential and commercial buildings, agricultural areas, and resource-extraction sites disrupt the natural landscape, creating a matrix of disturbance for many species-particularly largerbodied mammals (Gaynor et al. 2018). In these places, wide-ranging species can regularly encounter multiple types of disturbance including a matrix of natural and anthropogenic disturbances. Severity and frequency of natural disturbances, such as wildfire, that alter forest composition can simultaneously create risky environments (e.g., lack of cover or denning areas; Green et al. 2022; Olson et al. 2024) and reward centers (e.g., increased prey densities as a result of forest regeneration; Doherty et al. 2022). Natural disturbances, particularly large-scale events, can negatively influence mesocarnivore densities and movement (Kordosky et al. 2021a; Green et al. 2022; Collier 2024). In disturbed areas, an animal's perception of risk and reward is influenced by their exposure to natural and anthropogenic disturbance, which informs future decisions when interacting with disturbance features (Cristescu et al. 2013). When the different contexts in which individuals exist are not considered, we may misinterpret animal behavior and thus habitat use (Cowlishaw 1997; Montgomery et al. 2018).

Among disturbance features, roads and human development are major obstacles for wild animals (Jackson 2000; Dean et al. 2019). Roads fragment habitat, forcing animals to make tradeoffs between accessing resources in different patches and the potential mortality risks associated with crossing roads. However, these tradeoffs vary with spatial and temporal context. Road risk intensity varies significantly throughout the diel cycle and with the general level of traffic that a specific road receives (Gaynor et al. 2018). For example, large carnivores in Michigan, USA are known to avoid roads during hours of peak human activity (Kautz et al. 2021). Further, the amount of exposure an individual has to a disturbance (e.g., roads) may alter real and perceived risk, leading to variation in behavior (Mysterud and Ims 1998; Stillfried et al. 2017).

Here, we examined the context dependency of fisher (Pekania pennanti) habitat selection. Fisher are considered a relatively resilient and adaptive species (Powell et al. 2017). While fisher are well known to prefer contiguous forests with high canopy cover, their populations have expanded into humanmodified and fragmented landscapes (Powell and Zielinski 1994; Carroll et al. 1999; Loughry et al. 2012; LaPoint et al. 2013, 2015). Surprisingly, fisher populations are simultaneously contracting in parts of their range that consist of suitable habitat and low levels of disturbance (e.g., Washington, USA), while populations in the eastern United States are expanding despite the higher intensity of human development (Lofroth et al. 2010; Loughry et al. 2012; LaPoint et al. 2013). We examined habitat selection of fisher in a landscape with a gradient of disturbance to assess how individual context affects habitat selection. Our objectives were to understand how fisher habitat selection is influenced by (1) the proximity to roads and how this changes with time of day and the extent of human land use in the area, and (2) individuality and the general exposure of a fisher to natural (i.e., large-scale insect outbreak) and anthropogenic disturbance within its home range. Together, individuality is captured in three ways: (1) by incorporating varying availability by individual movement, (2) by incorporating individual-level response by random effects, and (3) by incorporating variation in individual response by a functional response. Identifying the nuances of fisher habitat selection of disturbed areas in this context provides a better understanding of when and why this species is tolerant of different levels of disturbance, and thus, in what types of landscapes we may expect fisher population expansion and persistence.

Methods

Study area

We collected data on fisher movement between January and August each year between 2021 and 2023 in the northeast United States (Fig. 1). The study was primarily conducted within the state of Rhode Island, USA, however fisher movement extended into bordering areas of Massachusetts and Connecticut, USA. Rhode Island is the second most densely populated

state in the United States, with 410 people/km² (US Census Bureau 2012). The study area is primarily composed of forest (49.5%), development (27.4%), and wetlands (13%; Fig. 1). Road density across the study area ranged from 0 to 31.1 km of total road length per km².

