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LETTER

The fine-scale movement pattern of Amur tiger (*Panthera tigris altaica*) responds to winter habitat permeability

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Abstract
The number of Amur tigers living in protected regions is increasing, and China has achieved significant progress in this regard, especially at the Sino-Russia border region around Hunchun where most of the Amur tigers are found in China. However, there is a need to increase the dispersal of Amur tigers further from the border as the region is not large enough to support the sustainable survival of the population. In the winter of 2012–2015 and January 2022, we tracked 38 Amur tiger snow traces and performed line transect and camera trap surveys in Hunchun to assess Amur tiger movements in response to the landscape and its permeability at fine scales. Our results showed that towns, shrubs, and forest roads are the main factors influencing Amur tiger movements. Furthermore, tiger paths were characterized by lower tortuosity in preferred habitats. This provides information for small-scale habitat modification to increase landscape permeability and facilitate dispersal.

KEYWORDS
landscape permeability, movement patterns, *Panthera tigris altaica*, path tortuosity

BACKGROUND

The Amur tiger (*Panthera tigris altaica*) is one of the world's most endangered large carnivores, found in the Russian Far East and Northeastern China (Wang et al., 2016). In China, the Chinese government banned tiger hunting in the 1950s, launched a national Natural Forest Protection Project to restore the Amur tiger habitat, and promoted forest vegetation restoration through policies such as returning farmland to forest (Jiang et al., 2017), and establishing the Hunchun Reserve in 2001 with a conservation policy to reduce pressure on the Amur tiger (Jiang et al., 2017). In 2016, the government established the Northeast Tiger and Leopard National Park, which includes the Hunchun Reserve, adjacent to the Sino-Russian border, to protect and restore wild populations of Amur tigers. Currently, the number of Amur tigers recorded in China has increased from 20 to 55 (Qi et al., 2021), of which more than 80% of the population is concentrated near the Sino-Russian border (Wang et al., 2018), which cannot support the sustainable existence of an Amur tiger population (Wen et al., 2022).

The expansion of cities, farmland, and roads has caused serious fragmentation of Amur tiger habitats. Researchers have tried to design ecological corridors to link the isolated landscapes in China. This was a huge project that required coordination between a number of government departments and was both time-consuming and costly (Li et al., 2017; Luan et al., 2011; Northeast Tiger and Leopard National Park Hunchun Bureau, 2022). Therefore, at this stage, the important issues facing Amur tiger conservation in China are how to increase the permeability between the habitats of Amur tigers, promote the dispersal of Amur tigers, and maintain the existing Amur tiger population before the completion of the ecological corridor. To solve this problem, our research team proposes to make small-scale habitat modifications to existing habitats, which is currently more feasible than constructing corridors. This requires an understanding of Amur tiger movement patterns across the landscape and landscape permeability.

Landscape permeability describes the relative potential for animals to move between habitat patches at a regional scale (Meiklejohn et al., 2010). The permeability of a landscape is determined by a combination of habitats where animals can move easily and barriers that prevent or redirect their movement (Singleton et al., 2002), hence assessing habitat permeability can help us identify landscape features and locations that facilitate or impede Amur tiger movement.

For tiger movement analysis, many researchers have studied factors such as home range, daily activity patterns, dispersal across the landscape, and landscape connectivity using data from satellite tracking collars (Goodrich et al., 2010; Hussain et al., 2022; Krishnamurthy et al., 2016; Rozhnov et al., 2011). In these studies, the time interval between localizations was usually between 20 min and 36 h, and the trajectory between localizations was straight ("Euclidean distance"). However, the trajectories collected at such long time intervals are likely to miss a good deal of detail concerning tiger movements (Hebblewhite & Haydon, 2010). Furthermore, our equipment does not support short-time-interval positioning. Therefore, field track was considered to be the best choice to obtain the movement trajectory of Amur tigers, as this can record more complete trajectory information at the micro-habitat scale, while detailed exploration of the trajectory shape and surrounding environment is possible, yet there is no temporal attribute.

Path tortuosity is the degree of curvature, or deviation from a straight line, of an animal's trajectory (Bascompte & Vilà, 1997); it can reflect animal landscape use and response to different types of habitats (Barraquand & Benhamou, 2008; Nams, 2005). In favorable habitats, path tortuosity may reflect animal foraging strategies (Gillis & Nams, 1998; Hein et al., 2003; Jiang et al., 2009; Wiens et al., 1995), such as in cases where resources are concentrated. In unfavorable habitats, such as habitat fragmented due to human landscape development (Smith et al., 2019), animals may increase path tortuosity to avoid obstacles or evade human disturbances (Kerley et al., 2002; Whittington et al., 2004).

Based on the above, we evaluate: (1) what are the factors that influence the path tortuosity of Amur tigers at fine scales; (2) how does the Amur tiger's path tortuosity change with these factors? On this basis, we then make clear recommendations on how to modify habitat structure to facilitate Amur tiger movement in the landscape.

Practitioner points

- Maintain forest roads and limit human use to increase landscape permeability for large carnivores.
- Use vegetation for land zoning to separate human activity from tiger habitat.
- This research provides new insights for landscape permeability assessment of wildlife in the future.

METHODS

Study area

This study was conducted in Hunchun, Jilin Province, China. Hunchun is located in the eastern part of Jilin Province (42°25′–43°30′ N, 130°03′–130°18′ E), and is situated in the northern part of the Changbai Mountains. The region has a mountainous terrain, with the highest peak reaching an elevation of 1477.4 m. The climate is characterized by a mid-temperate near-maritime monsoon climate, and it is covered by snow for almost half a year, providing conditions for our footprint tracking work.

