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Scale choices shape species adaptation predictions: Improving conservation modeling under global change

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Abstract

Ecological models must mimic observed patterns to predict species responses to global environmental change. However, the observation of patterns is scale-dependent, which poses a fundamental challenge for conservation policy under increasing anthropogenic pressure. This paper examines how choices on temporal and spatial modeling scales affect our understanding of species adaptation to changing environments, using tiger conservation in Nepal's Bardia National Park as a case study. Case study analysis revealed how tigers adapt to climate-driven habitat modification through mechanisms invisible at coarse modeling scales. Different temporal scales uncovered distinct patterns of human-wildlife coexistence, while spatial scales shaped our understanding of how habitat connectivity affects adaptation. This scale dependency of observation determines which processes we can discover and predict. We provide four novel recommendations for scale-aware ecological modeling under global change: explicit documentation of scale contexts, probability models to compensate for abstraction, sensitivity analyses of scale choices, and connected models across scales.

KEYWORDS

agent-based modeling, Bardia National Park, ecological modeling, human-wildlife coexistence, policy design, scale selection, tiger conservation

1 | INTRODUCTION

Stand close to Georges Seurat's "A Sunday Afternoon on the Island of La Grande Jatte," (Seurat, 1884–1886, Figure 1) and distinct colored dots become visible. Step back, and these dots form recognizable shapes—people, trees, water. Retreat further, and these shapes create patterns of light and shadow.

Each viewing distance reveals different aspects of the painting, contributing to our understanding of the whole. This analogy of scale-dependent observation applies to ecological systems. Our scale of observation shapes what patterns we will see emerging in real life and in ecological modeling (Galiana et al., 2018; McGarigal et al., 2016). A predator's movement may appear random when positions are observed once every hour, purposeful when observed at daily intervals, and territorially bounded when observed at yearly intervals (Malishev & Kramer-Schadt, 2021; Moorcroft & Lewis, 2013). A habitat may appear fragmented when observed in square kilometers but connected when examined in meters (Kramer-Schadt et al., 2004; Miguet et al., 2016). What part of the complexity of

FIGURE 1 Georges Seurat's "A Sunday Afternoon on the Island of La Grande Jatte" (1884–1886).

movement patterns, habitat use and boundaries is observed depends on the scale chosen, just as no single viewing distance captures a Pointillist painting's full complexity.

The scale dependency of ecological modeling presents a challenge in conservation, where multiple stakeholders value observations at different temporal and spatial scales, yet must work together toward common goals (Carter et al., 2012). Traditional ecological modeling approaches often adopt a single-scale perspective, typically aligned with the immediate needs of the commissioning stakeholder. A model developed for national park scientists might focus on yearly territory shifts to inform resource allocation, while one created for local community officers might track daily movement patterns to minimize human–wildlife conflict (Thatte et al., 2018). Both perspectives are useful, yet neither alone captures the full complexity of the system. This tension between scales of observation and scales of interaction can lead to incomplete or even contradictory management recommendations (Grimm & Railsback, 2012; Leroux et al., 2017).

For example, a continental-scale agent-based model of white stork migration across 700,000 km^2 of East Africa recommends avoiding wind development where corridors overlap with suitable wind sites (Oloo et al., 2018). In contrast, a turbine-blade-scale agent-based model (50 m resolution) of golden eagles in Wyoming shows birds successfully navigating around individual turbines, recommending fine-scale placement adjustments rather than regional exclusions (Sandhu et al., 2022). Agent-based models of the same conservation challenge can thus produce opposite management strategies, which in part depend on model scale.

In Bardia National Park, different stakeholders operate at different temporal and spatial scales, yet must coordinate tiger conservation efforts. Park scientists conducting annual territory surveys might conclude that tigers avoid human-dominated areas based on yearly GPS coordinates, potentially reducing conflict prevention measures. Meanwhile, local community officers tracking daily movement patterns could identify frequent tiger incursions into villages, recommending intensive conflict mitigation. These contrasting scale-dependent observations of the same tiger population could lead to contradictory management recommendations—complacency versus heightened vigilance—demonstrating how temporal modeling scales directly influence conservation policy decisions.

Ideally, policy makers would use ecological models to evaluate the effectiveness of management policies (Carter et al., 2012; Jhala et al., 2019). However, this requires that the models can demonstrate their utility for decision-making (Grimm & Railsback, 2012, Grimm and Berger, 2016).

In this paper, we use an agent-based model that simulates tiger territory formation in Bardia National Park to demonstrate how scale selection shapes our understanding of observable patterns and discuss policy consequences. This case study examines how different temporal and spatial scales affect our ability to capture movement patterns and territory formation, identify the challenges in simulating tiger behavior in human-dominated landscapes, and provide recommendations for scale-aware modeling to support conservation policy.

2 | CASE STUDY AREA: BARDIA NATIONAL PARK, NEPAL

Bardia National Park, established in 1988, encompasses 968 square kilometers of diverse habitats in Nepal's Terai lowlands (Figure 2). Water availability, primarily from the Geruwa River and its tributaries, shapes the landscape and influences the health and extent of grasslands, which cover approximately 15% of the park area (DNPWC & DFSC, 2022).

Grasslands and forests in this area support a high prey density of 92.6 animals per km^2, with chital (axis deer, Axis axis) being the most abundant at 62.7 individuals per km^2. The park is surrounded by a 507 km^2 buffer zone comprising 21 Village Development Committees with approximately 114,200 people across 17,228 households (Figure 1). The tiger population in Bardia National Park has increased from 18 individuals in 2009 to 125 in 2022 (DNPWC & DFSC, 2022; DNPWC, 2023). Studies in similar landscapes have documented territory sizes of 50 km^2 for males and 25 km^2 for females (Barlow et al., 2011). Bardia's current tiger population density suggests that tigers are adapting their spatial behavior to accommodate higher densities than typical territory size estimates would predict, potentially through increased territory overlap or shifts in resource use patterns.