Animal capture and monitoring

capture and handling followed Animal the institutional care and use standards approved by the University of Rhode Island Institutional Animal Care and Use Committee (#1676641-3). In each year, livetraps (Tomahawk 608S) were deployed to capture fisher from the beginning of January to the first week of March. Trapping locations were informed by fisher detections from a long-term camera trapping study (Mayer et al. 2022; Ganoe et al. 2024). In addition to bait (e.g., rabbit, squirrel, venison, beaver), a longdistance scent lure ("Caven's Gusto"; Minnesota Trapline Products, Pennock, MN, USA) and beaver castor were used in and around the trap site to attract fisher. Captured fisher were funneled into a metal handling cone (Appendix A, Figure S1) and were sedated with a combination of ketamine (32 mg/kg, range: 23.55-41.25) and midazolam (0.20 mg/kg, range: 0.13-0.33) administered via hand injection (Appendix A, Table S1; Green et al. 2018; Matthews et al. 2019).

Fisher were fitted with store-on-board global positioning system (GPS) radio collars (e-obs GmbH, Grünwald, Germany) with a handmade breakaway device. Males were fit with the 1C-light model (117 g), while females were fit with the lighter and more compact 1A model (69 g). To maximize battery life while achieving study goals of obtaining finescale location data, an accelerometer-informed GPS feature was used. Collars were programmed to take a burst of 2-6 location points from 1 to 10 s apart every 8 min when above the set activity threshold (48,400; Brown et al. 2012). When an animal was inactive or resting and the threshold was not reached, a point was taken every 8 h. Individuals were relocated via UHF radio-telemetry tracking to within 200 m every 2-4 weeks for data to be collected using a remote download device.



Fig. 1 Study area map in Rhode Island, USA and surrounding states showing land cover type and the distribution of locations from fisher GPS collars. State borders indicated by white border

Hypotheses of habitat selection

Our study area was subject to varied human disturbances (e.g., houses, roads, agricultural activities, resource extraction) that make movement across the landscape potentially risky for a mediumbodied mammal, particularly during the daytime when human activity is highest (Figs. 1 and 2). We proposed that the perception of risk is highly context-dependent for fisher and varies spatiotemporally depending on proximity to roads, time of day and thus exposure to human activity, and amount of human impact within an area. We hypothesized that fisher fine-scale habitat selection varied according to the interaction of these three factors while modulated by a functional response characterizing exposure to human land use within a fisher's home range. In addition to anthropogenic impacts on fisher movement, a large-scale defoliation event caused by an outbreak of spongy moth (Lymantria dispar dispar) occurred across the study area from 2015 to 2017 resulting in drastic changes to the forest structure (e.g., canopy loss, tree mortality, transition into early successional forest; Pasquarella et al. 2018). We hypothesized the severity of moth damage influenced fisher movement by potentially creating hunting opportunities, as habitat for prey species is created in forest gaps (Mitchell 2015). In combination,

- We hypothesized that human land use is a perceived risk to fisher and thus drives variation in their habitat selection. Therefore, we predicted that fisher would avoid human land use when human activity is highest by selecting areas farther from risky landscape features, particularly during daylight.
- 2) We hypothesized that human land use provides beneficial food sources for fisher given limited space for territories in the study area. Therefore, we predicted that fisher would select for areas in closer proximity to human land use when human activity is low and fisher can remain concealed. Thus, if fisher select for areas near roads, it would

occur at night in area with low human impact and high cover.

- 3) We proposed competing hypotheses for fisher selection of moth damaged areas that capture the possibility that these areas either provide rewards in the way of prey, or are risky to move through as they lack canopy cover that fisher prefer:
 - a. We hypothesized that moth damaged areas may provide habitat for prey that would attract fisher. Given that our location data relates to active movement of fisher and consequently may coincide with hunting activities, we predicted that fisher would select areas with more severe moth damage.
 - b. We hypothesized that due to the defoliation event and loss of canopy cover, moth damaged areas may prove to be unattractive and risky to a canopy-dependent species like fisher. We predicted that fisher would avoid areas of severe moth damage as they would areas of low cover.
- 4) We hypothesized that the contextual knowledge an individual has about their own experience with risky features (i.e., roads) within their home range informs how they move through those areas. Fisher living in areas with high human land use would have a different experience with anthropogenic features than those living in large areas of low human land use (e.g., contiguous forest). We predicted that selection near anthropogenic features is a functional response of a fisher's exposure to human land use within their home range.