In 2001, the Hunchun Reserve was established to protect the Amur tiger's habitat and relocate the residents within the core area of the reserve to nearby towns. Some abandoned logging roads remain in the Hunchun Reserve which are mainly used by reserve staff for patrol and monitoring work, as well as by farmers who work in the mountains. In winter, the reserve reduces the patrol frequency and farmers no longer work in the mountains, so there is less human activity on tertiary roads. Currently, the forest coverage rate in the northern part of the Changbai Mountains is 92%, with most forests having converted to secondary deciduous forests over the past 50 years (Li et al., 2009). The main vegetation types in Hunchun are broadleaf forests, including broadleaf mixed forests and secondary oak forests, as well as sparsely distributed coniferous forests dominated by fir trees. Research reports indicate that the habitat of Amur tigers has improved and that their populations are increasing (Jiang et al., 2017). Nowadays, Hunchun is the area in China with the highest density distribution and population abundance of Amur tigers (Figure 1) (Qi et al., 2021).

Snow footprint tracking and prey data collection method

Amur tiger tracks are generally difficult to locate. Before 2018, the Hunchun Reserve did not have an integrated real-time monitoring system, and camera traps were not

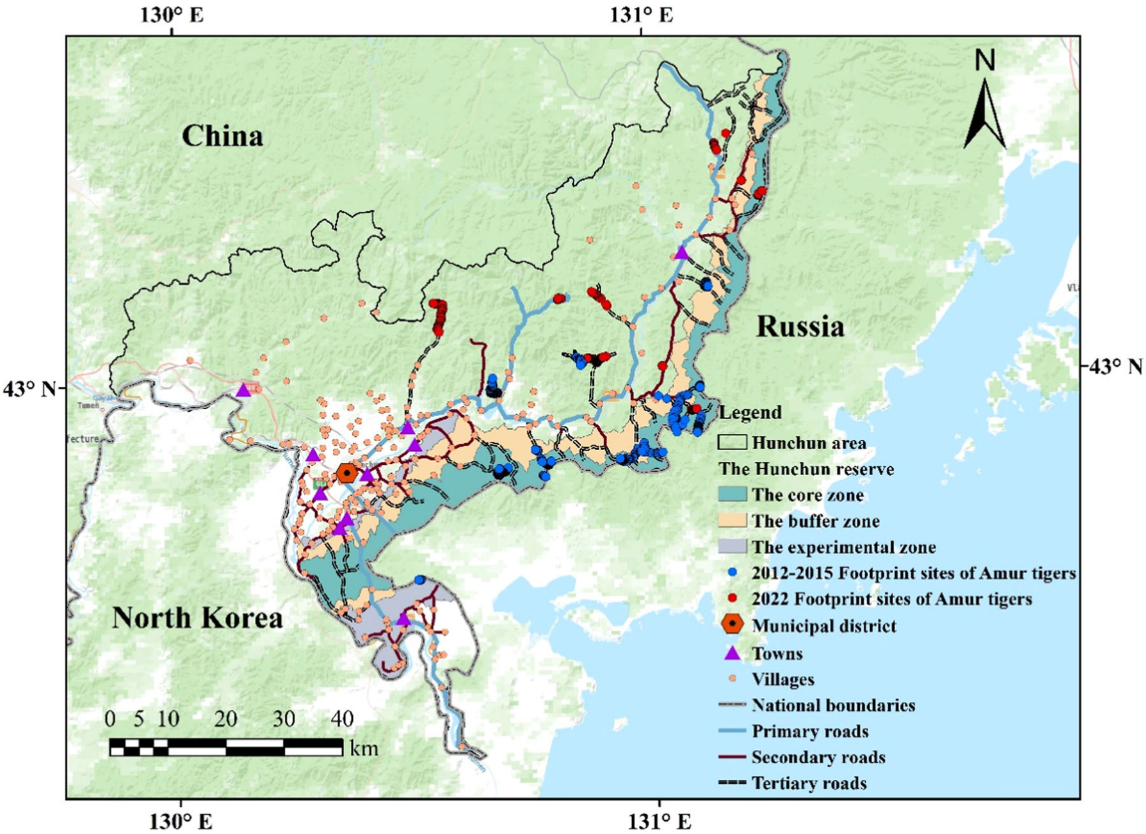

FIGURE 1 Location of the study area and Amur tiger footprint tracking sites in winters (2012–2015 and 2022).

widely used. The location of Amur tiger sightings was mainly determined by reserve staff patrols and reports from local residents after sightings. Accordingly, in January and December 2012, January 2013, and January 2015, we used line transect surveys to find Amur tiger tracks in areas where Amur tigers were frequently seen; 18 transect lines were laid out, each 5 km long with an interval of approximately 3 km between transects (Supporting Information Appendix S1: Figure S1). In January and February 2014, our team worked with the Hunchun Reserve to search for Amur tiger tracks, following each of the major east-west gullies in the reserve. To improve the efficiency of tracking Amur tiger footprints, in winter 2022, we used the integrated real-time camera trap monitoring system to locate Amur tiger occurrence sites, supplemented by line transect surveys and then visited these sites to find and follow tiger tracks. Each transect line was 3–5 km long and was placed at 3 km intervals across Hunchun, for a total of 56 transect lines (Supporting Information Appendix S1: Figure S1). When selecting sites for Amur tiger tracking, we prioritized untracked areas and did not limit ourselves to the reserve, with the aim of covering the entire Hunchun area.

Amur tigers are apex predators, and it is clearly important to avoid encounters with them for personal safety and not to disturb tigers' behavior during field tracking. Therefore, the direction of tracking was based on the freshness of the Amur tiger's snow tracks, judged by how much snow had frozen inside the footprints. If the snow was soft or slightly frozen, then the footprints were less than 24 h old. In this case, we followed the footprints in the opposite direction from the tiger's direction of travel. If the snow inside the footprints was frozen hard, the footprints were judged to be more than 24 h old and we tracked them in the same direction. For the January 2022 tracking, we relied on the integrated real-time camera monitoring system to select the locations where Amur tigers were present three days before the tracking began. This also provided a reference for determining the freshness of the footprints. Amur leopard (*Panthera pardus orientalis*) footprints were distinguished from the footprints of Amur tigers by measuring forefoot pad width. The width of the forefoot pads of female leopards is 5.5–6.5 cm, and that of male leopards is 6.5–7.5 cm (Pikunov et al., 2014); for tigers, 9.5–10 cm or larger than 10 cm for females and male Amur tigers, respectively.

