University of Alberta

Analysis of Space-Time-Action Systems in Woodland Caribou (*Rangifer tarandus*) using Hidden Markov Models

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: WHERE TO BE, WHAT TO EAT AND WHAT TO DO?

1.1 Introduction

This thesis addresses the study of animal actions in time and space through the application of doubly stochastic, multiple-observation hidden Markov models (HMMs) and frequent global positioning satellite (GPS) radio collar relocation data. Specifically, I show how GPS technology in conjunction with HMMs can be used to infer meaningful descriptions of woodland caribou (*Rangifer tarandus*) movement behavior. In addition, I show how HMMs can recognize moose (*Alces alces*) kill-sites solely from radio-collared wolves (*Canis lupus*), provide additional information pertinent to the estimation of kill rates and offer a portrayal of wolf behavior.

1.2 Background

Consider the actions a wild animal must undertake. At an elementary level, key activities are those that ensure adequate accumulation of water, shelter, and food. On the surface, activities that provide for these basic resources seem somewhat trivial. However, consider the complexity of choices an individual must make in order to accrue sufficient quantities of each in the face of realities such as predator avoidance, inter and intra-specific competition, environmental variation, territorial defense and the need to reproduce. The task of accruing sufficient resources is suddenly less than trivial.

Accumulation of resources by animals and the strategies by which they are accumulated have long been recorded in the scientific literature. Scott (1920) is often cited as the first author to quantify selection and MacArthur and Pianka (1966) were among the first authors to develop a simple optimal foraging model. How is it, though, that individuals are able to integrate space, time and action in such a way that allows them the potential opportunity to contribute to future generations regardless of the inherent uncertainty? The idea that the "actions undertaken by animals are important" is not new. Charles Elton (1927) wrote in Animal Ecology ...

"In solving ecological problems we are concerned with what animals do in their capacity as whole, living animals, not as dead animals or as a series of parts of animals. We have next to study the circumstances under which they do these things, and, most important of all, the limiting factors which prevent them from doing certain other things. By solving these questions it is possible to discover the reasons for the distribution and numbers of animals in nature".

Elton implies that the distribution and abundance of animals can be directly attributed to their actions, the circumstances under which the actions are taken, and the factors that limit their choice of activity at any given time. Andrewartha and Birch (1954) quote this passage in the opening chapter of their book, "The Distribution and Abundance of Animals", in an effort to emphasize that the separation between studies of animal abundance and distribution should be avoided. Turchin (1998) restates this assertion and points out that recent ecological theory has made it progressively more apparent that the relationship between environmental heterogeneity and animal movements can have sweeping effects on the distribution and abundance of organisms.

Despite efforts to shift from a phenomenological view of distribution and abundance of organisms to a more mechanistic view that explicitly incorporates space, time and action, modern analytical methods often fail (Garshelis 2001). A space-time-action system can be thought of as the tendency of animals to engage in certain activities, in certain places, at certain times and, requires that individuals decide where to be (site selection), what to eat (diet selection), and what to do (activity budget). Although these topics have been approached element-by-element, no method has yet been established to study all elements in unison.

For example, Habitat Suitability Indices (HSI) (e.g. U.S. Fish and Wildlife Service 1981, Wisdom et al. 1986) measure the suitability of each cover type for a given area for a given species. Models use considerable literature review, as well as professional and local knowledge in an effort to consolidate knowledge of species-habitat relationships to provide an index of habitat effects (0.0 to 1.0). HSI models assume a positive relationship between the index and habitat carrying capacity. Unfortunately, they invariably lack generalizability and precision, due in part to the paucity of scale-specific quantitative habitat data. In addition, they fail to account for the direct effects of processes such as disturbance.

In recent years, HSI modeling has been eclipsed by resource selection function (RSF) modeling (Manly 1993). Resource selection is defined as the process by which an animal chooses a particular resource (Johnson 1980). Studies in resource selection are widely applied in wildlife management to maintain habitat or to evaluate impacts of human activity (for example see Nielsen *et al.* 2003 and Ciucci *et al.* 2003). Notwithstanding its extensive application, RSF analyses, like its predecessor HSI, reveal disappointing predictability and generalizability in part due once again to the paucity of scale-specific habitat data. Other issues complicate the picture too. For example, "attractive sinks" can pose serious problems unless some function indicative of survival is included in the analysis (Delibes *et al.* 2001). The difficulty also seems related to scale and to problems inherent in averaging behaviors of individual animals (Nielsen *et al.* 2003).

Resource selection is scale-dependent in both spatial (resolution and extent) and temporal dimensions, but analysis across scales (landscapes, stands and sites) is seldom performed (Senft *et al.* 1987). In addition, individual animals likely have distinctive resource selection strategies, which are lost when results are pooled for a population. Regardless, the assumption is that selection of, or preference for, superior habitat relates to the fitness of an individual and hence to population growth or stability. Pooling data from many individuals potentially obscures individual selection of resources that are truly related to fitness and also incorporates resources used by individuals that have no bearing on fitness.

This is not to say that pooling is inappropriate. For example, if we allow that different individuals use different locations (habitat types) in different amounts and at different times in different amounts, then grouping similar bouts of activities that occur at similar spatial and temporal scales may allow researchers to appropriately aggregate resource selection data among individuals and decrease the ambiguity common to resource selection studies. For example, combining meaningful patterns of use with vegetation coverages at scales meaningful to several individuals may identify behavior specific habitats that are more important than is apparent from simply the time spent acquiring a specific resource.

In addition, the spatial extent and arrangement of resources (i.e. landscape context) varies by individual home ranges to the point that transitions between behavioral states (bout lengths) will likely also vary by individual. This would also be the case if landscapes were suddenly altered. An individual obliged to accommodate to relatively rapid changes in the spatial extent and arrangement of resources (e.g. fire or logging) should exhibit concurrent behavioral changes in bout length and transitions between behaviors. Individuals would be compelled to quickly gain knowledge of the "recent renovations" or its decisions (and indecisions) may, in fact, make it more vulnerable to processes such as competition, predation or energetic deficit. For example, caribou residing in forested uplands may be at reduced predation risk from wolves simply because diminished accessibility concomitantly diminishes the probability of wolf-caribou encounters. Abrupt changes, anthropogenic or otherwise, to the landscape (e.g. fire, logging or seismic lines) leading to improved accessibility by wolves (and other predators) would likely increase the odds of wolves encountering resident caribou. It follows that the probability of survival due to available resources (cover in the case of the caribou and travel routes in the case of the wolves) should shift away from the caribou toward the wolves in more accessible landscapes.

Several models have been developed to examine the strategies that individuals employ to acquire necessary resources. For example, the optimal diet model (MacArthur and Pianka 1966) attempted to describe the diversity of items in a diet and the trade-offs that accrue as a result of specializing and generalizing. Charnov (1976) modeled optimal use of food patches; the trade-offs that required balancing in this case were the relative costs of remaining within a patch (and thus depleting the resource) against the costs of finding a new patch that contained abundant resources.

Many of these models assume that environmental variation (the context in which individuals must make decisions) is constant and that the “predator” is aware of the average marginal value of all patches and the instantaneous value for each patch; it is clearly inappropriate to assign this degree of omniscience to any organism. Satisficing (Simon 1955), however, recognizes that where there are multiple and competitive objectives, the notion of securing the "best" solution is likely unrealistic. The satisficer acknowledges that real-world problems (predator avoidance, inter and intra-specific competition, environmental variation, territorial defense and the need to reproduce) are inherently uncertain and foregoes any hope of achieving true optimization. Satisficing, therefore, consists of two basic concepts: (1) satisfying a minimum requirement, and (2) choosing among a subset of behaviors when information-processing or time constraints limit the ability of a decision-maker to make an optimal decision (Ward et al. 1992).

Risk-sensitive foraging theory is based on the premise that fitness (in a Darwinian sense) derived from a predictable food source differs from fitness derived from an unpredictable, variable food source despite the fact that both food sources yielding the same average rate of gain. Experiments have shown that foraging animals are sensitive to the riskiness (defined as variance in amount of food or time since last meal) associated with alternative sources of food (Bateson 2002). For example, when offered the choice between a fixed feeding option that offered a constant food supply and a risky option that offered a variable food supply (no reward or high reward), individuals showed either risk-averse or risk-prone behavior. Preference of either the fixed or variable option seems related to a variety of factors, including the energetic status of the forager and the type of variance (time or amount) associated with the feeding.

In its most general terms, animal movement can be considered the process by which individual organisms relocate over space and time. Movement contributes to population demography (by supplementing or diminishing a population of individuals), rescue effect and genetic variability and, impinges upon important ecological processes such as intra and inter-specific competition and predation. Movement is especially important when both predator and prey are mobile; in such cases predators are able to actively search for prey which, are concomitantly able to avoid predators or other prey species that are part of a predators search image.

1.3 Problem Statement

In this era of unprecedented pressure to extract natural resources, biologists are increasingly facing demands that discourage the study of "pattern", which is often simple correlation devoid of causation. To facilitate our understanding of dynamic, spatially explicit processes, solutions to the conceptual and methodological problems associated with studying movement and resource selection are required. In short, analytical approaches that illustrate individual "space-time-action" systems will likely yield additional insight into the processes governing abundance and distribution of organisms.

The work presented in this thesis promotes a new direction in the study of animal movement, resource selection and the strategies by which these resources are accumulated. This approach explicitly recognizes the individual as the central unit of measure and clearly incorporates time, behavior and space at spatio-temporal scales that are meaningful to individuals.

1.4 Approach and Thesis Organization

To develop this approach I have used two existing data sets collected as part of two previous studies, one conducted on a population of woodland caribou in the Wabasca region of central Alberta (BCC 1998) and, the second on 3 wolf packs in west central Alberta (Kuzyk 2002). My first objective was to examine the applicability of hidden Markov modeling techniques to time-varying systems in ecology (such as animals moving across a landscape). I address this objective in Chapter 4 by simulating inferred movement behavior of woodland caribou. In Chapter 5, I deal with the issue of merely "inferring" proposed behaviors by evaluating HMM predictions of observer-confirmed kill sites solely from the GPS wolf relocation data; the objective here was to determine whether or not HMMs could correctly discover the kill-sites(i.e. the hidden states). In order to support these analytical chapters, I provide a representative review of resource selection and animal movement models in Chapter 2, which is followed by general hidden Markov model (HMM) theory in Chapter 3. A synthesis of the thesis and suggestions for future research is presented in Chapter 6.