Habitat selection analyses

We quantified habitat selection and movement patterns of fisher using step-selection functions (SSFs). SSFs compare habitat at a 'used' location (i.e., GPS location collected for an individual) to surrounding 'available' locations (Fortin et al. 2005; Thurfjell et al. 2014). The available locations associated with a given used location are determined by drawing potential movements an animal could have made from the previous GPS location using



Fig. 2 Distributions of variables of interest across the study area in Rhode Island, USA and surrounding states. a) severity of spongy moth damage across the region resulting in mass defoliation and tree mortality, b) road risk intensity, and c) the

movement distances (step lengths) and bearings (turning angles) drawn from distributions.

SSFs typically require regular intervals between locations, but our data were collected at various intervals, requiring that we standardize the data. Using the R (R Core Team 2023) package 'amt' (Signer et al. 2019), we identified sequences of locations occurring at regular intervals resulting in a dataset containing GPS locations at 8-min intervals with a 90 s tolerance and minimum of three locations per burst (Signer et al. 2019, Appendix B, Fig. S2). We then estimated the means and variances of movement parameters (i.e., step length, turning angle) by assuming they arose from gamma and von Mises distributions, respectively and using maximum likelihood to identify the most probable parameters given the empirical step length and turning angle data (Muff et al. 2020). Random steps were created by randomly drawing from these distributions for each used location, making an individual stratum that contains a given 'used' location combined with all associated random available locations (Muff et al. 2020). We conducted a sensitivity analysis of the ratio of available: used locations and identified 200:1 as a suitable ratio (Northrup et al. 2013, see Appendix

percentage of pixels within an area between roads that contain either development, agriculture (pasture, crops), or barren as classified in the National Landcover Database (2019)

B—Figure S3–S5 for more detail regarding modeling decisions). Covariates were then extracted at all 201 locations in every stratum for each individual.

Context dependency: interaction terms

Spatial and temporal covariates of interest included sunlight, roads, and human land use. Sunlight (sun) was calculated as the azimuth of the sun at each location in time using the R package 'suncalc' (Thierumel and Elmarhraoui 2022), where 0 represents the sun at the horizon (sunrise and sunset), negative values represent darkness and positive values represent daylight. To quantify risky features, we calculated the weighted distance from roads in ArcGIS (ESRI 2022) by combining two Euclidean distance rasters of 2 m resolution, (1) distance from major roads (i.e., highways, state routes) and (2) distance from minor roads (e.g., dirt roads; CT DEEP GIS 2021; MassGIS 2022; RIGIS 2016). Major roads were weighted more (0.70) than minor roads (0.30) to reflect their larger size and traffic volume and thus likely increased potential risk to fisher. The combined raster resulted in a single weighted distance to road (wRoad, Fig. 2b; see Appendix B-Figure S6 for more information regarding weight selection) that quantifies not only the distance to road but the use-intensity of the nearest roads. In this manner, the weighted distance to road (wRoad) is not a simple measurement of distance to road, but rather a gradient of the intensity of potential road risk where smaller values indicate higher risk (e.g., closer proximity to major roads). We expected fisher to select for distances to wRoad variably depending on the extent of human land use in the space between roads, which we define as zones. Using the same road layers as boundaries, we created polygons in ArcGIS within the road boundaries to create these zones. We defined human land use as developed, agriculture (pasture, cultivated crops), and barren landcover classes in the National Landcover Dataset (NLCD) from 2019 (Dewitz and USGS 2021). This metric is the inverse of landcover types that fisher are known to benefit from (i.e., forest, woody wetland, shrub). Using Zonal Statistics in ArcGIS, a raster was created totaling the number of cells with human land use within each zone between roads where higher raster values indicate higher extent of human land use within that zone (human; Fig. 2c).

