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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.

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 unicolor*), 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).

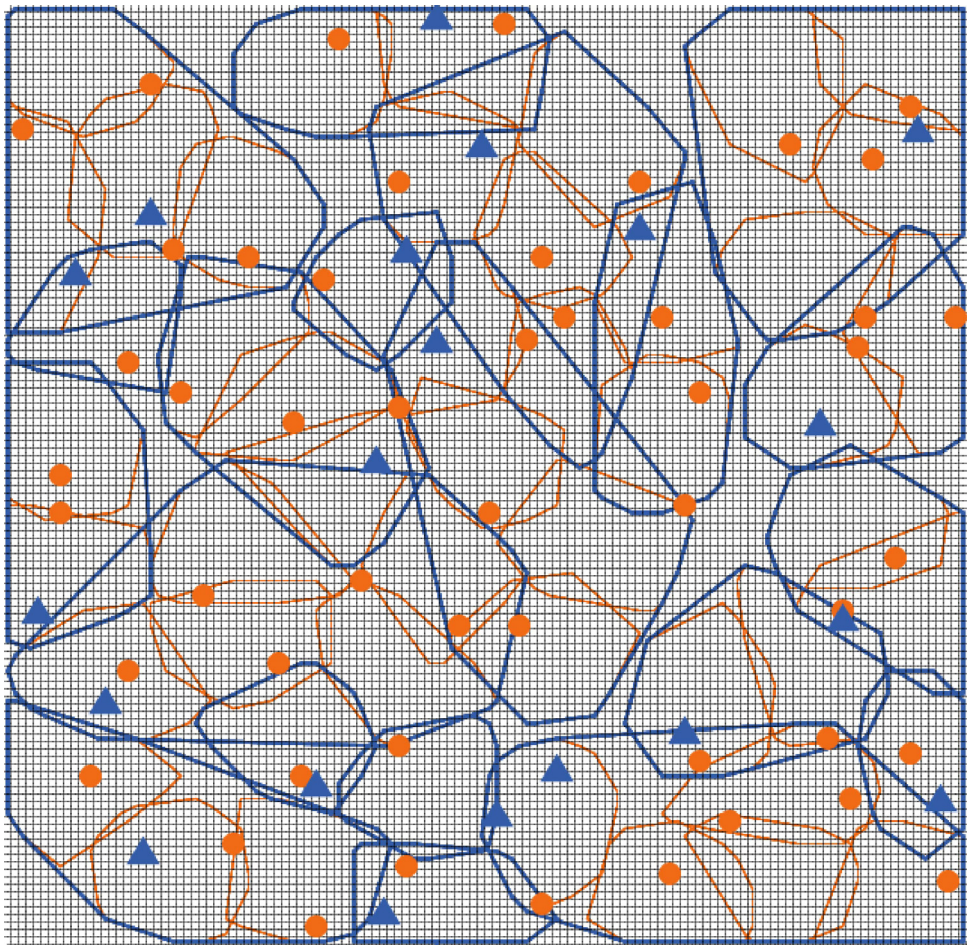

Fig. 1. Image of model landscape with 50 adult female tiger and 20 adult male tiger territories (shown as 100% minimum convex polygons) distributed across a landscape with square habitat cells (250 m × 250 m). Female tigers are indicated with orange circle and female territory boundaries are orange. Male tigers are indicated with blue triangles and male territory boundaries are blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Both male and female tigers exhibit site fidelity and maintain exclusive territories that are not shared with neighboring adults of the same sex (Seidensticker et al., 1999; Smith et al., 1987; Sunquist, 1981). Mean tiger territory size in Chitwan is 20.7 km^2 (range 10–51) for females and 54.4 km^2 (range 19–151) for males (Smith et al., 1987). Male territories encompass 1–6 female territories (Smith, 1993; Sunquist, 1981).

Female tigers breed at about 3 years old after establishing a territory. Gestation is 103 days (Karanth and Stith, 1999). Litter size in Chitwan is between 2 and 5 cubs with an average of 2.98 (Smith and McDougal, 1991). Interbirth period is approximately 2 years, however, the interbirth period can be considerably shorter if a mother's litter has died (e.g., through infanticide by adults males, Sunquist et al., 1999). Tigers disperse when they are about 2 years old and search for a location to establish their territory (Smith, 1993). Females will tend to settle closer to their natal range (mean 9.7 km, range 0.2–33 km) than males (mean 33 km, range 9.5–66 km, Smith, 1993). Dispersing tigers have higher mortality rates than resident tigers (Karanth and Stith, 1999). Dispersing males will often challenge other males for their territory and access to females. Infanticide by new resident male tigers is common (Barlow et al., 2009).

2. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2010, 2006). The model was implemented in NetLogo 5.0.4 (Wilensky, 1999) and the program used to simulate the tiger population on Chitwan National Park, Nepal, is available in the Supplementary Material.

2.1. Purpose

The proximate purpose of the model is to predict the dynamics of the number, location, and size of tiger territories in response to habitat quality and tiger density. 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. The ultimate purpose of the model, which will be presented in follow-up work, is to explore human-tiger interactions.

2.2. Entities, state variables and scales

Model entities are the square spatial units or habitat cells comprising the landscape, male and female tigers, and tiger territories (Fig. 1). All state variables characterizing these entities are listed in Table 1. Female territories consist of a set of habitat cells, which the females add to their territory based on prey availability and absence or rank of other females. Male territories consist of a set of up to six female territories (Smith, 1993; Sunquist, 1981), which the males

Table 1
Summary of state variables in model for female and male tigers and habitat cells.

Entity	Variable name	Description	Possible values	Units
Female	Age	Age in months	1–180	Months
	Fertile?	Indicates whether female is fertile	True/false	–
	Gestating?	Indicates whether female is gestating	True/false	–
	Males-in-my-territory	Identities of males overlapping female territory	Set of male identities	–
	My-mom	Identity of mom	Identity of female tiger	–
	My-offspring	Number of offspring in current litter	1–5	Individual cubs
	Natal-origin	Cell where female was initialized at or the centroid cell of mother's territory	0 – max *X*, 0 – max *Y*	Cell units
	Num-litters	Total number of litters the female has had up until current time	0 – max number of litters over lifetime	–
	Age-class	Indicates development stage of female	Cub, Juvenile, Transient, or Breeder	–
	Territory	Set of cells belonging to territory	Set of cell coordinates	–
	terr-orig	Cell that female was initialized at or first cell of territory	0 – max *X*, 0 – max *Y*	Cell units
	t-gestation	Indicates how long female has gestated	0–3 or 4	Months
	t-parenting	Indicates how long female has been a parent of current litter	0–24	Months
Male	Age	Age in months	1–180	Months
	Dominant-males	Identities of males that have beaten male in challenges	Set of male identities	–
	Females-in-my-territory	Identities of females overlapping male territory	Set of female identities	–
	Initial-male?	Indicates whether male was created at beginning of simulation	True/false	–
	Lost-territory?	Indicates if male lost a territory to a challenger	True/false	–
	Male-land-tenure	Total time male held onto territory	0 – entire breeding phase until death	Months
	My-mom	Identity of mom	Identity of female tiger	–
	Natal-origin	Cell where male was initialized at or the centroid cell of mother's territory	0 – max *X*, 0 – max *Y*	Cell units
	Age-class	Indicates development stage of male	Cub, Juvenile, Transient, or Breeder	–
	Territory	Set of cells belonging to territory	Set of cell coordinates	–
Cell	Owner-fem	Identity of female with cell in her territory	Identity of female tiger	–
	Owner-male	Identity of male with cell in his territory	Identity of male tiger	–
	Prey	Prey produced at cell	0 – max prey production	kg/month
	Is-churia?	Indicates whether cell falls within churia hill boundary (Chitwan landscape only)	True/false	–
	Is-park?	Indicates whether cell falls within national park boundary (Chitwan landscape only)	True/false	–

add to their territory based on their spatial proximity and absence or rank of other males.

Habitat cells have a side length of 250 m and are characterized by their prey biomass production rate (*prey*, kg/month) and whether or not they are part of a female or male territory (*owner-fem*, *owner-male*). Simulations were carried out on a small landscape of 40×40 cells (100 km^2), a larger landscape of 128×125 cells (1000 km^2), and the Chitwan landscape of 157×345 cells (3385 km^2 though only 1239 km^2 of it comprises park). The boundaries in the model landscapes were impermeable (i.e., the tigers and their territories could not extend beyond the boundaries). The small landscape size was chosen to develop and test the models of behavior and fine-scale interactions of a few tigers, whereas the larger landscape size was used to explore interactions of a larger tiger population. In addition, many protected areas are approximately the same size as the large landscape (Sanderson et al., 2006). Lastly, the Chitwan landscape was used to assess how well the model fits observed data. A time step in the model corresponds to 1 month and simulations were run for 1–20 years. One month is a suitably long enough time step for tigers to establish and maintain a territory. In addition, previous empirical studies reported data at the monthly time scale allowing for comparison with model results.