We used a handheld GPS to record the coordinates at the location where a direction change of more than 30° occurred in the animal path. At the points where the animal path went from one forest type to another forest type, we took a 10 m × 10 m sample quadrat and recorded the plant species and cover class. Furthermore, the step length, behavior (e.g., jumping, excretion, pawing the ground with hind feet, etc.), and corresponding occurrence points' coordinates and forest type were recorded. All coordinate data were exported, and information recorded during tracking was tabulated for processing and analysis.

We used line transect surveys and camera traps to collect prey presence point data (Manly et al., 2002). Based on the information collected on Amur tiger and prey occurrences (e.g. scat, tracks), we divided the areas where Amur tigers were often found into 2 km × 2 km grids. In each grid, we placed one camera station on ridges, animal trails, or vegetated areas. Each camera station was set up with two facing cameras. The line transect survey was described above. During the transect survey, we recorded the locations of the Amur tiger's main prey: wild boar (*Sus scrofa*), roe deer (*Capreolus pygargus*), and sika deer (*Cervus nippon hortulorum*) (Gu et al., 2018). We screened camera trap data for Amur tigers and prey occurrence points during the winter of 2014–2022 (December to March) and, together with data recorded during line transect surveys, predicted Amur tiger and prey distribution probabilities by MaxEnt models. These occurrence data were obtained opportunistically and are not considered systematically collected (Supporting Information Appendix S1: Figure S1) (Long et al., 2021).

Environmental data collection

We downloaded the GDEMV3 digital elevation data with a 30 m resolution from the geospatial data cloud at http://www.gscloud.cn/ and slope, aspect, and elevation data were extracted. Settlements, roads, rivers, croplands, and vegetation types were vectorized according to the Hunchun Forestry Bureau's forest maps, and the settlements were graded according to China's administrative divisions as municipal districts, townships, and villages. According to the Hunchun road classification design vector data provided by the Hunchun Forestry Bureau, the roads were divided into primary roads (i.e., highways), secondary roads (i.e., cement roads), and tertiary roads (i.e., abandoned forest harvest roads and forest trails). The nearest distances between each tiger's track to the nearest settlements, roads, rivers, croplands, and vegetation were calculated in ArcGIS 10.7. The four habitat types for vegetation classification were coniferous forest, broad-leaved forest, mixed needle-broadleaved forest, and shrub. Data on snow depth were taken from snow-cover products, MOD10A (see Supporting Information Appendix S1: Table S1).

Data analysis

Fractal analysis

Fractal analysis is one of many methods for describing animals' path tortuosity (e.g., straightness index, tortuosity entropy, and sinuosity) (Butschelet, 1983; Duffy et al., 2011; Liu et al., 2015). In many current studies, animal tracks are obtained from collars containing time series data, and the calculation of path tortuosity requires time series data. However, fractal analysis is a well-established method for calculating the tortuosity of trajectories without time series data and can be suitable for small sample sizes (Bascompte and Vilà, 1997). Time series data were not included in our trajectory data, so the fractal analysis was chosen to calculate the tortuosity of footprint chains to examine whether there are differences in the response of Amur tigers' movements to their surroundings at fine scales. The fractal analysis quantifies the path tortuosity by calculating the fractal dimension (D) which is constant over a range of scales. In a two-dimensional space, if the path is a straight line, the D value is 1; if the path covers the entire plane, the D value is 2. The D value is in Jiang et al. (2017) and Wang et al. (2016).

We used the Fractal Mean estimator 4.08 for analyses (Nams, 2006). Before applying fractal analysis, the correlated random walk was used as a null model, as recommended by Turchin, to test whether the path pattern differed from this model (Turchin, 1996). If the R_{diff}^2 value is positive when tested using the software's net distance procedure, the path data is different from the correlated random walk, and therefore, fractal analysis can be performed, otherwise, it cannot (Nams & Bourgeois, 2004).

After the above tests, we used the Fractal Mean program to set the divider size. The divider's lower limit should not be less than the sampling accuracy (Nams & Bourgeois, 2004). According to real measurements and published references, the average step of the Amur tiger was 1.5 m (Pikunov et al., 2014), so the lower limit of the divider for the path analysis was set to 2 m, and the upper limit of the divider was decided by reviewing the literature (Jiang et al., 2009; Nams & Bourgeois, 2004); the largest divider size was selected to be 50 m.

Based on the Fractal Mean estimator 4.08 program's calculations of the log (path length) and log (scale), regression analysis was performed. Because the slope between the log (path length) and log (scale) will be $1 - D$, $D = 1 - \text{slope}$, as the scale increases. To determine whether one model fits the data better than another, we compared the results of segmented regression to those of linear regression. If the segmented regression fits more precisely, D might change in the scale domain. We can then specify the scale domain in which the animal responses to the environment differ by identifying discrete breaks in the fractal dimension and the spatial scale (Doerr & Doerr, 2004; Etzenhouser et al., 1998; Nams & Bourgeois, 2004). Finally, the dimension log $(D - 1)$ was processed, allowing for further analysis of the relationship between the dimension and other variables (Nams & Bourgeois, 2004).

