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TIGMOD: an individual-based spatially explicit model for simulating tiger/human interaction in multiple use forests

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Abstract

The loss of tiger habitat and the greater dependency of tiger populations on multiple use forests has led to an increase in conflict between tiger and human forest use. Gaining a better understanding of this conflict through a combination of fieldwork and modeling is critical to the survival of tiger populations in these forests. TIGMOD is an individual-based spatially explicit, object-oriented model that simulates key aspects of tiger behavior and its interactions with wild and domestic prey through stochastic processes. It is a dynamic model driven by changes in states of tigers or prey that trigger the behavior and interactions appropriate to these changes. The model permits users to run the simulation based on different scenarios that explore the relationship between prey densities and tiger survivability, as well as those that examine the relationship between villager attitudes towards tiger killing of domestic prey and the likelihood of poisoning a tiger. Model output includes number of tigers born, starved, or poisoned, and number of wild and domestic prey killed. Model simulation results agree well with field observations and data in terms of prey density versus tiger survivability, number of days between two consecutive prey kills, simulated movement of tiger traversal of its home range, and number of cubs born per breeding female tiger. This study shows that tiger populations are sustainable at low density of domestic prey but not sustainable if domestic prey density increases to three or more per square kilometer. Additionally, change in behavior and attitudes of villagers towards tigers, such as increasing guarding of livestock and higher tolerance of domestic prey kills will significantly reduce tiger mortality caused by poisoning. TIGMOD is a useful tool for analyzing the interaction between tigers and humans in multiple use forests. It provides a means of understanding the right balance between forest use by tigers and use by villagers, which can lead to implementation of management strategies that optimize both.

Keywords: Tiger-human interaction; Individual-based object-oriented model; Dynamic simulation

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1. Introduction

Tigers (*Panthera tigris*) are highly endangered due to the habitat loss and fragmentation that has occurred since World War II. More recently, intensive poaching for traditional medicine has

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greatly increased the likelihood that many smaller populations will be driven to extinction (Kenney et al., 1995). Since 1970, efforts to conserve tigers have focused primarily on establishing a network of tiger reserves in the best remaining habitat. This approach is exemplified in global and national conservation strategies that aim to set aside at least 10% of national land in protected area systems. However, for tigers and other top predators, a system of protected areas alone is inadequate (Smith et al., 1998). Protected areas account for ca. 17–25% of tiger habitat throughout the world (Smith et al., 1987b; Dinerstein et al., 1996), while 75–83% of tiger habitat is in multiple use forests where human activity is a dominant landscape component. For tigers, these multiple use forests are critical; without them, most protected areas are too small and isolated to maintain viable tiger populations over the next 100–200 years. However, if levels of human activity increase, these multiple use forest lands no longer support tiger populations and become sinks (Pulliam and Danielson, 1991; Woodroffe and Ginsberg, 1998). Multiple use management is an often-cited solution offered by policy makers to deal with resource competition between local people and biodiversity conservation. It may be the only way to ameliorate the intense human competition for forest resources that are also needed to support viable tiger populations. However, multiple use management of these lands is confounded by the fact that there is little data on tiger-human conflict and there are no quantitative procedures for understanding the proper balance between competing uses. The one tiger study undertaken in a human-dominated landscape provides unique insight into these interactions (Chundawat et al., 1999). To obtain a more comprehensive understanding of tiger-human interaction in these multiple use landscapes, data from a diversity of tiger studies needs to be integrated into a quantitative framework that can provide guidance for balancing these competing uses.

Modeling provides this framework by formalizing the processes that govern a system. It helps to identify knowledge gaps, gain theoretical insights and is useful for predicting long-term response to changes in management practices (Liu and Ashton, 1998). Modeling is an essential tool for understanding the dynamics of tiger-human interactions because it is unrealistic to complete and replicate long term field studies for highly threatened, long-lived species living in rapidly changing landscapes. Furthermore, when field studies are conducted, the sample size is often small because tigers are secretive and live at low densities in thick vegetation. Although radio telemetry is a useful technique, the use of data concerning tiger behavior is limited by a lack of analysis tools. Modeling enables exploration of tiger response to different levels of human activities in diverse geographic settings under a wide range of conditions, some of which may not currently exist. In the past several years, many spatially explicit models have been developed to dynamically simulate mobile objects in geographic information systems (GIS). They can be generalized into two major categories: traditional layer-based GIS models and object oriented GIS models. Traditional layer-based GIS uses geometry-based data models. An object is represented as a geometric feature such as point, line, polygon or pixel, with all other properties of the object attached to the geometric features. The geometric features have fixed locations that are defined explicitly by their boundaries. Any change to these locations or boundaries requires update to the geometric features and to other properties built on the geometric bases. The rigid location-based system inevitably encounters serious limitations when applied to analysis of discrete objects moving through space (Raper and Livingstone, 1995; Bian, 1997).

In contrast to traditional layer based models, object-oriented GIS models mobile objects more efficiently because it treats location and time as explicit properties of an object. This permits frequent update of locations and time when an object moves. It is especially useful for building individual based models which ecologists recognize as an important way to simulate animal movement (Siniff and Jessen, 1969; Jones, 1977) and capture complex interactions of the ecological process (Liu et al., 1995). Recently, several investigators have used object-oriented GIS models to dynamically simulate the individual behaviors of animals in ecosystems (Bian, 1997; Zev, 1998; Westervelt and Hopkins, 1999). These models successfully simulated dynamic phenomena using the object oriented approach to represent objects and their relationships, permitting a closer mapping of reality into the modeling domain (Worboys, 1994).

This paper describes a prototype (TIGMOD) of an individual-based, object-oriented GIS model that dynamically simulates individual tiger behavior and interactions between tigers, natural prey, and domestic livestock grazing around the boundary of tiger habitat in the lowland forests of Nepal. TIGMOD models the dynamics inside protected areas, as well as the impacts of human activity in the surrounding region. The model is used to quantitatively test the density of wild prey needed to support a sustainable tiger population and the effects that different densities of domestic and wild prey have on tiger population sustainability. It helps predict population trends of tigers at diverse levels of human activities in boundary areas and provides insight into how to balance competing uses in these multiple use forests. The design of TIGMOD begins not with the specific analytic task to be performed, but with aspects of tiger behavior patterns and interactions needed to model the system. Once these aspects are correctly represented, the model can be used to answer a range of questions concerning tiger interactions with its environment by adding specific functions or changing the input parameters without altering the main structure of the simulation system. This paper begins with an introduction to the model structure and then focuses on the dynamic simulation of the interaction between tigers and their prey; both wild and domestic. Finally, we present results of model testing, sensitivity analysis and a discussion of the implications of this research.