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CHAPTER 2: A SELECTED REVIEW OF THE STUDY OF RESOURCE SELECTION AND ANIMAL MOVEMENT

2.1 Introduction

This chapter constructs a chronology of selected literature with regard to wildlife resource selection and movement, differentiating between analytical techniques that cater to the scale of one or more individuals and a population. I discuss some of the problems inherent at each scale as well as those that potentially result from inferring population level patterns from individual level analysis. To impose some structure, I have organized this review by taking a lead from Turchin's (1998) summary that indicates spatio-temporal density is the primary variable of significance to ecologists interested in distribution and abundance. Furthermore, I assert that resource selection and movement are key aspects that influence the spatio-temporal density of organisms.

I begin by discussing studies of resource selection and animal movement at the individual level and then shift from the scale of the individual to that of a population. At the population level I distinguish between studies that collect data as "points" (sited individuals or groups of individuals) and those that collect data as "grids" (pellet counts, track density etc.) I have further categorized movement and resource selection models following the publication by Starfield and Bleloch (1991) that distinguished between simulation models (which use computers to generate step-wise iterations from which conclusions are drawn) and analytical models that rely on the underlying mechanics of mathematical expressions from which conclusions are drawn.

2.2 Studies in Resource Selection

Preliminary research into resource use and availability has been typically descriptive. Most studies have taken the form of selection indices rather than formal hypothesis testing procedures. Researchers would simply report the number of individuals exploiting a resource and the degree (percentage) to which it was exploited. However, when resources are used disproportionately more than they are available, use of those resources is said to be selective (Johnson 1980). Forage selection (e.g. species, color, shape or size) and habitat selection (e.g. stand age, density or canopy height) are areas often considered of importance to biologists because they potentially identify the determinants of long term population persistence and, allow predictions of the consequences of changes in those resources due to anthropogenic and/or natural disturbance.

2.2.1 Selection Indices (Groups)

Several indices have been proposed to evaluate group selection. For example, using harvested mackerel, Scott (1920) calculated the ratio of resource use (prey type) to its availability (density) by dividing the average number of prey species per fish per unit of time by the number of prey species present per unit area. Total prey consumed or available was not included in this index and therefore, an estimate of preference is not actually obtained.

Savage (1931) presented a forage ratio and proposed that a value greater than 1 indicated the resource in question was exploited disproportionately more than it was available. Based upon this metric, the author indicated that the resource was preferred. One of the most widely used indices for analyzing selection is the electivity index (Ivlev 1961):

$$E_i = \frac{(r_i - P_i)}{(r_i + P_i)} \qquad 2.1$$

where, r_i is the relative abundance of prey (i) in a predator's diet and P_i is the relative abundance of prey (i) in the ecosystem. $E_i = -1$ corresponds to total avoidance, $E_i = 0$ represents non-selective feeding, and $E_i = 1$ corresponds to exclusive predation of prey. However, Ivlev's electivity index is not independent of prey density and, as such, it is significantly limited. Krueger (1972) compared 4 relative preference indices (RPI) to rank preference of twelve plant species by domestic sheep.

$$RPI_1 = \frac{fd \times D}{fr \times R} \qquad 2.2$$

$$RPI_2 = \frac{D}{R} \tag{2.3}$$

$$RPI_3 = \frac{fd \times D}{R \times 100} \tag{2.4}$$

$$RPI_4 = \frac{D \times 100}{fr \times R} \tag{2.5}$$

where:

$fd = \%\, frequency\, in\, diet$

$D = \%\ diet\ composition$

$fr = \%\ frequency\ on\ range$

$R = \%\ range\ composition$

In this study, the ranking of the 12 plant species by preference varied with RPI and the author concluded that, although they do provide additional information regarding preference, they were not an acceptable alternative metric for diet composition relative to forage availability.

Using different proportions of red and blue food pellets in a selective predation experiment, Manly *et al.* (1972) presented an index of selection (α) that measured the degree to which a forager (*Corturnix corturnix japonica*) was likely to opt for one prey type (pellet color) over another. The authors indicated that α remains constant if selection is independent of prey density, but will vary with prey density when prey selection is density dependent. Chesson (1978) advocated the use of Manly *et al.*'s (1972) measure for selective predation but proposed that its derivation from a simple stochastic model involving encounter and capture probabilities over multiple prey types resulted in increased applicability and interpretability under a wide range of biological conditions. Chesson (1983) subsequently summarized methods to estimate Manly *et al.*'s (1972) measure of food preference and indicated how it was related to some common foraging behavior models.

Jacobs (1974) modified the forage ratio and Ivlev's electivity index as they depend not only on the extent of selection, *per se*, but also upon the relative abundance of the food type being selected. The author indicated that use of either index should be avoided in cases where the relative abundance of food types is not equal.

Strauss (1979) reviewed reliability estimates for Ivlev's electivity index and the forage ratio. Using Monte Carlo simulations, the author reported that the statistical reliability of each index was a function of the relative abundance of the food items in the environment and proposed the use of a linear index of food selection that was not affected by the relative abundance of each food item. Strauss also cautioned that inadequate habitat sampling, differential availability of prey to the predator and differing digestibility of prey items were likely significant sources of error that limit interpretation of food selection studies.

Paloheimo (1979) reiterated the findings of Jacobs (1974) that the forage ratio and Ivlev's electivity index (measures of preference by predators of different prey or food items) depend on the relative abundance of the food items. However, Paloheimo asserted that the modifications proposed by Jacobs are similarly affected by relative abundance and offered an approach that standardized forage ratios that is independent of prey abundance. Paloheimo further pointed out that those measures of preference other than relative measures are not possible unless the detection radii, capture probabilities and distributions for all prey types are known.

Using spotlight transects Bowyer and Bleich (1984) studied the effects of cattle grazing selected habitats of southern mule deer (*O. h. fuliginatus*). The authors reported significantly fewer deer in meadows that were grazed by cattle compared to similar areas where cattle were prohibited. Deer pellets were also observed in significantly greater abundance on ranges that were not grazed by cattle. Total plant cover was significantly greater where cattle were absent and three important deer forage species were absent from cattle ranges. The authors also suggested that cattle grazing may limit deer numbers by reducing dense patches of *Muhlenbergia rigens* important for fawning.

Ready *et al.* (1985) developed an estimator of the sampling variance of Strauss' (1979) linear index of food selection, L_i, which accommodated for multiple predators and prey items, variability due to environmental heterogeneity and different feeding behavior in the predator group. The authors reported that variance decreased with an increase in the number of predators (fish in this case) sampled and, increased with increasing variance of prey (stomach contents). Furthermore, they indicate that uncertainty with regard to the degree of selectivity among the predators could be reduced with sample sizes of 10-15 for the predators and 700-1500 for total prey.

2.2.2 Selection Indices (Individuals)

Owen-Smith and Cooper (1987) assessed woody plant preferences of greater kudu (*Tragelaphus strepsiceros*) using plant and site based acceptability indices, feeding durations and forage ratios. In this study, the site-based acceptance index was defined as the ratio of 30 minute intervals during which the plant was used to 30 minute intervals during which the plant was available (within 10m). The plant-based acceptance index was defined as the ratio of the number of individual specific plant species eaten to the number species available (within neck reach). In this study, site-based acceptance indices distinguished between plants that were favored and those that were overlooked. Although no clear-cut pattern emerged based upon plant-based indices, the authors suggested this resulted from spatial auto-correlation of successive plants. The authors indicated that forage ratios were subject to errors in estimating the abundance and dietary proportions of less common plant species, especially when found in clumped distributions.

Cock (1978) reviewed the preference measures proposed by Scott (1920), Savage (1931), Larsen (1936), Cain and Shepard (1950), Ivlev (1961), Rapport and Turner (1970), Manly *et al.* (1972) and Jacobs (1974). Cock reported that only the measures presented by Cain and Shepard (1950), Manly *et al.* (1972) and Jacobs (1974) did not have major drawbacks, and of these three only Manly *et al.* (1972) allowed for exploitation of prey species. This implies that if exploitation of prey species is negligible, then the methods proposed by Cain and Shepard (1950) and Jacobs (1974) are quite appropriate. Furthermore, Jacobs (1974) pointed out earlier that the logarithm of the index presented by Cain and Shepard (1950) is favored when preference is high and that of Jacobs (1974) is suitable when preference is slight. Additionally, in this review, Cock (1978) discussed the utility of functional response models to predict preference and serve as null models. He presented Holling's (1959) disc equation adapted for two prey types, but recommends that it not be applied to predator-prey interactions where exploitation of the prey is considerable. In such cases, Cock advocates the use of Rogers (1972) random predator equation. For other reviews of resource selection indices, see Krueger (1972), Strauss (1979), Loehle and Rittenhouse (1982), Pearre (1982), Lechowicz (1982) and Manly (1993).

2.2.3 Hypothesis testing of resource selection (Groups)

Investigators concerned with objective examination of selectivity in resource selection studies typically use hypothesis testing to make inferences about populations. Numerous parametric and non-parametric tests for categorical and continuous data have been employed to test for selection of available resources.

Rondorf *et al.* (1990) studied preference (use vs. available) for food items of sub-yearling Chinook salmon (*Oncorhynchus tshawytscha*) in riverine and reservoir habitats of the Columbia River. They reported that caddisflies were predominant prey (64% by weight) in riverine nursery habitats while *Daphnia* and terrestrial insects predominated in reservoir habitats. The authors calculated a non-parametric "preference ranking" from the difference between "rank of use" and the "rank of available". They reported a positive correlation between preference and size of available prey items. Only rank in number of prey items available in the habitat was consistently correlated with rank in diet number. The authors suggested that the presence of *Daphnia* and terrestrial insects in the diet of reservoir salmon was likely associated with their high availability accompanied by a concomitant low availability of other food items. However, they suggested that use of *Daphnia* may result in a higher foraging cost per energy unit gained because of the small size of the prey.

Manly (1993) classified population level sampling strategies in resource selection studies as Design I. For example, using moose (*Alces alces*) distribution patterns, Neu *et* *al.* (1974) presented a mapping technique that used chi-square analysis (to test if a suite of resource categories were selected differently from relative availability) in tandem with a Bonferonni z statistic (to estimate which resource category within the suite was selected disproportionately). Marcum and Loftsgaarden (1980) also proposed the use of chi-square analysis. However, due to difficulties inherent in planimetric calculations (the standard method at that time) of area in large diverse regions or rugged terrain, they proposed a "random points, non-mapping" technique for studying habitat preferences. Aebischer *et al.* (1993) pointed out that Chi-square analysis inappropriately treats telemetry locations (rather than the individual) as the sampling unit. Johnson (1980) proposed a method based on a measure that calculated the average difference between the rank of use and rank of availability of specific resource elements across individuals. He then ranked the differences across individuals by resource elements and proposed that higher ranked elements implied relative preference over lower ranked elements. In addition, Johnson indicated true differences between ranked components could be tested using Hotelling's T^2 and a Bayesian decision procedure (Waller and Duncan 1969) for multiple comparisons. The author suggested the ranking approach had value because comparisons of resource-use were largely unaffected by inclusion of elements unimportant to the animal in the analysis. However, Alldredge and Ratti (1986) reported that the Johnson (1980) method did not detect differences in selection when the rank ordering for use and availability was the same in spite of the fact that percent used and percent available were quite different. Also, Aebischer *et al.* (1993) suggested that Johnson's method was unable to contend with differential habitat use by groups of individuals.