The final spatial covariate we included was moth damage severity (moth). From 2015 to 2017 a large-scale spongy moth outbreak occurred that covered over 4,000 km² of forest and encompassed the study area causing a mass mortality of trees (Pasquarella et al. 2018). At the time of our study, forest regeneration had begun in the form of rapid growth of shrubby plants (e.g., blueberry (Vaccinium angustifolium), huckleberry (Vaccinium membranaceum), pepperbush (Clethra alnifolia)), and the falling debris from dead trees have added structure to the forest floor, all of which may impact fisher habitat selection; fisher benefit from both structural complexity for hunting and canopy cover (Kelly 1978; Zielinski et al. 2004; Lofroth et al. 2010; Powell et al. 2017). A $30m^2$ moth damage severity raster was obtained from a 2017 Landsat dataset with increasing categories of damage (i.e., defoliation) from 1 (little to none; i.e., little to no canopy loss) to 4 (very severe; i.e., total canopy loss and subsequent tree mortality) (Fig. 2a; Pasquarella et al. 2018).

Context dependency: functional response terms

Additionally, we included the extent of human land use within a fisher's home range as a functional response covariate to examine how general exposure to human land use where a fisher lives may influence the selection of road risk intensity. The functional response demonstrates how fisher selection for road risk intensity is context dependent, not only in regard to daylight and amount of human disturbance in a zone, but is also dependent on the context of human land use within its home range. To estimate individual home ranges, we calculated the 95% autocorrelated kernel density estimates (AKDE) using the package 'ctmm' in R (Calabrese et al. 2016). To represent differences in exposure to human impacts, we defined "HR" as the total percent human land use in a fisher's home range using the NLCD in ArcGIS Pro. All variables were scaled across individuals to a mean of 0 and variance of 1, meaning a value of 0 for a covariate, represented the mean across all individuals and a value of 1 represented a covariate value 1 standard deviation above the mean. Under this approach, coefficient magnitudes are more comparable, with estimated coefficients reflecting the response to a 1 standard deviation change of a variable.

Modeling

We fit the SSF model using the glmmTMB R package (Magnusson et al. 2019) with a three-way interaction of *wRoad*, *human* and *sun*, additive effects of *moth*, and a functional response of *HR* (see Appendix C for full model notation and description). The SSF was specified as a Poisson regression model with stratum (i.e., step)-specific intercepts arising from a distribution with an estimated mean and large, fixed variance (Muff et al. 2020). The probability that an individual animal (*n*) selects the *j*th location at time *t* depends on the variables of moth damage (*moth*), road risk intensity (*wRoad*), extent of human land use in the zone between road boundaries (*human*), and time of day (*sun*) as,

$$Pr(y_{ntj} = 1 | moth_{ntj}, wRoad_{ntj}, human_{ntj}, sun_{nt}) = \frac{e^{\mu_{ntj}}}{\sum_{j=1}^{J} e^{\mu_{ntj}}}$$

where μ_{ntj} is the sum of all linear terms of variables and associated individual n regression coefficients $(\beta_n^{\text{variable}})$. To address our first three hypotheses, coefficients include the conditional, pairwise, and threeway interactions of wRoad, human and sun. All coefficient estimates occur when all other covariates are held at mean of 0, including when the functional response is at the mean HR. Conditional coefficients are interpreted as the effect of a variable when the other two variables are at their mean values. Pair-wise coefficients are interpreted as the change in slope of the combined conditional coefficients when the third variable is at its mean value. The three-way interaction coefficient changes the slope of all the combined coefficients when none of the three variables are at their mean value. Initially, we fit random effects to all coefficients, however the pairwise interaction of wRoad*sun had a population-level variance near zero, indicating little to no variation in individual responses, as such wRoad*sun was fit as a fixed effect in the final model.