2. Methods

2.1. Study area

The study area includes lands adjacent to Royal Chitwan National Park and the Park itself, which is located in the lowlands of Nepal (Smith et al., 1999). Field research supporting the model was conducted in the Terai forests in southern Nepal (Fig. 1). This study area was chosen because it typifies human tiger conflicts in multiple use forests and because of the availability of long-term data sets on tiger ecology and behavior collected in Royal Chitwan National Park. In the study area about 70% of the habitat is classified as sal (*Shorea robusta*) forest, 22% is a dynamic mosaic of alluvial grassland and riverine forest, and 8% is mixed deciduous forest that is found along streams in sal forests. In addition to the

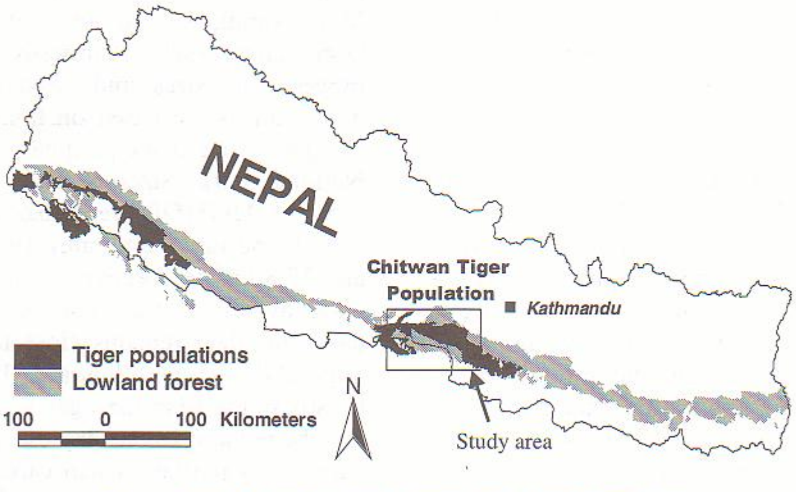


Fig. 1. Study area: terai forest of Nepal and tiger populations.

tiger, there are six medium sized ungulate species, all-important tiger prey, including five species of deer (*Cervus unicolor*, *Cervus duvauceli*, *Axis axis*, *Axis porcinus*, *Muntiacus muntjak*) and the blue bull (*Boselaphus tragocamelus*). Other prey include wild boar (*Sus scrofa*) and gaur (*Bos gaurus*). Land within Chitwan is well protected but there is some domestic livestock grazing along the edges and within the park. Outside the park, national forest land is variably impacted by human activity, primarily livestock maintenance and collection of fuel wood. The density of tigers is generally lower outside the park.

2.2. Overview of TIGMOD

TIGMOD is a spatially explicit, individual based object oriented model that simulates key aspects of tiger behavior and interactions with wild and domestic prey through stochastic processes. It is driven by changes in the state of the objects (tigers or prey) that trigger behavior and interactions appropriate to those changes. TIGMOD has a modeling environment that supports the mobility of objects, variable spatial attributes and time resolution, interaction with other individual objects, the creation of new individuals, and propagation of change in the state of one object through the system in space and time to affect all related objects.

The model requires input for a series of parameters that relate to tiger biology, tiger behavior given its particular state, and the length and time increment for the simulation run. Most parameters are based on data sets that have been acquired during previous field observation (McDougal, 1977; Smith et al., 1987a,b, 1989; Sunquist, 1981; Smith and McDougal, 1991; Karanth and Sunquist, 1992; Smith, 1993; Chundawat et al., 1999). Some parameters were set for multiple simulation runs, while other parameters were set per run. Model output includes: number of tigers that starve, are poisoned and are born, as well as the number of wild and domestic prey killed.

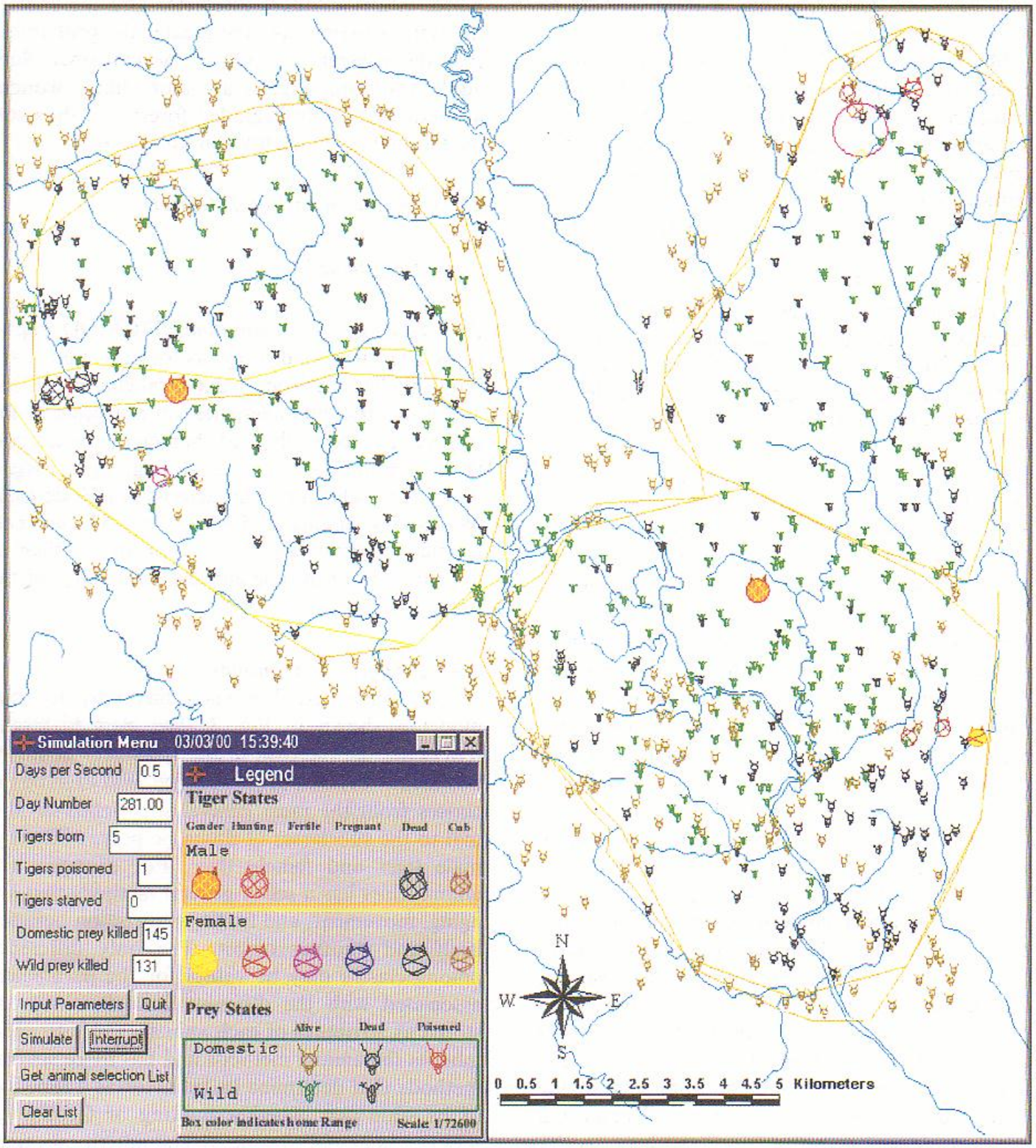
TIGMOD has an application that allows the user to randomly populate the core area of each tiger's home range with wild prey and populate the boundary area of the home range with domestic prey to imitate encroachment (Fig. 2). Some overlap of wild and domestic prey is permitted. Different combinations of wild and domestic prey densities can be created by the user and saved as separate versions using the version management capability of Smallworld (Newell and Easterfield, 1990). This capability enables the user to run TIGMOD with a diverse combination of prey densities without affecting any other combination already created.

Scenarios that explore the relationship between wild prey densities and tiger survivability can be tested with TIGMOD, as well as those that examine the relationship between the incursion of cattle into the tiger's home range and the likelihood of poisoning of tigers by villagers. The model provides a means of understanding the right balance in multiple use forests between use by tigers and villagers, which can lead to the implementation of management strategies that optimize both.