2.3. Process overview and scheduling

Each time step (1 month), the following processes are processed in the given order (Fig. 2). Model entities are processed in a randomized order, unless stated otherwise, and changes in state variables are updated immediately. The submodels implementing these processes are described in detail in Section 2.7 below. Note that in the program there are mutual links between tigers and territory cells, and males and females, which implies that these links have to be updated every time a tiger dies or a territory is changed or lost; these technical updates are not described in the following.

2.3.1. Mortality

Depends on sex, age, and on whether the tiger is a territory holder or disperser.

2.3.2. Update-age-stage-class

Tigers age and develop and may proceed to the next age class, i.e., cub, juvenile, transient, or breeder (Karanth and Stith, 1999).

2.3.3. Female-select-location

Upon reaching breeding stage, females select a location to begin establishing a territory.

2.3.4. Male-select-location

Upon reaching breeding stage, males select a location to begin looking for available females.

2.3.5. Update-female-territory

Females try to add habitat cells to their territory until the total amount of prey available reaches a certain threshold. They select new cells based on their prey availability and presence and rank, which are correlated to age, of other females. Within a time step, females can try up to 48 times to add a new cell. In other words, females can potentially add up to 3 km^2 to their territory in a time step, which is approximately the area added per month observed in the field (Sunquist, 1981). If the resulting set of habitat cells

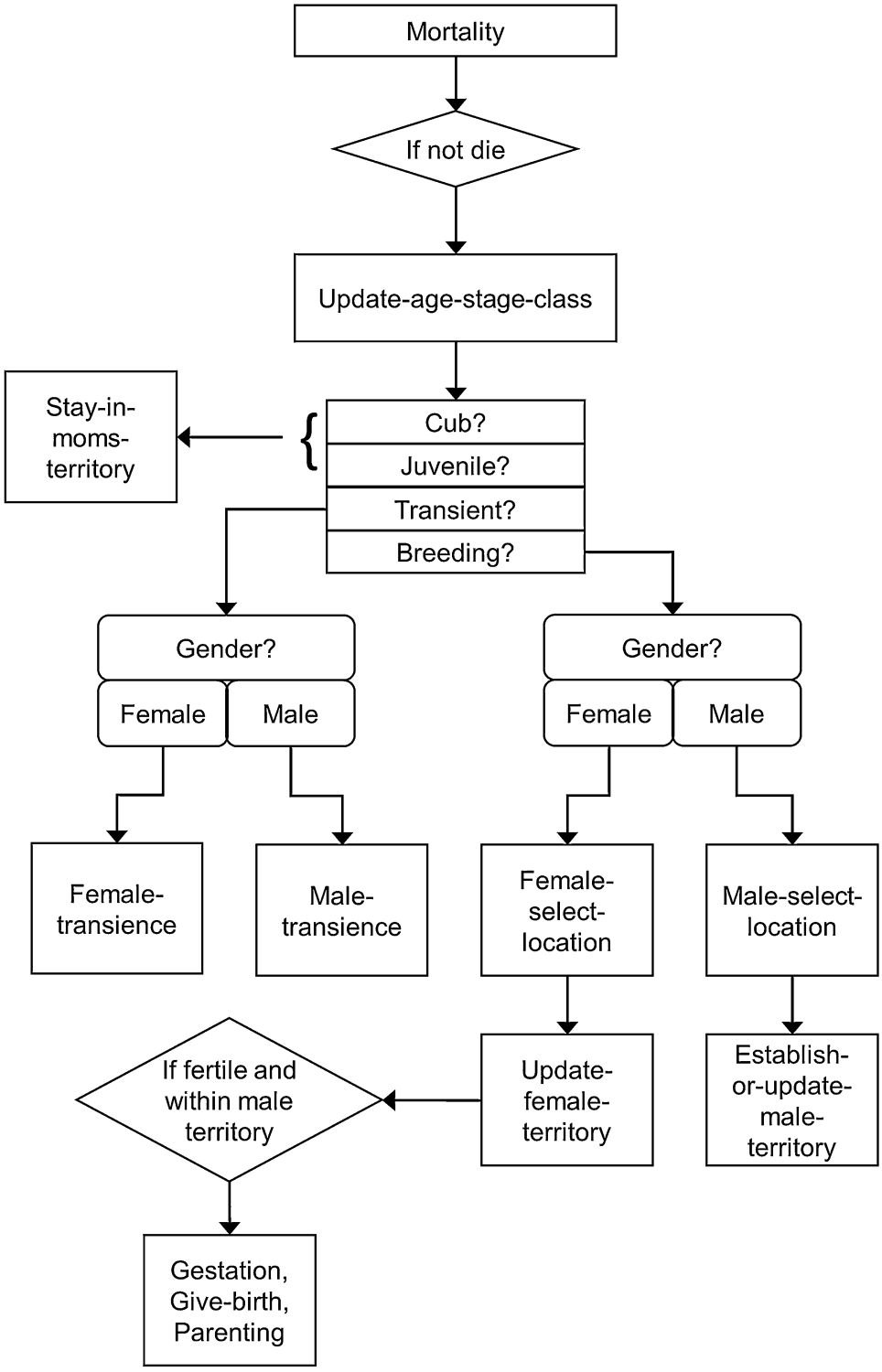

Fig. 2. Overview of model processes.

consists of two or more non-contiguous clusters of cells, all but the largest cluster are removed from the territory (*find-clusters*, *remove-clusters*).

2.3.6. Female-starvation

Females die if the total prey production within their territory is below 76 kg/month (derived from Miller et al., 2014) and the food within their territory has not increased.

2.3.7. Calculate-fem-centroid

Calculates the centroid of female territory, i.e., the cell which has the average *X* and *Y* coordinates of cells of the female's territory. These centroids are used to assign female to male territories.

2.3.8. Establish-or-update-male-territory

A model territory is established or updated. The selection of female territories to be added to a male's territory is based on the proximity of female territories (their centroids) and the rank of

nearby males. Males with less than six female territories may add territories; males with six female territories may replace, if possible, the female whose centroid is farthest away from the male's territory centroid by a closer female. This is done to prevent male territories from overlapping substantially.

2.3.9. Calculate-male-centroid

Calculates the centroids of male territories.

2.3.10. Parenting (female only)

Updates the time since a female gave birth; this determines when the female becomes fertile again and her cubs have to leave her.

2.3.11. Gestation (female only)

Updates gestation time and initiates reproduction (*give-birth*) when gestation time of a female is over.

2.3.12. Prob-mating

Determines whether fertile females mate with males and begins gestation period.

2.3.13. Plotting

Model output is plotted or written to files.

2.3.14. Calc-homerange

100% minimum convex polygon is drawn around each territory.

2.4. Design concepts

2.4.1. Basic principles

Acquisition and maintenance of territories reflect fundamental ecological relationships between organisms and their environment. How male and female territorial animals, like tigers, establish, defend, and modify territories, can be related to basic principles such as resource requirements and dominance relationships (Adams, 2001; Brown and Orians, 1970; Burt, 1943; Jacobs et al., 2008; Moorcroft et al., 2006). Having our model based on basic principles related to territory establishment allows application to other regions than Chitwan National Park. Furthermore, the model can be adapted and re-used for other organisms and contexts.

2.4.2. Emergence

Tiger population size and age distribution over time emerge from demographic processes and territory dynamics. Female territory dynamics emerge from prey biomass distribution and competition with other females. Male territory dynamics emerge from female territory locations and competition with other males.

2.4.3. Adaptation

Female tigers adapt their territories to changes in prey biomass and the presence of adjacent female territories, while males adapt their territories to the number and location of nearby female territories and the presence of adjacent male territories.

2.4.4. Fitness

Individual tiger fitness is indirectly modeled as access to prey and mates through the formation and adaptation of territories.

2.4.5. Interaction

Competition for habitat cells is a direct interaction for both females and males. Males also interact directly as they can expel other males from their territory to gain access to females. In such cases, to trigger estrous in females, infanticide can occur.