To account for individuality in animal behavior, we included individual random effects in the model, whereby we allowed the coefficient for each covariate to vary by individual. Each individual's coefficient for a given covariate is treated as a random effect with mean μ^{variable} , which is further modulated by the functional response, which is simultaneously estimated by modeling the population-level means of the conditional and interaction effects related to *wRoad* with an interaction with the variable *HR_n* as,

$$\mu^{\text{wRoad}} = \alpha^{\text{wRoad}} + \omega^{\text{wRoad}} \times \text{HR}_n$$

$$\mu^{\text{wRoad:human}} = \alpha^{\text{wRoad:human}} + \omega^{\text{wRoad:human}} \times \text{HR}_{...}$$

$$u^{\text{wRoad:sun}} = \alpha^{\text{wRoad:sun}} + \omega^{\text{wRoad:sun}} \times \text{HR}_{\text{wRoad:sun}}$$

$$\mu^{\text{wRoad:human:sun}} = \alpha^{\text{wRoad:human:sun}} + \omega^{\text{wRoad:human:sun}} \times \text{HR}_{\dots}$$

To address our fourth hypothesis, our model allows an animal's response to weighted distance to road risk (*wRoad*) to be influenced not only by the extent of human land use in the zone between roads (*human*) and daylight (*sun*) but is also a function of the context in which an animal lives (i.e., extent of human land use in their home range (*HR*)). Estimation was all done simultaneously in a single model (see Appendix C for full model notation). Due to model complexity and the multitude of factors (e.g., social dynamics, competition, etc.) influencing animal behavior that we were unable to account for in our sampling design, we define Type I error at $\alpha = 0.10$ in determining statistical clarity (Dushoff et al. 2019). Additionally, we define relative selection strength (RSS) as the exponentiated value of the relative intensity of use of a location dependent on a 1 *SD* unit of change in a covariate (Fieberg et al. 2021). We predict RSS using the observed ranges of covariate values for *human*, *sun*, and *wRoad*. RSS values below 1 correspond to selection less than it is available, and RSS values above 1 correspond to selection more than is available.

Results

Data collection

From 2021 to 2023, we collected data on 43 individual fisher (21 females, 22 males) resulting in 46,907 GPS locations (Fig. 1 & Appendix B, Fig. S2). Data collected ranged from January to August of each year with an average of 76 days on-air for each individual. Upon visual inspection of tracks, three individuals exhibited wide exploratory movements beyond their home range, with one female returning to her initial home range and both males establishing a new home range > 8 km away from their initial territory. As exploratory movements were clearly visually distinct, we removed any associated locations using visual inspection (Appendix D-Fig. S7) and all remaining locations were used in the analysis and home range calculations. Average home range sizes of animals varied by sex with males having larger home ranges (95% AKDE = 38.2 km^2) than females (95% $AKDE = 6.7 \text{ km}^2$). The percentage of human land use (HR) within home ranges varied from 3 to 55%, and 5 to 44%, respectively, and was not correlated to the size of an individuals' home range.

Individual random effects and interaction context dependency

We observed wide variation in individual random effect responses to *moth* and the conditional effects of *wRoad* and *human* (Fig. 3). Estimated



Fig. 3 Conditional variable effects for individuals $(\beta_n^{\text{variable}})$ for **a**) moth damage, **b**) road risk intensity (*wRoad*), **c**) extent of human land use within zone between roads (*human*), and **d**) the pair-wise interaction of *wRoad* and *human*, when all other variables are held at mean 0, including the functional response. Population level mean indicated by black horizonal line with 90% confidence interval as shaded region. Red-dotted line at 0 indicates selection in proportion to availability. Mean and 90%

