Chapter 18

Modeling the Interaction between Humans and Animals in Multiple-use Forests: A Case Study of Panthera tigris

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ABSTRACT

THE LOSS OF ANIMAL HABITAT AND THE GREATER USE OF FORESTS by humans in various parts of the world have increased the conflict between humans and wildlife, especially for those animals with geographically large home ranges. As a result, much effort has gone into preserving a network of reserves of the last remaining prime habitat. Biologists, however, have realized that these areas alone are not sufficient to sustain populations and that the multiple-use regions that surround these core areas are essential for species' survival (Smith, Ahearn, and McDougal 1998). While the concept of multiple use is attractive, finding the right balance between competing uses is difficult or impossible without a computational framework in which to analyze these competing uses. The advent of object-based geographic data structures has given scientists such a framework and has spawned a number of dynamic individual-based models for analyzing the interaction of animals with their environment. One of the most difficult challenges associated with these models is the simulation of movement and the relationship between movement and behavior. Various analytic models have been proposed, and implementation of state-based movement has been designed using knowledge from domain experts. With the recent use of GPS collars for tracking animals, scientists now have quantitative information on the nature of animal movement. This quantitative data offers an unprecedented opportunity to better understand the relationship between an animal's state and its behavior at different spatial and temporal scales. The findings from these analyses can be used to calibrate and test the individual-based object models in an effort to understand

the short- and long-term consequences of geographically specific management proposals and practices. This chapter explores these issues in the context of the tiger as a prototype for modeling the interaction between humans and animals in the wild.

INTRODUCTION

Over the past thirty years, there has been significant emphasis on establishing protected areas for conservation of the best remaining habitat. However, for keystone species like tigers, Panthera tigris, which often require large geographic areas for their survival, these protected areas may not be enough. Studies have shown that protected areas only account for 17–25% of all tiger habitat and that 75–83% of tiger habitat is in multiple-use forests with significant human activity (Smith, McDougal, and Sunquist 1987, Wikramanayake et al. 1999). The concept of multiple use is an often-cited solution by policy makers for balancing human activities in forests with conservation needs. However, the development of a quantitative framework for balancing the various needs in a multiple-use forest is in its early stages (Ahearn et al. 2001). Additionally, information on human–animal interaction is limited, especially for large carnivores like tigers (Kenney et al. 1995, MacKinnon, Mishra, and Mott 1999). In fact, resource selection by individual animals, a prerequisite for understanding this interaction, is notoriously difficult (Garshelis 2000) and has only recently been approached within an analytic framework (Franke, Caelli, and Hudson 2004, Jonsen et al. 2003, Brillinger et al. 2004). The fundamentals of animal movement and its relationship to behavior are the subject of this discussion. To provide context for this discussion, the movement and behavior of the tiger (Panthera tigris) will be examined in the context of the new analytic frameworks.

MODELING MOVEMENT AND BEHAVIOR OF ANIMALS

Early models for animal movement employed random walk models (Brownlee 1911) and diffusion models (Dobzhansky and Wright 1943). However, these models assumed spatial isotropy of movement and were considered too simple as a general principle of animal movement (Turchin 1998). Dice and Howard (1951) and Skellum (1951) examined dispersal movements to calculate neighborhood size. Meta-population models proposed by Levins (1970) extended Wright's shifting-balance theory by creating an implicit spatial structure among populations. Hanski (1991) and McCullough (1996) extended metapopulations to include spatially explicit and individually based realistic models of animal movement among subpopulations that have been used to examine the effects of fragmented habitat connected by corridors. Siniff and Jessen (1969) were the first to realistically simulate animal movement and emphasize the importance of space as a medium for ecological interaction. Turchin (1998) proposed four general types of movement by animals. They include simple random walk, random walk with directional persistence, random walk with directional bias, and random walk with persistence and directional bias. Individual-based movement models (IBMMS), which have been widely adopted by ecologists, use these principles of movement to model individuals and their interaction with each other and their environment. An example of a spatially explicit individual-based model is TIGMOD (Ahearn et al. 2001). It used general principles of movement and behavioral information from tiger field studies to model the interaction between tigers and humans and to analyze tiger survivability given different levels of human interaction and prey abundance and varying management practices.