We added a random effect when combining the two sets of data for analysis (data from 2012 to 2015 and 2022) because the time interval between the two sets of data was considered too long. The habitat variables (Supporting Information Appendix S1: Table S1), probability of prey occurrence, and frequency of behavior (the behavioral data from field tracking) in the Amur tiger footprint chain were used as independent variables, while the Amur tiger's path tortuosity was the dependent variable. The variables without significant correlation were added to the initial model to avoid the issue of collinearity between the variables, based on Spearman rank correlation (calculated in R software); an absolute value of the correlation coefficient between two variables greater than or equal to 0.5 was determined as correlated (Sachot et al., 2003). We standardized independent variables before running the linear mixed-effects model. Dredge in the MuMln package was used to select the best model with the lowest AIC_c, and the best model was used to predict the tortuosity value map of Amur tigers in the Hunchun region in winter.

Presence probability of prey species

Because tiger movement may be driven by prey distribution, we used the MaxEnt model to assess the presence probability of prey in the Hunchun area. Due to the time interval of footprint chain collection, estimates of prey occurrence probabilities were based on yearly groupings. We predicted the habitat suitability for wild boar, roe deer, and sika deer in winter 2014–2015 and winter 2018–2022. Then, these probability maps were summed to derive a final map that represents prey occurrence probability (Grenié et al., 2020). Since our camera trap data started in 2014, we determined that the prey data from 2014 to 2015 corresponds to the response analysis of Amur tiger footprint chain data from 2012 to 2015; we used prey survey data obtained after 2018 to correspond to the response analysis of Amur tiger footprint chain data in the winter of 2022.

The regularization multiplier (RM) and feature type (FC) can have an impact on MaxEnt model predictions (Merow et al., 2013). Using the MaxEnt model's default settings can result in model overfitting and erroneous predictions (Radosavljevic and Anderson, 2013). Among the MaxEnt FCs, linear (L) is always used, quadratic (Q) requires at least 10 samples, hinge (H) requires at least 15 samples, and product (P) and threshold (T) require at least 80 samples (Elith et al., 2010). In addition, the prey occurrence point data does not follow the method of random sampling or systematic sampling, and there is expected to be sampling bias or spatial autocorrelation, resulting in model overfitting. This influence was eliminated by spatially filtering the prey occurrence points using the SDMtoolbox tool in ArcGIS 10.7 (Boria et al., 2014; Brown, 2014; Wang et al., 2017), obtaining 22, 13, and 25 occurrence points of sika deer, wild boar, and roe deer, respectively, in winter 2014–2015, and 37, 38, and 79 occurrence points of sika deer, wild boar, and roe deer, respectively, in winter 2018–2022.

Based on the filtered occurrence point data, the model FC combinations were set to L, LQ, LH, and LQH for the 2014–2015 sika deer and roe deer, and L, LQ for wild boar, and L, LQ for the 2018–2021 sika deer, wild boar, and roe deer. The RM was set to 1–6 for each species model. We used the ENMeal package (Li et al., 2022) and the kuenm package (Cobos et al., 2019) to adjust the MaxEnt model. Kernel density analysis was used to create a bias file based on all winter prey occurrence points to reduce the impact of occurrence point data bias (Long et al., 2021). Bias files were also incorporated while generating models. Multicollinearity was considered where $|r| > 0.7$ in Pearson correlation analysis of the habitat variables needed for prediction, and the variables of little ecological significance were eliminated. The final variables for model prediction are displayed in Supporting Information: Appendix S1.

Habitat suitability of Amur tiger and spatial distribution of path tortuosity

We predicted the winter habitat suitability of the Amur tiger from 2014 to 2022 using the MaxEnt model. Because the distribution of prey is a major factor influencing the habitat occupancy of large carnivore populations (Karanth et al., 2004), the prey presence probability data were considered when creating the Amur tiger distribution prediction model. Spatial filtering (as above) resulted in 54, 41, 96, and 37 occurrence points of sika deer, wild boar, roe deer, and Amur tiger, respectively, in winter 2014–2022. Accordingly, the FC combinations for 2014–2022 were set to L, LQ, LH, and LQH for roe deer, wild boar, and Amur tiger from 2014 to 2022, and all FC combinations were set for roe deer from 2014 to 2022. The RM was set to 1–6 for each species model. Variables with $|r| > 0.7$ and little ecological significance were excluded from the analysis. Finally, using linear regression mixed-effects modeling, we related the predicted winter habitat suitability map of the Amur tiger with the spatial distribution of path tortuosity. Because the trajectory analysis scale of the Amur tiger is within the range of 50 m, the accuracy of the maps was set to 50 m × 50 m, and the accuracy of the variable layers involved in the model were uniformly resampled to 50 m × 50 m.

Finally, we analyzed the relationship between habitat suitability and tortuosity by checking Pearson's correlation of values in each grid cell, resampled to 7 km × 7 km. The grid size was based on the daily activity distance of female Amur tigers (7 km) (Goodrich et al., 2010), recognizing that the successful expansion of the Amur tiger population is based on the effective dispersal of female tigers.

RESULTS

Response of Amur tiger movement to habitat characteristics

We tracked 25 Amur tiger snow tracks in January and December 2012–2015, and 13 snow tracks in January 2022. We screened 35 snow tracks for examination, totaling 29.485 km in length, eliminating paths that were less than 150 m in length because the length of the path used for fractal analysis should not be less than three times the divider size (here, 50 m) (Jiang et al., 2009). Amur tigers' movement paths were significantly different from the correlated random walk model ($R_{diff}^2 = 0.727$, $p < 0.001$). Therefore, a fractal analysis of the travel paths of Amur tigers was performed. Linear regression models were developed between log (path length) and log (scale), showing a high fit ($R^2 = 0.94$, $p < 0.001$), while segmented regression was not well-supported, indicating that there was no qualitative change in the fractal dimension at the scale of 2–50 m, that is, there was no significant difference in how Amur tigers responded to habitat in the 50 m scale range.

Factors affecting Amur tiger movement

There were three main factors influencing the Amur tiger movement (Figure 2). The value of Amur tiger path tortuosity showed that the closer to tertiary roads, the lower the path tortuosity, and the closer to shrub vegetation and to townships, the higher the path tortuosity (Figure 2). Behavioral data and prey occurrence probabilities were not selected in the best model of animal path tortuosity, maybe due to insufficient sample size.