population-level coefficients were positive for both moth $(\beta_{moth} = 0.07, p < 0.001)$ and wRoad $(\beta_{wRoad} = 0.23, p < 0.001)$, indicating selection for areas with more severe moth damage and areas with lower road risk when all other covariates are held at mean 0, including the functional response (Fig. 3a-b). Additionally, we observed 51 and 58% of individuals had support for positive selection for moth and wRoad, respectively. The conditional population-level effect of human was statistically clearly negative ($\beta_{human} = -0.18$, p < 0.001), and over 81% of individuals avoided the human covariate (Fig. 3c). The pairwise population-level interactions of both *wRoad x human* ($\beta_{wRoad:human} = -0.07$; Fig. 3d) and wRoad x sun ($\beta_{wRoad:sun} = 0.23$) were statistically clear (p = 0.07, p < 0.001, respectively), however the pairwise interaction of human x sun $(\beta_{human:sun} = -0.003, p = 0.95)$ was not. Additionally, the response of the 3-way population-level interaction was statistically unclear at the mean level of the functional response $(\beta_{wRoad;human;sun} = 0.05, p = 0.25).$

confidence intervals of each individual random effect represented by point and associated vertical line, respectively. Statistical significance (whether confidence interval includes zero or not) indicated by opaqueness, where darker points represent selection for (positive values) or against (negative values) the variable in question and transparent points represent no selection. Y-axis scales are not uniform across panels



Fig. 4 Mean coefficients as a functional response of the extent of human land use within a fisher's 95% AKDE home range. Model variables include road risk intensity (*wRoad*), extent of human land use within zone between roads (*human*), and the azimuth of the sun (*sun*)

Context dependency: functional response

The conditional effect of *wRoad* ranged from positive to negative as the extent of human land use in a home range increased (Fig. 4). Fisher with less human land use within their home range had positive coefficient values for wRoad (i.e., selection for areas with lower road risk). We observed the opposite pair-wise response of wRoad x sun, with fisher selecting for areas with lower road risk at night when they have a higher extent of human land use in their home range. However, these interactions are all modulated by the 3-way interaction of wRoad, human and sun (Fig. 4). While the conditional effect of wRoad $(\beta_{wRoad:HR} = 0.03, p = 0.48)$, pair-wise effect of wRoad x human ($\beta_{wRoad:human:HR} = -0.002, p = 0.96$) and the 3-way interaction of wRoad x sun $(\beta_{wRoad:human:sun:HR} = -0.008, p = 0.74)$ were statistically unclear, the pair-wise effect of wRoad x sun was statistically clear ($\beta_{wRoad:sun:HR} = 0.12, p = 0.08$).

Fisher were least likely (RSS = 0.05) to select areas with lower road risk in zones with moderate to high human disturbance when their home range had the highest extent of human land use (Fig. 5). At night, for fisher with 20–55% human land use in their home range, all RSS values regardless of the extent of human land use in each zone, were below 1 for areas with low road risk and above 1 for areas with high road risk, suggesting that at night these animals select to be in areas with higher road risk than what is available to them (Fig. 5). Regardless of a fisher's home-range-level exposure to human land use, they were generally likely to be in areas with low road risk during the day. The strongest selection (RSS = 280) for this was in zones with high human land use by fisher with the most exposure to human land use in their home range (Fig. 5). In other words, individuals that avoided road risk the most were those with the most human land use in their home range, particularly when they were in zones of high human land use during the day. Fisher with low exposure to human land use during the day. Fisher with low exposure to human land use in their home road risk regardless of time of day or amount of human land use in a zone.

Discussion

Understanding the influence of individuality and context dependency on animal habitat selection is crucial for making robust and mechanistic inferences on species' resource use. We were able to show that fisher proximity to road risk is not only influenced by the extent of human land use and time of day but also that to understand the effect of one of these variables, requires considering the context of the

Fig. 5 Gradient of relative selection strength (RSS) with respect to time of day (columns), extent of human land use in areas between roads and road risk intensity (wRoad; rows) all as a function of the amount of human disturbance within a fisher's 95% AKDE home range. RSS values of 1 indicate selection for location as it is available, RSS < 1 indicate selection for location less than available, and RSS > 1 indicates selection for location more than available. The median percentage of human land use within a home range is represented by the vertical dotted line



others simultaneously. Further, fisher response to these factors depends on the context within which an individual lives.