With the advances in GPS, there is now a plethora of data on animal movement at very high spatial and temporal scales (Moen et al. 1996. Schlecht et al. 2004). This data has resulted in phenomenological studies that describe the pattern of habitat use (Merrill 2000, Blake et al. 2001) and has been used by a limited number of researchers to develop spatio-temporal models to predict movement. Some of the models have used stochastic differential equations calibrated from the GPS data to simulate animal movement (Brillinger et al. 2004), while others have used Markov models to infer the behavior and sequences from GPS data and to generate movement based on the state probabilities, state transitions, and state observations (Franke, Caelli, and Hudson 2004, Jonsen et al. 2003). At issue with respect to these quantitative models is how well they capture the complexity of the movement and behavior of individuals as it relates to the environment in which they move, the other individuals with whom they interact, and their own geographic strategies for resource usage.

At this point, it may be useful to distinguish between an animal's state and its behavior. We use state to define an animal's physiological condition (e.g., its age, whether in estrus, pregnant, hungry, alive), and behavior is an animal's actions in response to its state and its environment.

A CONCEPTUAL MODEL FOR TIGER BEHAVIOR

While the acquisition of high-resolution spatial and temporal information regarding animal movement is a recent phenomenon, a wealth of behavioral information has been acquired from field studies over the years that has led to an understanding of the relationship between behavior and movement at coarse spatial and temporal scales. From these studies, conceptual models for behavior have been developed which describe general strategies for resource usage, mating, hunting/foraging, and home-range delineation. In the following discussion, we will describe a conceptual model for the tiger.

Tiger behavior and movement

Our conceptual model for tigers is based on the field research of Smith (1993), Smith, McDougal, and Sunquist (1987), Smith, McDougal, and Miquelle (1989), Smith and McDougal (1991), Smith, Ahearn, and McDougal (1998), Seidensticker and McDougal (1993), Sunquist (1981), Karanth and Sunquist (1995), Chundawat, Gogate, and Johnsingh (1999), and Miquelle et al.(1999) that provides detailed information on predatory, reproductive, territorial, and dispersal behavior. Each of these behaviors can be further subdivided based on an animal's state. For example, there are a variety of behaviors that fall under reproductive behavior that are a function of an animal's changing reproductive state. Scent marking intensifies during a female's pre-estrus state, and she gradually marks throughout her entire home range. Once estrus occurs, her movement becomes more rapid and continuous as she begins repeated calling, day and night, to help the resident male to find her. Thus, we have a set of different behaviors, each in response to a changing physiological state. Each behavior has a specific movement pattern associated with it, which can be described by rate of movement and degree of directional persistence.

Tiger home ranges are established based on resource availability and sex. Home ranges tend to be fuzzy boundaries that are sometimes breached by small forays beyond a territorial boundary or in response to changing resource needs or conditions. Male tiger home-range spans vary from 35–150 km~~2~~ in the Royal Chitwan National Park (Smith, McDougal, and Sunquist 1987) to >800 km~~2~~ in the Russian far east (Miquelle et al. 1999). The male home-range circumscribes 2 to 7 female home ranges. Prey are killed on average every seven days if the animal is at least 200 kg (i.e., Cervus unicolor) but can be of higher frequency if the prey size is smaller. The tiger will remain near its kill for 2–3 days and begin hunting again between 3 and 5 days after it last fed (Sunquist 1981, Chundawat, Gogate, and Johnsingh 1999). Females with cubs will increase their frequency of hunting until cubs are 16–17 months old, at which time their rate of killing has doubled or tripled. Male tigers visit their females three to five times a month. If the female is fertile, the male will remain to mate with her for 2 to 3 days and copulate over 100 times. If not, he may just spend a few minutes with her and move to the next female. Females become fertile every 20–30 days on average and give birth to 2–5 cubs after 102 days. Cubs remain with their mother until they are 18–22 months old.