2.3. Conceptual model of tiger behavior and human interaction

Tigers establish home ranges based on habitat type, quality and prey availability. A tiger home range has fuzzy boundaries within which individuals generally remain. If tigers move outside their home range it is usually for a brief period and for a specific purpose such as hunting (Smith et al., 1989). Male tigers have a home range that encompasses one or more female home ranges. TIGMOD simulates two adjacent adult male tiger home ranges; each circumscribes two female home ranges. The sizes and configurations of these home ranges are based on home range estimates of tigers living at the periphery of Royal Chitwan National Park. Sizes of male tiger home range used for TIGMOD were 46.6 and 70.1 km^2. Female home range estimates were 22.1, 20.0, 26.2, and 37.3 km^2, respectively, (Smith et al., 1987a).

On average, a tiger kills one prey every seven days and then remains close to its kill for 2–3 days while it feeds (Sunquist, 1981). If the kill is livestock, the time the tiger remains with the kill may be reduced to one day due to human interference and a partially eaten carcass remains; if the kill is wild prey, it is rarely disturbed and eats


Simulation Menu 03/03/00 15:39:40

Days per Second 0.5
Day Number 281.00
Tigers born 5
Tigers poisoned 1
Tigers starved 0
Domestic prey killed 145
Wild prey killed 131

Fig. 2. A TIGMOD simulation after 281 days.

until gorged. Interruption in feeding causes tigers to hunt more frequently when they kill domestic prey. Tigers will start to hunt prey again 3–5 days after a feeding. Female tigers with cubs hunt more frequently because they kill to feed their cubs in addition to themselves. A tiger that does not find prey within 10 days begins to experience stress and will increase its rate of movement. After 30 days of unsuccessful hunting, a tiger will die or weaken beyond recovery.

Male tigers make three to five visits a month to each female within its home range. If the female is fertile the male will remain to mate. A female is fertile on average every 20 days. If she becomes pregnant she gives birth within 102 days of conception. When cubs are born they remain close to their mother for the first 18–22 months of life and fertility of the female is suppressed for about 600 days (Smith, 1993).

Tiger movement patterns, characterized by the distance and direction a tiger moves per day, are determined by tiger activities. When looking for prey or a female, male tiger movement usually has an external bias in the direction of a hunting area or the female. Males begin to move toward the target, may be distracted, but resume moving toward their goal until they find prey (if hunting) or enter a female tiger home range (if mating). Once a male tiger enters a female home range, it will move slower. A male seeking an estrous female can be characterized as a random walk with directional bias. If the male tiger is within 400 m of the female, he will move directly towards her. A tiger seeking prey will have a similar movement pattern. After prey is killed, the tiger tends to stay nearby. In the absence of specific behavior a tiger will begin to move in a given direction and may persist in that direction before redirecting itself. This type of movement is characterized as random walk with persistence.

As discussed above, most tiger habitat is in multiple use forest lands where human activities play an important role in the ecological system. In the study area, the local use of lowland forests has caused significant degradation of the forest through intensive harvest of primary products such as fuel wood, lopped branches for livestock fodder and grazing around the boundary of the tiger's home range. As forest use by human and livestock intensifies, natural prey is displaced by domestic livestock and consequently, tigers kill more livestock. As the number of cattle killed within a given time period and spatial proximity increase, villager become increasingly motivated to poison the carcasses to prevent further killing of domestic livestock. The more cattle that are killed within a square kilometer and the shorter the time between kills, the greater the probability that the villager will poison the carcasses. Subadult, dispersing tigers, are more likely wonder around the heavily degraded forest and thus suffer the highest mortality (Smith, 1993).

2.4. Computer model of TIGMOD

2.4.1. Data model

2.4.1.1. Object representation. TIGMOD represents the tiger and prey as objects that have physical characteristics, behavioral characteristics, and geometric characteristics; all are fields in the respective objects. Physical characteristics describe the condition of the animal (e.g. *age*, *weight*, *alive*). The behavioral characteristics include *feeding*, *hunting*, *mating*, and *giving birth*. The geometric characteristics are the *location* of the tiger at any given point in time and the *home range* of the tiger.

2.4.1.2. Object relationships

Class hierarchy. The class hierarchy for our model is shown in Fig. 3. The class hierarchy represents the increase in the specificity of methods (behavior) that are associated with each of the classes from the most general super-class of animal to the subclasses of domestic prey, wild prey, male tiger and female tiger. For example, the animal class has a set of general methods that are aging, movement, and finding a direction between itself and another object. The only difference among classes may be values for the parameters associated with the different animals; these are stored as attributes of each animal. The tiger class inherits the animal methods and has more specific methods that determine its behavior as a function of its state (e.g. whether hunting or feeding on prey). Male and female tigers inherit all tiger methods and have additional unique methods. For example, a male tiger regularly visits females in his home range and has a method, *visit next female*, which schedules that event. A female has methods for becoming fertile, getting pregnant, and giving birth.

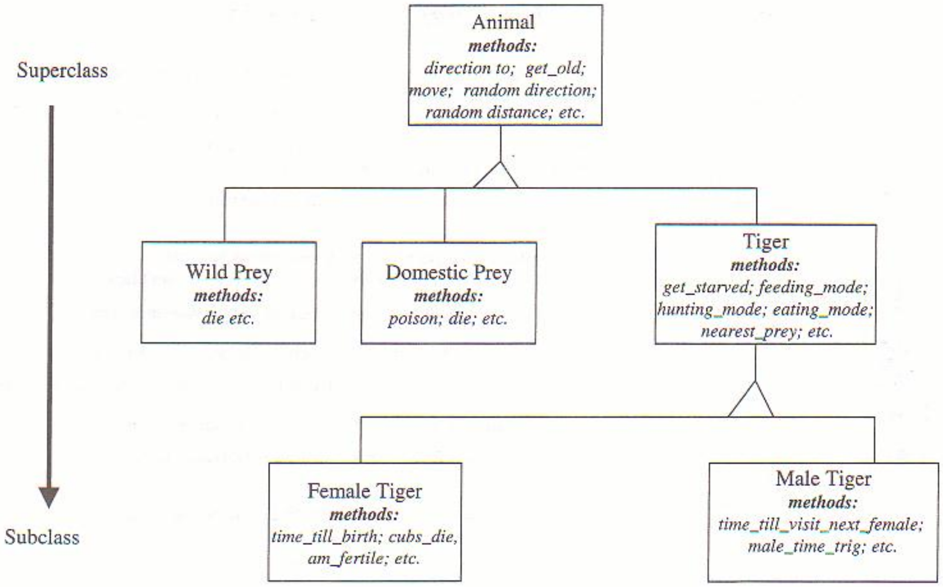


Fig. 3. Class hierarchy of TIGMOD data model. Methods are cumulatively inherited by subclasses from their superclasses.

Associations (relational joins). Objects that are closely coupled need a stronger bond to efficiently define their relationships. Smallworld implements these bonds as relational join fields in the object model. The TIGMOD object model has relational joins between male and female tigers and also between a tiger and its prey (Fig. 4). The functionality between the male and female tiger is one to many (1:*n*); one male can have one or more females within its home range or zero female tigers if it is a juvenile. The female has a 1:*n* relationship with itself (e.g. a female tiger can have zero, one or more female cubs) and a 1:*n* relationships with a male tiger (e.g. a female tiger can have zero, one or more male cubs). Both male and female tigers have 1:0 relationships with prey (e.g. a tiger can have a relationship with zero or one prey at a time).

2.4.2. Dynamic mechanism of TIGMOD

Dynamics of TIGMOD are driven by the interaction of the tiger's state and its environment. State-based relationships, event scheduling, functional events and movement are actions that occur due to a combination of an object's state and its interaction with other objects or its environment. For example, if a mating male comes close enough to a fertile female and spends a period of time with her, her *pregnant* attribute will change from *false* to *true* which then triggers a method to *schedule* her *time until birth* attribute. This change will trigger change in the *type of movement* she will exhibit.