2.2.4 **Hypothesis testing of resource selection (Individuals)**

Manly (1993) categorized individual resource selection studies into one of two sampling approaches (Design II or III). In the first, "use" is measured by individual, but "availability" is measured at the population level. Alternatively, both "use" and "availability" are assessed individually. In studies such as these, estimates of population parameters and associated variability as well as inference to the population level obligates investigators to assume individuals are a random sample of the larger population and that resource selection between individuals in time and space is fixed. Under these assumptions, Manly (1993) pointed out that inferences to populations, hypotheses testing and estimating parameter variation are superior if the individual is considered the experimental unit rather than the observations from a single animal. However, this sampling approach also offers investigators the option to consider variation between individuals *per se (*e.g. selection for one resource over others), differences in age, gender, or selection strategies can also be examined using this sampling approach.

Many authors have used categorical data to examine resource selection. For example, Talent *et al.* (1982) used categorical data and Wilcoxon's signed rank test to examine habitat use by mallard broods in south-central North Dakota and Pietz and Tester (1983) used the Freeman-Tukey goodness-of-fit test (Bishop *et al.* 1975) to study habitat selection by radio-collared snowshoe hares in north-central Minnesota.

Hohman (1985) studied the feeding ecology of individual ring neck ducks (*Aythya collaris*) in northwestern Minnesota. Food use by adult hens prior to increased gonadal activity varied with habitat. Ducks utilizing ephemeral wetlands consumed mainly plant material whereas invertebrates comprised 1/2 of the diet in semi-permanent and permanent wetlands. Juveniles consumed mostly invertebrates, the proportion of which varied with age-class. Availability of food items was important to their selection.

Heisey (1985) proposed log linear modeling in conjunction with the Manly *et al.* (1972) selectivity measure to examine whether resource selection by radio-collared white-tailed deer (*Odocoileus virginianus*) was influenced by attributes other than the resource (e.g. by time of day and by individual). Using the "random points", non-mapping technique outlined by Marcum and Lofftsgarden (1980), Gionfroddo and Krausman (1986) examined summer resource (habitat) selection of radio-collared sheep (*Ovis canadensis mexicana*). Alldredge and Ratti (1986) used the Quade (1979) test and data from 10 radio tagged gray partridge to test differential habitat selection between 5 categories of agricultural land-cover. Following a significant F-statistic, the authors used the least significant difference (LSD) method to determine which of the five habitats were different from the others. However, Aebischer *et al.* (1993) pointed out that use of the

Quade test is invalid because of the unit-sum constraint (proportional use of one habitat type depends on all other habitat types).

Dunn and Braun (1986) used discriminant function analysis to describe summer habitat use by adult female and juvenile sage grouse. The authors indicated that sage grouse selected habitat near edges which were associated with greater amounts of cover, but where cover was more homogenous in terms of density and size. Within these sites, grouse selected roost sites alongside shrubs that were larger than average. No difference was detected in the habitat used by adult females and juvenile sage grouse.

Alldredge *et al.* (1991) used one way ANOVA's to examine shrub cover and height at fawn birth sites selected by 13 radio-collared pronghorn antelope (*Antilocapra americana*) and 50 fawn bedding sites. Used sites were compared to 47 random sites selected from areas used infrequently by parturient females. No differences in shrub cover were detected between birth and bedding sites, however, significant differences existed between used and unused sites. The authors found no difference in shrub height between birth sites, bedding sites and unused sites. In this study, the authors used solar-powered radio transmitters to relocate 7 fawns daily over a period of 3 weeks. Shrub height and percent canopy cover were measured at 72 bed sites and these were compared to shrub height and percent canopy cover at 228 random sites located within fawn home range. Significant differences existed between bedding sites and random locations.

Aebischer *et al.* (1993) pointed out that many techniques used in the analysis of habitat use based on radio-tagged animals have problems associated with sampling level, data pooling across individuals, non-independence of habitat proportions, differential habitat use by groups of animals and, arbitrary definitions of habitat availability. They advocated the use of compositional analysis for proportional (use/availability) habitat use by individual animals as a basis for analysis and point out that compositional analysis can be applied to questions such as the effects of age class and season. The authors compared utilized with available habitats at two scales: 1. home range selection within the overall study area and; 2. habitat use within the home range. Regardless of scale, compositional analysis allows habitat ranking by relative use. Significant between-rank differences can also be established.

Cooper and Millspaugh (1999) introduced and promoted the application of discrete choice models to wildlife resource selection studies. Discrete choice models use continuous or categorical data to estimate the likelihood that an individual will select a resource as a function of its' attributes and those of all other available resources. When combined with GIS technology, discrete choice models allow flexible delineation of resource availability for individuals over time and space. The effects of alternate management actions and hypotheses can also be explored. Using discrete choice models the authors reveal the importance of factors relating to thermal regulation, hiding cover, and potential forage in elk (*Cervus elaphus*) bed site selection.

Osko *et al.* (2002) studied moose (*Alces alces*) habitat preferences in response to changes in availability at the individual level. Although, it is unclear whether degree of disturbance was responsible for the apparent differences in proportional habitat use rather than habitat availability, this study challenged the notion that habitat preferences are fixed and endorses the notion that habitat availability influences apparent preferences.

2.3 Studies of Animal Movement

Movement models date back to early 1900, among the first were Pearson and Blakeman (1908) used diffusion to model random migration and Brownlee (1911) who applied diffusion models to the spread of epidemics.

Dobzhansky and Wright (1943) modeled the dispersal of fruit flies and Skellam (1951) modeled range expansion of small mammals. Patlak (1953a; 1953b) extended the simple random walk model of dispersal, but it was largely overlooked at the time. Rohlf and Davenport (1969) used computer-simulated random walks to mimic dispersal behavior. The past two decades have seen many refinements in the models and in methods of applying the models to data.

Investigations of animal movement in natural environments generally fall within one of three general frameworks: (1) phenomenological studies which describe patterns of habitat use, but do not address the underlying mechanisms (With 1994, Wiens *et al.*

1997); (2) theoretical analyses that usually make oversimplified assumptions about movement and it's underlying mechanisms (Skellam 1973, Stinner *et al.* 1983, Turchin 1989) and; (3) individual-based movement models (IBMM's) tailored to context and organism-specific conditions which yield little generalized information (Turner *et al.* 1993, 1994).

2.3.1 Animal movement (Groups)

The movement of groups of animals is often treated as a diffusion process (Okubo 1980), which when combined with terms that describe ecological processes such as density dependence, population drift or attraction becomes progressively more biologically meaningful.

2.3.1.1 Diffusion

Diffusion is the process whereby a flux of particles advances from regions of high concentration to regions of low concentration in proportion to the gradient of concentration. If one assumes that successive steps taken by an organism are independent and random, passive dispersal of a collection of random-walks in a one-dimensional, homogenous environment can be described by the following differential equation.

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} \tag{2.6}$$

where D is the rate of diffusion, u refers to the concentration of particles (the collection of random walks) and x refers to the spatial derivative. Two-dimensional simple diffusion is completely analogous to the one-dimensional case

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) \tag{2.7}$$

In this case, u is the spatio-temporal density of organisms, where x and y are Cartesian spatial coordinates and t is time. Simple diffusion can also be expressed using polar rather than Cartesian coordinates

$$\frac{\partial u}{\partial t}=\frac{1}{r}\left[\frac{\partial}{\partial r}\left(rD\frac{\partial u}{\partial r}\right)+\frac{\partial}{\theta}\left(\frac{D}{r}\frac{\partial u}{\partial \theta}\right)\right] \tag{2.8}$$

where

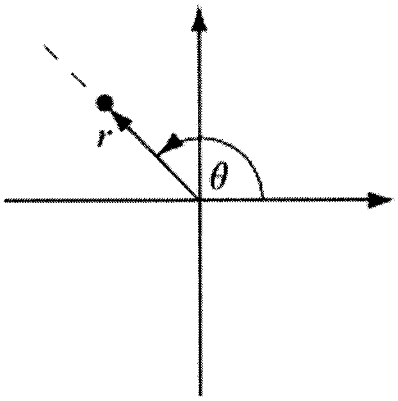

Figure 2.1Calculating θ from polar coordinates

Determining the density of a population at any given point in time and space by diffusion requires specification of an initial condition (IC) and two boundary conditions (BC). Several types of each condition are commonly used to represent ecological problems. An "absorbing boundary condition" sets the population density at the domain boundary to zero $(\mu(0,t)=0)$. This condition results in the immediate mortality of any organism crossing the boundary when hostile habitat exists outside of the modeled domain. A "reflecting boundary condition" sets the number of organisms dispersing per unit area (flux) at the domain boundary is set to zero $(\partial\mu(0,t)/\partial x=0)$ resulting in no net movement of organisms across the boundary. This is useful for describing diffusion on islands or other insularised systems. In cases where the domain boundaries are extremely distant from the point location of interest to the point that their effects can be ignored, "the zero at infinity boundary condition" $(\mu(\infty,t)=0)$ is most suitable.

An initial condition such as "point release" is useful for modeling mark-recapture releases. Point release assumes that all individuals are released at a single point in space ($x = 0$) and that the density of individuals at t = 0 is infinite. In reality, marked organisms cannot be released in this fashion. However, the assumption that all individuals are released at a single point in space and that the density of individuals at t = 0 is infinite is acceptable if the spatial extent into which organisms are released is much larger that the release site. For example, it may be appropriate to assume a point release if one were modeling an forest insect outbreak that begins in a small patch, but has the potential to spread to the entire forest. "Area release", on the other hand, improves biological authenticity. However, the region from which individuals will diffuse requires complete specification.

2.3.1.2 Spatially Explicit Population Models

Spatially explicit population models (SEPMs) primarily describe population dynamics but, in addition to expressing births and deaths, they incorporate movement terms. The three variables of primary importance in SEPMs are population density (of one or more interacting species), space (from one to three dimensions) and time, each of which can either continuous or discrete. A spectrum of models can, therefore, be developed ranging from continuum models in which all variables are continuous to cellular automata in which all variables are discrete. The choice of whether to parameterize with continuous or discrete variables should be made based upon the biological nature of the system being modeled. For example, species that reproduce annually may be modeled using a discrete time-step of one year; whereas those that are not restricted to a distinct reproductive season should be modeled on a continuous basis.