Movement by tigers can be characterized by the direction and distance a tiger travels per unit time and is functionally dependent upon its state. A male tiger has an external bias to its direction when moving to the next hunting area or visiting the next female. Once a male enters a female's home range, his movement will slow as he seeks his mate, and his movement may be characterized as a random walk. If he is within 1 kilometer of the female, he is likely to roar and move directly towards her. If she is not fertile, he assumes a random walk through her home range until he meets her or moves on to his next female. If he is hunting, he assumes a random walk once he enters his hunt~~er~~ area and searches for prey. After prey is killed, the tiger will remain near the kill until it is finished.

Human interaction and cattle grazing

Human interaction with tigers takes various forms from poaching of tigers and their prey, to loss of habitat, or poisoning of tigers by villagers whose cattle have been killed by tigers. Human behavior toward tigers is complex. In multiple–use forests, one of the primary human uses for these forests is cattle grazing. The problem with cattle grazing is that it cascades through the ecosystem to eventually affect tiger viability. Grazing reduces regeneration, resulting in forest degradation and eventually forest fragmentation. This deterioration of habitat quality reduces the natural prey base and increases the likelihood that a tiger will kill domestic prey. If a sufficient number of prey are killed within a given geographic region, a domestic carcass will be laced with an insecticide by the owner, and when the tiger comes back to finish its meal, it will be poisoned and die. The motivation to poison tigers is dependent on the number of kills a tiger makes in an area and the number of kills in turn depends on local grazing pressure. At higher domestic stocking rates, a tiger is more likely to remain in the area killing cattle.

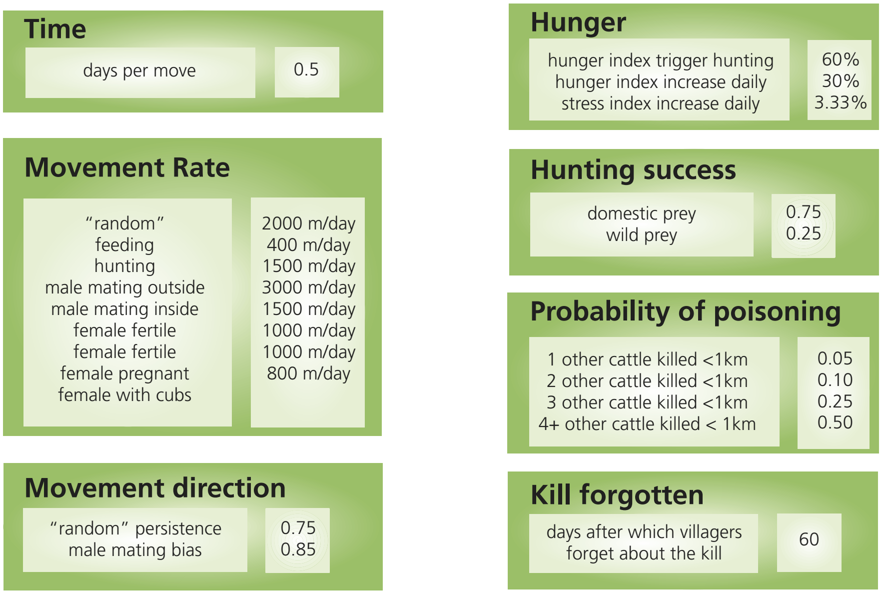
An important management question concerning tigers and other large area-sensitive predators is: What is the probability of dispersal across a real, human-dominated landscape? (Smith, 1993). Estimating the probability of dispersal is a vexing problem that field biologists have not been able to address because the dispersal of a single individual is too rare an event to hope to observe, even with intensive monitoring. However, it is not difficult for field biologists to observe and document the behavior of a tiger living in poor-quality habitat typical of a potential habitat corridor and then use this behavior or sets of behavior to model an individual animal's movement through a corridor. Such modeling also can help managers explore the effects of various management actions designed to increase the likelihood of successful dispersal.