2.4.6. Sensing

Females can sense total prey available to them within their territory and the prey abundance of cells neighboring their territories. Males know the number of females within their territory and nearby as well as the location of the corresponding female territories. Females sense whether or not a habitat cell adjacent to their territory is owned by another female, and males sense whether or not other males are nearby.

2.4.7. Stochasticity

Stochasticity was incorporated into many processes to account for natural variation. The initial locations and ages of tigers, mortality, challenges between males, females taking habitat cells from adjacent females, male selection of females to move toward, litter size, gender of cubs, and mating all include elements of stochasticity. See Section 2.7 for details.

2.4.8. Observation

Individual and population-level processes were observed. These included reproduction (i.e., litter size and lifetime reproductive success for females), mortality (i.e., infanticide and mortality rates for different age classes), dispersal (i.e., distance from natal range to post-natal territory), resource selection (i.e., prey biomass for females and females for males), male and female land tenure (i.e., time that breeding animal held onto territory before dying or dispersing), territory size and spatial distribution, and tiger population size and age structure.

2.5. Initialization

Prey biomass production rates (kg/month/cell) used in the models were calculated by combining empirical rates of average daily prey consumption by female tigers and information on female territory sizes in Chitwan. Specifically, using daily consumption rates of 5.5 kg/day (Sunquist, 1981), we estimated that female tigers consume 167.3 kg/month. Assuming tigers consume 10% of the standing prey biomass (Karanth et al., 2004), then 1673 kg/month is on average available to a female tiger within her territory. The upper and lower limits of prey biomass production per cell were then calculated by scaling the average monthly prey biomass available to a female in her territory (1673 kg) to the largest (51 km^2 or 816 cells) and smallest (10 km^2 or 160 cells) observed female territory sizes reported in Smith (1987). Thus, the lower limit for prey biomass production was 2.05 kg/month/cell (i.e., 1673/816) and the upper limit was 10.46 kg/month/cell (i.e., 1673/160). These prey biomass production values were used for various simulation experiments (see Section 2.8 below).

2.6. Input data

The current model version does not include any input of data describing dynamics in drivers, environmental conditions, or disturbances. Future model versions, however, will include seasonal variations in prey biomass production rate and human disturbances.

2.7. Submodels

All model parameters are listed in Table 2. For some of the complex submodels, we used tags, e.g., "*R*1", that link the description of this model rule to the corresponding NetLogo code in the program. This applies to "female-select-location", "male-select-location", "update-female-territory", and "establish-or-update-male-territory" processes.

Table 2
Summary of parameter information used in agent-based model of tiger territory and population dynamics in Chitwan National Park, Nepal.

Parameters	Values	Reference	Notes
Age-classes		Karanth and Stith (1999) (Page 103)	Based on long-term field data of tigers across sites.
Breeding	3+ years old		
Transient	2–3 years old		
Juvenile	1–2 years old		
Cub	0–1 years old		
Litter size distribution[a]		Kenney et al. (2014) (Appendix A)	Based on long-term field data of tigers in Chitwan.
1	0		
2	0.23		
3	0.58		
4	0.17		
5	0.02		
Maximum number of cells female can add to territory per time step[a]	48 (3 km^2)	Sunquist (1981) (derived from Table 15 on page 37)	This value represents an approximation of the average area added to female's territory per month from observed data.
Annual survival[a]		Karanth and Stith (1999) (Page 103)	Survival rates were parameterized from field data on tigers, leopards, and cougars.
Breeding male	0.8		
Breeding female	0.9		
Dispersal male	0.65		
Transient male	0.65		
Transient female	0.7		
Juvenile	0.9		
Cub	0.6		
Annual fecundity[a]		Kenney et al. (2014) (Appendix A)	Based on long-term field data of tigers in Chitwan.
Probability that 3-year old resident female breeds if fertile	0.9		
Probability that 4+ year old resident female breeds if fertile	1		
Maximum possible dispersal distance from natal range[a]		Smith (1993) (Table 1 on page 173)	Based on long-term field data of tigers in Chitwan.
Transient male	66 km		
Transient female	33 km		
Prey thresholds[a]			
Minimum within territory	76 kg/month	Miller et al. (2014) (Page 127)	Model estimates 2.5 kg/day to maintain basal metabolic rate of female Bengal tiger in Bangladesh. This converts to: (2.5 kg/day × 365 days)/12 months
Maximum within territory	167.3/month	Sunquist (1981) (Page 91)	From empirical data, estimates female tiger in Chitwan consumes 5–6 kg/day. This converts to: (5.5 kg/day × 365 days)/12 months
Probability that dominant female will take territory cell from subordinate female if cell has highest prey[a]	0.25	This study	Based on expert opinion.
Proportion of prey within territory utilized by female tiger[a]	0.1	Karanth et al. (2004) (Page 4854)	Based on field data of large carnivore guilds across different sites in Asia and Africa.
Radius in which breeding males will search for nearby breeding females[a]	3 km	Ahearn et al. (2001) (Table 1 on page 90)	Based on long-term field data of tigers in Chitwan.
Max number of female territories a male can overlap[a]	6	Kenney et al. (2014) (Appendix A)	Based on long-term field data of tigers in Chitwan.
Litter sex ratio at birth	50:50	Karanth and Stith (1999) (Page 103)	Based on long-term field data of tigers across sites.
Gestation period	3 or 4 months with equal probability	Sunquist et al. (1999) (Page 7)	Gestation is 103 days, which is between 3 and 4 months. Model randomly selects either 3 or 4 months.
Search criteria for dispersing females to determine location of territory origin[a]			Based on expert opinion.
Ideal area in which no other female territory occurs	12.57 km^2 (2 km radius)	This study	
Less-optimal area in which no other female territory occurs	3.14 km^2 (1 km radius)	This study	
Probability that the dispersing male dies after losing challenge[a]	0.25	Kenney et al. (2014) (Appendix A)	Based on long-term field data of tigers in Chitwan.
Probability that the resident male dies after losing challenge[a]	0.6	Kenney et al. (2014) (Appendix A)	Based on long-term field data of tigers in Chitwan.
Probability offspring die due to infanticide following successful challenge[a]		Pusey and Packer (1994) (derived from Fig. 1 on page 279)	Based on long-term field data on African lions in Tanzania's Serengeti National Park.
Juvenile	0.24		
Cub	0.79		

[a] Parameters that were included in sensitivity analysis.

2.7.1. Mortality

Observed age-specific annual survival rates were used to derive monthly background mortality rates. The observed survival rates are identical to those used in Karanth and Stith (1999). When a female with dependent offspring (i.e., cubs and juveniles) dies, then her offspring die as well. Tigers die when they reach 15 years old, considered their maximum age in the wild (Smith and McDougal, 1991).

2.7.2. Update-age-stage-class

The age of each tiger increases by 1 month at each time step. Age-classes were based on those used in Karanth and Stith (1999). Tigers are considered "cubs" from birth to 12 months old, "juveniles" from 12 to 24 months old, "transient females" or "transient males" from 24 to 36 months, and "breeding males" or "breeding females" after 36 months of age. Male breeders who have lost their territory become "floater" males with a mortality rate equal to transient males. Females become fertile at 36 months.

2.7.3. Female-select-location

When females reach 3 years they move to a location where they establish the origin point of their territory. The following describes the steps involved in selecting that location.

1. The female identifies all cells within 33 km of her natal origin (*R*1). We chose 33 km as the search radius because this is the maximum observed distance females traveled from their natal range to establish their home range in Chitwan (Smith, 1993).
2. Of those cells, she identifies cells that have no other female territory within 2 km and have no other transient female present (*R*2).
3. Of those cells meeting that criteria, she selects and moves to the cell that has the highest mean prey within 2 km (*R*3).
4. If no cells meet that criteria, then she identifies cells within 33 km of her natal range that have no other female territory within 1 km and that have no other transient female present (*R*4).
5. Of those cells meeting that criteria, she selects and moves to the cell that has the highest mean prey within 1 km (R5).
6. If no cells meet the abovementioned criteria, then she dies (*R*6). This is analogous to her dying from no food because she is unable to establish a territory in any suitable areas.

2.7.4. Male-select-location

When males reach 3 years old they move to a location from which they will try and establish a territory. The following describes the steps involved in selecting that location.