3 | ILLUSTRATION USING AGENT-BASED MODELING

To examine how scale choices affect our understanding of tiger behavior, the Bardia case study combines simple agent-based modeling with field observations. ABM allows for studying complex ecological systems and investigating emergent properties (DeAngelis & Grimm, 2014; Grimm & Railsback, 2012; McLane et al., 2011). This simple agent-based model serves to illustrate scale-dependent concepts rather than provide detailed mechanistic predictions about tiger behavior. A simple model simulated tigers moving through the national park's core and buffer zones, incorporating elevation maps and GPS locations to reflect the landscape. Within this environment, tigers follow random walks in circular territories—50 km^2 for males and 25 km^2 for females—based on observations from the Sundarbans (Barlow et al., 2011).

Due to a lack of available data on territory sizes of tigers in Bardia, the model uses imposed territory sizes instead of a mechanistic model where animal decisions are represented (e.g., Imron et al., 2011; whereas Carter et al., 2015 let territories emerge from prey and conspecific density).

Movement parameters were derived from a GPS collar study of tigers (Naha et al., 2016), where 6 tigers were tracked with 1–3 h fix intervals (fix acquisition rate

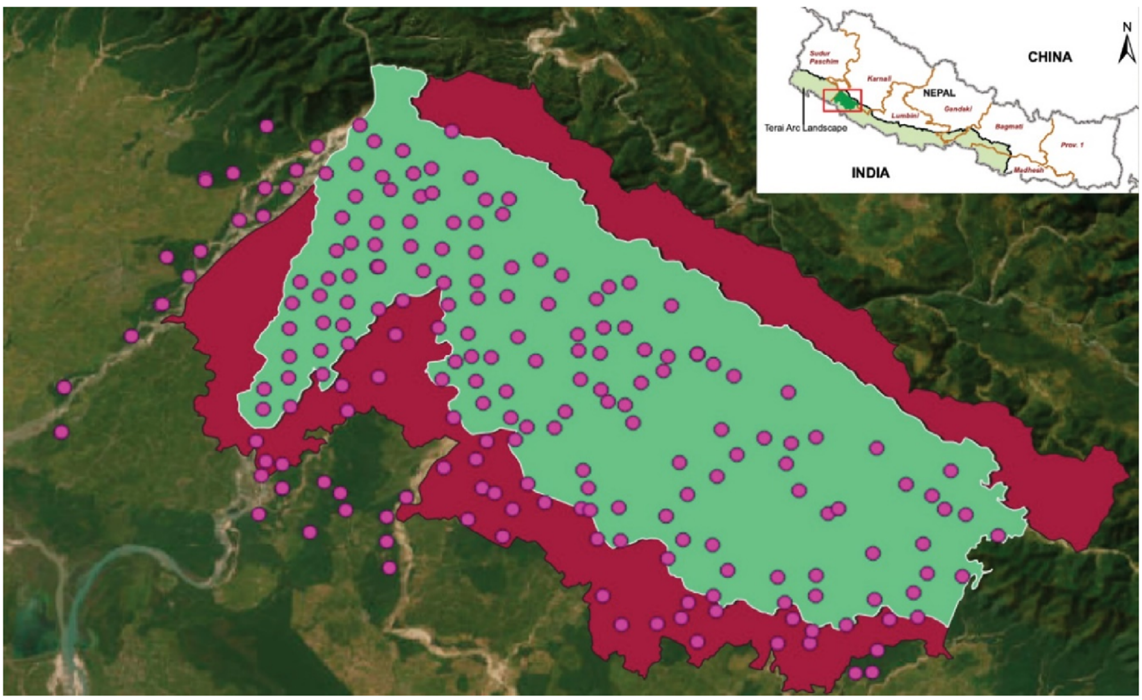

FIGURE 2 Geographic location and tiger distribution in Bardia National Park, Nepal. Bardia National Park is shown in green, (968 km^2), the buffer zone in red, (507 km^2). Pink dots represent individual tiger locations documented in the 2022 national tiger survey (DNPWC & DFSC, 2022). The inset map (top right) shows Bardia's location within Nepal's Terai Arc Landscape.

of 66%) which reports not just the mean of daily movement distances (4.6 km), but also the range (0.1–23 km) which greatly expedites the formulation of movement in an ABM. Furthermore, it reports the propensity of tigers to cross rivers of different widths. However, because it concerns Sundarbans, which as a mangrove habitat does not resemble Bardia, the generalizability of these parameters for our example is limited. Because our example is illustrative rather than definitive, we accepted this limitation.

The specific technical details of this model are less important than its demonstration of how scale choices affect pattern recognition in ecological modeling. In our model the movement was implemented using polar coordinate sampling, where each daily position was determined by coordinates (r, θ), with $r = R\sqrt{u}$ and $\theta = 2\pi v$ (R is territory radius, u, v are uniform random numbers), for two key reasons:

The $\sqrt{r}$ transformation in the polar coordinate sampling ($r = R\sqrt{u}$) corrects for the increasing area at larger radii within circular territories. Without this transformation, random points would cluster toward territory centers, but the square root scaling ensures uniform spatial coverage across the entire territory area (Moorcroft & Lewis, 2013). This approach matches observed patterns of how tigers utilize their home ranges in similar landscapes (Simcharoen et al., 2014), creating naturalistic movement patterns within bounded territories for this simple illustrative model.

1. It created a bounded territory while allowing random exploration, matching observed carnivore behavior (Mitchell & Powell, 2004).
2. The $\sqrt{r}$ transformation ensured uniform spatial coverage within the territory (Moorcroft & Lewis, 2013), matching observed patterns of how tigers utilize their home ranges in similar landscapes (Simcharoen et al., 2014), while creating more naturalistic movement patterns near territory boundaries (Mitchell & Powell, 2004).

This approach allowed explicit testing of scale-dependent territory size assumptions, crucial for investigating how tigers adapt their spatial requirements in human-dominated landscapes.