The simplest continuum model is the Skellam (1951) diffusion (equation 2.9) model adapted to include exponential growth

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \alpha u \tag{2.9}$$

where D is the rate of diffusion and a is the intrinsic rate of increase for a local population. In essence, equation 2.9 states that the population density, $u(\mathrm{x}, t)$ can change as a result of local demographics and redistribution in space. The Skellam (1951) model can be expanded to include two dimensions:

$$\frac{\partial u}{\partial t} = D\left[\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right] + \alpha u \tag{2.10}$$

Continuum models that explicitly include reproduction and diffusion are termed reaction diffusion models (Turchin 1998). However, diffusion models have been criticized (Skellam 1973, Stinner *et al.* 1983, Turchin 1989) because they assume organisms proceed at infinite velocity along infinitely random paths. Biologically, this implies that the probability exists for an organism to move an infinite distance from its current location in an infinitely small amount of time; second, the assumption of infinitely random paths implies that an organism's movement trajectory remains unpredictable even at very small time scales.

Non-diffusion continuum models such as the telegraph equation

$$\frac{\partial u}{\partial t} = -\frac{1}{2\lambda}\frac{\partial^2 u}{\partial t^2} + \frac{\gamma^2}{\partial x^2}\left[\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right] \tag{2.11}$$

where γ is the organisms finite velocity and λ is the organisms rate of changing direction were developed to account for the unrealistic assumptions of diffusion.

Local population growth can be combined with telegraph dispersal in the following form:

$$\frac{\partial u}{\partial t} = -\frac{1}{2\lambda}\frac{\partial^2 u}{\partial t^2} + \frac{\gamma^2}{\partial x^2}\left[\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right] + au \tag{2.12}$$

where a is the intrinsic rate of increase for a local population.

2.3.1.3 Reaction-Diffusion Networks

In ecology, reaction-diffusion networks study the dispersal of organisms (through diffusion) within a network of discrete patches (i.e. space is no longer continuous) for which internal multi-species population dynamics are governed by Lotka-Volterra competition (Levin 1974, Caswell and Etter 1993).

$$S_1(n+1) = S_1(n) + a^* S_1(n) - b^* S_1(n)^* S_2(n) \tag{2.13}$$

$$S_2(n+1) = S_2(n) + e^*b^* S_1(n)^* S_2(n) - c^* S_2(n) \tag{2.14}$$

where $S_1(n)$ and $S_2(n)$ represent the number of species 1 and species 2, respectively, a is the natural growth rate of species 1 in the absence of predation, c is the natural death rate of species 2, *b* is the death rate per encounter of species 1 due to predation and, *e* is the efficiency of turning predated species 1 into species 2.

Levin (1974) modeled dispersal of individuals of two competing species between two patches in order to illustrate the importance of a spatial component in modeling ecological interactions. In patchy environments, Levin concluded that distinct patches are likely to be initially colonized by different species and evolve independently as a result. Relatively poor invaders are thus able to establish themselves due to the random chance of early arrival. Levin's model also indicated that species richness within a patch should increase as a result of patchiness alone (regardless of patch type), but should diminish as ability of species to migrate increased.

2.3.1.4 Coupled Map Lattices

Whereas continuous systems are described by differential equations, discrete systems are described by difference equations. Analysis of population dispersal using coupled map lattices is accomplished by developing systems of difference equations in which time and space are discrete. The general form of a difference equation is:

$$x_{t+1} = f(x_t) \tag{2.15}$$

where the function *f* determines the value x_{t+1} from x_t.

Hassell *et al.* (1991) constructed a coupled map lattice in which patches were modeled as a tessellated, rectangular two-dimensional complex. Each patch was occupied by "hosts" and "parasitoids" whose dynamics occurred according to the Nicholson-Bailey model:

$$H_{t+1} = RH_t \exp(-aP_t) \tag{2.16}$$

$$P_{t+1} = cH_t[1 - \exp(-aP_t)] \tag{2.17}$$

where *H* is the host density, *R* is the intrinsic net reproductive rate of the host, *P* equals the parasite density, and *c* is the average number of parasitoids emerging from a parasitized host.

The model assumes that parasitoids search independently of each other and encounter hosts at random (implies that the fractions of hosts which escape parasitism is related to parasitoid density), both parasites and hosts exhibit a clumped distribution and, in the absence of a parasitoid, the host population increases exponentially (the host population is limited only by the parasitoid). Dispersal of hosts and parasites to the eight neighboring cells occurred in a fixed proportion to that of the original patch. The model resulted in a number of outcomes, including extinction of hosts and parasites, crystal lattice, spatial chaos and spiral waves.

2.3.1.5 Cellular Automata

Cellular automata (CA) are discrete dynamical systems in which relatively simple rules are local and invariant. CA use these rules to emulate the seemingly random way in which the laws of nature operate. In studies of population redistribution, space is represented by a uniform grid of inter-connected cells, time advances in discrete steps and population densities (absent, low, medium, high) are computed for each cell based upon its current state (population density) and that of its neighbors.

Even with very simple deterministic rules, CA are capable of producing complex random-looking spatio-temporal patterns such as homogeneity, chaos, periodic patterns and localized structures capable of traversing the CA domain (Wolfram 1983). An example of a simple CA rule set is: “If a cell is off, it turns on if exactly three of its neighbors are on. If a cell is on, it stays on if exactly two or three neighbors are on; otherwise it turns off”. When a cell is on, it is considered "alive", but will “die” if more than three neighbors are alive (density dependence); similarly, a live cell with fewer than two live neighbors dies (Allee effect). This simple deterministic rule (Conway 1970) produced life-like behaviors (moving, growing, reproducing and evolving).

2.3.1.6 Interacting Particle Systems

Interacting particle systems (IPS) (probabilistic cellular automaton) are stochastic equivalents of deterministic CA in which population density and space are discrete and, time is either discrete or continuous. Particles multiply or decline according to rates usually dependent on those immediate to their neighborhoods. Interacting particle system approaches have been applied to meta-population dynamics and are closely related to percolation.

Durrett and Levin (1994) point out that modeling space as a discrete variable has the advantage of dividing the effects of local and distant interactions. Their model assumed space (x) was represented by a cellular array (in one or two dimensions), each cell maintained a maximum of one particle, which died at rate, δ, or reproduced at rate α. A daughter particle dispersed randomly to a neighboring cell (to one of two cells in the one dimensional case or one of cells in the two dimensional case). If the neighboring cell was occupied, the disperser died. Durret and Levin made use of an IPS model to illustrate dissolution of spatial pattern when birth rates are too low or death rates too high and, using previously published research, discuss organism dispersal and competition.

2.3.1.7 Spatial Contact Processes

According to Mollison (1986), there are four classes of spatial contact processes (SCP); linear stochastic contact models, linear deterministic contact models, non-linear stochastic models and non-linear deterministic contact models. SCPs are a class of models that combine IPSs and continuum reaction-diffusion models; however, a crucial element central to SCPs is a frequency distribution that describes the location of offspring relative to that of its parent. For example, individuals may reproduce with probability α, but location (distance, s) of the offspring relative to its parent is selected from a probability distribution $V(s)$. The probability of a new individual at location x over $(t, t+dt)$ is:

$$P(N \rightarrow N+1) = \alpha \overline{N(x,t)dt} \tag{2.18}$$

where $N(x,t)$ refers to the number of individuals at location x time t, and $\overline{N}(x,t)$ is the integration $\int N(x-s,t)dV(s)$ over the entire spatial domain of the process. Essentially, equation 2.18 states that for the offspring of a parent to appear at location x, it had to be born at some location s units away (the probability of which is $\alpha N(s,t)dt$) and then travel *x*-*s* (with the probability specified by *V*(*s*)). In the case where space is discrete, the number of individuals is the sum over the entire lattice.

2.3.2 Animal movement (Individuals)

Many modeling strategies aggregate individuals and their interactions with the environment, but following several important publications (Huston *et a.l* 1988, DeAngelis *et al.* 1992, Judson 1994), individual based movement models (IBMMs) were widely adopted by ecologists. This approach acknowledges two fundamental biological principles. The first points out that individuals are behaviorally and physiologically distinct. The second recognizes that interactions among individuals are inherently localized, i.e., organisms are influenced mostly by nearby organisms.

2.3.2.1 Linear Dispersal Models

The best-known linear dispersal model is McArthur and Wilson's (1967) stepping-stone model. In this model McArthur and Wilson explored the effect of stepping-stone islands on the exchange of individuals between source and far off recipient islands. They were interested in calculating the probability that an individual on the recipient island came from the stepping-stone island rather than the source island. Their model included widths of the source, stepping-stone and recipient islands, distances from source to recipient and stepping-stone to recipient, mean dispersal distance (which could be varied by taxa) (Figure2.3), a term to account for an individual leaving the source island at an angle that would allow it to intercept the stepping-stone island (figure 2.3) and various survivorship probability density functions (exponential, normal). The model

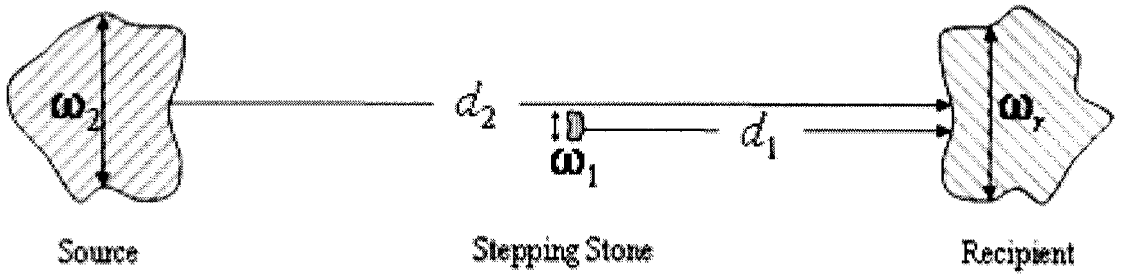

Figure 2.2 McArthur and Wilson (1967) stepping stone model

indicated that even very small stepping-stone islands could significantly increase the number of individuals reaching a recipient island.