2.4.2.1. Associations (state-based relationships). State-based relationships are relationships in which a change in the state of a characteristic of

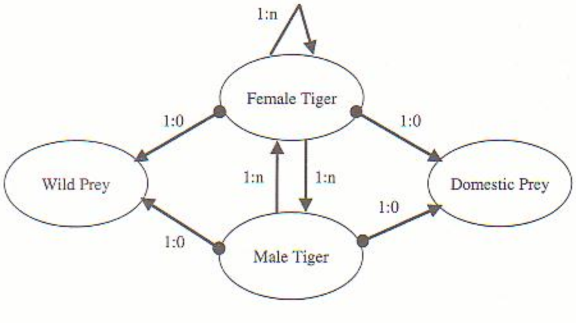


Fig. 4. Object relationships in TIGMOD shown 1:n relationships between tigers (e.g. a tiger can have a relationships with 0, 1 or many tigers) and 1:0 relationships between tiger and prey (e.g. a tiger can have a relationship with zero or one prey).

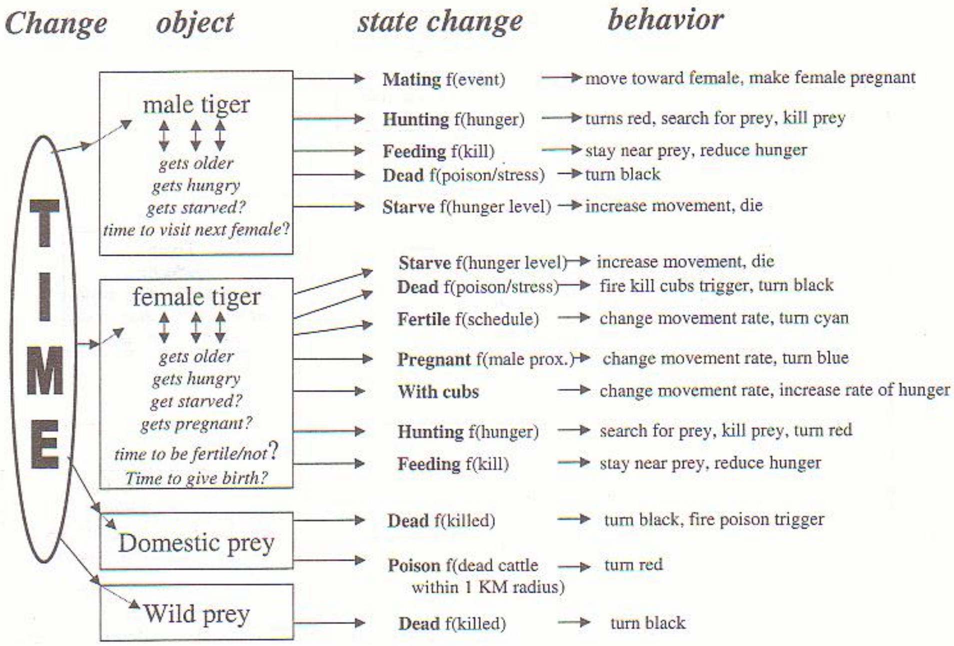


Fig. 5. Diagram of the dynamic interactions in TIGMOD.

an object imparts changes on the object itself or other related objects. These types of relationships create a dynamic environment that drives the model. Each animal has a *time* attribute that is updated for each change in the simulation menu clock that keeps track of the model time. A change in the time attribute triggers methods that govern all time-related attributes (Fig. 5). These include attributes related to states, as well as to scheduled events.

2.4.2.2. Event scheduling. Events can be either periodic or functional. Two types of events can be scheduled in TIGMOD by setting the event schedule tied to each object. Periodic events scheduled are *time until fertility* and *time until visit next female*. Fertility status is changed to its opposite state every 20 days by scheduling the *time until fertility* variable for current time plus 20 days, after each change in its fertility status. The movement toward the next female is scheduled once the male tiger is within 1 km of the female whom it is currently visiting and has remained with her for an average of 3 days. The functional event scheduled is *time until birth*. *Time until birth* is an event scheduled when a fertile female is in close proximity to a male. It schedules a birth 102 days in advance and suppresses fertility for 600 days. At the end of that period, two to four cubs are born. After birth of her cubs, the female tiger's rate of hunger increases, her movement becomes more confined and she is closely followed by her cubs.

2.4.2.3. Periodic and functional events. Periodic events in TIGMOD are *fertility* and *visit next female*. They are triggered *by time until fertility* and *time until visit female*. Functional events are triggered by a change in the tiger's state or its interaction with other animals. Functional events in TIGMOD include *birth*, *hunting*, *feeding*, *starving*, *poisoning* and *dying*. Each tiger has an attribute called *hunger index* that has a range between 0 and 100, with 0 representing the state of no hunger and 100 being the state of maximum hunger. A tiger is in the *hunting mode* when its hunger index is greater than 60. A tiger's hunger index increases 30 each day (40 for females with cubs). Once the tiger reaches a threshold hunger index (default is 60), its behavior changes to the hunting mode and it begins to search for prey.

The search proceeds with the tiger scanning a 0.4 km radius to find the nearest prey. The tiger then pursues that prey and kills it with 0.25 probability of success if the prey is wild and 0.75 if the prey is domestic (both are input parameters). If unsuccessful, the tiger continues to move randomly with a persistence of 0.75 and will again scan for nearby prey. If successful, its movement pattern changes to *feeding mode* and its hunger index decreases by 25 for each day of feeding. For wild prey a tiger feeds for 2–3 days. If the prey is a domestic animal, the tiger only feeds for 1 day (they are often scared off by villagers). When a tiger kills domestic prey in the simulation, a 1 km radius is scanned around the dead prey. If a kill has occurred in the past 60 days, a trigger is fired to initiate poisoning. The probability of poisoning increases from 0.05, if two domestic prey were killed to 0.10, if three are killed, to 0.25 if four are killed and 0.50 if five or more are killed. These probabilities are input parameters that can be changed along with number of cattle killed before poisoning begins and the time period for triggering poisoning. If the villagers poison a carcass the *tiger will die*. If no prey is found and the hunger index rises above 90, the starvation index is increased by an increment of one each day. If no prey is found after 30 days, the tiger dies of starvation, otherwise the index is reduced to zero. The *starvation index* is an attribute of the tiger that ranges from 0 (no starvation) to 30 (death).

2.4.2.4. Movement. Movement is a complex functional event. Turchin (1998) identified four general types of movement for animals: simple random walk, random walk with directional persistence, random walk with directional bias and random walk with persistence and directional bias. These different movements are a function of the state of the individual and the discrete time interval over which the model is run. In the absence of specific field data on tiger movement, we chose a modeling approach that focuses more on behavioral aspects of individuals rather than on models that relate more directly to population redistribution. TIGMOD is designed with maximum flexibility for type of movement that can be selected and the parameters of that movement for a given type of behavior.