This illustrative ABM simulated potential spatial arrangements of tigers under increasing population density and examined implications of territory overlap. The visualization (Figure 3) revealed two key insights: extensive territory expansion into buffer zones, and increased tiger-tiger conflict as population numbers increased. While these visualizations proved valuable for stakeholder engagement with nature guides and conservation officers, who could relate the patterns to their field observations, the model's lack of mechanistic underpinnings limited its utility for direct policy exploration. These model outputs guided subsequent field investigations by highlighting potential scale-dependent patterns, rather than providing quantitative predictions for testing.

In March 2024, we collected field observations (exploration path in Figure 4, panel I) and held workshops with local stakeholders in Bardia National Park. Field observations found several discrepancies closely related to how scale choices had been implemented in the model. One example was local fishing communities' temporal

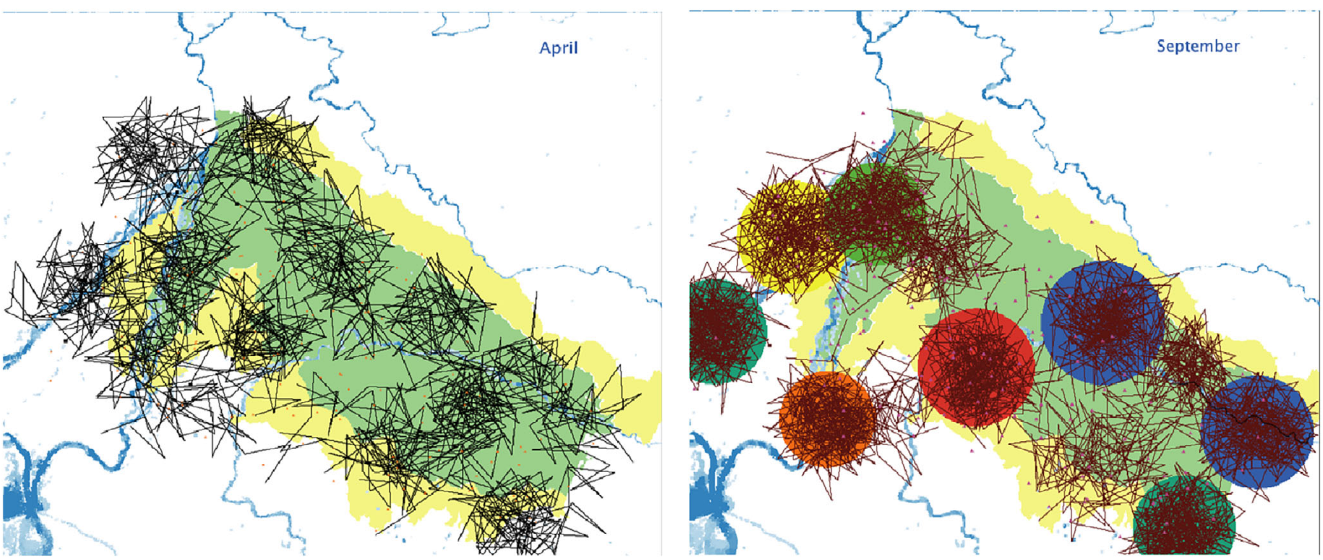

FIGURE 3 Visualization of agent-based model output showing tiger territories in Bardia National Park (green is the national park core, yellow buffer zones). Black lines show movement paths of individual tigers, with colored circles delineating territory boundaries.

FIGURE 4 Field evidence of tiger adaptation in Bardia. In panel I marker (A) 4 km by 2.5 km area in which six unique fresh footprints of tigers were observed by the lead author in March 2024. Marker C is next to what is locally referred to as "Love Island". Panel II, fishing in tiger territory (between markers B and C) (temporal partitioning). Panel III, fresh tiger footprints in fresh tire marks.

partitioning. Panel II demonstrates temporal partitioning, where local fisherwomen cease activity at 3:00 PM, allowing tigers to use the same riverine areas during afternoon and evening hours without human–wildlife conflict. This represents a coexistence strategy that enables tigers to maintain access to water resources in human-dominated landscapes.

This is an indirect form of adaptation where tigers benefit from predictable human behavioral patterns. Such daily rhythms are invisible in daily-scale models. There were also interesting points of convergence. The model suggested that the number of tigers in Bardia and the typical movement pattern used would lead to impossibly close proximities of tigers to each other.

And indeed, our workshops revealed that in Bardia tigers are increasingly coming into conflict with one another, leading to tigers exploring community forests and buffer zones as prospective territories.

There is the unusual observation of multiple tigers sharing a small riverine island (Figure 4).

This proximity between tigers diverges from previously documented territory sizes in similar landscapes (e.g., Kanagaraj et al., 2013; Thatte et al., 2018), suggesting that some tigers show adaptation to increased population density. How this will develop in the future is unknown. Despite these convergences, the illustrative ABM's limitations demonstrate how scale choices determine which processes we can discover (Evans et al., 2013; Fraser et al., 2013; Levin, 1992). In Bardia, tigers seem to have adapted through mechanisms invisible at our model's scale. Our model was spatially explicit, but tigers' activities were not coded to be habitat dependent.

This became particularly evident during field investigations, where we observed tigers utilizing diverse micro-habitat features that our model did not capture but were crucial to predicting where tigers would go. New grass growth in burnt areas provides hunting opportunities (Figure 5, panel IV), dried riverbeds serve as movement corridors (Figure 5, panel V), and dense grass thickets offer concealment (Figure 5, panel VI). These diverse micro-habitats, invisible in daily simulations, allow multiple tigers to share small spaces without the predicted lethal conflicts.

The model's limitations reflect our methodological focus: examining how scale choices shape ecological understanding rather than predicting tiger behavior. Without territory emergence mechanisms or validated behavioral parameters for Bardia, the model cannot generate testable quantitative predictions. Instead, it demonstrates that regardless of model sophistication, the chosen temporal and spatial scales predetermine which ecological processes can be observed. This is a fundamental constraint for conservation modeling that must be acknowledged before developing predictive models.