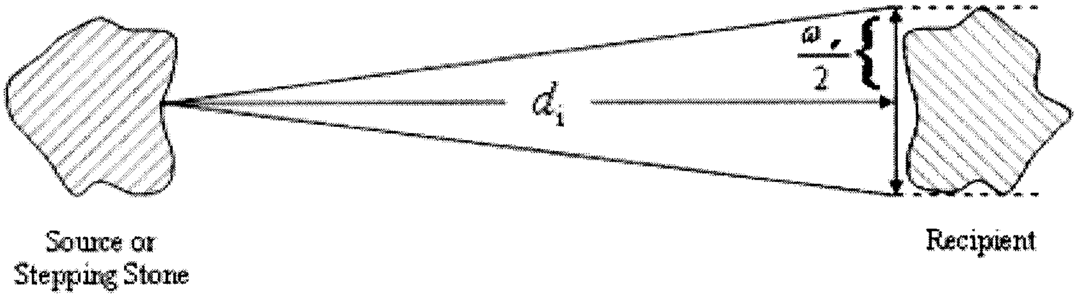

Figure 2.3 Accounting the angle at which an individual leaves an island

According to McArthur and Wilson, the probability that an individual arrived from a stepping-stone island was simply the proportion of individuals arriving at the recipient island from the stepping-stone:

$$p(A_i) = \frac{n_1}{n_1 + n_2} \tag{2.19}$$

where n_1 refers to the number of individuals arriving from the stepping-stone island and n_2 refers to the number of individuals arriving from the source island. Using a normally distributed survivorship probability density function, McArthur and Wilson estimated the number of individuals passing from one island to another some distance away to be:

$$n_i = \tan^{-1}(\omega_r / 2d_i)\alpha\omega_i^{\,2}\left(\sqrt{\frac{2}{\pi}}\frac{e^{-d_i^{\,2}/2}}{d_i}\right) \tag{2.20}$$

The relative contribution of the stepping-stone island to the recipient, $n_1/(n_1+n_2)$, can be calculated directly from expression 2.20. By varying the relationships outlined in equation 2.20 and using $\omega_r = \omega_1 = d_1 = \Delta$, McArthur and Wilson developed isoclines to illustrate the rapidly increasing importance of stepping-stone islands of almost all sizes as their relative distance to the recipient island decreased.

Although the simplifying assumptions of linear dispersal models are considerable, they have made significant contributions to the study of how the underlying structures of communities develop and exposing the close relationship between movement and spatial population dynamics.

2.3.2.2 Random Walk Models

Although movement of individuals is often treated as a simple random walk (SRW), they too are prone to over-simplification in terms of features such as spatial dimension, constant move length or duration and independence between steps. SRWs in one dimension assume an individual moves a distance, Δx, for time step, Δt, and that moves to the right occur with probability a and those to the left with probability β, where

$$\alpha + \beta = 1 \tag{2.21}$$

A random walk is dubbed isotropic when $\alpha = \beta$ and anisotropic when $\alpha \neq \beta$. The position of the individual after n time steps is

$$m = n_r - n_l \tag{2.22}$$

where n_r equals the number of moves to the right and n_l the number to the left. The probability that an individual will be found at position m after n steps is

$$p(m,n) = \frac{n}{n_r n_l} \alpha\beta$$

(2.23)

One can expand the random walk model to two-dimensional space quite easily. Jones (1977) applied a simple random walk in two-dimensional space to describe patterns of population distribution for cabbage butterflies (*Pieris rapae*). Processes such as taxis, kinesis and density dependence are natural extensions of random walk models (Rohlf and Davenport 1969). In addition, random walks may be augmented by varying the length of, and/or imposing directional bias on successive moves. In this case, length and angle are randomly selected from distributions with each consecutive angle correlated with the preceding one (Siniff and Jensen, 1969, Skellam 1973, Kitching and Zalucki 1982, Kareiva and Shigesada 1983, Othmer *et al.* 1988).

2.3.2.3 Simulation Models of Individual Movements

Historically, individual based movement models (IBMMs) were referred to as computer simulations and were considered distinct from random walk models (the former principally biological in nature and the latter primarily mathematical). IBMMs assume each decision to move is comprised of a combination of stochastic and deterministic factors. For example, the decision to remain in one location over a period of time is likely probabilistic in character, yet in certain localities at certain times, the probability of remaining stationary may be very high. During the hottest portion of a mid-summer day, a well-satiated, undisturbed caribou, for instance, would likely be bedded; the probability of being so may even be 1.0, in which case, the action is deterministic. Although IBMM's are capable of modeling variation among individuals and the interaction between them, most are quite complex, often requiring arbitrary estimates for some model parameters. Ruckelshaus *et al.* (1997) suggest that less detailed models would improve the match between model complexity and the quality of the available data.

Although IBMMs contribute little or nothing in the way of general ecological theory, their utility lies in providing a direct approach to fitting model parameters to empirical data to specific scenarios. They are particularly useful in management and identifying areas where research is lacking.

2.4 Conclusion

Much of the research effort illustrated by selected studies in this chapter has been applied to describing reliable, easily observable patterns between two or more variables. As biologists, we are pleased at the discovery of these reliable associations, but are often more intrigued with "why" the association exists in the first place. Inevitably, we are frequently left with the daunting challenge to speculate about the nature of underlying biological mechanisms that produced the observed pattern. One possible way to reduce this uncertainty is to characterize these processes in terms of signal models, which have at least three benefits; (1) to provide a theoretical description of the signal processing system, (2) to improve our understanding of the process that created the signal, (3) to provide an effective, practical framework for system prediction and recognition. Hidden

Markov models belong to a class of probabilistic signal models called Bayesian Networks. I present an application of hidden Markov models to woodland caribou movement and behavior in Chapter IV and therefore, I examine the fundamentals of hidden Markov modeling in the next chapter.

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CHAPTER 3: HIDDEN MARKOV MODELS

3.1 Introduction

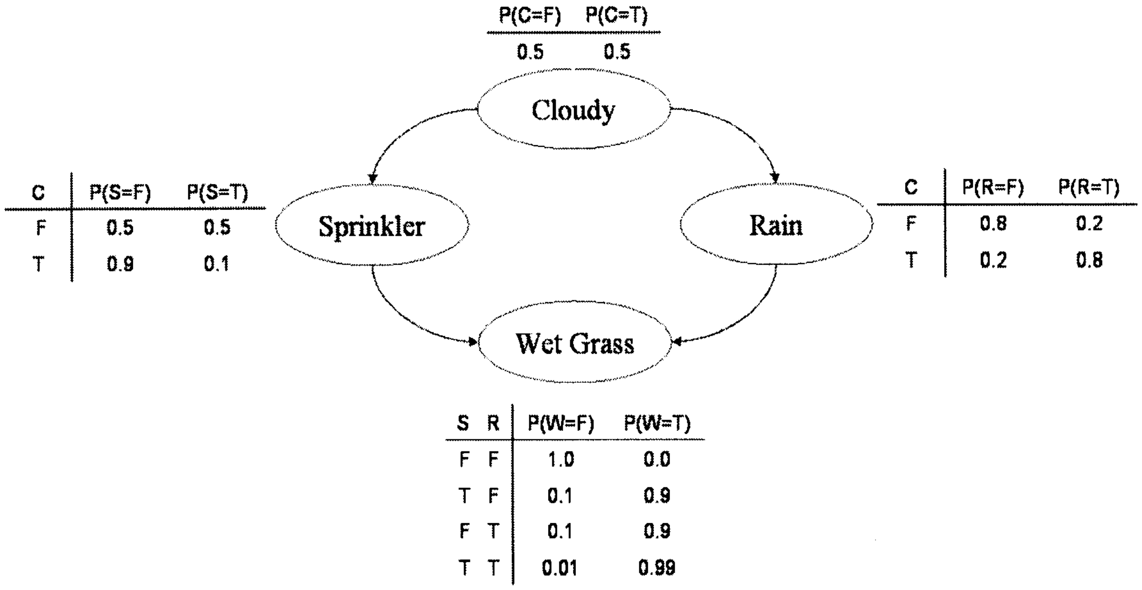
Hidden Markov models (HMMs) belong to a class of probabilistic models called Bayesian Networks. Bayesian probability theory permits one to model uncertainty and outcomes by combining prior knowledge with observational evidence. For example, you may speculate that a fire (outcome) has started based on the observation that a smoke detector sounds; you cannot, however, be certain. It is possible some other mechanism caused the alarm to sound, for example, the steam from a shower. This uncertainty can be characterized using a Bayesian Network (BN), the components of which are: a set of variables, a graphical structure connecting the variables, and a set of conditional probability distributions.

3.2 Bayesian Networks

A BN is commonly represented as a graphical model that consists of nodes (the random variables) and arcs (Gharamani 2000). By convention, node A is a parent of node B if a directed arc flows from A to B; intuitively, node B is a child (or equivalently, progeny) of node A. Node A can have several descendants (node C is a child of node B which is a child of node A). A directed path is a sequence of nodes such that each node in the sequence is a parent of the one following. A directed arc is placed from node A to node B if B is conditional on A. The absence of an arc between two variables indicates independence; that is, the probability of one of the variables does not depend upon the other. Construction of a BN occurs as follows: decide upon all of the important system variables, use causal knowledge to guide the connections made in the graph and specify the conditional probability distributions based upon defined dependencies.

If the variables are discrete, a conditional probability table (CPT) specifies the probability that a child node will result in one of the outcomes described in the CPT.

Consider the following example[1] (Figure 3.1), in which all nodes have two possible outcomes; true (T) and false (F). The event "grass is wet" (W=true) has two possible causes: either the sprinkler is on (S=true) or it is raining (R=true). For example, we see that Pr(W=true | S=true, R=false) = 0.9 (second row), and hence, Pr(W=false | S=true, R=false) = 1 - 0.9 = 0.1 (each row must sum to one).



P(C=F)	P(C=T)
0.5	0.5

C	P(S=F)	P(S=T)
F	0.5	0.5
T	0.9	0.1

C	P(R=F)	P(R=T)
F	0.8	0.2
T	0.2	0.8

S	R	P(W=F)	P(W=T)
F	F	1.0	0.0
T	F	0.1	0.9
F	T	0.1	0.9
T	T	0.01	0.99

Figure 3.1 A simple Bayesian Network

Since the Cloudy node has no parents, its CPT specifies the prior probability that it is cloudy (in this case, 0.5). In Bayesian network terms, a HMM is represented by associating state nodes with a transition matrix and observation nodes with a state dependent observation matrix (Figure 3.2).

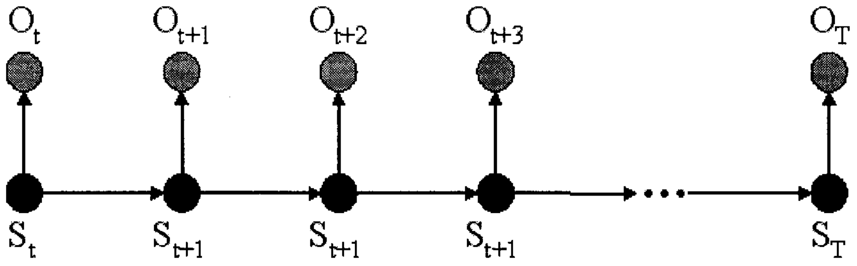


Figure 3.2 Bayesian network representation for an HMM

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[1] This example is discussed fully in Bosia, L., von Rohr, P. 2003. "A Class for Discrete Bayesian Networks in Darwin" at http://cbrg.inf.ethz.ch/bio-recipes/BayesNet/code.html

Before discussing HMMs, however, I first focus on the more simple case of first-order Markov chains.