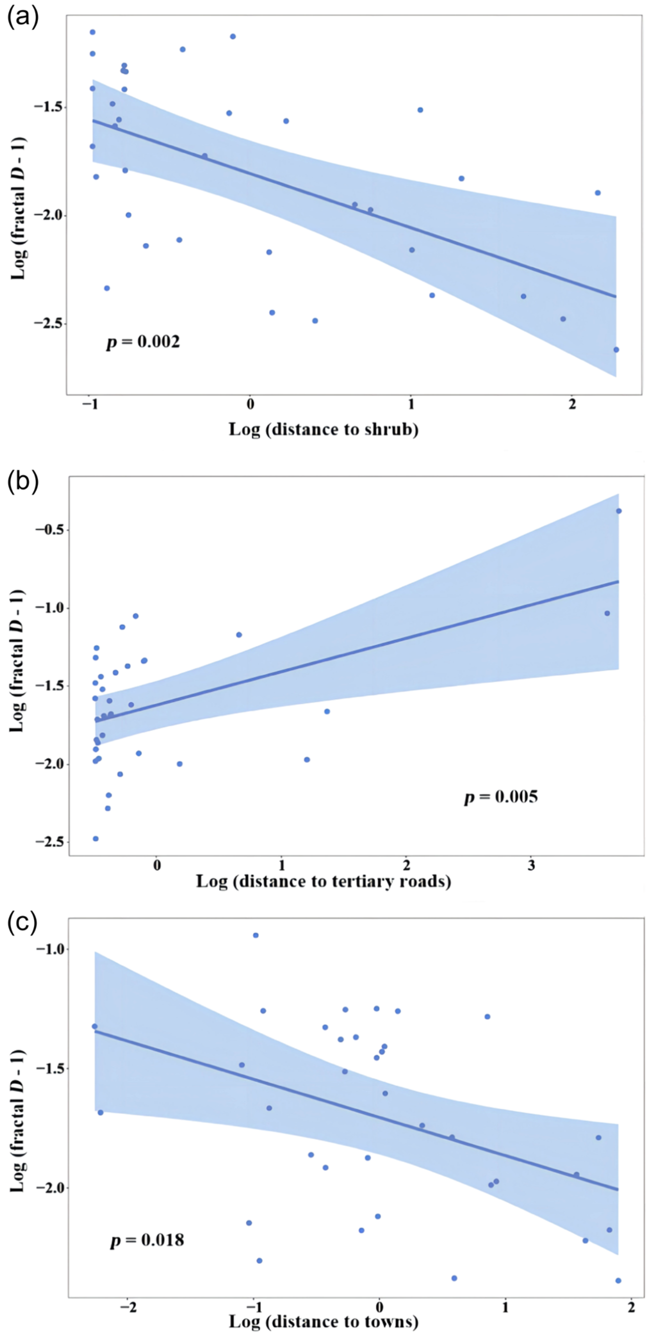

FIGURE 2 Plots of linear mixed effects model fit of log (fractal $D-1$) with log (distance to shrub) (a), log (distance to tertiary roads) (b), and log (distance to towns) (c) at scales of 2–50 m. Path tortuosity is quantified by fractal D, which is subject to log $(D-1)$ normalization. The explanatory variables are calculated and plotted as normalized values. The linear mixed effects model $R^2_m = 0.380$, $R^2_c = 0.391$, $AIC_c = 55.221$.

Winter habitat suitability of Amur tiger

The optimal model parameters FC for the winter distribution of Amur tigers from 2014 to 2022 were LH, RM = 5, and AUC = 0.918; the optimized model was used to predict the winter habitat suitability of Amur tigers in the Hunchun area (Figure 4a). The contribution and importance of predictor variables in the model were ranked using the jackknife method. The results showed that the probability of prey distribution had the greatest influence on the winter distribution of Amur tigers, with a contribution of 63%, followed by distance from settlements, distance from cropland, and distance from deciduous forest (Figure 3).

Spatial distribution prediction of Amur tiger's path tortuosity

We used the fractional dimensions evaluated at the 2–50 m full-scale range to develop the best model for predicting the spatial distribution of Amur tiger tortuosity. The path tortuosity of the Amur tiger in Hunchun in winter was predicted using the regression coefficients of the best model (see Supporting Information Appendix S1: Table S2). The raster calculator in ArcGIS 10.7 produced maps of fractal dimension spatial prediction with an accuracy of 50 m. Pearson analysis determined that tiger habitat suitability was negatively correlated with path tortuosity ($r = -0.212$, $p = 0.043$) (Figure 4c).

DISCUSSION

This study explored the fine-scale movement patterns of Amur tigers in Hunchun based on snow tracks, finding low path tortuosity and high permeability where the habitat is suitable, and vice versa, while winter habitat suitability predictions showed that prey, human settlements, cropland, and broad-leaved forest vegetation were the main variables influencing Amur tiger distribution. The optimal linear mixed-effects model showed that Amur tiger path tortuosity was negatively correlated with distance to towns and shrub vegetation, and positively correlated with distance from tertiary roads. These results provide important implications for fine-scale habitat modification to increase landscape permeability. While the behavioral data collected during our field tracking were not part of our best models, they make a significant contribution to explaining the relationship between the movement trajectories of Amur tigers and the characteristics of their surrounding environment.