1. The male identifies the centroids of all female territories that "belong" to a male and those that do not belong to a male (*R*1).
2. If the male has previously lost a challenge to a resident male, then he distinguishes those females belonging to unchallenged and challenged males (*R*2).
3. The first choice for the male is to move to the closest cell within 66 km of his natal range that is the territory centroid of a female not belonging to a male (*R*3). The male cannot move to that location if another dispersing male has already moved to it. This ensures that young males from the same cohort do not all clump on the same female. The natal range is defined as the centroid of the dispersing male's mother's territory at birth. We chose 66 km as the search radius because this is the maximum observed distance males traveled from their natal range to establish their home range in Chitwan (Smith, 1993).
4. If no "unoccupied" female exists within 66 km, then the male will select a female closest to his natal range and that belongs to an unchallenged male (*R*4). This ensures that the male will not continually challenge the same resident male, and instead keeps looking for females across the landscape. Also, no other dispersing male must be present at that centroid. If a male without a territory moves to a female's centroid that is occupied by a resident male, it might challenge that resident male in the next time step (see Section 2.7.8).

2.7.5. Update-female-territory

Adult breeding females update the size and shape of their territories based on the location of prey resources and adjacent female territories. The following steps are involved in updating territories for female tigers (Fig. 3).

1. Cells neighboring an existing female territory are categorized as being vacant (i.e., not belonging to another female's territory) or owned by another female (*R*1). Neighbors are defined as the four cells sharing a border (not a vertex) with the territory cells. This allowed territories to be more concentrated in space.
2. If the cell is owned, then the female determines if the owner female is "subordinate" to her (*R*2). This is based on age, with middle-aged females being the most dominant, young adult females moderately dominant, and older females the least dominant; the dominance relationships are listed in Table S1, which is implemented in the NetLogo procedure *subord?*.
3. If there are neighboring cells not owned by other females, then she will add a vacant neighboring cell with the highest prey biomass production (*R*3).
4. If there are both vacant and subordinate cells and if a vacant neighboring cell has an equal or higher prey biomass production than a neighboring cell owned by a subordinate female, then she adds the vacant cell to her territory (*R*4).
5. If, instead, the highest prey biomass production of a neighbor cell belonging to a subordinate female is greater than the highest prey biomass production of a vacant neighboring cell, then she has a 25% probability of adding the cell from the subordinate female to her own territory (R5). Otherwise, she adds the vacant cell even though it has a lower prey biomass production than the cell from the subordinate female (*R*6).
6. If there are no vacant neighbor cells, then she adds the cell belonging to a subordinate female with the highest prey biomass production (*R*7). Although females are highly territorial and sometimes demonstrate aggression toward each other along the edges of their respective territories, doing so incurs a cost (Smith et al., 1987). In other words, a female does not attempt to co-opt a portion of another female's territory unless it is necessary and beneficial to her.
7. Addition of new cells to her territory ceases when 10% of all available prey biomass production (i.e., prey biomass cropped by tigers, Karanth et al., 2004) in her territory within one time steps equals 167.3 kg/month (Table 2) (*R*8).
8. Females can also shift their territories in space if nearby prey resources are higher than those currently obtained within the female's territory. A female achieves basal metabolic energy demands when she has access to 76 kg/month of prey within her territory (Table 2). This number is based on estimates of energetic requirements (2.5 kg/day) applied to female tigers in Bangladesh (Miller et al., 2014). A female will replace a cell from the edge of her territory with the lowest prey biomass production with a neighboring cell of higher prey biomass production once she has met her energetic minimum of 76 kg/month within her territory (*R*9). The edge of her territory consists of all the cells in her territory that share exactly one border with another territory cell.
9. The territory must be contiguous, with all cells sharing at least one border with each other. If gaps occur between cells, then the female moves to the largest group of cells, and all smaller,

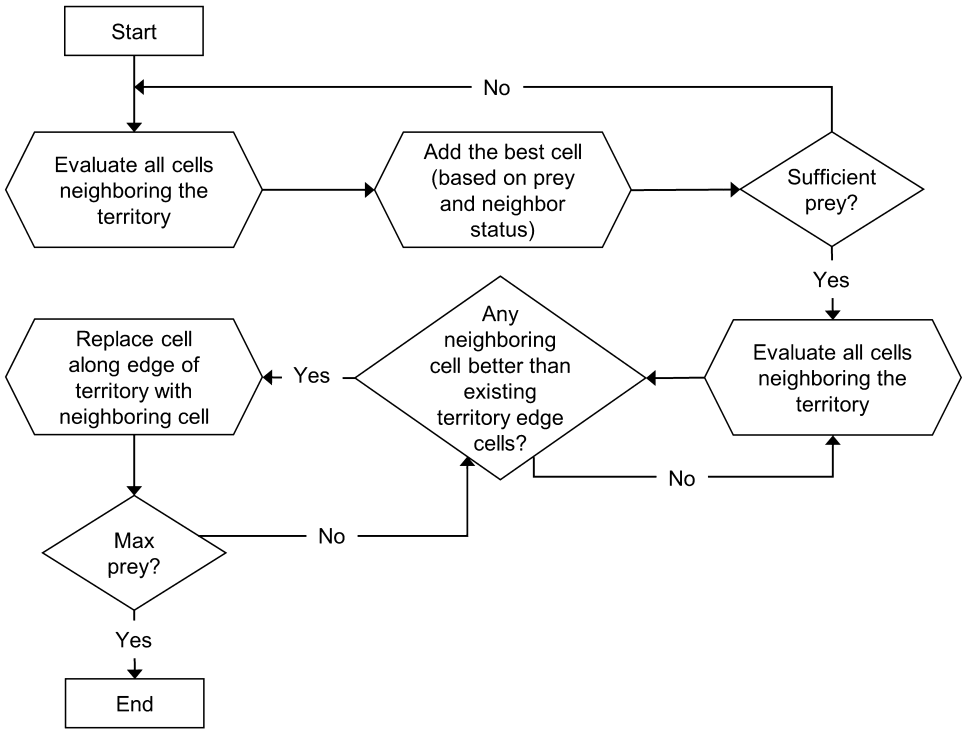

Fig. 3. Structure of female tiger territory submodel.

isolated groups of cells (or single cells) are removed from the territory (*R*10; procedures *find-clusters*, *remove clusters*).

2.7.6. Female-starvation

Females die if the total prey within their territory is <76 kg/month (i.e., basal metabolic requirement) and the food available to them within their territory did not increase from the previous time step. Non-increasing access to food in her territory indicates that she is hemmed in by other dominant females and is unlikely to ascertain more food. If the starving female has offspring, then they die as well.

2.7.7. Calculate-fem-centroid

The centroids of all female territories are determined and assigned to their respective female. The centroid is determined by the arithmetic means of the *X* and *Y* coordinates of all cells belonging to the female's territory. The state variable "owner-fem-centroid" of the cell at the centroid's location is assigned to the female territory holder.

2.7.8. Establish-or-update-male-territory

Adult males establish or update the size and shape of their territories based on the location of nearby adult females and other adult males. Essentially, a male territory represents all the territories of females that he has exclusive access to. Male territories contract or expand when they lose or gain access to female territories. A male territory can overlap a maximum of six female territories (Sunquist, 1981). The "establish-or-update-male-territory" submodel requires information about the territory centroids of females and males. Territory centroids are calculated in the "calculate-fem-centroid" and "calculate-male-centroid" processes. The following describes the steps involved in establishing and updating a male's territory (Fig. 4).

1. If male already has a territory comprising one or more female territories (i.e., he is a resident male), then his territory size and shape is updated based on changes in territories of the females he already overlaps (*R*1).
2. If a male does not have access to any females (i.e., dispersing male), then he identifies all of the females that have territory centroids within 3 km of himself (Table 2, *R*2).
3. If a male is a resident breeder (i.e., already overlaps female territories), then he identifies all females that have territory centroids within 3 km of the territory centroids of the females he overlaps (*R*3). This allows the male to expand his territory based on the location of female territories already within his territory.
4. In some cases, a female territory centroid is beyond 3 km but her territory shares a border with the resident male's territory (i.e., the combined territories of the females he overlaps). We assume that a male would be aware of this neighboring female based on territorial markings (Smith et al., 1987). Thus, the resident male also identifies those neighboring females (*R*4).
5. Of the nearby females (i.e., within 3 km or sharing a territorial border), the male identifies which of them do not "belong" to another male. He then adds the territories of the closest available females to his own (R5). If the male already has access to six females, then he cannot add any more even if they are available.
6. However, if the centroid of an available female's territory is closer than the farthest territory centroid of a female belonging to a male with six females, then he will replace the farthest female with the closer female's territory (*R*6). This reflects the idea that it is energetically more efficient to defend a territory with females that are closer to each other.
7. If no available females are nearby, a dispersing male identifies all nearby females belonging to other males (*R*7). The following behaviors (8–10) do not apply to "floater" males, as they previously lost their territory and do not initiate challenges with resident males any longer.
8. The dispersing male (excluding floaters) randomly chooses one of the males overlapping those nearby female territories to challenge for access to his female(s) (*R*8). The dispersing male