3.3 First-Order Markov Chains

Discrete 1st-order Markov chains assume a system can be described by N distinct states, which undergo transitions at discrete, regular time intervals. The initial likelihood of state q_i is expressed by π_i and transitions between states are governed by a set of transition probabilities, a_{ij}, such that:

$$a_{ij} = p[q_{t+1} = j \mid q_t = i] \tag{3.1}$$

where

$$a_{ij} \geq 0 \quad \forall j,i \tag{3.2}$$

and

$$\forall i, \sum_{j=1}^{N} a_{ij} = 1 \tag{3.3}$$

Hence the probability of the system being in the next state (q_{t+1}) depends exclusively on the current state (q_t). Rabiner and Juang (1993) presented a simple example for modeling weather prediction. Consider a weather system comprised of three states: rainy (R), sunny (S) and cloudy (C). The likelihood of transition between each state is represented by probabilities (aij) within the stationary matrix A:

Table 3.1 Transition Matrix For Weather Example

		t+1		
		(R)	(S)	(C)
	(R)	0.60	0.20	0.20
t	(S)	0.33	0.33	0.33
	(C)	0.30	0.50	0.20

Based on A we are able to calculate the probability of observing a particular state sequence and the likelihood of correctly predicting the next state. For example, the probability of observing a series of days that follows the sequence rainy, rainy, sunny, rainy, cloudy (replacing 1 for rainy, 2 for sunny and 3 for cloudy is;

$$\mathrm{P(O|Model)} = p[1, 1, 2, 1, 3|\mathit{Model}] \qquad 3.4$$

$$= p[1]\,p[1|1]\,p[2|1]\,p[1|2]p[3|1] \qquad 3.5$$

$$= \pi 1 \bullet a_{11} \bullet a_{21} \bullet a_{12} \bullet a_{31} \qquad 3.6$$

$$= (0.33)(0.60)(0.20)(0.33)(0.20) \qquad 3.7$$

$$= 2.61\mathrm{x}10^{-3} \qquad 3.8$$

where π_1 is the probability of state 1 (rainy) given no history.

The Markov chain is a simple, but powerful method that can describe biological processes such as community succession (McAuliffe *et al.* 1988, Tanner et al 1996) and, population structure and abundance (Leslie 1945) that are stochastic in nature and, where each state corresponds to an observable (physical) event. Markov chains, however, are too restrictive to be applicable to problems where the process of interest is hidden and dynamic (i.e. non-stationary). Solutions to these problems require a simple extension of the Markov chains to include the case where an observation is a probabilistic function of the state. The resulting hidden Markov model is said to be a doubly stochastic, first order method for representing time varying systems.

3.4 Hidden Markov Models

Hidden Markov models have been widely employed in speech recognition (Levinson *et al.* 1983, Rabiner 1989), automated cartographic applications (Caelli *et al.* 2001a), genetics (Henderson *et al.* 1997) and human movement modeling (Caelli *et al.* 2001b).

Assuming a finite number of observations, hidden states and time samples, discrete HMMs can be defined by three basic components: (1) a vector containing the prior probability of each hidden state (π vector), (2) the state transition probabilities (A matrix: the first-order Markov component) and (3) the probability of the observations given a state (B matrix). More formally, a discrete2 HMM, λ is defined by:

$$\lambda = \{\pi, A, B\} \tag{3.4}$$

where

$$\pi = p(S_i); A = p(S_j(t+1)/S_i(t)); B_l = p(O_k^l / S_i) \tag{3.5}$$

for states (S_j, j=1, M), independent observation variables, O_k, and observations (k, k=1, Nl).

Given suitable estimates of these quantities, solutions (Rabiner, 1989) are well known for: (1) generating (predicting) observation and state sequences from the model by Monte Carlo sampling methods; (2) determining the most likely behavioral "state" sequence given the model and an observation sequence (the Viterbi algorithm) and (3) updating the model estimate given new observations (the Baum Welch algorithm).

3.5 A Coin-Tossing Example

Consider the following problem. You are seated on one side of a barrier and a second person is seated on the other. At regular time intervals, the other person completes 1 coin toss choosing randomly among three biased coins for a total of 5 tosses. Although you are informed of the result from each coin toss, you are not informed which of the coins produced the result (i.e. the choice of coin is "hidden" from you). After 5 coin tosses, you have an "observation (O)" sequence that consists of a series of heads and tails; a typical sequence may be:

= {O1, O2, O3, O4, O5}

= {H, H, T, H, T}

where

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[2] Continuous HMMs are not conceptually different from the discrete case except for replacing individual probabilities by continuous probability density functions.

$$\begin{aligned} H &= heads \\ T &= tails \end{aligned} \tag{3.6}$$

Using the HMM to determine the most likely coin sequence that produced the above observation sequence, requires that the choice of coin at each time step be governed by: 1) a transition matrix (A) (Table 3.2);

Table 3.2 "A" Or State Transition Matrix for Coin Example

		Coin at t+1		
		(Coin 1)	(Coin 2)	(Coin 3)
Coin at t	(Coin 1)	0.20	0.20	0.60
	(Coin 2)	0.33	0.33	0.33
	(Coin 3)	0.30	0.40	0.30

where

$$a_{ij} = p[q_{t+1} = j \mid q_t = i] \tag{3.7}$$

2) a state dependent observation matrix (B) (Table 303).

Table 3.3 "B" or state dependent observation matrix

	(H)	(T)
Coin 1	0.30	0.70
Coin 2	0.60	0.40
Coin 3	0.90	0.10

where

$$b_j(k) = p[o_t = v_k \mid q_t = j], \quad 1 \leq k \leq M \tag{3.8}$$

defines the bias of each coin and, 3) an initial state distribution (π_i). For example:

$$\pi_1 = 0.33 \quad \pi_2 = 0.33 \quad \pi_3 = 0.33$$

Given these parameter values for λ, we can determine the most likely state (coin) sequence. Extension to the multiple-observation HMM simply involves augmenting λ to include a set of B matrices each corresponding to a unique observation set. Parameter estimation is described below.

3.6 Algorithms

3.6.1 Model Estimation and Prediction of Optimal State Sequences.

Given an observation sequence; the Baum Welch procedure estimates model parameters (**A**, **B**, π) that maximize the probability of the observation sequence given the model. The Viterbi procedure, on the other hand, estimates the most likely state sequence given the observation sequence.

To grasp the Viterbi and Baum Welch algorithms, an understanding of the mechanics of the *forward* and *backward* operators is crucial. Also, solutions to the following three problems must first be understood before using HMMs:

1. Given a sequence of observations $\mathrm{O} = \mathrm{O}_1, \mathrm{O}_2, \ldots, \mathrm{O}_\mathrm{T}$ and a complete model $\lambda = \{\pi, A, B\}$, compute $p(O \mid \lambda)$, the probability of the observation sequence given the model.
2. Given λ and an observation sequence, O, uncover the most likely "*hidden*" state sequence.
3. Given an observation sequence, adjust $\lambda = \{\pi, A, B\}$ to maximize $p(O \mid \lambda)$.

3.6.2 The Forward Operator

The first problem (computing $p(O \mid \lambda)$) is solved using the *Forward* part of a two-part technique called the *Forward-Backward Procedure* (the *Backward* component is used to solve problem 3). The *Forward* operator calculates the joint probability of a partial observation sequence and a given state in a step-wise manner. It is defined as

$$\alpha_t(i) = \mathrm{P}(\mathrm{O}_1, \mathrm{O}_2 \ldots \mathrm{O}_\mathrm{t}, \mathrm{q}_\mathrm{t} = \mathrm{S}_\mathrm{i} \mid \lambda) \tag{3.9}$$

where $\alpha_t(i)$ is solved in a step-wise manner. Initially, $a_1(i)$ is set for all states according to π_I and the probability of the observation b_i given state I (Equation 3.10). With the exception of $a_T(i)$, a solution for all remaining $a_t(i)$'s is generated iteratively (Equation 3.11) demonstrating how $q_j(t+1)$ may be reached from all N states at time, t. The likelihood of being in state j at time $t+1$ is equal to the summation of the probability of being in all N states at time t ($a_t(i)$ for all states, i), the state transition probabilities (a_{ij}) and the probability of observing o_i given state j, as follows:.

1. Initialization:

$$\alpha_1(i) = \pi_i b_i(O_1) \qquad 1 \le i \le N \tag{3.10}$$

2. Induction:

$$\alpha_{t+1}(j) = \left[\sum_{j=1}^{N} \alpha_t(i) a_{ij}\right] b_j(O_{t+1}) \qquad 1 \le t \le T-1 \tag{3.11}$$

$$1 \le j \le N \tag{3.12}$$

3. Termination:

$$p(O \mid \lambda) = \sum_{i=1}^{N} a_T(i) \tag{31.4}$$

Accordingly, this stepwise, trellis-like procedure determines the probability of every possible state sequence that can result given the observation and the state.

3.6.3 The Backward Operator

The Backward operator calculates the probability of a partial observation sequence (O_{t+1}, O_{t+2} … O_T) given state i at time t and model λ

$$\beta_t(i) = P(O_{t+1}, O_{t+2} \cdots O_T, q_t = S_i \mid \lambda) \tag{3.15}$$

where $\beta_t(i)$ is solved step-wise as follows:

1. Initialization:

$$\beta_T(i) = 1 \qquad 1 \le i \le N \tag{3.16}$$

2. Induction:

$$\beta_t(i) = \sum_{j=1}^{N} a_{ij} b_j(o_{t+1}) \beta_{t+1}(j) \qquad 1 \le i \le N \tag{3.17}$$

3.6.4 The Viterbi Procedure

The solution to the second problem (uncovering the most likely "*hidden*" state sequence) is achieved by employing the Viterbi procedure which is often considered to be a special case of the forward operator because it is similarly initialized using π and b_i. However, the Viterbi procedure differs from the forward operator by back recording the "discovered" state sequence in an additional array (ψ).

1. Initialization

$$\delta_1(i) = \pi_i b_i(o_1) \qquad 1 \le i \le N \tag{3.18}$$

$$\psi_1(i) = 0 \tag{3.19}$$

2. Recursion

$$\begin{aligned} \delta_t(i) &= \max_{1 \le i \le N} \left[\delta_{t-1}(i) a_{ij}\right] b_j(o_t) && 2 \le t \le T, 1 \le j \le N \\ \psi_t(j) &= \arg \max_{1 \le i \le N} \left[\delta_{t-1}(i) a_{ij}\right] && 2 \le t \le T, 1 \le j \le N \end{aligned} \tag{3.20}$$

3. Termination

$$P^* = \max_{1 \le i \le N} \left[\delta_T(i)\right] \tag{3.21}$$

$$q^*_T = \arg\max_{1 \le i \le N} \left[\delta_T(i)\right] \tag{3.22}$$

Backtracking

$$q^*_t = \psi_{t+1}(q_{t+1}), \qquad t = T, T-1, T-2, \cdots, 1 \tag{3.23}$$

The solution to the third problem (re-estimating the model parameters) is accomplished by an iterative procedure in which $P(O \mid \lambda)$ is maximized locally using the Expectation-Maximization algorithm, termed the Baum Welch procedure in this literature.