FIGURE 5 Field evidence of micro-habitat use enabling tiger coexistence (taken between markers A and B of Figure 4, panel I). Panel IV, new grass growth in burnt areas provides hunting opportunities, panel V, tiger footprints on dried riverbed showing use of seasonal corridors, and panel VI with tiger paths through dense grass thickets.

4 | SIGNIFICANCE OF SCALE SELECTION IN ECOLOGICAL MODELING

Our experiences confirm key principles on how scale choices impact understanding of ecological interactions and, consequently, any approach to policy design and effectiveness evaluation.

First, different scales reveal different aspects of the system (Levin, 1992; Wu et al., 2006). Extremely high-resolution modeling may not always provide additional actionable insights for the questions we are addressing. Second, some patterns only emerge at specific scales (Peterson et al., 1998; Schneider, 2001). Third, cross-scale feedback loops create emergent constraints by revealing how interactions between different scales generate unexpected limitations or boundaries in a system (Cumming et al., 2006; Peters et al., 2007). Fourth, the scale of observation determines what mechanisms we can discover (Schneider, 2001; Wiens, 1989). Following these principles, we next discuss the impact of temporal scale and spatial scale on simulating tiger movement patterns.

4.1 | Temporal scale impacts perceived use of space

While behavioral ecologists typically employ finer temporal resolutions for studying wildlife interactions, conservation management and policy decisions often rely on annual monitoring reports, population surveys, and yearly occupancy data. This creates a disconnect between research temporal scales and management temporal scales that can have significant conservation consequences.

The first scale choice concerns time. Even in a simplified theoretical model, not intended to be spatio-temporally explicit in resembling Bardia, we must choose what each discrete time unit represents. Some observations occur at yearly intervals, others at hourly intervals. Our models inevitably form an abstraction at an aggregated temporal level above the microsecond scale of actual processes. Consider a simplified model of a single tiger making a random walk through an area containing human settlements. Even in such a simplified model that does not yet incorporate factors such as barriers, energy, or hunting — which will be discussed in later sections—the seemingly arbitrary choice of time scale significantly affects our conclusions.

Figure 6 presents conceptual demonstrations of four panels of a buffer zone where wildlife and human populations coexist, while simulating tiger movements at different temporal resolutions: yearly (a), monthly (b), daily (c), and hourly (d). Human-dominated spaces are represented by huts and fenced livestock areas in red icons. Start and end points of the tiger's annual journey remain the same across all panels.

Panel (a), simulating yearly movement, shows a displacement of the tiger from one region to another. This yearly time scale suggests that the tiger's movement is confined within the forested dense vegetation area, seemingly avoiding human-dominated spaces.

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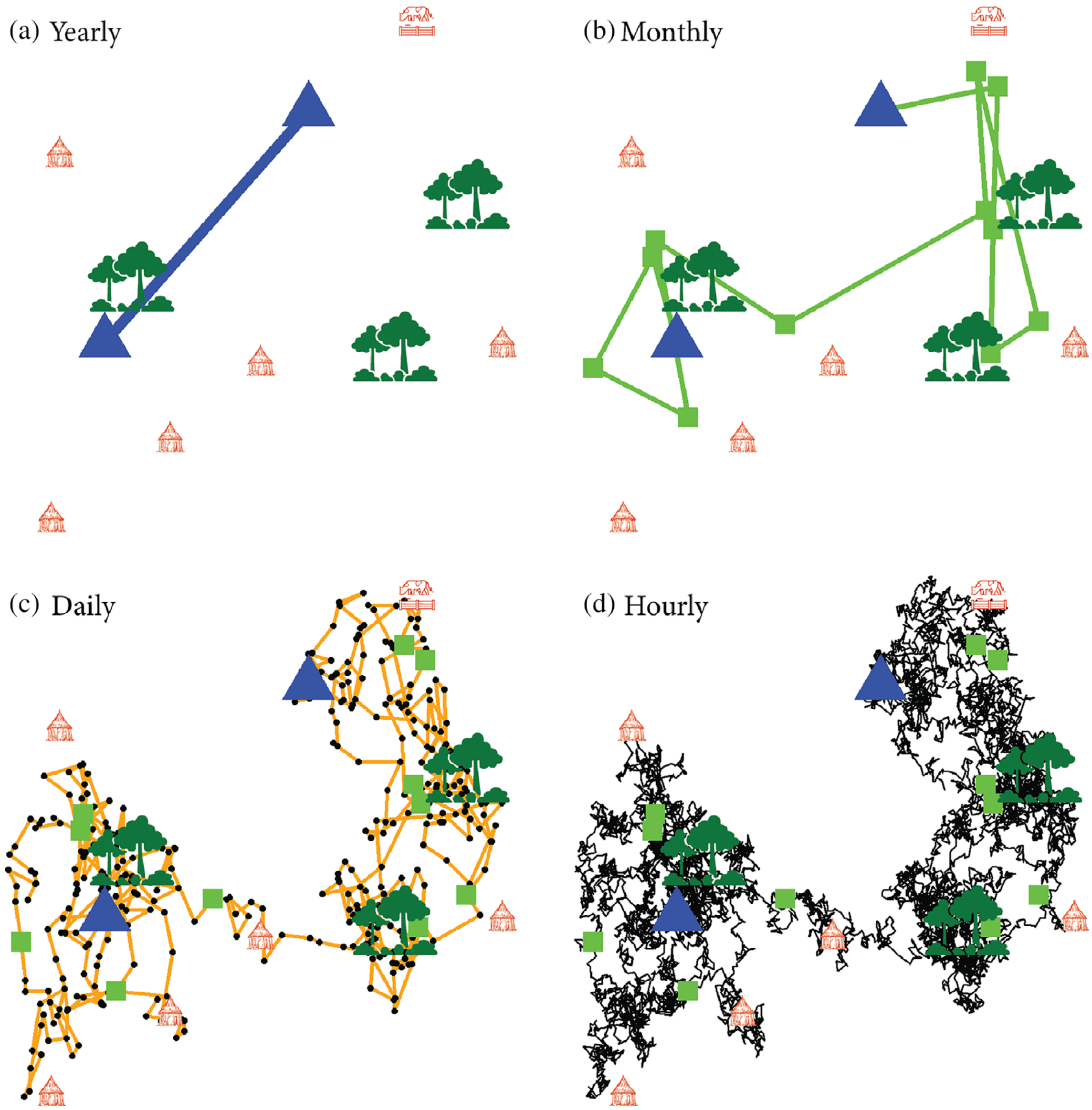