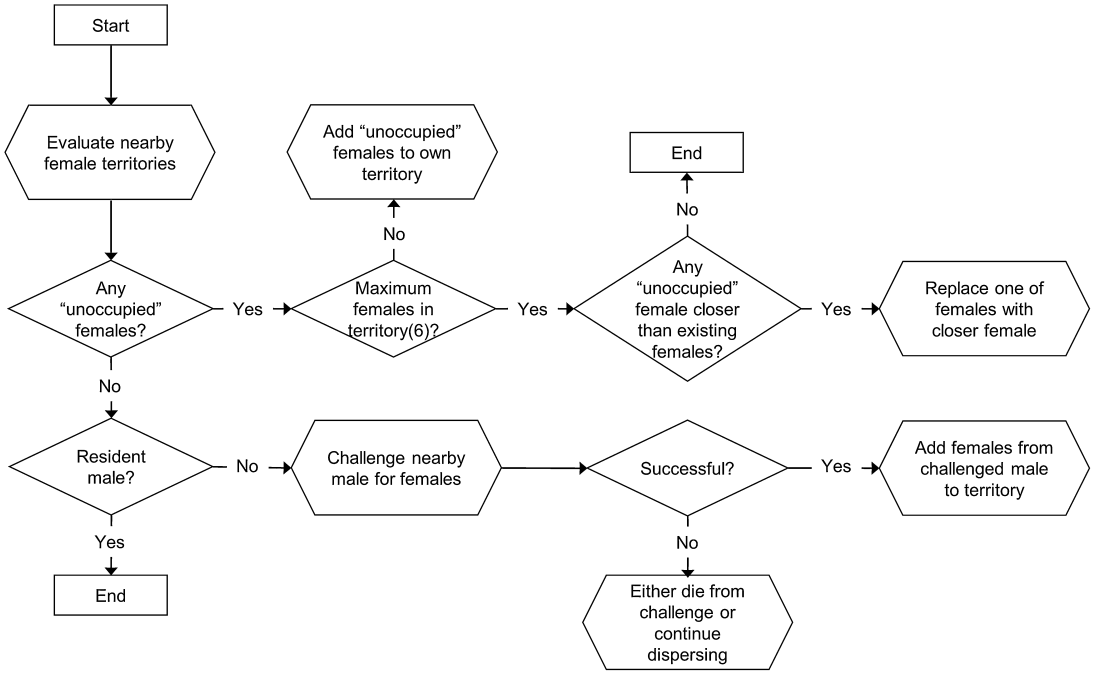

Fig. 4. Structure of male tiger territory submodel.

cannot challenge a resident male that he has lost to in the past. The probability of various outcomes of the challenge is listed in Table 3 (NetLogo procedure *prob-winning*).

9. If the dispersing male wins the challenge, he adds the territory of the female(s) previously belonging to the resident male to his own territory (*R*9). If the females had offspring, then there is a certain probability that they die due to infanticide (*R*10), a commonly observed phenomenon in the wild among territorial animals. Probabilities that a cub and juvenile die due to infanticide are in Table 2. These probabilities are based on the empirical data from African lions (Pusey and Packer, 1994).
10. If the dispersing male loses the challenge, but survives, then he continues dispersing. He remembers the male he lost to (*R*11) and cannot challenge him again in the future.

2.7.9. Calculate-male-centroid

See calculate-female-centroid.

Table 3
Probability that dispersing male tiger successfully challenges resident male tiger for territory as a function of age. Based on Kenney et al. (2014).

Age of resident male	Age of dispersing male		
	3	4	5
3	1	1	1
4	0.5	0.55	0.65
5	0.45	0.5	0.55
6	0.4	0.45	0.5
7	0.35	0.4	0.45
8	0.4	0.45	0.5
9	0.45	0.5	0.55
10	0.5	0.55	0.6
11	0.7	0.75	0.8
12	1	1	1
13	1	1	1
14	1	1	1
15	1	1	1

2.7.10. Parenting

After giving birth to a litter, a female's offspring are dependent on her for 2 years. During that time she is not fertile and hence incapable of giving birth to another litter. In this submodel, parenting time starts at zero when litter is born and parenting time increases by one each time step. If parenting time is 24 (i.e., 2 years), unless induced by infanticide, the female becomes "fertile" again and is capable of giving birth to another litter if she is within an adult male's territory. At that time, the cubs turn 2 years and become transients.

2.7.11. Gestation and give-birth

Once pregnant the female gestates for 3 or 4 months. She is no longer fertile during that period. Since gestation is about 103 days in the wild, the model randomly selects 3 or 4 months as the gestation period so that the average gestation period for all females is approximately 3.5 months. In this submodel, gestation time is reduced by one each time step. If gestation time is zero, the female proceeds to reproduce (see NetLogo procedure *give-birth*). She gives birth to a litter of size and male:female ratio according to probabilities in Table 2. Each offspring stays within the territory of its mother until it becomes a transient adult.

2.7.12. Prob-mating

Once females reach the age of 36 months or 3 years, they become fertile and are capable of giving birth to litters. They have a 90% annual probability of successfully mating within their first reproductive year. That probability increases to 100% after they turn 4 years of age.

2.7.13. Plotting

Plots of total population size, age structure, and territory sizes of males and females are updated each time step.

2.7.14. Calc-homerange

Using the package "adehabitat" in the R software (R Development Core Team, 2009), the 100% minimum convex polygon (MCP) surrounding each female and male territory is drawn.

The MCP is used to visualize each territory and compare to empirical results from the field. NetLogo and R were linked by using the R extension for NetLogo (Thiele and Grimm, 2010). For runtime reasons, this procedure was not used when numerical output of the model was produced.

2.8. Simulation experiments

We conducted various simulation experiments on different landscapes to illustrate and assess model behavior. First, the model was simulated on a 40×40 landscape with four different prey biomass patterns: homogenous (prey biomass production of 5 kg), random (prey biomass production between 2.05 and 10.46 kg), smoothed random (a moving window passed over each cell to create slight gradient), and left-right gradient going from lowest (2.05 kg) to highest (10.46) prey biomass production. We used these different patterns to visualize configurations of 1–4 female territories. No other outputs were evaluated. These simulations were run for 12 time steps (1 year) with reproduction and mortality processes turned off.

The model was then simulated on 125×128 landscape to examine how a single female territory size varies with respect to habitat quality, i.e., cell-based prey biomass. We first created a "reference" landscape, in which the prey biomass production at each cell was drawn from a uniform distribution with the bounds set to the lower (2.05 kg/cell/month) and upper (10.46 kg/cell/month) limits of prey biomass production derived from Chitwan data. Next, we created landscapes where the prey biomass production values varied from 10% to 200% of those selected from the uniform distribution used in the reference landscape. The simulation was run for 12 time steps and replicated 100 times for each parameterization with a random seed to assess variation. Reproduction and mortality processes were turned off. Aside from female territory size, no other model outputs were evaluated.

We also assessed how mortality processes, such as female starvation, male challenges, and infanticide, are density dependent in the model. We created a 125×128 landscape with prey biomass production per cell set to the midpoint (6.255) of the lower (2.05 kg) and upper limit (10.46 kg) in Chitwan. The model was initialized with 50 adult females and 20 adult males. The distributions were random while making sure that initial positions of females were not closer than 12 cells (3 km) and males were not closer than 20 cells (5 km). The ages of the adult tigers were randomly selected from a range of adult breeding ages ($\geq$3 and <11 years old). Mortality was deactivated over the first 4 years to get territories established and reach quasi-stationary (i.e., stable population size over time) population dynamics more rapidly. Once the population reached a quasi-stationary point after 200 time steps, 50% of the adult females and males were removed from the model, and then various mortality processes and total tiger population size were evaluated for the next 20 years. Simulations were replicated 5–50 times with a random seed to assess variation. The standard deviation in several model outputs appeared to stabilize after 30 replications, so we therefore assessed model outputs for all subsequent analyses using 32 replicates (4 nodes with 8 processors; see Supplementary Materials and Table S2).