3.7 The Baum Welch Algorithm

The first step in re-estimation is to define $\xi_t(i,j)$, which is the joint probability of being in state i at time t *and* state j at time t+1, given the observation sequence and the model, that is;

$$\xi_t(i,j) = P(\mathrm{q}_\mathrm{t} = \mathrm{S}_\mathrm{i}, \mathrm{q}_{\mathrm{t}+1} = \mathrm{S}_\mathrm{j} \mid \mathrm{O}, \lambda) \tag{3.24}$$

Intuitively, for each time step, the forward and backward operators are employed to converge at time t and t+1 respectively. $\xi_t(i,j)$ can be re-written within the context of the forward and backward variables in the following form;

$$\xi_t(i,j) = \frac{\alpha_t(i) a_{ij} b_j(o_{t+1}) \beta_{t+1}(j)}{\sum_{i=1}^{N} \sum_{j=1}^{N} \alpha_t(i) a_{ij} b_j(o_{t+1}) \beta_{t+1}(j)} \tag{3.25}$$

where the numerator is $P(q_t = S_i, q_{t+1} = S_j, O \mid \lambda)$ and the denominator is $P(O \mid \lambda)$.

The second step requires that the probability of being in state *i* at time *t*, $\gamma_t(i)$ be calculated. This quantity is calculated by summing all $\xi_t(i,j)$ across all *j* states.

$$\gamma_t(i) = \sum_{j=1}^{N} \xi_t(i,j) \tag{3.26}$$

The expected number of transitions from S_i can be determined by summing $\gamma_t(i)$ over time and the expected number of transitions from S_i to S_j can be determined by summing $\xi_t(i,j)$ over time. We now have enough information to re-estimate $\lambda = (\pi, A, B)$ as follows;

$$\hat{\pi} = \text{the expected number of times in } S_1(i) = \gamma_1(i) \tag{3.27}$$

$$\hat{a}_{ij} = \frac{\text{the expected number of transitions from } S_i \text{ to } S_j}{\text{the expected number of transitions from } S_i} \tag{3.28}$$

$$\hat{b}_j(k) = \frac{\text{the expected number of times in } S_i \text{ while observing } v_k}{\text{the expected number of times in } S_i} \tag{3.29}$$

where

$$\sum_{t=1}^{T-1} \gamma t(i) = \text{the expected number of transitions from state } i \text{ given } O$$

$$\sum_{t=1}^{T-1} \xi_t(i,j) = \text{the expected number of transitions from state } i \text{ to state } j \text{ given } O$$

Based on the observation sequence, it is therefore possible to iteratively re-estimate $\hat{\lambda}$ until the function converges a maximum likelihood estimate of the HMM parameters, given the initial model and observation sequence. Following re-estimation, the Viterbi procedure may be re-employed to determine the degree to which re-estimation of $\hat{\lambda}$ has improved model performance. The model can then be used to generate observation sequences that are evaluated against the training data.

3.8 Generating Observation Sequences from the Model.

Given suitable estimates of π, **A** and **B**, a HMM can generate an observation sequence by Monte Carlo sampling. The simulation can take one of two forms; it can either be unconstrained or constrained depending on whether one or both distributions are randomly sampled.

3.8.1 Unconstrained Monte Carlo Sampling

Unconstrained Monte Carlo sampling reflects complete sampling of both state and observation distributions to determine a new observation value. Beginning at time zero, the procedure assumes a state based upon the initial state distribution (π); a new state is subsequently randomly selected from the distribution of all possible state transitions given the state assumed at time zero; an observation is then randomly selected from the distribution of all possible observations given the new state. This procedure continues iteratively for all T as follows:

1. Set $t = 1$.
2. Select state $q_1 = S_i$ according to π.
3. Select state q_{t+1} from q_t according to A.
4. Select O_{t+1} given q_{t+1} according to B
5. Set $t = t + 1$. (Return to step 3 if $t < T$, else terminate).

3.9 Assessing HMM Performance

3.9.1 Absolute Average Distance between Actual and Predicted Observation Sequences

Absolute Average Distance (AAD) returns a comparison of two ordered sequences in terms of amount of error rather than simply assessing the error. It provides a measure of how incorrect the prediction is rather than simply scoring it correct or incorrect. AAD is calculated as follows:

$$AAD = \frac{1}{N}\sum_{i=1}^{N} | d_i | \tag{3.30}$$

where d_i is the difference between the actual and the predicted observation at any given time step.

3.9.2 Log Likelihood

Log likelihood is the traditional metric used to evaluate the likelihood that the predicted sequence arose from the model or not. It is this metric that is used to optimize the model; once the difference between two models converges around an arbitrary user-defined threshold, no further re-estimation takes place.

3.10 Conclusion

Signal models can offer a theoretical description of the signal processing system, improve our understanding of the process that created the signal and provide an effective, practical framework for system prediction and recognition. In addition, they may characterize biological processes and allow further insight into the nature of underlying biological mechanisms. In the next chapter, the application of multiple-observation HMMs as an individual-based predictive modeling technique is explored. In addition, the degree to which state and observation components of HMMs can encapsulate use of space, movement and behavior in woodland caribou is assessed.

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CHAPTER 4: ANALYSIS OF MOVEMENTS AND BEHAVIOR OF CARIBOU (RANGIFER TARANDUS) USING HIDDEN MARKOV MODELS[3]

4.1 Introduction

Quantification of wildlife resource selection is critically important in impact assessment and management planning but continues to be notoriously difficult (Garshelis 2000). New models that detail the spatial-temporal behaviors of individuals therefore need to be explored. Investigations of animal movement in natural environments generally fall within one of three general frameworks: (1) phenomenological studies which describe patterns of habitat use, but without addressing the underlying mechanisms (With 1994, Wiens *et al.* 1997), (2) theoretical analyses that usually make oversimplified assumptions about movements and their underlying mechanisms (Skellam 1973, Stinner *et al.* 1983, Turchin 1989) and, (3) individual-based movement models (IBMM's) tailored to context and organism-specific conditions that yield little generalized information (Turner et al 1993, 1994).

Many modeling strategies aggregate individuals and their interactions with the environment, but following several important publications (Huston *et al.* 1988, DeAngelis *et al.* 1992, Judson 1994) IBMM's were widely adopted by ecologists. This approach acknowledges two fundamental biological principles: first, individuals are behaviorally and physiologically distinct and, second, interactions among individuals are inherently localized, i.e., organisms are influenced mostly by nearby organisms. Although IBMM's are capable of modeling variation among individuals and the interaction between them, most are quite complex, often requiring arbitrary estimates for some model parameters.

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[3] A version of this chapter appears as Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models, Ecological Modelling, Volume 173, Issues 2-3, 1 April 2004, Pages 259-270 Alastair Franke , Terry Caelli and Robert J. Hudson

In this study I explore multiple-observation HMMs as an individual-based predictive modeling technique and assess the degree to which state (bedding, feeding and relocating) and observation (distance traveled and turn-angle) components of HMMs can encapsulate use of space, movement and behavior in woodland caribou that reside year-round in central Alberta, Canada. To describe this "space-time-action" system (the tendency of animals to engage in certain activities, in certain places at certain times), I encoded the contribution of distance traveled and turning angles in the form of multiple-observation hidden Markov models.

The most common HMM structure is a doubly stochastic, first order (unit time lag) model for representing time-varying systems (such as animals moving across a landscape). Assuming a finite number of observations, hidden states and time periods, discrete HMMs can be defined by three basic components: (1) a vector containing the prior probability of each hidden state, (2) the state transition probabilities (A matrix: the first-order Markov assumption) and, (3) the probability of the observations given a state (B_l matrices). More formally, a discrete[4] HMM, λ is defined by:

$$\lambda = \{\pi, A, B\} \tag{4.1}$$

where

$$\pi = p(S_i); A = p(S_j(t+1)/S_i(t)); B_l = p(O_k^l/S_i) \tag{4.2}$$

for states (Markov, j=1, M), independent observation variables, l, and observations (k, k=1, N_l). Given suitable estimates of these quantities, solutions (Rabiner, 1989) are well known for: (1) generating (predicting) observation and state sequences from the model by Monte Carlo sampling methods; (2) determining the most likely behavioral "state" sequence given the model and an observation sequence (the Viterbi algorithm); (3) updating the model estimate given new observations (the Baum Welch algorithm). I do not present details of the Viterbi or Baum Welch solutions here (see Rabiner 1989),

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[4] Continuous HMMs are not conceptually different from the discrete case except for replacing individual probabilities by probability density functions.

however, these techniques have been widely employed in speech recognition (Levinson *et al.* 1983, Rabiner 1989), automated cartographic applications (Caelli *et al.* 2001a), genetics (Henderson *et al.* 1997) and human movement production (Caelli *et al.* 2001b).

In accord with the HMM formulation, transitions between the same or different behavioral states can be predicted from the state transition matrix (the model Markov matrix, A) and the state-dependent observation matrices (model B matrices). The latter defines the context sensitive nature of the behavioral states and can be quantified using Bayes rule. The π vector refers to the (aggregated or steady state) likelihood that an individual is bedding, feeding or relocating.

4.2 Methods

The issues related to developing a HMM for caribou movement involve determining the optimal number of states, the behaviors to which they correspond, and the types observations to make. I examined the possibility of 3 "hidden" states that corresponded to bedding, feeding and relocating. In most large herbivores, including caribou, these activities typically account for over 90% of time spent over all activities. Furthermore, I assume that "distance-between-location" (DBL) and "turn-angle (TA)" are suitable observations for encapsulating movement behavior and use of space.

The Boreal Caribou Committee and Alberta Pacific Forest Industry provided the dataset (15 minute fixes during a 10 day period in August, 1998). Point locations from twelve caribou were collected by satellite tracking using collars outfitted with Lotek Global Positioning System 1000 (GPS) location technology (Lotek Engineering Systems, Newmarket, Ontario 1998) and differentially corrected using N3Win (Lotek Engineering Systems, Newmarket, Ontario 1998), which reduced location error to less than 10m (Rempel and Rogers 1997). Collar number, date, time, latitude, longitude, activity, and ambient temperature were converted to *Arc Info* ™point coverage format.