Relationship between habitat permeability and path tortuosity

Our study used the habitat suitability value as an indicator to evaluate landscape permeability, based on the hypothesis that landscapes with lower landscape resistance are more suitable habitats, and vice versa

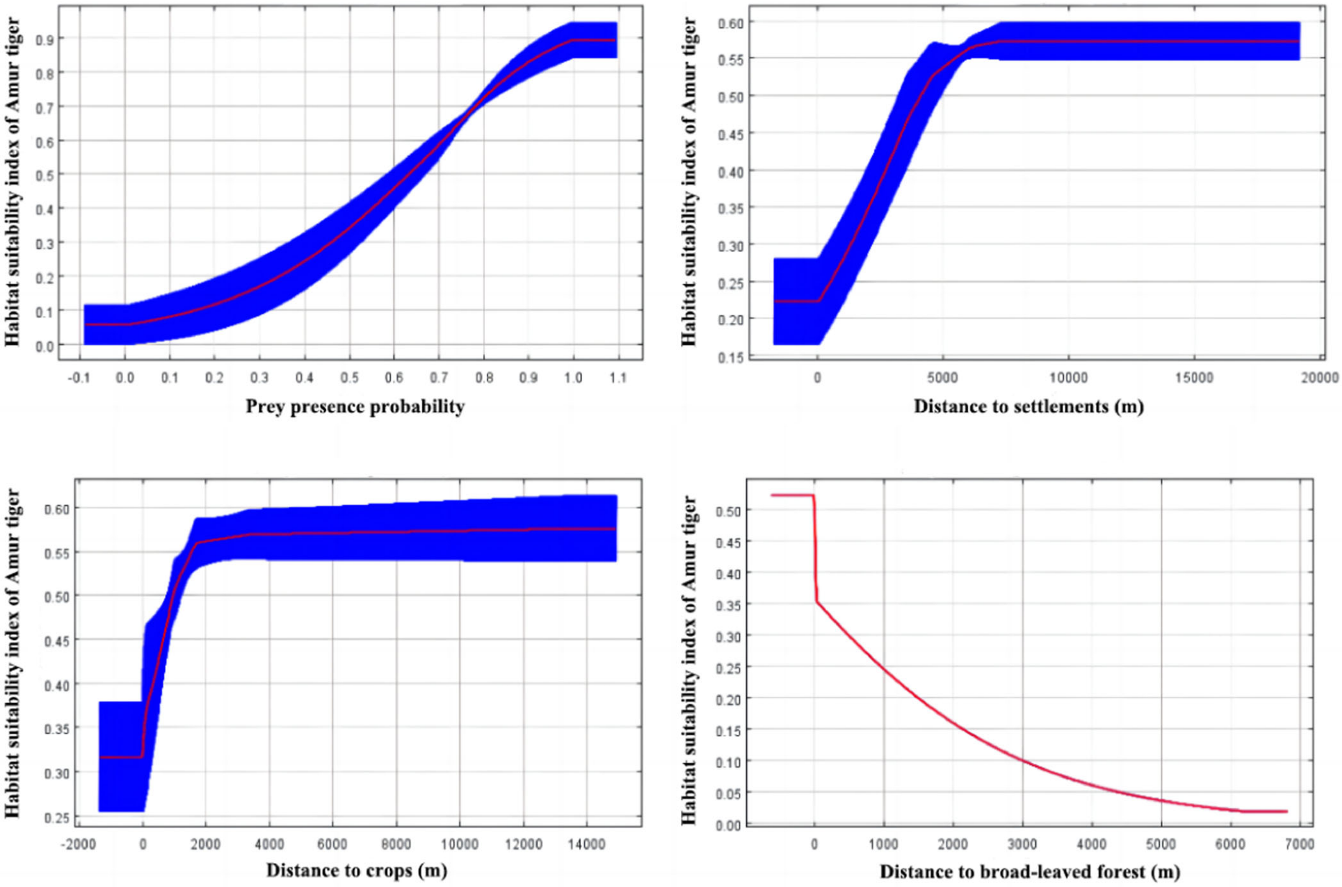

FIGURE 3 Response curves for the four variables in the Maxent model with the highest contribution. The contribution percentage of the prey presence probability is 62%, the distance to human settlements is 9.7%, the distance to croplands is 7.3%, and the distance to broadleaf forests is 4.7%.

(Guerry & Hunter, 2002). Evidently, combining movement pattern analysis with habitat suitability models to determine Amur tiger permeability across the landscape can provide more information than habitat suitability models alone.

Previous studies on the path tortuosity of herbivores (e.g., ungulates, African elephants *Loxodonta Africana*) have discovered that they have a higher path tortuosity in favorable habitats (Duffy et al., 2011; Jiang et al., 2009), which is in contrast to our results. There are two possible reasons for this. The first reason may be related to the distribution patterns of resources required by animals across the landscape and the different ways in which animals access them. In habitat areas with dispersed resources, these animals will rely on a highly tortuous path to improve foraging efficiency (Etzenhouser et al., 1998). Conversely, tigers need to capture large prey and they are directional when moving through the landscape (Sunquist, 1981). In this study, suitable Amur tiger habitat was in areas with a high occurrence probability of prey, meaning that tigers did not have to spend too much time searching for prey. Additionally, Amur tigers follow prey tracks over long distances, moving more in a straight line than in a prey trail, and after locating prey, the Amur tiger likely chooses the shortest route to wait, track, and deduce where the prey will pass before finally attacking the prey (Zaitsev, 2012). Therefore, Amur tigers may exhibit lower path tortuosity. However, in the case of African lions (*Panthera leo*), large herbivores tend to gather around water sources, and lions adopt a more regional (more tortuous) limited search strategy near water sources to minimize search efforts (Valeix et al., 2010), contrasting with our results and illustrating that the tortuosity of an animal's path is related to its hunting strategy.

Another more likely reason influencing tortuosity is the influence of habitat structure. The predicted habitat suitability map shows that the areas with poor habitat suitability are those where anthropogenic features are densely distributed. Anthropogenic features fragment the habitat and reduce habitat permeability for animals, hindering their movement (Jiang et al., 2014; Stevens & Boness, 2003; Whittington et al., 2004). Notably, however, areas with high suitability for Amur tigers were also areas with a dense distribution of tertiary roads, and we suppose that tertiary roads likely facilitate Amur tiger movement and reduce tortuosity (see below).

