



# Modeling tiger population and territory dynamics using an agent-based approach



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## ABSTRACT

Effective conservation planning of globally endangered tigers (*Panthera tigris*) requires a good understanding of their population dynamics. Territoriality, an essential characteristic of many wildlife species, plays a crucial role in the population dynamics of tigers. However, previous models of tiger population dynamics have not adequately incorporated territoriality. We therefore developed and implemented a spatially explicit agent-based model of tiger population dynamics shaped by different territorial behaviors of males and females. To allow for predictions to new conditions, for which no data exist, territories are not imposed but emerge from the tigers' perception of habitat quality and from their interactions with each other. Tiger population dynamics is deduced from merging territory dynamics with observed demographic rates. We apply the model to Nepal's Chitwan National Park, part of a global biodiversity hotspot and home to a large (~125) population of tigers. Our model matched closely with observed patterns of the real tiger population in the park, including reproduction, mortality, dispersal, resource selection, male and female land tenure, territory size and spatial distribution, and tiger population size and age structure. The ultimate purpose of the model, which will be presented in follow-up work, is to explore human-tiger interactions and assess threats to tiger populations across contexts and scales. The model can thus be used to better inform decision makers on how to conserve tigers under uncertain and changing future conditions.

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## 1. Introduction

Tigers (*Panthera tigris*) are a globally endangered species, with their remaining populations throughout South Asia threatened primarily by habitat loss, prey depletion, and illegal killing by people (Dinerstein et al., 2007; The World Bank, 2011). Effective tiger management and conservation planning requires a good understanding of tiger population dynamics (Lindenmayer et al., 1993; Margules and Pressey, 2000). Territoriality, an essential characteristic of many wildlife species (Adams, 2001; Burt, 1943), plays a crucial role in the population dynamics of tigers (Sunquist, 1981). As demonstrated in various wildlife species, for example, territorial behavior influences social organization, mating, disease transmission, demography, and the spatial distribution of individual animals

(Craft et al., 2011; Moorcroft et al., 2006). By exerting a strong effect on population regulation (Dhondt et al., 1992; Wang and Grimm, 2007), territoriality likely influences the susceptibility of tigers to anthropogenic and natural disturbances (Letcher et al., 1998).

Integrating territoriality in computer models of tiger populations can give us tools to evaluate future impacts of various threats. However, previous models of tiger population dynamics, while making important contributions, have not adequately incorporated territoriality. For example, the models of Kenney et al. (2014, 1995) and Karanth and Stith (1999) do not include real spatial data or dynamic territories and are therefore not useful for simulating tiger population response to changing habitat conditions (e.g., infrastructure development) on spatially heterogeneous landscapes. The spatially explicit model of Ahearn et al. (2001) imposed territory sizes on males and females and did not include conspecific interactions, thus limiting the ecological and conservation questions that the model can address. To help fill these information gaps, we developed and implemented a spatially explicit agent-based model (ABM) of tiger population dynamics shaped by different territorial behaviors of males and females. In this paper we describe the model and how it has been tested and

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then applied it to Nepal's Chitwan National Park, part of a global biodiversity hotspot and home to a large (~125) population of tigers (Carter et al., 2015; Myers et al., 2000).

The design of our model was determined by basic principles underlying territorial behavior observed across a range of species (Börger et al., 2008). Territories or home ranges are mechanisms by which animals acquire resources such as food, but also shelter and mates (Brown and Orians, 1970; Burt, 1943). As such, the size and spatial structure of animal territories or home ranges are strongly related to environmental resource abundance and distribution (Mitchell and Powell, 2007; Moorcroft et al., 2006). Since territory size is correlated with food productivity across landscapes, the population densities of many bird and mammal species are inversely related to their home range or territory sizes (Makarieva et al., 2005).

Territories and home ranges are also influenced by the location, behavior, and identity of conspecifics. Agonistic interactions between animals in adjacent territories (or core parts of home ranges) are costly, with outcomes including loss of resources, mates, injury, and sometimes death (Jacobs et al., 2008). Direct interactions with neighbors (e.g., fights) and indirect interactions, such as avoidance of negative encounters, can influence territory size and shape (Moorcroft et al., 2006). In general, territory size is reduced by interactions among neighbors or with potential settlers (Adams, 2001). Such interactions redistribute resources among competitors, affecting individual fitness. Agonistic interactions also somewhat decouple territory size and shape from landscape food supply (Adams, 2001).

Furthermore, for many wildlife species, including conservation-priority species like the tiger, agonistic interactions between males for females are common and influence male territories and their reproduction in a different way than females (Bond and Wolff, 1999; Creel, 1998; Pusey and Packer, 1994; Sunquist, 1981). Male competition for access to females, for example, can completely displace males from a territory (Piper et al., 2000), significantly reducing fitness of the displaced male. Appropriation of a male territory by another male is also sometimes followed by infanticide, triggering estrous in the resident female and potentially allowing the new male to quickly sire a litter with her (Barlow et al., 2009; Pusey and Packer, 1994). The significant consequences of male-male competition on dispersal, reproduction, and population size and structure provide strong rationale for developing a model with separate but interacting female and male territory processes.