FIGURE 6 Illustration of how observations of tiger movement change with the temporal scale at which observations are made. Panels (a)–(d) represent tiger movements at yearly (a), monthly (b), daily (c), and hourly (d) scales. Human settlements and livestock are represented with red icons. Panel (a) (Yearly) suggests minimal interaction with human settlements. Panel (b) (Monthly) shows periodic approaches to human settlements, indicating potential human–wildlife conflict. Panel (c) (Daily) and Panel (d) (Hourly) show frequent incursions into human-dominated zones.

In Panel (b), which represents monthly movement patterns, we begin to see that the tiger's path is more intricate. The monthly simulation reveals that the tiger might approach areas closer to human settlements during certain months, a detail that the yearly model could not capture.

Panel (c) further refines our understanding by simulating daily movement patterns. At this resolution, the tiger travels larger distances and spends considerable time in or near human-dominated landscapes, something invisible in the coarser time scales. Finally, Panel (d)'s hourly movements present the most detailed and complex pattern. Here, we see the tiger frequently visiting human-dominated areas, and spending hours there.

The progression from yearly to hourly temporal scales demonstrates how coarser temporal resolutions can systematically underestimate both the spatial extent of tiger habitat utilization and the frequency of potential human-wildlife interactions. A yearly model might suggest that human-dominated areas are safe from tiger incursions, potentially leading to complacency in wildlife management policies. If we take the yearly data at face value, we may infer that the tiger traversed the center of the map diagonally, while it is visible in all other panels that it was never at the center of the map. In contrast, an hourly model shows frequent tiger visits to human-dominated areas, requiring vigilant management strategies. With coarse time scales, time-dependent effects such as seasonality also disappear. Seasonality affects the activities of various actors in the ecosystem, including herbivores and tigers.

During certain moments in the crop cycle, herbivores may be attracted to farms to eat agricultural crops rather than forest growth. As these herbivores move outside the core forest, the risk of tigers following them into human-dominated areas increases (Sharma et al., 2013).

Conservation policies, such as burning grasses in the winter to prevent overgrowth and facilitate grazing, influence the areas used by herbivores and, consequently, the areas frequented by tigers (Wikramanayake et al., 2004). Moreover, tigers adapt their activities seasonally to conserve energy, spending more time in shaded or water areas during the hot seasons (Barlow et al., 2011). These seasonal patterns are not observable when considering a yearly temporal scale.

Energy use adds another factor to our understanding of tiger activities and movement patterns simulated (Harte et al., 2024). Individual-based energy budget models have quantified how movement costs accumulate across temporal scales: Turning angles increase energetic costs by 10%–50% compared to linear movement, while step length variations across hours and days affect overall dynamic body acceleration and daily energy expenditure (Kramer-Schadt et al., 2004; Malishev & Kramer-Schadt, 2021).

The energy costs associated with fine-scale movement patterns —acceleration, deceleration, and directional changes—accumulate differently across temporal scales. A model that captures daily or hourly movement patterns (such as those in panels (c) or (d) of Figure 6) reveals the need for frequent intermediate kills to fuel these complex movement patterns, whereas coarser temporal resolutions mask these energy requirements.

4.2 | Spatial model resolution need not match spatial data resolution

Tigers rely on rivers, lakes, and water holes for survival. These water bodies can also act as movement barriers, especially in landscapes with significant human activity requiring the same resource (e.g., irrigation, fishing or washing). When rivers are simulated, the question arises of how much space they occupy and how they are represented in discrete grid cells (hereafter referred to as "patches").

Rivers are dynamic systems where flow regimes, channel morphology, and connectivity change in response to climate variation, seasonal patterns, and anthropogenic pressures (O'Briain, 2019). Climate change is expected to modify temperature and precipitation patterns, leading to altered seasonal discharge that can fragment continuous river networks into disconnected pools or conversely reconnect previously isolated habitats (Fuller et al., 2015).

Therefore, the projected changes in rivers can directly influence how tigers move around their habitat. As rivers are dynamic entities, simulating rivers requires networks of patches whose extent changes with fluctuating water volume, such as during rainy seasons or high rainfall events. Depending on water volume, the number of patches that belong to a water body changes. Simulated water patches should inherently be connected to each other; otherwise, they do not make sense (Zeller et al., 2012). A river stream might be divided over two different patches in such a way that only 10% of each patch is corresponding to water. However, when such a patch would become "land," the simulated river might end up being disconnected, abruptly ending in one patch and then continuing in the next. Tigers do not need an entire patch to be blue to be able to use it patch to replenish thirst, cool down or play.

In agent-based models, space is typically discretized into "patches"—square grid cells of uniform size that represent discrete spatial units. In our conceptual demonstrations, we show three spatial resolutions: 625 patches (each around 1.5 km^2), 2500 patches (each around 0.4 km^2), and 10,000 patches (each around 0.1 km^2) for the 968 km^2 park area. At the finest resolution (0.1 km^2), a patch might contain partial habitat features like a river segment, while at the coarsest (1.5 km^2), entire habitat complexes are aggregated into single units.

Figure 7 illustrates conceptual representations of spatial resolution effects for modeling rivers as barriers. The Bardia case illustrates the impact of spatial scale selection for modeling rivers as barriers. Tigers can swim across narrow channels but are reluctant to cross wide bodies of water (Naha et al., 2016).