The model was then simulated on the Chitwan National Park, 157×345. We rescaled the minimum and maximum prey abundances per cell across Chitwan estimated using Geographic Information Systems (see Supplementary Material) to the lower and upper limits of prey biomass production. Initially 28 adult female tigers were released within the park based on observed individuals in Karki et al. (2013). Because tiger density is higher in the lowland portion of the park, we distributed 4/5 of females in the lowlands and 1/5 in the Churia hills (Karki et al., 2013). The distributions were random while making sure that initial positions of females were not closer than 12 cells (3 km). Female territories initially consisted only of the cell of their origin location. Similarly, 14 adult males (equal to observed males in Karki et al., 2013) were distributed randomly in the landscape (4/5 in lowlands, 1/5 in Churia hills) with a minimum distance of 20 cells (5 km), but they did not initially have a territory. The ages of the adult tigers were randomly selected from a range of adult breeding ages ($\geq$3 and <11 years old). Mortality was deactivated over the first 4 years to get territories established and reach quasi-stationary population dynamics more rapidly.

The Chitwan simulation was allowed to reach a quasi-stationary point after 200 time steps, and then model output was evaluated for the next 20 years. Simulations were replicated 32 times with a random seed to assess variation. All processes were turned on for these simulations. All model outputs were evaluated, including those related to reproduction, mortality, dispersal, resource selection, male and female land tenure, territory size and spatial distribution, and tiger population size and age structure.

A local sensitivity analysis of the Chitwan model was performed by varying key input parameters from their reference value and comparing outputs. Specifically, sensitivity was calculated as the ratio of the relative change of the parameter ((reference value – new value)/reference value) and the relative change of the output quantity. Outputs were tiger population size, total breeding animals, and female territory size over time. Most parameters were varied by $\pm$5% from their reference value. For integers, we selected the next value below and above. For distance parameters, such as maximum dispersal distances, we selected values 0.5 km below and above the reference value. If a parameter was set to a maximum, i.e., 100%, then we only selected a lower value. For litter size, defined by a probability distribution, we tried two alternative distributions, one that was steeper and one that was flatter than the reference. We simulated each parameterization for 120 months (10 years) after discarding the first 200 runs, and replicated 32 times with a random seed to assess variation.

3. Results

Females establish territories that overlap areas with highest prey biomass available to them (i.e., not already taken by a neighboring female), with the territory shape and size corresponding to the spatial distribution of prey (Fig. 5). When simulated on a larger landscape, average female territory size has a power law relationship with the landscape-level average prey biomass (Fig. 6). Further, as population size increased following removal of 50% of adults, rates of infanticide, male deaths from challenges, and adult female deaths more than doubled (Fig. 7 and Table 4). These rates eventually leveled off and the tiger population stabilized after 20 years on this artificial landscape.

3.1. Model testing

We compared a number of model outputs across a 20-year time frame to empirical data on tiger behavior and ecology in Chitwan. By comparing model output to several patterns observed in the field we can increase our confidence that the model performed well (Grimm et al., 2005).

3.1.1. Reproduction

Average litter size in the model was 2.98 cubs (SD = 0.69 cubs), which not surprisingly corresponds exactly to observed litter sizes in Chitwan, as litter sizes were directly imposed in the model. Females gave birth to an average of 12.46 cubs (SD = 7.85) during their lifetime, suggesting that females gave birth to an average of 4 litters. Similarly, long-term field data from Chitwan indicated that females had 4–5 litters over their lifetime (Smith and McDougal,

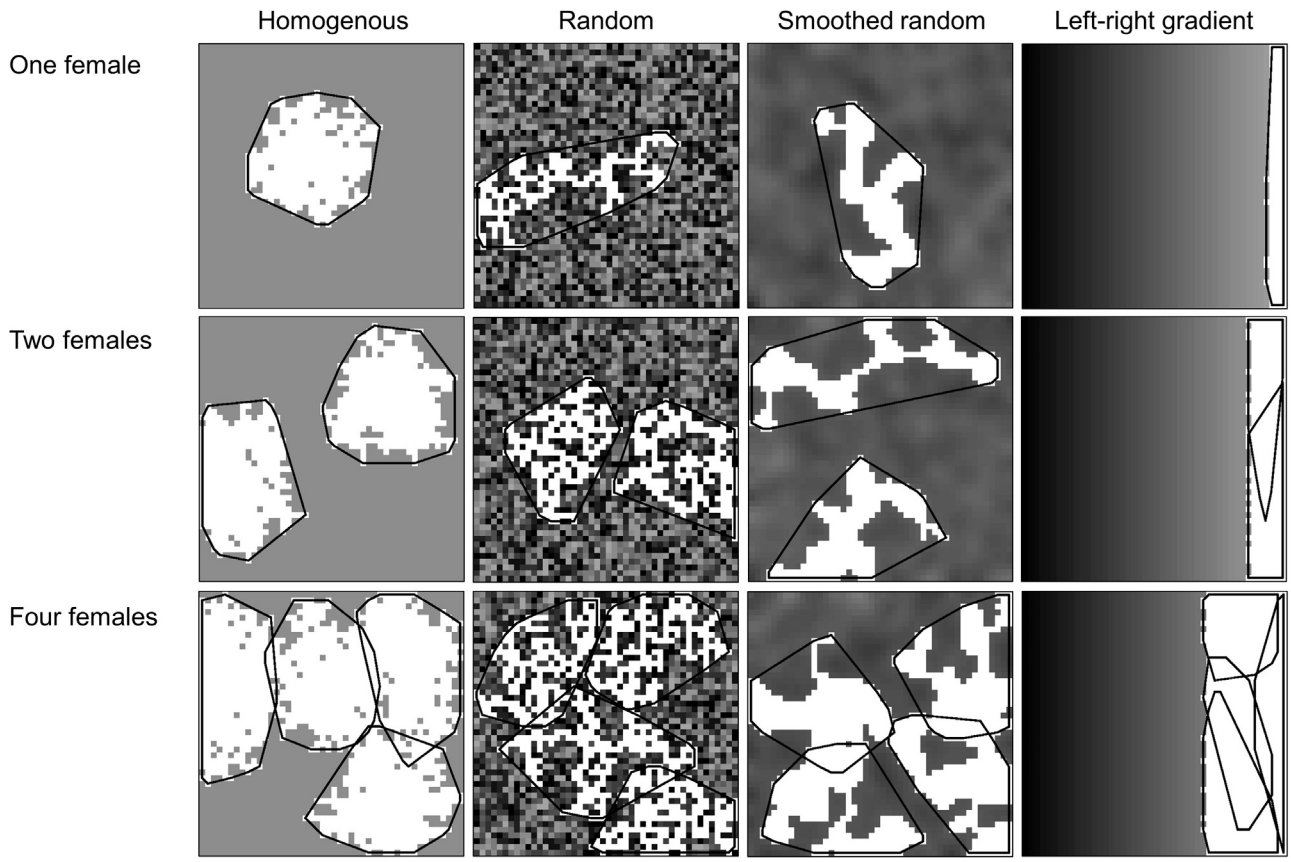

Fig. 5. Female tiger territories in model landscapes with differing spatial distributions of prey biomass production. Cells belonging to a territory are white. A 100% minimum convex polygon is drawn in black around each territory.

1991). The average lifetime reproductive success (i.e., cubs reaching dispersal age) of females was 3.64 (SD = 3.19). Field-based data indicates that female average lifetime reproductive success is 4.5 (SD = 3.4) (Smith and McDougal, 1991).

3.1.2. Mortality

The mean number of cubs and juveniles that died from infanticide per month in the model was 1.47 (SD = 3.58). Observed infanticide rates can be high in Chitwan, with 12 cubs from a portion of the park believed to have died due to infanticide in the span of 1 year (Barlow et al., 2009). Although not directly comparable to model output, the observed rates indicate that an average of >1 infanticide per month across the park is within reason. An average of 0.54 females (SD = 0.78) died per month in the model, and an average of 0.3 males (SD = 0.6) died per month from challenges.

3.1.3. Dispersal

On average females in the model dispersed 18.02 km (SD = 8.8 km) from their natal range and males dispersed 29.62 km (SD = 17.44 km) from their natal ranges. Observed average dispersal distances for females was 9.7 km (range = 0.2–33 km) and 33 km (range = 9.5–65.7 km) for males in Chitwan (Smith, 1993).

3.1.4. Resource selection

The average prey biomass cropped by an adult female per month was 157.62 kg (SD = 26.73 kg). Males overlapped an average of 2.64 (SD = 1.89) females. Males in Chitwan have been observed to overlap up to 6 females, however, most males appear to overlap between 2 and 3 females (see Fig. 27 in Sunquist, 1981).

Table 4
Rates (mean and standard deviation) of different mortality processes in 2-year intervals evaluated for 20 years following a 50% reduction of adult tigers from an artificial population.