TIGMOD REVIEW

Introduction

The principles behind individual-based models (IBMM) are that each individual is an autonomous entity that is behaviorally and physiologically distinct and that interaction among individuals is localized (Franke, Caelli, and Hudson 2004). GIS software constraints until recently have stymied efforts to create robust, extensible, geographically based IBMM (Raper and Livingstone 1995, Westervelt and Hopkins 1999, Ling 2000). With the advent of object-oriented (OO) geographic systems in the last ten to fifteen years, these constraints have disappeared. The critical difference from previous generations of GIS software tools is that OO systems make the object the unit of analysis, not its geometry. The result of this paradigm shift is that location and time are treated as explicit properties of an object, permitting the frequent updating of space–time attributes. It also results in the creation of an autonomous individual that can interact in a unique fashion with other individuals (Ahearn et al. 2001). In the case of the tiger in TIGMOD, the tiger objects have two geometry fields, location (a point) and home range (a polygon). TIGMOD was created to give an analytic framework for the enormous amount of behavioral data that has been collected for tigers in order to better understand its behavioral dynamics and to demonstrate that an IBMM could be used effectively to analyze the proper balance to strike in multiple–use forests. It was designed, however, not with a specific analytic task to be performed but with the goal of capturing the patterns of behavior and interactions needed to model the system. Once these aspects are correctly captured, questions concerning changes to the system could be answered (Ahearn et al. 2001).

Key features of TIGMOD are that it supports mobility of objects, variable spatial attributes and temporal resolutions, interaction with other individual objects, the creation of new individuals, and the propagation of change in the state of one object through the system in space and time to affect all related objects. Model inputs include: an array of information on movement (rate and direction) as a function of ten unique states of the tiger, ~~a~~ three-probability estimate on the likelihood of tiger poisoning, a rate of hunger, a probability of hunting success, and an input for temporal resolution (fig. 1).



Time

days per move	0.5

Movement Rate

"random"	2000 m/day
feeding	400 m/day
hunting	1500 m/day
male mating outside	3000 m/day
male mating inside	1500 m/day
female fertile	1000 m/day
female fertile	1000 m/day
female pregnant	800 m/day
female with cubs	

Movement direction

"random" persistence	0.75
male mating bias	0.85

Hunger

hunger index trigger hunting	60%
hunger index increase daily	30%
stress index increase daily	3.33%

Hunting success

domestic prey	0.75
wild prey	0.25

Probability of poisoning

1 other cattle killed <1km	0.05
2 other cattle killed <1km	0.10
3 other cattle killed <1km	0.25
4+ other cattle killed < 1km	0.50

Kill forgotten

days after which villagers forget about the kill	60

Figure 1 :Input parameters for TIGMOD with default values (from Ahearn et al. 2001).

Data model

Tiger and prey are represented as objects that have physical, behavioral, and geometric characteristics, all being fields in the description of the respective object. Age, weight, and whether alive are examples of physical characteristics; feeding, hunting, mating, and giving birth are examples of behavioral characteristics, and location and home range are examples of geometric characteristics. Class hierarchies were created with animal as a super class, prey and tigers as subclasses, wild and domestic prey as subclasses of prey, and male and female as subclasses of tiger. All methods were inherited from the super classes above any subclass. Closely coupled objects are modeled with relational joins. A male tiger can have one or more females in its home range, females can have two or more male and female cubs, and tigers can be hunting 0 or 1 prey.