In Bardia, this observation is relevant as Bardia's water levels change due to seasonal variation and due to factors, such as climate change and glaciers melting. With rivers becoming increasingly narrow, a prediction that needs to be tested is whether there is sufficient water to provide a safe boundary between settlements and tiger habitats. In the ground truth panel 7A, the villages are not secure as they are close to a narrow point in the river.

In the lower panels, the river is abstracted into a rasterized representation as it is commonly found in ABMs, in one of two ways:

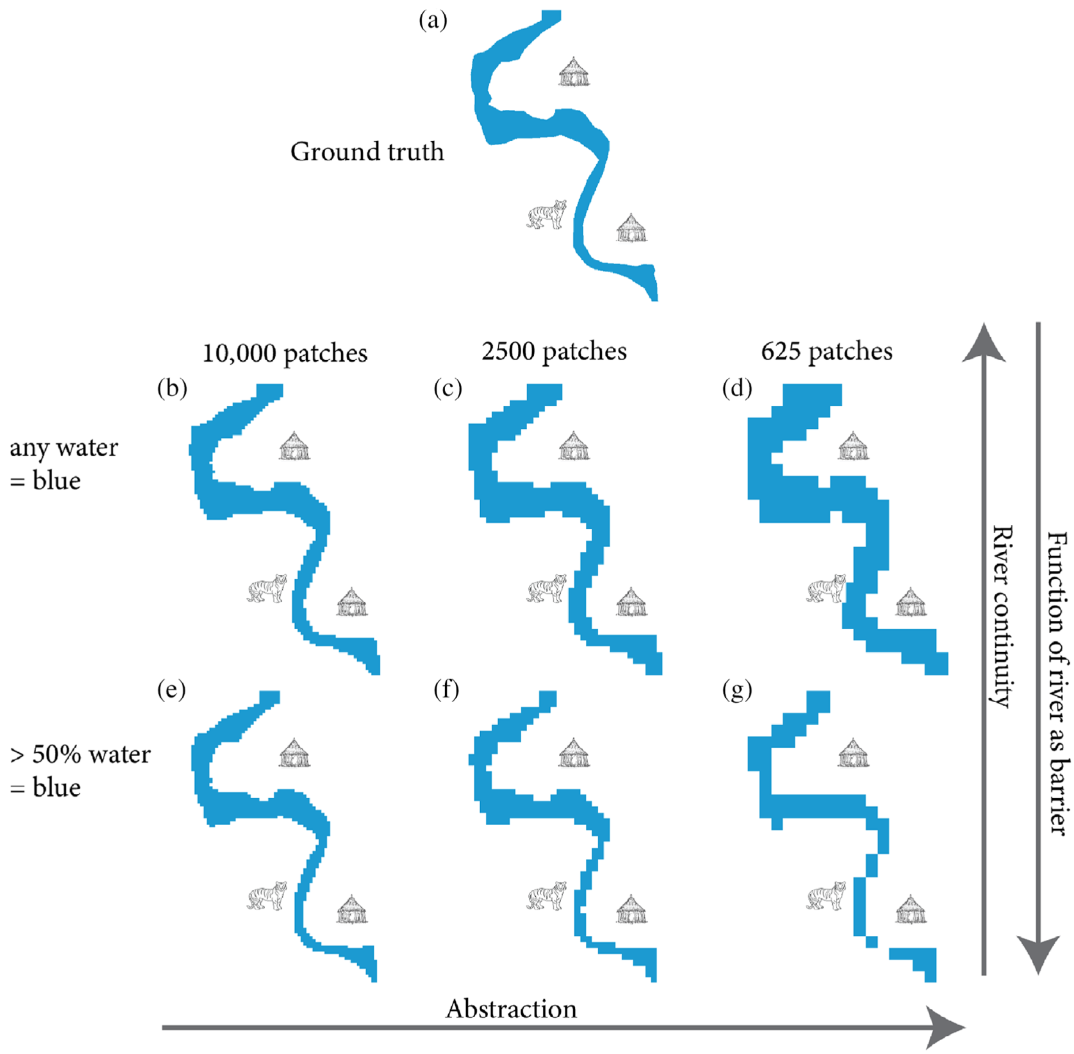

FIGURE 7 Illustration of how spatial resolution affects the modeling of rivers and their function as barriers in tiger habitats. Human settlements are represented with icons. The top panel shows the ground truth representation of a river where tigers can cross at narrow points. Lower panels demonstrate how rasterization at different resolutions (10,000, 2500, and 625 patches) affects the river's representation under two different water classification rules: Patches with any water are marked blue (middle row) versus patches with >50% water coverage are marked blue (bottom row).

1. If any of the ground truth patches contain water, the rasterized version at a lower resolution of that patch will be a water patch,
2. If over 50% of the ground truth patches contain water, the rasterized lower resolution will be a water patch.

As a result, in panels 7b and e, the tiger is able to cross the river in the same location as in the ground truth panel. In panels 7c and d, patches are increasingly less fine-grained. Even though the exact same data from panel 7a are represented, the river is so wide that it would be impossible for the tiger to cross. If we were to consider panel 7d from a policy-making perspective, we could infer that there is no danger to the human settlement at all. In panels 7f and g, with patches less fine-grained with a different rule, tigers can cross the river. In panel 7g, the river is disconnected, stopping in one location and continuing in another. This progression from high to low resolution in the model reveals that the choice of spatial scale and the rule to down-sample to a coarser scale affects our conclusions about the tiger's ability to cross rivers and interact with human settlements.

A high-resolution model indicates frequent river crossings and potential human-tiger conflicts, while a low-resolution model could either indicate that rivers act as effective barriers, potentially leading to complacency in wildlife management policies, or to the alarming conclusion that tigers can walk directly to human settlements.

There are several ways in which river data can be obtained from publicly available resources, such as digital elevation maps and satellite data. These data sets can be used to infer where the river should be flowing. The datasets come with an inherent resolution, for example, 30 by 30 m, and it might be attractive to assume that this resolution of the data is the most useful model resolution as well. However, we would argue that the usefulness of the spatial model resolution is not dependent on the spatial data resolution (which may be downsampled or upsampled later), but on the resolution of the represented activities, which primarily requires theory and content knowledge.