Direction. All individuals in the model move independently unless they have a relationship in which their movements are linked (e.g. mother and cubs). The two aspects of movement, direction and rate are modeled as a function of individual state. Table 1 summarizes the movement direction and distance for each state that is exhibited by the male and female tiger. Direction can take one of four general forms. The simplest is the movement of one individual directly toward another. An example of this type of directional movement occurs when prey is located and the tiger moves directly toward it. Another type of directional movement is one in which the direction is a normal random variant with a mean in the direction of the object and a user defined standard deviation (S.D., σ). This type of movement simulates the movement of a tiger after it makes a kill and remains in the area of the kill. Random movement with a probability of persistence in a direction is a third type of movement in TIGMOD. The direction of persistence is selected from a random variant with a mean in the direction of the earlier move and a user defined S.D. (σ). An example of this type of movement occurs when a tiger is cruising its territory. For this state, the default value for the probability of persistence is set at 0.75 with σ equal to 10°. If there is long distance attraction between two objects, the movement direction is random with a bias. This is represented as a random directional component with a probability of bias in a direction that is selected from a random variant with a mean in the direction of the object of attraction and a user defined σ. A male tiger that is mating and heads toward its next female typifies this type of movement. These two types of movement, random with directional bias and random with persistence, are illustrated in Fig. 6.

Distance. Distances that tigers move are rarely uniform and are usually determined by the tiger's state. For example, if a male is mating, he often travels very quickly to a female home range and then slows to search for her. Field data show that movements can be characterized by a greater number of smaller movements than longer movements. Given lack of information on the precise distributions of movement rate we chose to model

Table 1
Movement characteristics under different tiger behaviors

	Movement characteristics with default values	
Behavior	Rate (distance per day) μ, mean rate of movement	Direction μ, mean direction movement, σ, standard deviation of movement direction
Looking for prey	χ^2 random variable ($\mu = 1500$ m, $\sigma = 1500$ m)	Random with bias: moves in a random direction with a probability of bias of 0.75 in a direction selected from a normal random variable with μ, direction of prey and σ, 10°
Found prey	Moves to the location of prey	Moves in the direction towards the prey
Feeding	χ^2 random variable (μ, 400 m, σ, 400 m)	Movement is directed to prey location as selected from a normal random variable with μ, direction to prey and $\sigma = 5°$
'Random'	χ^2 random variable (μ, 2000 m, σ, 2000 m)	Random with persistence: moves in a random direction with a probability of persistence of 0.75 in a direction selected from a normal random variable with μ, earlier direction and $\sigma = 10°$
Mating (male), outside female domain	χ^2 random variable ($\mu = 3000$ m, $\sigma = 3000$ m)	Random with directional bias: moves in a random direction with a probability of bias of 0.85 in a direction selected as normal random variable with μ, direction of female and $\sigma = 10°$
Mating (male), inside female domain	χ^2 random variable ($\mu = 1500$ m, $\sigma = 1500$ m)	Random with directional bias: moves in a random direction with a probability of bias of 0.85 in a direction selected as a normal random variable with μ, direction of female and $\sigma = 10°$
Mating (male), within 400 m of female	Moves to location of female	Moves in the direction toward female
Fertile (female)	χ^2 random variable ($\mu = 100$ m, $\sigma = 1000$ m)	Random with persistence: moves in a random direction with a probability of persistence of 0.75 in a direction selected from a normal random variable with μ, earlier direction and $\sigma = 10°$
Pregnant (female)	χ^2 random variable ($\mu = 1000$ m, $\sigma = 1000$ m)	Random with persistence: moves in a random direction with a probability of persistence of 0.75 in a direction selected from a normal variable with μ, earlier direction and $\sigma = 10°$
With cubs (female)	χ^2 random variable ($\mu = 800$ m, $\sigma = 2000$ m)	Random with persistence: moves in a random direction with a probability of persistence of 0.75 in a direction selected from a normal random variable with μ, earlier direction and $\sigma = 10°$

movement as a χ^2 random variable with mean and S.D. set as a parameter for each behavioral state (Table 1).

2.5. Simulation and analysis methods

2.5.1. Modeling environment

The simulation model was developed in the Smallword GIS software package (Smallworld, 1999) using its native computer language Magic. Magic is an object-oriented language that comes with a comprehensive set of objects and methods for the various spatial and non-spatial data structures supported by Smallworld. The data model was created using both Smallworld Case tool and the Magic language. The simulation was run on an Alpha workstation running the NT operating system.

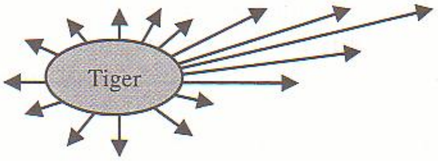


Fig. 6. A vector diagram of the probability of a tiger moving in a given direction for the movement characterized by a random walk with persistence or a random walk with external bias. The longer the vector the greater the probability of a tiger moving in that direction. The longest vector is the direction of the previous move in the case of persistence or the direction of a female in the case of external bias.

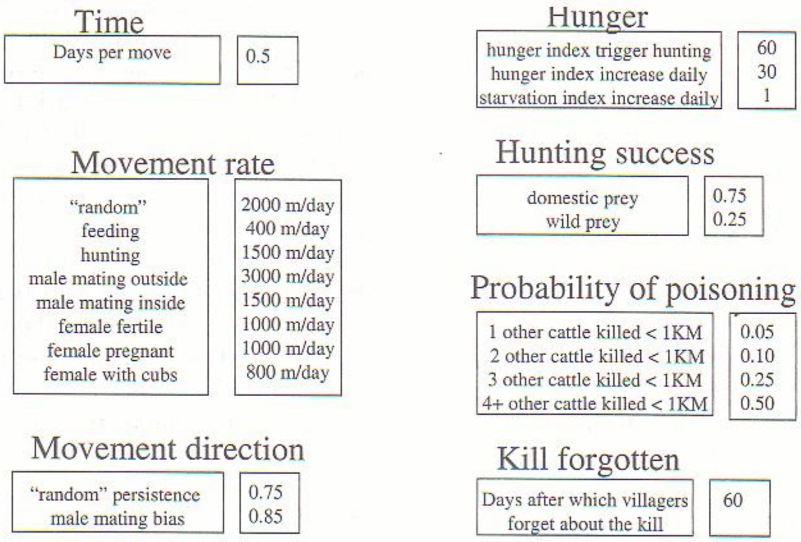


Fig. 7. Input parameters for TIGMOD with default values.

2.5.2. Input and output

The initialization of the model starts with creating male and female tiger objects and their home ranges. Data are then input for the physical characteristics of the tigers (e.g. age, size, fertility status). Wild and domestic prey are incorporated into the model using the PREYSIM application. This application, also written in Magic, allows the user to create different densities of wild and domestic prey within user defined regions, saving the resulting database scenarios as different versions of the database. A menu permits the user to input model parameters controlling: the number of times per day tigers move, movement rates and direction for different states, the onset of hunger, the probability of hunting success for both wild and domestic prey, the probability of poisoning for a given number of cattle killed within a 1 km region, and the period of time villagers remain motivated to poison (Fig. 7). Model output includes tigers born, starved, and poisoned and wild and domestic prey killed (Fig. 2). The length of model runs was 365 days with a time step of 0.5 days. The time step of 0.5 (two movements per day) was chosen to capture the periodicity of the tigers activities while minimizing the use of computer resources.

2.5.3. Visualization and cartographic representation

The cartographic representation of prey and tigers is state dependent. If the male tiger is alive he is orange, if he is hunting he is red, and if he is dead, he turns black. Immature tigers (< 2 years old) are brown and small. Females are smaller than males and have five cartographic representations, yellow (normal), red (hunting), cyan (fertile), blue (pregnant) and black (dead). Prey are either brown (livestock) or green (sambar) and are black if they have been killed. Livestock carcasses that have been poisoned are red (Fig. 2). These state-based cartographic representations are very useful for monitoring activities of the model as it runs. Fig. 2 shows a simulation run for 58 days at a prey density of four cattle and four sambar per km^2. Note the many states of the various tigers and prey as reflected in their colors. The female and her cub located in the northern part of the eastern region have both been poisoned. The cattle they ate is red indicating they have been poisoned.