TIGMOD is a dynamic model that is driven by the tiger's internal state and its relationship with its environment. In some instances, states are dependent on the environment (e.g., a male tiger stays longer with a female if she is fertile) and sometimes they are not (e.g., a female becomes fertile every ~20–30 days). A change in time drives the model affecting state-based relationships (e.g., relationship between hunger and desire to hunt), functional events (e.g., a female becomes pregnant if she is fertile and within close proximity of a male) and scheduled events (e.g., she gives birth ~102 days after conception (fig. 2). These in turn determine the pattern of tiger movement (Table 1). Movement is characterized by rate and direction. Rate and direction of movement is functionally dependent on state. Distance traveled in a time step is modeled as a chi squared random variable. Direction is modeled as four different behaviors: direct movement when the tiger is going directly to a spotted prey or toward a female's calling; directed movement when a tiger heads back toward its kill; random movement with a directional bias when a tiger cruses its home range; and random movement with an external bias when a male heads toward a female home range.

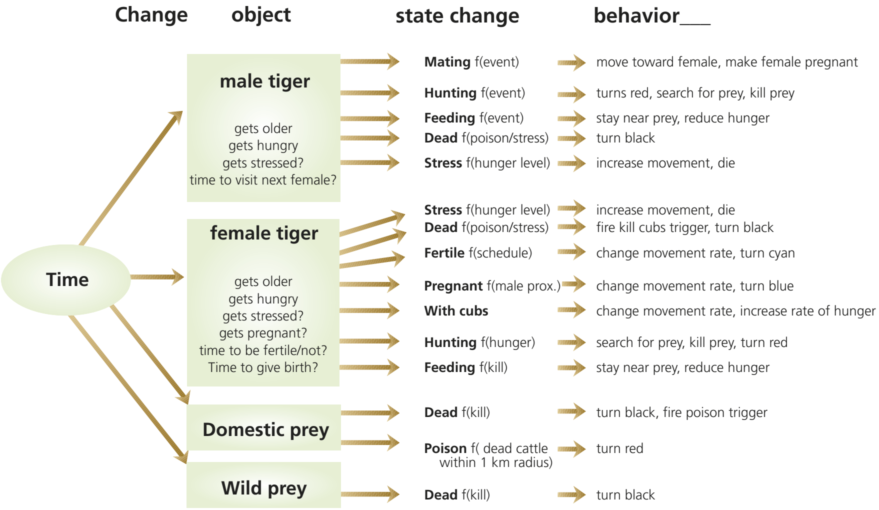


Figure 2: Diagram of the dynamic interactions in TIGMOD (from Ahearn et al. 2001).

	Movement Characteristics with default values	
Behavior	Rate (distance per day) μ= mean rate of movement σ= standard deviation of movement rate	Direction μ= mean direction of movement σ= standard deviation of movement direction
Looking for prey	χ^2 random variable (μ= 1500 meters, σ= 1500 meters)	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 μ= 10 degrees
Found prey	Moves to the location of prey	Moves in the direction of the prey
Feeding	χ^2 random variable (μ = 400 meters, σ= 400 meters)	Movement is directed to prey location as selected from a normal random variable with μ = direction to prey and σ= 5 degrees
"Random"	χ^2 random variable (μ = 2000 meters, σ= 2000 meters)	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= previous direction and σ= 10 degrees.
Mating (male): outside female domain	χ^2 random variable (μ = 3000 meters, σ= 3000 meters)	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 σ= 10 degrees
Mating (male): inside female domain	χ^2 random variable (μ = 1500 meters, σ= 1500 meters)	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 σ= 10 degrees.
Mating (male): within 400 meters of female	Moves distance to female	Moves in the direction of female
Fertile (female)	χ^2 random variable (μ = 1000 meters, σ= 1000 meters)	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= previous direction and σ= 10 degrees.
Pregnant (female	χ^2 random variable (μ = 1000 meters, σ= 1000 meters)	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= previous direction and σ= 10 degrees.
With cubs (female)	χ^2 random variable (μ = 800 meters, σ= ~~2000~~ meters)	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 = previous direction and σ= 10 degrees.