Factors influencing Amur tigers' movement

Effects of human disturbances on the movements of Amur tigers

The linear mixed effects model shows that the closer the tigers are to townships, the higher their path tortuosity

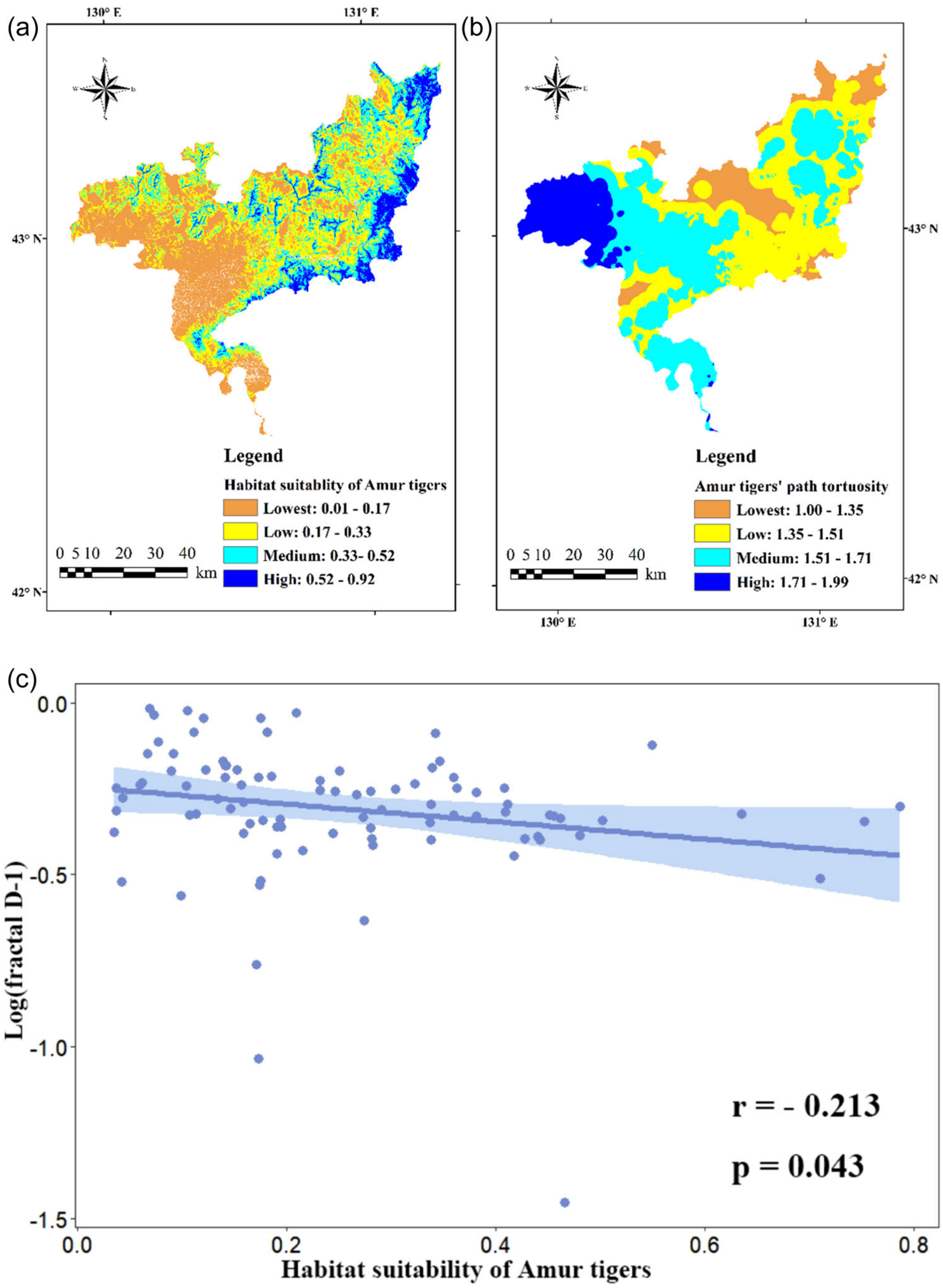

FIGURE 4 (a) Habitat suitability of Amur tigers predicted using winter occurrence point data of the Amur tiger from 2014 to 2022 by MaxEnt at 50 m resolution, (b) path tortuosity value distribution map at 50 m resolution of the Amur tiger predicted by the linear mixed-effects model, and (c) Pearson analysis of the relationship between extracted habitat suitability values and path tortuosity values at 7 km resolution. Fractal dimension values were normalized.

will be, and the MaxEnt model results show that the suitability index is lower as the distance to residential areas increases, within a range of 0–5 km. These results suggest that Amur tigers will take a circuitous route to avoid being close to areas with higher human activity. At larger spatial scales, village density is one of the most important factors affecting the occurrence probability of Amur tigers (Long et al., 2021), and many studies have found that large carnivores rarely occur in areas with dense infrastructure, preferring areas with low human activity (Klaassen & Broekhuis, 2018; Markovchick-Nicholls et al., 2008). Here, we obtained similar results at fine scales, and it is possible that tigers perceive anthropogenic disturbance more acutely than we observed; this needs further investigation.

The MaxEnt model results for the Amur tiger show that the suitability index for the species is lower closer to agricultural areas, and this has also been tested in previous studies on the species (Jiang et al., 2014). Croplands in Hunchun are mainly concentrated near settlements, where human interference is high, and during winter, croplands cannot provide cover for the Amur tigers, resulting in avoidance behavior.