2.5.4. Model testing

The model was run with five different density levels of wild prey (one, three, four, six and eight sambar per km^2) and six different combinations of domestic and wild prey (one wild and one, three, and six domestic prey; and three wild with one, three, and six domestic prey). Each combination was run at least 6 times and each run required about 15 min. using the time period of 365 days with 2 increments per day. During a run, the movements, behaviors and reproductive status of tigers were displayed in 'real time' and the numbers of tigers born, starved and poisoned were monitored and recorded in the simulation menu (Fig. 2). Additionally, the numbers of wild and domestic prey killed were also tabulated. A paired difference test between the effects that different density combinations had on tiger survivability was conducted at $t_\alpha = 0.05$ level.

2.5.5. Sensitivity analysis

Three parameters that affect tiger/human interaction were examined for sensitivity of tiger survival. The three parameters are*: time villagers remain angry and motivated to poison tigers*, *guarding of domestic prey*, and *delaying the onset of poisoning domestic prey carcasses*. The three parameters chosen for the testing affect the ratio of domestic to wild prey kills and/or the likelihood that local people will poison a livestock carcass. Settings for each parameter reflect the cultural influences and villager attitudes toward tigers. Government policies can influence attitudes through education, management practices and incentives. For example, encouraging villagers to guard their cattle more intensely reduces the probability that domestic prey are killed, which decreases tiger mortality from poisoning. Also, villager education regarding the economic benefit tigers contribute through tourism, may decrease the length of time they remain angry after domestic livestock are killed, and increase the number of kills tolerated before they resort to poisoning.

The prey density combination used for this analysis is d3w3 (i.e. three domestic and three wild prey per km^2). At least six runs were made for each parameter setting. The probability of tiger hunting success when pursuing domestic cattle was tested for three probability levels — 0.25, 0.50 and 0.75. These probabilities relate to how well the villagers guard their domestic livestock. The number of cattle that need to be killed within 1 kilometer before villagers will start poisoning cattle carcasses was tested at two, three and four kills. This was done by shifting the poisoning probability for the second kill of 0.05, the third kill of 0.10, the forth kill of 0.25 and the fifth or more kills of 0.50, up one level. Length of time that villagers remain angry enough with tiger-killed livestock to poison the carcass was tested for 60, 120 and 360 days. This was accomplished by counting only those kills that occurred during the earlier 60, 120 or 360 days and within the 1 km radius. For each of these parameters, differences in tiger mortality between successive changes were compared using a $t_\alpha = 0.05$.

3. Results

3.1. Model consistency with field data

Four aspects of the model were examined for consistency with field data — prey density versus tiger survivability, number of days between two consecutive prey kills, effects of the simulated movement on tigers traversal of its home range, and number of cubs born per breeding female.

The model is consistent with field data on the minimum level of prey required to support breeding tigers. Based on field surveys of prey abundance as measured by number of deer pellet groups per 10 m^2, the minimum number of pellet groups required to support breeding tigers is 0.5 groups per 10 m^2 (Smith, 1993). This converts to 3.8 sambar deer per km^2 (Smith et al., 1999). In our model, all populations survived at this prey population density. At sustainable prey densities, the model is also consistent with field data concerning the number of days between prey kills by tigers. Prey were killed on average once every 7.7 days with a standard deviation of 0.002 for 6 simulation runs with prey density set at d0w8. This compares with studies that have estimated an average of 7 days between prey kills (Seidensticker and McDougal, 1993).

The validity of the tiger's movement pattern was tested by comparing the pattern of prey distribution at model initialization with the pattern of prey kills after the first 365 days in the model

Table 2
Nearest neighborhood analysis of dead prey distribution used to examine tiger movement

Dead prey	Dead prey density (km^2)	Actual average distance between dead prey (km)	Perfectly random average distance between prey (km)	Perfectly clustered: average distance (km)	Perfectly dispersed average distance prey (km)
330	2.163	0.32	0.34	0	0.73
347	2.246	0.31	0.33	0	0.72
279	1.806	0.32	0.37	0	0.78
311	2.013	0.33	0.35	0	0.76
308	1.994	0.32	0.35	0	0.76

run. The distribution of kills provides a cumulative measure of the complex interactions associated with movement. Distribution of the prey at model initialization was random, so if movement patterns of tigers are not biased toward a particular part of their home range, resulting kill patterns should also be random. To test the distribution of prey kills, a nearest neighbor analysis (NNA) (McGrew and Monroe, 1993) was performed for five different runs in which all tigers survived the full 365 days and an equal number of domestic and wild prey was killed. The first step in an NNA is to create an index for a random distribution, a maximally dispersed distribution, and a perfectly clustered distribution. These measures are calculated as a function of point densities and a set of empirical equations used to calculate each index (De Meer, 1997) (Table 2). The actual average distance between dead prey ranges from 0.31 to 0.32 km, while the average distance between live prey at model initialization ranged from 0.33 to 0.37 km. These results confirm that the distribution of kills in the study area was random in a set of five different simulation runs and there was no bias in tiger movement.

The average number of tigers born to the four female tigers was 5.8, with a standard deviation of 0.56 for 11 replicates (with no fatalities), in the first year of simulation, an average of 11.6 tigers per 2-year period. This is consistent with field data in which it was estimated that four female tigers would have 12 surviving cubs per birthing interval of ca. 2 years (Smith and McDougal, 1991).

3.2. Simulation runs

The simulation runs were divided into two sets. The first set of runs only included wild prey at different densities. The second set was run with different combinations of wild and domestic prey densities. The results for both sets of runs are summarized in Fig. 8.

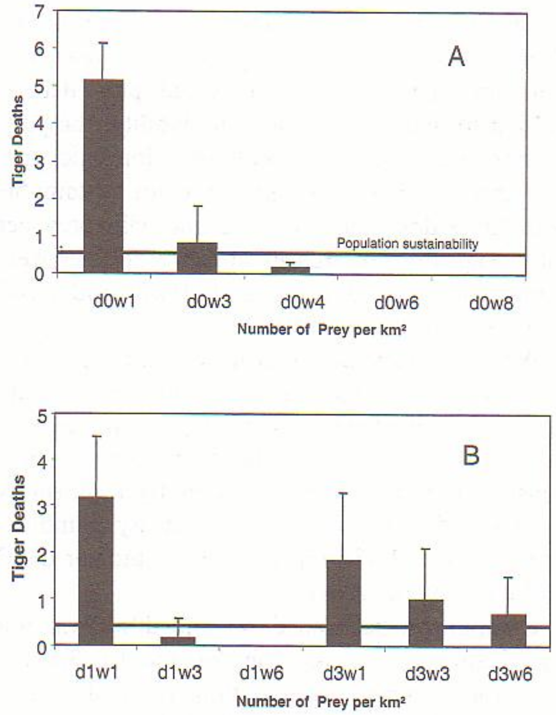


Fig. 8. Tiger mortality at different prey densities (A) without domestic prey; (B) with domestic prey. Error bars are equal to 1 S.D. The horizontal line is the level of mortality that can sustain a tiger population.