Context dependency: interactions

As we predicted, fisher avoided road risk during the day supporting our first hypothesis that they will avoid human disturbances when human activity is high (Figs. 5 and 6). Given fisher also selected for areas of high road risk at night, our results support our second hypothesis that territory limited fisher (e.g., those with home ranges with high human land use) will utilize risky areas when human activity is low (Figs. 5 and 6). The avoidance of roads during periods of high human activity but use of areas near roads at night suggest that risk is high during the day but there may be rewards associated with roads, potentially in the form of roadkill and scavenging opportunities that attract fisher at night. At the mean functional response value, it was statistically clear that fisher avoided roads (Fig. 3b), particularly when there was high human land use in zones between those roads (Fig. 3d). Selection for areas of lower road risk during the day did not vary across individuals (Fig. 3f), indicating this is a standardized population-level response to road risk when human activity on those roads is high. These findings may also suggest that fisher utilize times of lower human activity to cross roads in order to access habitat within their home range. Recent studies on fisher in the western U.S. have indicated that fisher seek refugia by minimizing human activity in their core home range (Kordosky et al. 2021b). Our findings provide additional support for the avoidance of human activity reflected by the strong avoidance of roads by all individuals, particularly if they are in a zone with high human land use. The diel partitioning of habitat selection we observed in our study could also be indicative of behavioral plasticity that may be facilitating fisher population expansion in recent years into highly disturbed landscapes in Eastern North America (LaPoint et al. 2015; Moncrief and Fies 2015; Triska et al. 2020). Lastly, our findings highlight the importance of considering the context-dependent nature of spatio-temporal factors affecting animal behavior. This includes considering individuality, variable interactions and a functional response.

In addition to risks and potential rewards created by human development, our study area also

Fig. 6 Infographic summarizing the relationship between time of day, proximity to road (selection for road risk intensity), and extent of human disturbance for fisher living in home ranges with varying degrees of human development



experienced a mass defoliation event that drastically changed the forest canopy and forest floor during our study (Pasquarella et al. 2018). We observed individual variation in response to the severity of moth damage with some individuals avoiding severely damaged areas, while the majority selected for areas with more severe moth damage (Fig. 3a). In the western part of their range, fisher regularly experience transformations in forest structure caused by wildfires that is known to increase stress, reduce abundance and lower survival (Kordosky et al. 2021a; Green et al. 2022). In contrast, in southern New England, fisher do not experience high intensity wildfires and respond quite differently to similar, lower intensity forest change. Our findings support the hypothesis that moth disturbed areas may be creating habitat for prey. When fisher are highly active (i.e., hunting) at night they are selecting to use those areas with moth damage. In the years following the defoliation event, understory growth and woody downed debris have increased in these areas. In this context, our results support the literature that fisher are known to benefit from forest floor complexity as it creates opportunities for ambushing prey (Powell 1993; Powell and Zielinski 1994; Carroll et al. 1999; Weir and Harestad 2003).

Our hypothesis that there may be risk associated with increased exposure from the loss of canopy was not supported as it appeared that the rewards of potential hunting opportunities were worth the risk of exposure for all individuals but two male fisher in our study (Fig. 3a). In a previous study of the distribution of fisher in the same study area, we found that fisher occupied areas without moth damage year-round, and utilized areas with moth damage in the winter months (Ganoe et al. 2024). These combined results may indicate that moth damaged areas are beneficial for food sources, particularly in winter when prey items are less abundant. It also may indicate that moth damaged areas are less suitable for denning opportunities with less cover and protection for young in summer as fisher are known to be more selective when resting (Olson et al. 2024). However, fisher responses to moth damage may shift as forest succession continues and as tree cavities are formed in dead standing trees (Powell et al. 1997; Green et al. 2019; Kordosky et al. 2021b). There is also potential that fisher use of moth damaged areas may be informed by changes in habitat selection of other competitors, like bobcat (Parsons et al. 2019). Identifying the underlying mechanistic process of prey availability and competition would be better supported and understood if levels of relative prey density were known in moth damaged areas of this region, thus further investigation of predator–prey interactions in these areas is warranted.