Years after shock	Number of offspring killed per month from infanticide		Males that died per month from challenges		Adult females that died per month	
	Mean	SD	Mean	SD	Mean	SD
0–2	0.9128	2.7120	0.1992	0.4851	0.3438	0.5925
2–4	0.9310	2.6889	0.2201	0.5129	0.4961	0.7149
4–6	1.2357	3.4623	0.2383	0.5493	0.3372	0.5496
6–8	1.1628	3.0302	0.2604	0.5569	0.4701	0.6825
8–10	1.4622	3.5121	0.2826	0.5751	0.5234	0.7290
10–12	1.7526	4.1649	0.2956	0.6498	0.5443	0.7849
12–14	1.6654	3.9045	0.3607	0.6649	0.6953	0.8952
14–16	1.8125	3.8827	0.3529	0.6289	0.6393	0.9028
16–18	1.6641	3.6369	0.3503	0.6626	0.6510	0.8206
18–20	2.1068	4.1725	0.4036	0.6764	0.6953	0.9239

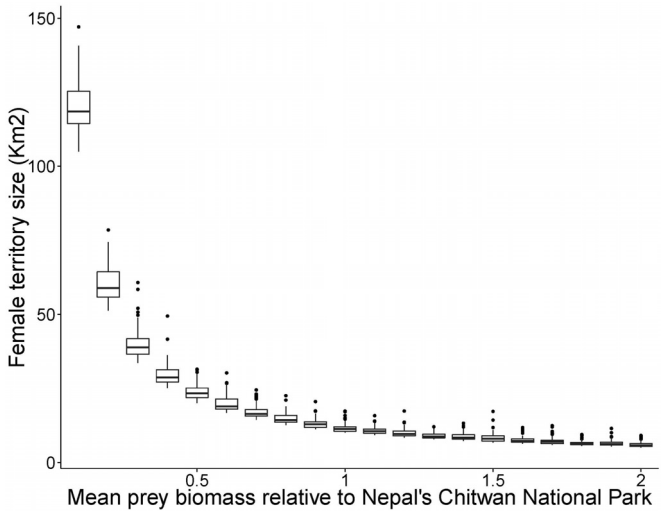

Fig. 6. Territory sizes for a single female tiger with respect to prey biomass. '1' represents mean prey biomass production from Nepal's Chitwan National Park. Values left and right of '1' are proportional to the mean value. Boxplots represent the 25th and 75th percentiles of female tiger territory size across 100 model replicates. Whiskers represent the 95% conference limits, black lines with boxes represent medians, and circles outside whiskers represent outlier values.

3.1.5. Land tenure

Female land tenure was 6.74 years (SD = 4.27 years) and male land tenure was 2.02 years (SD = 1.87 years) in the model. Female and male land tenure is 6.1 and 2.8 years, respectively, from field data collected in Chitwan (Kenney et al., 1995; Smith and McDougal, 1991).

3.1.6. Territory size and spatial distribution

Average female territory size was 21.09 km^2 (SD = 7.46) and was 56.07 km^2 (SD = 44.01) for males in the model. Mean territory sizes observed in Chitwan were 20.7 km^2 (SD = 9.2) and 54.4 km^2 (SD = 35.8) for females and males, respectively (Smith et al., 1987). A snapshot of the model running in Chitwan illustrates the spatial distribution of female and male territories (Fig. 8).

3.1.7. Tiger population size and age structure

Average tiger population size was 158.5 (SD = 19.55), with 106.48 (67.18%) of them greater than 1 yr old. The tiger population was stable across the 20-year period, which is expected since the landscape did not change nor was human-induced mortality (e.g., poaching) included. Age structure of the modeled population was 37.87% breeding adults, 12.26% transients, 17.05% juveniles, and 32.82% cubs (Fig. 9). Long-term field data in Chitwan found the tiger population was 45% breeding adults, 7% transients, 18% juveniles, and 30% cubs (Barlow et al., 2009). Further, variation in breeding adults in the model was lower than other age classes, corresponding to field-based data (Barlow et al., 2009). Average number of breeding females and breeding males in the model across the 20-year period was 43.35 and 16.67, respectively. Previous studies in Chitwan indicated a breeding population of 45 females and 20 males (Smith and McDougal, 1991). Kenney et al. (2014) suggest that the total tiger population estimated from camera traps is approximately 2.9 times greater than the number of breeding females in a population. If so, our model results would equate to a total tiger

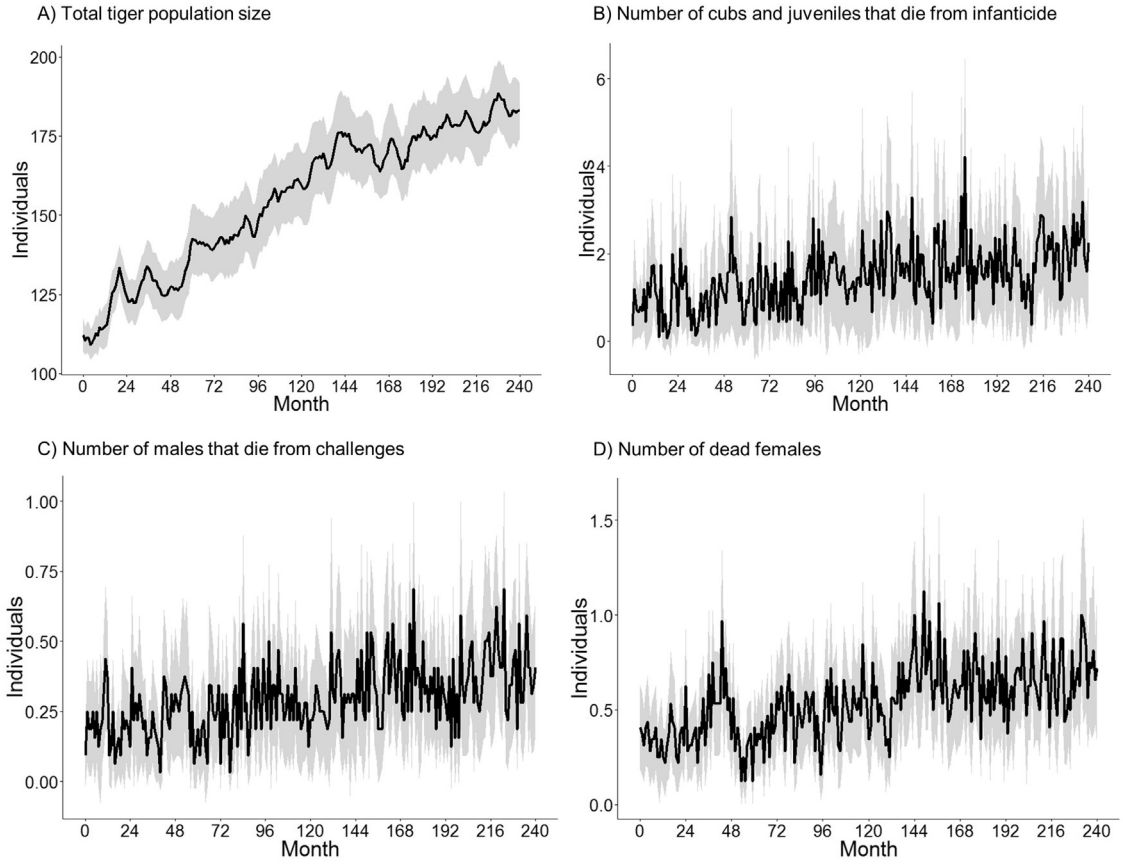

Fig. 7. Mortality processes were evaluated over 20-year time period with respect to total tiger population size following a removal of 50% of adults from the landscape. (A) Total tiger population size, (B) number of cubs and juveniles killed from infanticide, (C) number of males that died from challenges, and (D) number of females that died. Black lines show mean value, with confidence limits (95%) for the mean in gray.