The first set of runs used only wild prey and showed statistically significant differences in the number of tiger fatalities between d0w1 (i.e. zero domestic prey per km^2 and one wild prey per km^2) and d0w3 at a $t_\alpha = 0.05$ and between d0w3 and d0w4 at a $t_\alpha = 0.10$ level. The difference between tiger fatality levels for d0w4 and d0w6 were not significant (Fig. 8a). These results indicate there is a threshold for prey density between 3 and 4 prey per km^2 at which tiger populations are sustainable. Home range sizes in the study area and model were similar (20–37 km^2 for females and from 46 to 70 km^2 for males) and for these home range sizes in the wild, a prey density of approximately 3.8 sambar per km^2 is required for a sustainable population.

Encroachment of domestic prey into tiger habitat as simulated in the second set of runs, resulted in increased adult tiger mortality due to poisoning. At densities of one domestic and one wild prey per km^2 (d1w1) the tiger population was not sustainable because of starvation and poisoning. When the total number of prey was increased to four prey per km^2, the threshold prey density needed to maintain population viability, the population was sustainable with one domestic prey and three wild prey per km^2 but not sustainable with three domestic prey and one wild prey per km^2 (Fig. 8b). Differences in tiger fatalities were significant between d1w1 and d1w3; and d1w3 and d3w1 at a $t_\alpha = 0.05$.

When domestic prey density was three prey per km^2 or greater, increases in wild prey density reduce tiger mortality, but tiger populations were never sustainable at this level of domestic prey density (Fig. 8b). Differences in tiger mortality were significant between prey density combinations d3w1 and d3w3 at a $t_\alpha = 0.05$ and for d3w3 and d3w6 at the $t_\alpha = 0.10$ level.

Comparison between d1w3 and d0w4 was not significant at $t_\alpha = 0.05$ (Fig. 8a and b). Simulations for both prey combinations resulted in tiger fatalities of 0.17, levels that have been shown to allow survival. These results suggest that a moderate level of cattle grazing in national forests is not detrimental to tigers.

3.3. Model sensitivity to parameters related to tiger/human interaction

3.3.1. Time interval villagers remain angry and motivated to poison tigers

We examined model sensitivity to length of time villagers were motivated and organized to poison carcasses. Increasing the length of time that villagers remained angry from 60 or 120 days to 365 days had a strong negative effect on tiger survival ($t_\alpha = 0.01$), however, survival differences were not significant when the time villagers stayed angry was reduce to 60 days from 120 days. These data suggest that increased education on endangered wildlife conservation may lead to greater tolerance of tiger predation on livestock and significant decrease in tiger mortality (Fig. 9a).

3.3.2. Guarding of domestic livestock

Closely monitoring grazing livestock in areas that are more open decreases the probability that tigers will kill cattle. This reduces the ratio of domestic to wild animals killed and consequently fewer tigers are poisoned. We examined this phenomenon by reducing the probability of tiger killing success for domestic prey from 0.75 to 0.50. There is no statistical difference in tiger fatalities between 0.75 and 0.50 probability of success in killing domestic prey at the $t_\alpha = 0.05$. There is, however, a statistically significant difference in the ratio of domestic to wild kills, which declines from 1.03 to 0.86, when the probability of success in killing domestic prey drops from 0.75 to 0.50. The difference between tiger mortality when guarding is increased, and probability of success in killing of domestic prey drops to 0.25, is significant at $t_\alpha = 0.05$ (Fig. 9c). The implication of these results is that increased guarding reduces tiger mortality due to poisoning.

3.3.3. Delaying the onset of poisoning carcasses

Some ethnic groups that have lived adjacent to tigers for a long time appear to tolerate occasional killing of livestock as part of living near protected areas. If few livestock are killed near their village, local people may not make the effort to lace the carcass with poison, but as the number of kills increases, people will become more motivated to

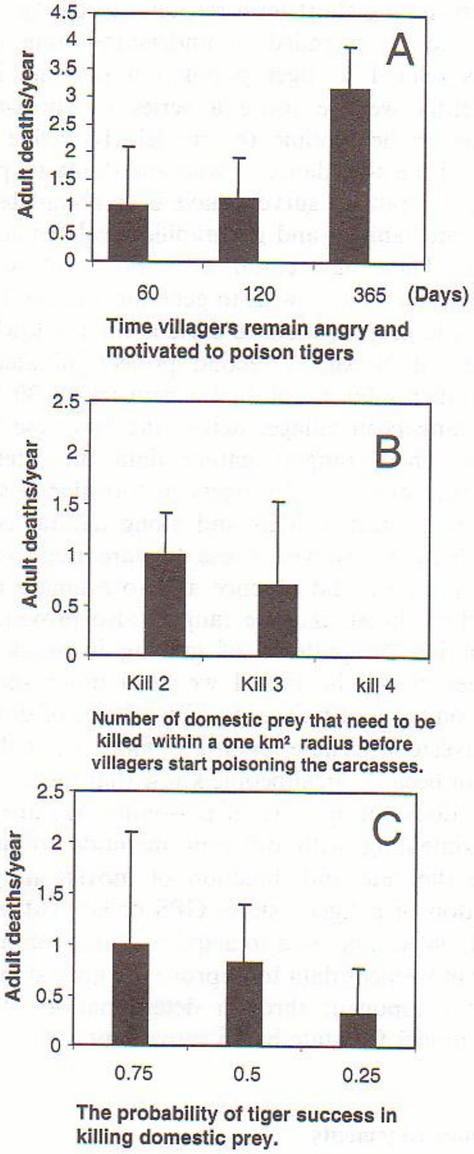


Fig. 9. Tiger mortality resulting from various responses to domestic prey kills by local villagers: (A) the duration of time that villagers are motivated to poison a carcass is increased from 60 days to 365 days; (B) the poisoning response threshold is increased from the second kill to the fourth kill; (C) the probability of a tiger successfully killing domestic prey is reduced from 0.75 to 0.25.

poison the offending animal. We examined the effect of villager motivation to poison by varying the parameter, number of cattle, that need to be killed within 1 km radius before villagers will start poisoning cattle carcasses (Fig. 9b). There is no significant difference in tiger mortality due to poisoning between the second and third cattle killed within 1 km radius. However, there is a significant difference between the third and forth cattle killed within one kilometer radius at $t_\alpha = 0.05$.

4. Discussion

TIGMOD offers an alternative approach to modeling the interaction between tigers and humans because it is driven by behavioral data available from long-term tiger studies (McDougal 1977; Sunquist, 1981; Smith et al., 1987a, 1989; Smith and McDougal 1991; Smith, 1993). The output of the model was consistent with field observations in four aspects — minimum prey density to support sustainable tiger populations, the number of tigers born, the number of days between consecutive prey kills, and movement pattern. The inclusion of low levels of domestic prey at the boundaries of the tigers home range resulted in low levels of tiger poisoning and the same overall prey density (four prey per km^2) was needed to sustain tigers as if all prey had been wild. When levels of domestic prey were greater than or equal to three per km^2, poisoning increased to levels that were no longer sustainable for tiger populations. This phenomenon held even when wild prey populations were increased well above normally sustainable levels (e.g. three to six wild prey per km^2). Human interaction with tiger was modeled by testing the sensitivity of three parameters that affect the ratio of domestic to wild prey kills and the likelihood that local people will poison a livestock carcass. Changes in all three parameters, *time villagers remain angry and motivated to poison tigers, guarding domestic prey, and delaying the onset of poisoning domestic prey carcasses* resulted in statistically significant differences in tiger mortality. These results suggest that by altering management practices and by educating local villagers about the value of the ecological resources in their forests may significantly reduce tiger mortality caused by poisoning.