5 | RECOMMENDATIONS FOR SCALE SELECTION IN POLICY-DRIVEN ECOLOGICAL MODELING

Our analysis has revealed multiple areas where making spatial and temporal scale choices can potentially lead to consequential challenges when policies are derived from these simulations.

To mitigate these problems, we make four recommendations.

The following recommendations focus on making scale choices explicit rather than prescribing solutions to scale issues, as optimal temporal and spatial resolutions depend on specific research questions, system characteristics, and available computational resources. Rather than suggesting universal scales, we provide approaches for documenting and justifying scale selection decisions.

5.1 | Be explicit where patterns fall on spatial and temporal scales

When developing an ABM of an organism, it is essential to consider the different temporal and spatial scales at which the organism operates and at which its fate is determined. This includes the lifespan of the organism and the scale of migration patterns (arctic terns vs. snails) (Alerstam et al., 2003), but also the scale at which smaller yet consequential events happen (Peterson et al., 1998). For instance, while tigers may range over large areas across seasons, their survival can depend on split-second decisions during individual hunting attempts—highlighting how processes at very fine temporal scales can have long-term consequences. Therefore, explicit documentation of scale contexts becomes crucial.

This documentation should acknowledge that there are fine-scale processes present at a detailed level of abstraction, which could or could not be aggregated into broader patterns. Not only is there a lower-bound limit on what processes the agent-based modeling can represent, but there is also an upper-bound. The behavior of animals, which falls within the ABM, may lead to changes in policy, which falls outside the ABM. For example, if burning of grasses is not having the desired effect, policies will be adjusted that will affect deer behavior. In this case, policy adjustments would affect ecological interactions (i.e., that of deer and grass).

To position the scale at which our model produces patterns, we suggest plotting out various simulated activities, mapping their position on spatial and temporal scales. This representation was inspired by the work of Steele (1978, as cited by Levin, 1992), but hydrologists similarly map out phenomena on different spatiotemporal scales (Blöschl & Sivapalan, 1995): Glaciers move at a different time scale from storm fronts and span a different space scale from canals.

Figure 8 shows different spatial and temporal resolutions for tigers. Hunting sessions are plotted on the bottom left (small spatial scale, small temporal scale), the entire lifespan of a tiger on the top right (large spatial scale, large temporal scale). The shaded area labeled ABM1 depicts the spatiotemporal context of a hypothetical model. Activities in the bottom left affect activities in the top right but might not be explicitly included in the model. This graphical representation makes explicit at what level new patterns could emerge, and what patterns fall within and outside of the scope of a model.

5.2 | Include a probability model to compensate for abstraction

Including uncertainty at more abstract low-resolution levels can accommodate missing interactions at higher-resolution levels. For example, a confrontation between two tigers may be implemented as a moment when two tigers occupy the same patch in a simulation.

Such confrontations are rare with many patches (high-resolution spatial scale), and extremely rare with few time steps (low-resolution temporal scale).

When modeling at a yearly time step, the probability that two tigers will ever occupy the same patch is minute. Within the space of a year however, many intermediate daily and hourly steps will have taken place. In all 24 h of those 365 days, there were many rolls of the dice. During at least some of those 8760 occasions, tigers will have met other tigers in their proximity—with drastic emergent consequences, such as mating and subsequent cubs, or fighting and subsequent death. If the modeler chooses not to represent all 8760 occasions for computational or other reasons, representing the uncertainty directly is an

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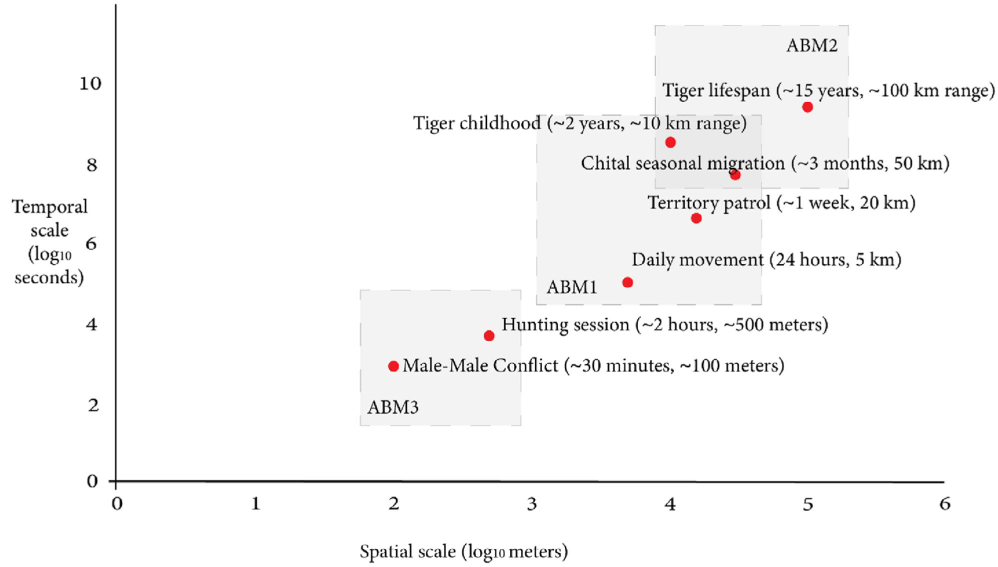

FIGURE 8 Illustration of the positioning of tiger and prey activities on spatial (x-axis) and temporal (y-axis) scales. Bottom-left patterns take place in a short time span and limited space. Top-right patterns occur at a longer duration on larger areas. The shaded square ABM1 denotes the scope of a hypothetical agent-based model encapsulating simulated activities. Each ABM covers a different scope in terms of temporal and spatial scale to reveal different emergent patterns.

option. Rather than representing tiger location as a single patch, tiger location may be represented as an area that a tiger peruses during the space of a month. With these approaches, confrontations between two tigers can be assessed as a probability based on the percentage of overlap between the two perusal areas.