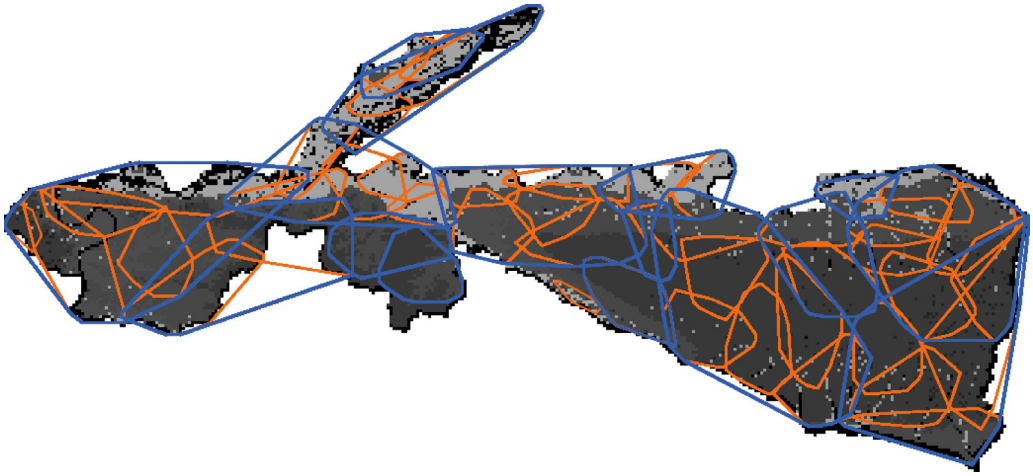

Fig. 8. Snapshot of spatially explicit agent-based model of tiger population and territory dynamics for Chitwan National Park, Nepal. Territories are outlined with 100% minimum convex polygons. Territories of females are orange and blue for males. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

population of 125.72, which matches recent camera trap data from Chitwan (125 individuals, Karki et al., 2013).

3.2. Sensitivity analysis

Chitwan model outputs were most sensitive to changes in the survivorship parameters (Table S3), which is to be expected. In particular, lowering the breeding female annual survival 5% decreased total tiger population size and total number of breeding animals by approximately 25%. Female territory size was most sensitive to amount of prey cropped from total prey biomass and maximum prey resources needed for stable territory. However, those parameters did not disproportionately impact female territories. Changing litter sizes so that there an equal probability of having 1–5 cubs/litter lowered tiger population size by 6% compared to the reference tiger population size (Table S3). Having most breeding females have 3 cubs/litter (i.e., litter size peak distribution) changed model outputs by <1% from the reference. For all of the other parameters, the changes in model outputs were proportionally similar to or less than (i.e., >−1 and <1) the changes to parameter values.

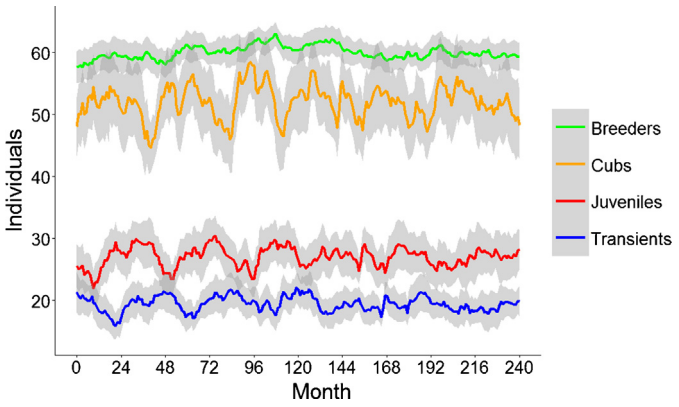

Fig. 9. Tiger population size and structure in Chitwan National Park, Nepal, simulated for 20 years and replicated 32 times. Colored lines show mean size of different age classes, with confidence limits (95%) in gray. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

To the best of our knowledge, this is the first ABM to simulate both female acquisition of spatially heterogeneous food resources and male acquisition of females through agonistic interactions. In the model, females search for the best prey resources near them and add those resources to their territories, which are exclusive of other females. Female territories are constantly being modified due to the presence of neighboring females that are competing for the best prey resources. Males seek exclusive access to as many females as possible to increase their reproductive potential. To claim females, males establish territories that encompass the territories of those females he can successfully defend from other males. We also demonstrate how these distinct territorial behaviors, interwoven with reproduction, dispersal, and mortality processes, regulate population structure on a landscape representing Chitwan National Park, Nepal.

Inter- and intra-sexual dynamics mediated by habitat quality across the model landscapes reproduced several patterns we expect from theories about resource use and conspecific interactions. For example, territory size reflected food productivity, with average territory size decreasing predictably with increasing landscape-level prey resources. In addition, individuals in the model demonstrate habitat preference, with territories being optimized to overlap areas with the highest prey biomass. Territorial dynamics also regulate populations. For example, adult male deaths due to challenges for females increase as the population of males increases. This additional mortality depresses the overall size of the tiger population not only by removing breeding males but also through infanticide, which increases with greater number of challenges. Likewise, as the population of breeding females increases, dispersing females are more likely to die from starvation as they are unable to establish a resident territory large enough to provide sufficient food. Further, female tigers can only disperse and reside in areas that are not occupied by resident females. The spatial distribution of territories thus dictates where the population can expand.

Previous ABMs of territorial dynamics typically represent territories as static in size or with simple shapes, such as circles (Ahearn et al., 2001; Grimm et al., 2003; Kostova et al., 2004; Letcher et al., 1998; Wiegand et al., 2004). In contrast, territories in our model are more flexible and realistic, and they constantly optimize size and shape by overlapping highest prey resources while recognizing the boundaries of nearby territories. Furthermore, our model improves on previous models of tiger space use in Chitwan (Ahearn et al.,

2001; Kenney et al., 2014, 1995). These previous models did not include dynamic territories, were based on hypothetical densities of prey, and simulated movements and behaviors for which empirical data are scarce and difficult to collect throughout most of the tiger's geographic range. Our model utilized empirically derived and easily replicable estimates of prey biomass across the landscape and simulated biologically relevant interactions at scales that are relatively easier to parameterize. The prey resources in our model were static over time, however, because large-scale seasonal shifts in prey biomass do not appear to occur in Chitwan. Fine-scale prey biomass fluctuations due to predator presence, and broader changes in prey due to climate change, represent important future research activities.

Our model matched closely with observed patterns of the real tiger population in Chitwan National Park. Some of this realism was imposed by using observed litter size, and age-specific survival rates, or by calculating prey production rates from observed home range sizes. However, it should be noted that none of the model parameters were determined by fitting the full model to data, i.e., by calibration. Most of the parameters used in the model were measured directly from the field. Several parameters were best-estimates derived from the literature (e.g., the area a breeding female can potentially add to her territory in 1 month). These parameters fortunately had little effect on model outcomes according to the sensitivity analysis.

It thus seems that many of the realistic key patterns of territory dynamics emerged from model behaviors. Spatial structure and distribution of territories related to the spatial distribution of prey resources and presence of conspecifics. For example, the riverine/grassland areas near the northern edge of the park had a higher tiger density and smaller territory sizes (Fig. 8), indicating higher preference for those areas by tigers than the Churia hills where prey biomass is lower. Also, dispersal allows for the tigers in the model to avoid conflict with each other and take advantage of as much of the Chitwan landscape as possible. Territory dynamics and associated mortality processes regulated population size and structure on the Chitwan landscape.

Detailed energy considerations regarding the fitness of an individual were not used in the present model. For example, energy intake by females could be used to determine litter size and survivorship. The probability of a male winning a challenge could be related to how much recent energy he consumed from prey. Such considerations would be useful in exploring subtle issues of how differences in competitive ability may arise through genetic-based or chance differences in the foraging histories of individuals, or what determines the number of survivors in a litter. Also, although some aspects of learning behavior are included (memory of defeats and victories in challenges), others, such as a tiger's gradual learning about the environment, were not considered in this model. Field data to parameterize such relationships do not currently exist. Instead we used rules of thumb on behavior and minimum energy requirements of a territory for survival to simplify the model and encourage its use as a management tool.

The close correspondence of model outputs to observed patterns suggests the model can be a very useful tool for wildlife researchers and conservation planners. In Chitwan, for example, the current model can serve as a baseline for future studies aiming to evaluate the potential effects of different human resource use patterns (e.g., forest degradation and fragmentation), conservation policies (e.g., forest reforestation), tiger poaching and prey hunting rates, and various land uses (e.g., roads) on the tiger population. Our model builds off previous ABMs of territorial behaviors and incorporates basic principles of resource requirements and conspecific relationships. When adapted somewhat to other contexts, the model can test different anthropogenic and natural impacts on tiger populations elsewhere across their range. For example, habitat-specific data on prey densities and empirical estimates of territory sizes would theoretically allow application of the model to other sites, such as those in India and Russia. In addition, by making simple adjustments to territory behaviors (e.g., allowing for greater overlap or less site fidelity), the overall model structure is useful and easily adaptable for understanding population and territory dynamics of many other territorial wildlife species, such as cougars (*Puma concolor*) and jaguars (*Panthera onca*).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.06.008

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