TIGMOD is different from analytical modeling approaches requiring data that cannot be easily obtained in the field. For example, despite 30 years of tiger research, data as basic as population sizes are not estimated with the accuracy needed to model extinction probabilities. Other implicit spatial models (Kenney et al., 1995) do not incorporate real spatial data and, therefore, are not useful for exploring the response to site specific differences in human behavior and habitat conditions. TIGMOD, as an individual-based and spatially explicit object oriented simulation model, can easily incorporate specific ecological and landscape conditions such as habitat quality and the spatial configuration of habitat types that describe the land supporting tiger populations and the range of human response to tiger depredation. The spatial aspect of the model is critical to tiger conservation because management options vary considerably depending on specific landscape configuration and the variability in human patterns of livestock protection and grazing. TIGMOD was built based on the behavior of tigers in relation to their environment. It is not limited to a specific task but has the flexibility to address a wide array of questions related to tiger study.

Currently, many reserves occur within a matrix of larger forest fragments connected by corridors of varying forest quality. These forest areas continue to degrade due to increasing human demand for forest resources. Fortunately for tigers, multiple use management is gaining increasing support among local people in the lowlands of Nepal because they are beginning to recognize the value of ecological services and the economic benefits of sustainable managed forestlands. This study is the first attempt to create an individual-based model for tigers that helps evaluate various management options for meeting the needs of both tigers and local people, while finding the right balance between these competing uses.

This study does not consider the effect of poaching on tiger sustainability. Most of the data pertaining to human interaction with tigers and some aspects of tiger behavior were induced from field experience and requires a more systematic process for data collection. The time period of the simulation was a year, which is adequate for understanding short term response to change, but needs to be extended to understand long term issues related to tiger population sustainability. Currently we are using a series of short-term studies to help refine the model. To refine our data on the abundance of wild and domestic prey, 230 prey transect surveys have been completed in different habitats and geographic localities across Nepal. These data combined with classified TM digital data will allow us to generate a natural and domestic prey abundance surface for the lowland forests of Nepal. A second project initiated in December 1999 established a network of 30 ‘citizen’ rangers in villages across the Nepalese lowlands. These rangers gather data on rates of domestic predation by tigers in forestlands adjacent to protected areas and along habitat corridors between reserves. These data are used to map tiger presence and absence and to estimate rates of killing livestock. The rangers also provide information on patterns of grazing livestock. To further refine the model we need more specific data on rates of poisoning of carcasses of domestic livestock. These data are more difficult to obtain because local people know that the government does not approve of poisoning. We are also experimenting with different methods to determine the rate and direction of movement as a function of a tiger’s state. GPS collars (Moen et al., 1996) will be used to acquire a large sample of tiger movement data to improve the animal movement component through determination of the best model for state-based movement.

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References

Bian, L., 1997. Modeling Mobile Objects in Three-dimensional aquatic systems using object oriented design. GIS/LIS 1997, ASPRS.

Chundawat, R.S., Gogate, N., Johnsingh, A.J.T., 1999. Tigers in Panna: preliminary results from an Indian tropical dry forest. In: Seidensticker, J, Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, pp. 123–129.

De Meer, M.N., 1997. Fundamentals of Geographic Information Systems. Wiley, p. 486.

Dinerstein, E., Wikramanayake, E., Robinson, J., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Connor, M., 1996. A framework for identifying high priority areas and actions for the conservation of tigers in the wild, World Wildlife Fund-US, Washington D.C., pp. 72.

Jones, R.E., 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 45, 195–212.

Karanth, K.U., Sunquist, M.E., 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. J. Trop. Ecol. 8, 21–35.

Kenney, J.S., Smith, J.L.D., Starfield, A.M., McDougal, C.W., 1995. The long-term effects of tiger poaching on population viability. Conserv. Biol. 9, 1127–1133.

Liu, J., Ashton, P.S., 1998. FORMOSAIC: an individual-based spatially explicit model for simulating forest dynamics in landscape mosaics. Ecol. Model. 106, 177–200.

Liu, J., Dunning, J.B. Jr, Pulliam, H.R., 1995. Potential effects of a forest management plan on Bachman's Sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conserv. Biol. 9, 62–75.

McDougal, C., 1977. Face of the Tiger. Rivington Books and Andre Deusch, London, p. 182.

McGrew, J.C., Monroe, C.B., 1993. Statistical Problem Solving in Geography. Wm. C. Brown Publishers, Dubuque, IA.

Moen, R., Pastor, J., Cohen, Y., Schwartz, C., 1996. Effect of Moose Movement and Habitat use on GPS Collar Performance. J. Wildlife Manage. 60 (3), 659–668.

Newell, R.G., Easterfield, M., 1990. Smallworld GIS: version management-the problem of the long transaction. Smallworld Technical Paper 4, pp 9.

Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. (Suppl.) 137, S50–S66.

Raper, J., Livingstone, D., 1995. Development of a geomorphological spatial model using object-oriented design. Int. J. Geog. Info. Sys. 9, 359–383.

Siniff, D.B., Jessen, C., 1969. Simulation model of animal movement patterns. Adv. Ecol. Model. 6, 185–219.

Smallworld, 1999. Smallworld Systems, Cambridge England.

Seidensticker, J., McDougal, C., 1993. Tiger predatory behavior, ecology and conservation. Symp. Zool. Soc. (London) 65, 105–125.

Smith, J.L.D., 1993. The role of dispersal in structuring the Chitwan tiger population. Behaviour 124, 169–195.

Smith, J.L.D., McDougal, C., 1991. The contribution of variance in lifetime reproduction to effective population size in tigers. Conserv. Biol. 5, 484–489.

Smith, J.L.D., McDougal, C., Sunquist, M.E., 1987a. Land tenure system in female tigers. In: Tilson, R.L., Seal, U.S. (Eds.), Tigers of the World: the Biology, Biopolitics, Management and Conservation of an Endangered Species. Noyes Publications, Park Ridge, NJ, pp. 97–109.

Smith, J.L.D., Wemmer, C., Mishra, H.R., McDougal, C., 1987b. A conservation strategy for tigers. In: Tilson, R.L., Seal, U.S. (Eds.), Tigers of the World: the Biology, Biopolitics, Management and Conservation of an Endangered Species. Noyes Publications, Park Ridge, NJ, pp. 464–473.

Smith, J.L.D., McDougal, C., Miquelle, D., 1989. Communication in free-ranging tigers (*Panthera tigris*). Anim. Behav. 37, 1–10.

Smith, J.L.D., Ahearn, S.C., McDougal, C., 1998. A landscape analysis of tiger distribution and habitat quality in Nepal. Conserv. Biol. 12, 1338–1346.

Smith, J.L.D., McDougal, C.W., Ahearn, S.C., Joshi, A., Conforti, K., 1999. Metapopulation structure of tigers in Nepal. In: Seidensticker, J., Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, pp. 176–189.

Sunquist, M.E., 1981. The social organization of tigers, Panthera tigris, in Royal Chitwan National Park, Nepal. Smithsonian Contribution to Zool. 336, 1–98.

Turchin, P., 1998. Quantitative Analysis of Movement: Measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, p. 396.

Westervelt, J.D., Hopkins, L.D., 1999. Modeling mobile individuals in dynamic landscapes. Int. J. Geog. Info. Sys. 13, 191–208.

Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128.

Worboys, M.F., 1994. Object-oriented approaches to geo-referenced information. Int. J. Geog. Info. Sys. 8, 385–399.

Zev, Y., 1998. The effect of habitat heterogeneity on species diversity patterns: a community level approach using an object-oriented landscape simulation model (SHALOM). Ecol. Model. 111, 135–170.