Table 1: Movement characteristics for different tiger behavior (from Ahearn et al. 2001).

Human interaction is modeled for one aspect of cattle grazing at the forest boundary: the likelihood that a cow killed by the tiger will be poisoned by villagers. The first aspect of interaction deals with the likelihood of a cow being killed by a tiger based on the difficulty of killing. This is determined by the method for grazing by the villagers. In some instances, cows are guarded, resulting in a lower probability of kill, and other village groups just send their cows into the forest unguarded, resulting in a higher probability of kill. The other two factors that determine the likelihood of poisoning are probabilities based on the number of kills within a geographic region (e.g., 1 km radius) and the length of time villagers are annoyed about the kill. All probabilities related to all three factors are user inputs and can change depending on geographic location and the level of education of the villagers. For instance, if the villagers know that tigers bring in tourist money, then they may be more tolerant of cattle kills and the probably of poisoning is reduced.

TIGMOD can be run at different time-step increments and for different durations. Ahearn et al. (2001) also ran the model with differing amounts of domestic and wild prey densities in order to understand tiger viability.

MODELING COMPLEXITY: A NEW SOURCE OF DATA

TIGMOD was developed as an IBMM using expert knowledge of the relationship between the tiger's state and its relationship to other tigers and its environment. While this model proved effective in simulating tiger behavior and tiger viability as a function of different management conditions, it has several limitations: (1) it wasn't calibrated with spatio-temporal geographic information for tiger movement, (2) it made significant assumptions about the nature of tiger movement given different behavioral states, and (3) it modeled a subset of tiger behavior.

The availability of high-resolution spatial and temporal information from GPS collars on animals provides us with a new source of spatio-temporal data and enables us to understand better the relationship between an animal's state and its behavior at different spatial and temporal scales. As discussed above, there have been a number of studies that have used GPS to examine the pattern of habitat use (Merrill 2000, Blake et al. 2001) and a limited number that have used it to measure quantitatively the nature of movement and its relationship to behavior (Brillinger et al. 2004, Franke, Caelli, and Hudson 2004, Jonsen et al. 2003). The critical question is: How well do these models capture the complexity of the movement and behavior of individuals as they relate to the environment in which the animals move, the other individuals with whom they interact and their own geographic strategies for resource usage? For this discussion, we will concern ourselves with the Hidden Markov Model (HMM), as this type of model has the interesting properties of imputing behavior and movement characteristics from a spatio-temporal signal although it is recognized that other models (e.g., Brillinger et al. 2004) show equal promise.

HMM

Hidden Markov Models (HMM) are in a class of stochastic signal models that characterize the statistical properties of a signal. They are an extension to the idea of discrete Markov chains, which characterize the probabilities of state transition sequences. In Markov chains, each state relates to an observable, physical event. In contrast, in HHM the observation is a probabilistic function of the state, which results in a doubly stochastic process where one process is observable and one is hidden. The ergodic HMM assumes that every state can be reach from any other state (Rabiner et al. 1989).

An HMM is characterized by N, the number of states in the model; M, the number of distinct observations; **A,** a state transition matrix; **B,** the observation probability distribution; and $\boldsymbol{\pi}$, the initial state distribution. HMM is often described by:

$$\lambda = (\pi, \mathbf{A}, \mathbf{B}).$$

The three problems for HMMs include: 1) generating estimates of observations and state sequences, 2) determining the most likely state sequence given λ and an observation sequence, and 3) updating the model given new observation data (Rabiner et al. 1989, Franke, Caelli, and Hudson 2004).

For theoretical reasons, good initial estimates of λ λ are necessary to ensure optimal model parameterization, with particular importance given to good initial estimations of **B.** There are various techniques for making estimates, including manual segmentation of observation sequences, maximum-likelihood segmentation with averaging, and segmentation with k-means clustering (for a definitive review of HMM, see Rabiner et al. 1989). As we discuss below, selecting the number of states for the A matrix often requires significant information on the state and associated behavior of the animal being modeled.