The fragmentation of wildlife habitat due to linear infrastructure left by forest logging may now facilitate the least-cost movement for animals through the landscape and present opportunities for foraging for food. For example, grizzly bears (*Ursus arctos*) had less tortuous movements when they were closer to forest roads within the logging area (Roever et al., 2010), consistent with our study, although Grizzly bears and tigers may be using them for different purposes. As we found traces of Amur tigers urinating, defecating, and pawing the ground with their hind feet on the forest roadside during the actual tracking, it is likely that Amur tigers use roads to patrol and mark their territories, especially to reduce energy consumption in the heavy snow season (Gittleman, 1993; Kerley et al., 2002; Pikunov et al., 2014). These forest roads are not tortuous, so the path tortuosity of the Amur tiger is low. For cougars (*Puma concolor*), lower-class roads are used when passing through human-dominated areas, also taking into account the energy cost of moving (Dickson et al., 2005), while other large carnivores have been shown to use roads at night because of reduced human activity at night (Kautz et al., 2021). Hence, we suppose that reduced human activity during winter also promotes forest road use by Amur tigers.

Impact of vegetation on the movement of Amur tigers

Broad-leaved forests are more suitable for Amur tigers' survival than shrubs, wetlands, coniferous forests, and other vegetation types (Jackson, 1995). The increased path tortuosity near shrubs in our results may be that Amur tigers do not prefer shrub vegetation or such vegetation types may impede tigers' movement through the landscape, resulting in higher tortuosity. However, in studies of human-tiger conflict, tigers have been found to use dense shrubs as beneficial cover when capturing their prey (Miller et al., 2015). During our field-based tracking, we also found traces of Amur tigers jumping over low shrubs at the roadside, suggesting that Amur tigers are capable of moving through low shrub vegetation and that winding paths around shrub vegetation may be the result of concealment behavior.

Impact of prey on the movement of Amur tigers

The prey occurrence probability variable in the linear mixed effects model may have been insignificant in influencing Amur tiger tortuosity due to its prediction being limited to a small scale. However, prey probability had the greatest impact on the Amur tiger's habitat suitability in the MaxEnt model. At scales above 1 km, the abundance of ungulate animals is considered the most critical factor driving the distribution of Amur tigers (Long et al., 2021). Together, this suggests that at both a microscale of 50 m and larger scales such as 1 km, prey populations are the primary driving force for large carnivore movements during winter, also validating the idea that prey is a major factor influencing the distribution of large carnivores [Karanth et al., 2004]. This highlights the importance of combining different methods to analyze factors affecting animal movement in landscapes, to avoid missing crucial information.

Quantifying path tortuosity using fractal analysis

In this study, we used fractal analysis to calculate the tortuosity of animal movement paths. However, fractal analysis has been criticized because fractals describe objects with self-similarity and scale-independent properties, but objects in nature are not fractals in the true sense, so using fractal analysis to calculate the features of the object in this context could be deemed inappropriate (Halley et al., 2004; Loke & Chisholm, 2022). Despite this, many researchers continue to use fractal analysis to study natural phenomena because fractals can be used as simple models to approach the messy and multi-scale nature of natural phenomena (Halley et al., 2004; Melaschenko & Hodges, 2020; Opps et al., 2020; Troup et al., 2020). It has also been demonstrated that the properties of fractal dimensions can be used to examine the spatial scale domain of animal-environment interactions (Nams, 2005). For example, the fractal dimension is constant over a range of scales, and if there is a discontinuity in the fractal dimension, it indicates that animals' path structures change from one scale to another and that the animal responds differently to the environment. Our results showed that the fractal dimension of Amur tigers was almost constant at the fine scale range of 2–50 m, in contrast to martens (*Martes americana*) and ungulates (Jiang et al., 2009; Nams & Bourgeois, 2004). The range of scales at which qualitative differences in tiger pathways occur can be tested in the future.

CONSERVATION IMPLICATIONS

Through our research, we have gained a better understanding of landscape characteristics and location information that promote or hinder the movement of Amur tigers. Based on these findings, we propose recommendations for small-scale habitat modification to enhance landscape permeability for Amur tigers, helping them to disperse: First, the tertiary roads in Hunchun may serve as corridors that facilitate the movement of tigers to other areas and so should be well maintained to minimize human disturbance and to monitor usage by tigers. Forest roads can be constructed in areas where habitat suitability has been reduced by anthropogenic landscape disturbance and supplemented with food to attract prey, thus encouraging Amur tigers to use the roads to disperse to other areas. Second, to reduce the incidence of human-tiger conflict, large areas of tall shrubs or conifers could be planted around areas of high human activity to separate them from areas where Amur tigers are active, thereby significantly reducing the probability of human and tiger space use overlap. Third, small patches of low shrubs could be planted near to areas where fodder is added to attract prey during tertiary road construction, facilitating Amur tiger stalking and capture behavior when hunting.

FUTURE RESEARCH PERSPECTIVES

Here, we tested the relationship between landscape permeability and path curvature and discussed whether path curvature can serve as a proxy indicator of landscape permeability, and in the process we have provided potential new directions for research in landscape permeability assessments. This study was conducted during the winter season and we expect that different seasons may result in variations in animal movement patterns due to changes in the landscape (Rozhnov et al., 2011); we recommend exploring movement patterns during different seasons. Additionally, combining footprint tracking with collar data can be used to verify the relationship between path curvature and landscape permeability. Finally, it will also help to model relationships between path tortuosity and landscape permeability in different landscape types to indicate landscape-specific permeability.

AUTHOR CONTRIBUTIONS

Ying Wang: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); visualization (lead), writing—original draft (lead); writing—review and editing (equal). **Wannian Cheng**: Data curation (equal), investigation (equal). **Yanhui Guan**: Investigation (equal). **Jinzhe Qi**: Investigation (equal). **Nathan J. Roberts**: Writing—review and editing (equal). **Dusu Wen**: Investigation (equal). **Zhigang Cheng**: Investigation (equal). **Feng Shan**: Investigation (equal). **Yan Zhao**: Investigation (equal). **Jiayin Gu**: Conceptualization (equal); data curation (equal); supervision (lead); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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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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