ABMs (also referred to as individual-based models) have the flexibility and capacity to incorporate these principles of territoriality (DeAngelis and Grimm, 2014). ABMs explicitly represent individual behaviors and local interactions (Grimm and Railsback, 2005; Semeniuk et al., 2011, 2012). By simulating the life of individual animals, ABMs operate at a scale at which population dynamics are based (DeAngelis and Mooij, 2005; Letcher et al., 1998). Furthermore, in an ABM, population dynamics are not pre-defined by aggregate-level equations but emerge due to events and behaviors at the individual level (Grimm and Railsback, 2005; Semeniuk et al., 2012). In terms of territoriality, individual behaviors and interactions can be directly informed by observations in the field (Watkins et al., 2014), if they exist, or used to guide field data collection. An ABM approach is especially useful for modeling species inhabiting spatially heterogeneous environments and for which social dynamics strongly influence population structure (DeAngelis et al., 1998; Federico et al., 2013; Watkins et al., 2014).

ABMs have incorporated territories and home ranges in the past. Some of the earlier uses of ABMs integrated territories and home ranges into population models; however, they treat territories and home ranges as equal or static in size or represent them with overly simplistic shapes, such as circles (Ahearn et al., 2001; Grimm et al., 2003; Kostova et al., 2004; Letcher et al., 1998; Wiegand

et al., 2004). Other studies have explicitly modeled more complex shapes and sizes of territories and home ranges as functions of intraspecific interactions and/or resource spatiotemporal heterogeneity (Giuggioli et al., 2011; Mitchell and Powell, 2004; Moorcroft et al., 2006; Nabe-Nielsen et al., 2013; Van Moorter et al., 2009). These studies provide very useful insights; however, they do not integrate territory or home ranges into population dynamic models.

The recent models by Wang and Grimm (2007, 2010) and Liu et al. (2013) are different, as they incorporate dynamic territories into population modeling of the common shrew (*Sorex araneus*) and the wood mouse (*Apodemus sylvaticus*), respectively. In the wood-mouse model (Liu et al., 2013), only females are considered; territory acquisition is based on vegetation cover and the presence of conspecifics. In the common shrew model (Wang and Grimm, 2007, 2010), territory acquisition for both females and males was based mostly on food resources, although males preferred locations where females were present.

Our model thus builds on the resource-based acquisition of territories used by Wang and Grimm (2007, 2010), but adds further rules representing interactions between females and males. In our model, female tiger territories fluctuate based on local prey biomass production and the presence of neighboring female territories (Smith et al., 1987). Male tigers try to overlap the territories of multiple females, with young males challenging resident (i.e., territory-holding) males for access to their females (Smith, 1993; Sunquist, 1981). Tigers in the model reproduce, disperse, establish and modify territories, and die, with other tigers dispersing to and establishing territories in the gaps left by dead tigers. By applying the model to Nepal's Chitwan National Park, where empirical data on tigers and their habitat have been collected for several decades, we demonstrate its utility at simulating tiger population dynamics in a real landscape. The model presented here does not include interactions with humans, but the ultimate purpose of the model is to explore the consequences of various threats on tigers (e.g., poaching and resource depletion), as well as feedbacks of tiger behaviors on human communities. As such, the model can be a useful tool for informing decision-makers on how to conserve tigers under uncertain and changing future conditions.

### 1.1. Study site and biological background

The model was parameterized for Nepal's Chitwan National Park (27°20' N to 27°43' N, 83°5' E to 84°46' E), where long-term tiger behavioral and ecological data have been collected (Barlow et al., 2009; Eisenberg and Seidensticker, 1976; Seidensticker and McDougal, 1993; Seidensticker et al., 1999; Shrestha, 2004; Smith and McDougal, 1991; Smith, 1993; Smith et al., 1999, 1987; Sunquist, 1981). The park is situated in south central Nepal and located in a river valley basin along the flood plains of the Rapti, Reu, and Narayani Rivers with an elevation range of 150–815 m. Climate in Chitwan is subtropical with a summer monsoon season from mid-June to late-September, and a cool dry winter. The park consists of *Sal* (*Shorea robusta*) forest, *khair* (*Acacia catechu*) and *sissoo* (*Dalbergia sissoo*) riverine forests, and grasslands dominated by species of the genera *Saccharum*, *Themeda*, and *Imperata* (Carter et al., 2013; Chaudhary, 1998).

Tigers are obligate carnivores that crop approximately 10% of available prey in a landscape, with females in Chitwan consuming 5–6 kg of prey/day (Karanth et al., 2004; Sunquist, 1981). Tiger prey is abundant in Chitwan, consisting primarily of spotted deer (*Axis axis*), barking deer (*Muntiacus muntjak*), hog deer (*Axis porcinus*), wild boar (*Sus scrofa*), sambar (*Rusa unicorn*), and gaur (*Bos gaurus*). Prey biomass generally corresponds to land cover, with prey biomass highest in grassland/riverine forest complexes (Eisenberg and Seidensticker, 1976; Shrestha, 2004; Smith et al., 1987).

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