CARIBOU EXAMPLE OF HMM

Franke, Caelli, and Hudson (2004) implemented a HMM for caribou using GPS data acquired every 15 minutes for 12 caribou. They examine three "hidden states" (**A** matrix, as probabilities) feeding, bedding, and relocating, which typically occupy over 90% of the caribou's activity. They selected distance between locations and turn angle as observations that encapsulate movement as related to behavior. Distance was assigned to four intervals: stationary, short, medium, and long; turn angle was assigned four categories: ahead, left, right, back (the **B** matrix, as probabilities).

They compared their model with a traditional time-series method and found much greater PC (percent correct) and significantly less AAD (average absolute difference) for the HMM when used to predict an observation sequence from λ. Perhaps more important, the state transition probability matrices (A matrix) showed that caribou tended to forage for short periods and bed and relocate for longer periods and that the animals were most likely to bed after relocating and forage after bedding. Both of these behaviors of movement and transition are support by field observation. Through examination of the transition matrices, Franke, Caelli, and Hudson (2004) also were able to deduce the differing land-use strategies of the individual caribou. In summary, they believed their model was very effective for predicting behavior but recognized that resource selection is scale dependent and their implementation of HMM avoided integration across ecological scales. Nevertheless, Franke, Caelli, and Hudson (2004) have made a strong argument for using HMM for the derivation of behavioral states and generating observation sequences for the woodland caribou.

HMM FOR TIGER MODELING

The conceptual model for the tiger described above reveals the complexity of the relationship between the tiger's state and its behavior. In considering the use of HMM for i[illegible]ting tiger behavior from movement and in generating movement from $\lambda\lambda$, several issues are at hand: Can a tiger's movement be described by a first-order Markov process? How are different temporal scales accommodated? Are there state changes that result in the generation of different movement rates and patterns for the same behavior? Are certain behaviors and therefore movement patterns dependent on the state of other entities?

Can a tiger's movement be described by a first-order Markov process? A first-order Markov process assumes that the current state is wholly dependent on the previous state. This is not as limiting as it sounds as dependencies propagate through the model. However, not all behaviors are first order. There is a significant amount of research that indicates that animals may possess a cognitive map of their environment (Poucet 1993, Bennett 1996) and that animals may use that map to develop geographic strategies of resource use. Our own preliminary analysis of GPS data obtained in the Royal Citwan National Forest in Nepal indicates that the tiger may have a hunting strategy that minimizes disturbance between hunts and maximizes usage of her home range by sequencing hunts in different geographic regions of her home range over a one-month period (fig. 3). The strategy may also be part of her establishing and maintaining her home range.