Context dependency: functional response

We found the response of fisher to road risk was a function of the amount of human disturbance within their home range, supporting our fourth hypothesis that environmental context influences the habitat selection patterns of individual animals. We found that a fisher's selection for intensity of road risk was drastically different at night depending on how much human land use they are exposed to. This suggests that fisher utilize diel partitioning to mitigate risk associated with roads in heavily human disturbed areas (Fig. 6). This may also suggest that fisher in areas with low human disturbance (i.e., low human land use, lower road risk) that are not frequently exposed to roads may perceive them as highly risky. Alternatively, they may not be aware of advantages brought by scavenging opportunities, or perhaps the risk-reward tradeoff of scavenging near roads does not outweigh the reward of hunting and scavenging in alternative habitat they have available to them, thus they avoid those areas near roads (Frid and Dill 2002; Gaynor et al. 2018; Brehm et al. 2019).

The results of our functional response analysis gives insight into how fisher may respond to disturbance across their range. Fisher have been documented as canopy-cover dependent species, and our results support the literature that developed this understanding (Powell and Zielinski 1994; Carroll et al. 1999; Weir and Harestad 2003; Powell et al. 2017; Kordosky et al. 2021b). Overall, the Rhode Island fisher population avoided road risk during the day, especially when individuals lived in areas associated with less human land use and thus, more cover (e.g., forest, woody wetland, shrub). Fisher distributions in the northeastern United States are limited mostly by natural rather than anthropogenic barriers and have expanded into more developed areas (Hapeman et al. 2011; LaPoint et al. 2015). In other parts of their range where fisher may not have a long history of encountering roads (e.g., extensive wilderness areas in Canada and western United States), we may expect individuals to respond differently to human development (e.g., oil and gas exploration, recreation, urbanization) than individuals with extensive experience with roads and development. Rhode Island has a widespread fisher population even though availability of what would be traditionally known as prime fisher territories (contiguous forest) is limited and fragmented (Ganoe et al. 2024) which would require crossing roads to connect habitat. Thus, fisher tolerance to roads in our study area may be informed by the need to adapt to human disturbances in order to utilize the available habitat and find mates. Our results show plasticity in fisher responses to roads and human development through diel partitioning, however, this plasticity remains reliant on access to large zones with low human disturbance (Ganoe et al. 2024).

Conclusion

Overall, we found support for the importance of accounting for individuality and the context dependent nature of spatio-temporal factors in habitat selection analyses. Our findings provide evidence of fisher plasticity to a highly human modified landscape given their individual experiences. At the populationlevel it was important that during the daytime fisher consistently selected areas with low intensity of road risk, but selection of areas of higher road risk depended on the extent of human land use a fisher was exposed to. Our research clarifies the importance of incorporating context-dependency in fisher habitat selection in heterogeneous environments. Managers conservation ecologists should consider and individuality and animal exposure to varying levels of disturbance when implementing wildlife movement studies and attempting to understand the limitations of fisher adaptability to human activities.

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Author Contributions LG, CB, and BG conceived and designed the study; LG, AM, and CB conducted the field data collection; LG, JN, and BG discussed and performed the data management, analysis and visualization; BG supervised the study; All authors contributed to the concepts within the original draft, edits, and finalization of the manuscript. All authors have read, commented on, and agreed to the published version of the manuscript.

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Data Availability Data and model code available from Zenodo: https://doi.org/10.5281/zenodo.12764759.

Declarations

Conflict of interest The authors declare no competing interests.

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