Alternatively, the model need not represent movement at all but could focus only on space use in which tigers add patches until their energy requirements are met (Carter et al., 2015; Wang & Grimm, 2007). This may be less computationally intensive and simpler. In principle, working with probabilities is standard practice when the mechanistic basis is unknown or not the focus, because it still captures important variation without requiring finer-scale details. This solution does require assumptions on the distributional properties of movements, and on the shape of movement areas. Ideally, each of these assumptions would be supported by empirical data but at least should be made explicit in the model description.

5.3 | Run structural sensitivity analysis

Sensitivity analyses are commonly used to study the effect of one choice of parameter over another and are not generally used to study the structure of the simulated model world itself. However, the same reasoning holds. A modeler can choose two reasonable specifications of temporal scale (e.g., one step every 24 h vs. one every 12 h), and two reasonable specifications of spatial scale (e.g. 625 patches vs. 2500 patches) to reveal different requirements for the programmed routines, which would provide information in itself. But if all else remains equal, results and conclusions drawn from the 2×2 specifications can be compared.

If they are the same, this would provide confidence that the specific scale choices that were made were not the primary drivers of the conclusions. The goal of the sensitivity analysis would not be to broaden the scope, as the different settings would all concern the same shaded rectangle in Figure 8. The sensitivity analysis would serve to substantiate that small, arbitrary, differences in these choices do not affect the primary conclusions.

5.4 | Make multiple connected models at different scales

Modelers do not have to restrict themselves to a single model but might specify different models at different levels of abstraction to describe the same system. Even if models are not merged directly, it would be beneficial to have multiple models to describe multiple aspects of the system as shown in Figure 8. In an ecosystem of models, there can be a low-resolution, high-abstraction model, which is computationally efficient as processes are represented through computed probabilistic behavior (following recommendation 2). The added value would be that the formal basis for the shape of the probability distribution of this behavior pattern would be constructed with a separate ABM at a high-resolution fine-grained level. This second ABM can show the emergence of the pattern that we do not need to concern ourselves with in the top-level model. The benefit is that if we ever want to study the impact of other factors on this low-abstraction level, for example, whether the pattern still emerges with increased temperature due to climate change, the modeler can return to the highly abstracted model and run it with the new temperature parameters.

If the emergent pattern changes, adjustments can be made to the top-level, fine-grained model to account for the fact that the emergent behavior at the higher abstraction level no longer holds. Such multi-level or hierarchical modeling approaches —where a detailed, fine-grained model helps calibrate a simpler, coarse-scale model—represent one promising direction for agent-based modeling. Multi-level and hierarchical modeling approaches more broadly have been discussed in the agent-based modeling literature (e.g., Grimm et al., 2005; Grimm et al., 2006), and several research groups have implemented models that operate across multiple hierarchical levels and scales (e.g., Berger et al., 2006; Kramer-Schadt et al., 2005).

6 | CONCLUSION

Our discussion of scale selection in ecological modeling demonstrates how different temporal and spatial resolutions affect our understanding of species adaptation to changing environments. This understanding becomes critical as conservation policies must address both immediate responses, such as temporal partitioning between humans and wildlife (Carter et al., 2012), and longer-term adaptations in territory use and resource selection (Mitchell & Powell, 2004). The many changes that ecosystems are experiencing result often in fragmented landscapes and a decrease in forest cover (Sodhi et al., 2004; Tucker et al., 2018) and alter how species use their habitats across different temporal and spatial scales (Peters et al., 2007).

Conservation practitioners must manage multiple species using limited resources (Walston et al., 2010), while addressing scale-dependent responses to habitat modification (Wu et al., 2006).

Ecological models can provide sandboxing tools to test policies in silico (Grimm & Railsback, 2012). However, making ecological models that can capture the emergent patterns over different temporal and spatial scales remains a challenge (DeAngelis & Grimm, 2014; McGarigal et al., 2016). The model can be used to make predictions, which can be verified through empirical observations, providing a measure of validation (Evans et al., 2013). By making observations before and after the intervention, understanding of the ecosystem can improve, which can in turn benefit the modeling (Levin, 1992). The Bardia case study illustrates how the combination of agent-based modeling and field validation reveals scale-dependent adaptations that would be missed by single-scale approaches. The observed temporal partitioning between humans and tigers, and the emergence of territories based on resource availability rather than fixed boundaries, shows how different scales of observation lead to different conservation implications (Moorcroft & Lewis, 2013).

Our recommendations for scale selection in ecological modeling—documenting scale contexts, incorporating probability models, conducting sensitivity analyses, and developing multi-scale models—offer practical approaches to bridge the gap between modeling abstractions and observed animal behavior, by making scale-dependent assumptions explicit and testable.

These four recommendations change model scale choices from an implicit technical constraint into an explicit theoretical consideration when addressing scale-dependent patterns in ecological modeling. It may not be necessary to implement all four for every agent-based model, but they can be used to show that these choices do not affect conclusions in a particular use case. In this way, conservation policies can be evaluated across the multiple scales at which ecological processes occur, leading to more effective management strategies for human-wildlife coexistence.

AUTHOR CONTRIBUTIONS

Indushree Banerjee: Writing—original draft (lead); Model development and data analysis (lead); Writing—review and editing (equal). **Maurits Ertsen**: Conceptualization (equal); Writing—original draft (supporting); Writing—review and editing (equal); funding acquisition (lead).

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CONFLICT OF INTEREST STATEMENT

None of the authors have any competing interests.

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DATA AVAILABILITY STATEMENT

Available upon request to Dr. Indushree Banerjee at: i.banerjee@tudelft.nl.

ETHICS STATEMENT

The workshops and data collection for this study were conducted as part of larger research projects which received formal ethics approval from the Human Research Ethics Committee (HREC) TU Delft.

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