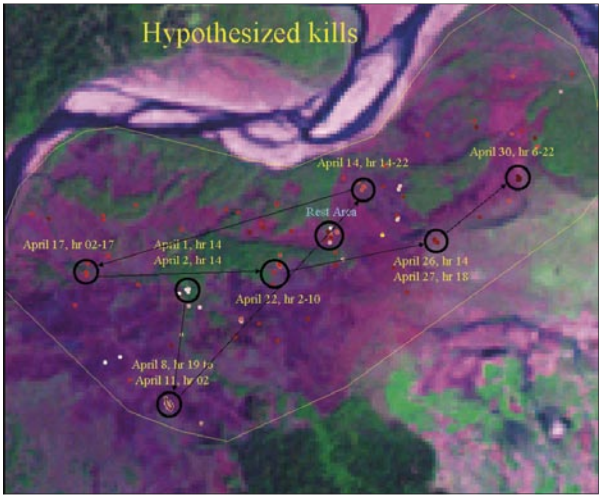


Figure 3: Hypothesized hunting/kill areas

Are there state changes that result in the generation of different movement rates and patterns for the same behavior? For the tiger, the answer is yes. When a tiger's state starts to change from satiated to hungry, her behavior becomes that of a hunter. The rate at which she becomes hungry and her strategies for hunting may be a function of her reproductive state. When she is pregnant, she gets hungrier sooner. When she has cubs, her hunting increases until she is essentially hunting continuously when the cubs are 12 to 18 months old. Between the cubs' birth and when they are two months old, her home range is reduced by 50% (Smith, 1993). Thereafter, she carries or leads the cubs from place to place until they are big enough to follow her and assist in the hunt.

Are certain behaviors and therefore movement patterns dependent on the state of other entities? The answer for the tiger is yes. The clearest example is the behavior of the male toward his females. If a visited female is not fertile, he may spend only minutes with her. If she is fertile, he will spend several days.

How are different temporal scales accommodated? Tigers operate at numerous temporal scales. Hunting occurs at 5–7 day intervals, home range traversal occurs every 24–28 days, and dry and wet season variation occurs biannually. Males also visit their females periodically. A model that truly mimics tiger behavior must operate at these multiple temporal scales.

DISCUSSION

The above analysis suggests that it may be difficult to use a single HMM to incorporate the complex states and corresponding behaviors of a tiger. Perhaps multiple HMMs, which correspond to different states, might be more appropriate. However, determining these states is no small task. It requires detailed, close-range, behavioral observations, information on rates, variability, and directional persistence of movement, and observation of anecdotal data such as presence of a kill or tracks of another tiger. Together, this information provides clues to an animal's behavioral rules. For example, finding a kill and determining the GPS time when the tiger reached the kill site allows one to infer the behavior (hunting) prior to the kill time. Similarly, behavior post feeding can be inferred to be either territorial patrolling or long-range movements designed to take a tiger to another potential hunting site.

To obtain behavioral data needed to model movement, it is important not to disturb an animal when making continuous close-range observations. However, in dense vegetation sound attenuates rapidly, and it is often possible to approach a tiger close enough to hear the crunching of bones as it feeds on its prey or the sharp copulatory growls a female makes while mating. Following an animal closely provides opportunity to gather a variety of data from which an animal's behavioral state may be assessed. For example, patrolling can be distinguished from long-distance movements between hunting localities based on data on rates of movement versus rates of scent marking and inspection of scent marks which can determined by observing tracks going up to scent marks (Smith, McDougal, and Maquelle 1989). Having both the behavioral information from following a tiger and the GPS data, which provides quantitative information on movement, will enable us to evaluate the number and type of HMMs that may be need to model tiger movement. It will also help us to calibrate the HMM by determining the number of states needed for the A matrix, the initial approximations for the B matrix, and estimates of $\boldsymbol{\pi}$.

CONCLUSIONS

This chapter has reviewed individual-based models as a framework for understanding the interaction of animals and humans in multiple-use forests. It as also examined the potential for using GPS data to calibrate these models and to provide new insight into the relationship between animal movement, behavior, and an animal's physiological state. TIGMOD, an individual-based model for emulating the behavior of tigers in multiple-use forests was a first attempt to capture different movement patterns in response to behavior and physiological states. This conceptual model has begun to capture some of the complexity of animal movements. Statistical models such as the HMM can strengthen the movement dynamics of individual-based models, but there are limitations to the use of HMM. Stochastic events such as the appearance of another tiger (e.g., an estrous female, a male challenger) can alter the matrices describing the HMM.

What is clear is that modeling this complexity is a key challenge if we are to create individual-based models for animals that can be used for understanding both resource allocation and the interactions between humans and animals in multiple-use forests. The key to making advances is a close reiterative interaction between modeler and field biologist. For an endangered species where sample sizes are limited, management problems are site specific, and there simply is not time to examine the outcome of experimental management scenarios, modeling may be the only alternative for exploring management options.

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