Distance-between-locations and turning angles were calculated from UTM coordinates and resulting observation sequences were used to train models for all individuals. Where locations were not acquired, DBL was standardized by dividing total distance traveled by the number of elapsed 15-minute intervals. DBL data were subsequently clustered, resulting in four discrete observations; distances of less than 20m between locations were considered equal to zero (i.e. the caribou was stationary: observation value O=1), those greater than 20m and less than 100m were considered "short" distance moves (O=2), those greater than 100m and less than 250m were considered "medium" (O=3), distances equal to or greater than 250m were considered "long" (O=4) distance moves. Turning angles were clustered in the following manner: 316° through 45°, 46° through 135°, 136° through 225°, 226° through 315° were assigned "ahead" (O=2), "right" (O=3), "back" (O=5) and "left" (O=4) respectively. In the case where an animal remained stationary (according to the distance between location calculation) between fixes, the assigned observation was "stationary" (O=1).

My initial interest was to determine the degree of association between observation sequences predicted by HMMs and the data for each individual. Commonly used measures that indicate the degree of correspondence include Percent Correct (PC) and the Average Absolute Difference (AAD). Accordingly, HMMs for each individual were estimated using the Baum Welch procedure (Rabiner, 1989). I used PC and AAD scores for both observations and compared HMM performance within and between all individuals as well as with more traditional time series analysis from data collected from four individuals (caribou 502, 506, 508 and 509). In addition, I trained, estimated and evaluated these models using the full dataset (FDS) and split-half datasets (training on the first half sequence and testing on the remaining unseen sequence, SDS) on each of the four caribou (502, 506, 508 and 509). These animals were selected based upon different spatial distributions of satellite telemetry point locations (Figure 1). Caribou 508 presented a formation of "very clustered" point locations, whilst those for caribou 509 were considered "somewhat clustered". Point locations for caribou 502 were "widely" distributed and those of caribou 506 were "ambiguous" (both diffuse and clustered). Apart from apparent differences in use of space, the four individuals were residents of the same region, their locations were recorded over the same 10 days at the same interval and total number of fixes was similar (range 618 to 630); all four were cows of similar age, but whether these individuals had a calf is unknown.

I examined estimated model parameters for differences in relative bout length, transition and state-dependent observation probabilities. Finally, by combining DBL and TA in the form of multiple-observation HMMs, I have predicted typical space-time-action systems for the caribou subset purely from estimated model parameters using Monte Carlo sampling methods.

4.3 Results

Correspondence between models trained and estimated using the FDS and SDS are summarized in Table 4. Sample variances for the dependent measures in both groups

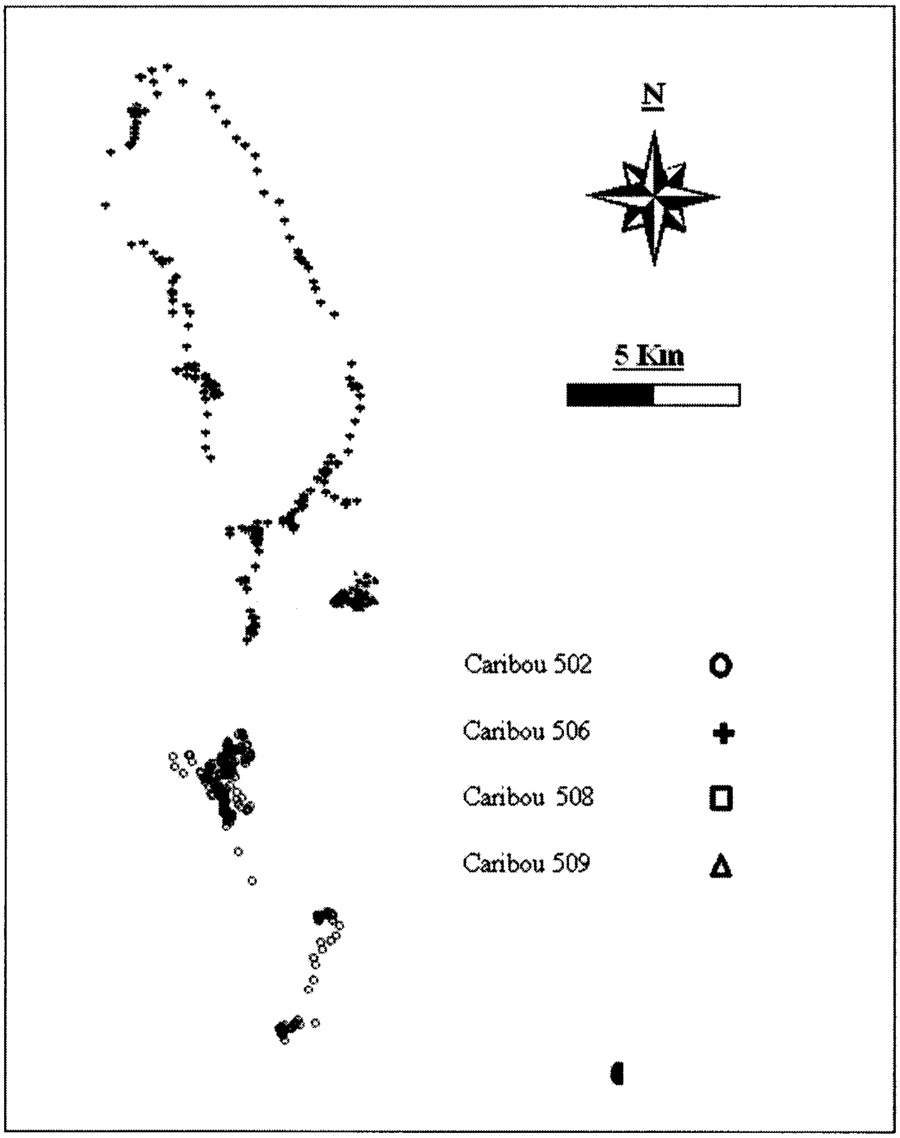

Figure 4.1 GPS telemetry point locations for caribou 502 (bottom left), 506 (top left), 508 (bottom right), and 509 (centre) between August 3 and 12, 1998.

were equal and two-sample T-test for equality between means showed no difference in either PC or AAD between the FDS and SDS, demonstrating the initial robustness of model parameter estimation using either the full data set or the split-half procedure – involving testing on data not used in training.

Percent Correct values for all individuals ranged from 0.72 to 0.95 (Mean=0.76±0.08), those for caribou 502, 506, 508 and 509 were 0.73, 0.75, 0.95 and 0.75 respectively. Such scores indicate that the underlying models could, on average (Monte Carlo sampling) predict the correct observation at the correct time-step between 73% and 95% of the time. Absolute Average Distances for all individuals ranged from 0.08 to 0.41 (Mean = 0.32±0.12) for DBL and TA respectively. Mean AAD within the caribou subset was (0.31±0.15). These results indicate that among the four individuals in the caribou subset, an incorrect prediction was on average only 0.31 units (on a 4 point scale) incorrect. These results are encouraging as they indicate excellent prediction in so far as incorrect predictions were less than one discrete unit from observed values for DBL and TA.

Table 4.1 Percent Correct and Absolute Average Difference for models trained and estimated for all caribou using Full and Split-half Data Sets

Model	PC Non-partitioned	PC partitioned	AAD Non-partitioned	AAD Non-partitioned
502	0.73	0.73	0.40	0.39
504	0.81	0.81	0.29	0.29
505	0.72	0.74	0.41	0.38
506	0.75	0.79	0.38	0.31
508	0.95	0.96	0.08	0.05
509	0.75	0.73	0.37	0.39
510	0.75	0.74	0.37	0.38
511	0.79	0.78	0.31	0.32
512	0.76	0.72	0.36	0.42
513	0.94	0.93	0.13	0.14
515	0.74	0.79	0.39	0.29
522	0.74	0.71	0.37	0.43

Time-series equations and coefficients estimated for caribou 502, 506, 508 and 509 are also reported in Table 4.2. Although the number of proceeding time-steps required for prediction in each auto-regression model varied by individual (2^{nd} to 10^{th} order), without exception, the greatest predictive power was contained in the first term of each model (Table 4.2). This provides clear evidence for a first-order Markov process as used in the HMM formulation. Other biological systems have also been well represented by first order processes (Tanner 1996, Yemshanov and Perera 2002).

Time-series model
$502 = 0.502*(t_{-1})+0.065*(t_{-2})$
$506 = 0.733*(t_{-1})+0.013*(t_{-2})+-0.028*(t_{-3})+ -0.026*(t_{-4})+0.108*(t_{-5})$
$508 = 0.604*(t_{-1})+ -0.261*(t_{-2})+ 0.196*(t_{-3})+ -0.074*(t_{-4})+ -0.000*(t_{-5})+ 0.063*(t_{-6})+-0.017*(t_{-7})+ -0.006*(t_{-8})+ -0.037*(t_{-9})+ 0.117*(t_{-10})$
$509 = 0.464*(t_{-1})+0.115*(t_{-2})+-0.089*(t_{-3})+ 0.086*(t_{-4})+ 0.009*(t_{-5})+ -0.085*(t_{-6})+ 0.170*(t_{-7})+ -0.075*(t_{-8})$

Table 4.2 Autoregressive time-series models for caribou 502, 506, 508 and 509

A comparison of model-data correspondence between HMMs and time series analysis is shown in Table 4.3. Here it can be seen that the HMMs consistently outperformed the time series (autoregressive) model on both measures.

Table 4.3 Model-data correspondence comparing time-series analysis and HMM analysis for caribou 502, 506, 508 and 509.

	Model Type			
	Time Series Analysis		HMM Analysis	
Caribou ID	PC	AAD	PC	AAD
502	0.47	0.76	0.73	0.40
506	0.57	0.69	0.75	0.38
508	0.84	0.16	0.95	0.08
509	0.58	0.48	0.75	0.39

Estimated multiple observation HMM parameters for caribou 502, 506, 508 and 509 are shown in Tables 4.4, 4.5, 4.6 and 4.7, respectively. The Markov structure (A matrices) permits interpretation of behavioral transitions (the likelihood that an individual will remain in or change states) and relative bout lengths. For example, in the case of caribou 502 (Table 4.4), the probability is 0.21 that this individual will bed in the next time step given relocating in the current time step. Similarly, given bedded (the current state), the likelihood is 0.11 that the next state will be foraging.

Cells aligned along the principal diagonal of the transition matrix are indicative of relative, behavior-specific bout lengths. Generally, models indicated that the caribou showed a propensity to forage for short periods, but would bed and relocate over long periods. In addition, the animals were most likely to bed after a relocating bout and forage after a bedding bout. Such relocating behavior is supported by evidence indicating average distance moved per time step among all 12 animals showed a typical diel cycle, with long periods of relatively stationary behavior during the hottest part of the day and relocating behavior during relatively cooler parts of the day (Figure 4.2).

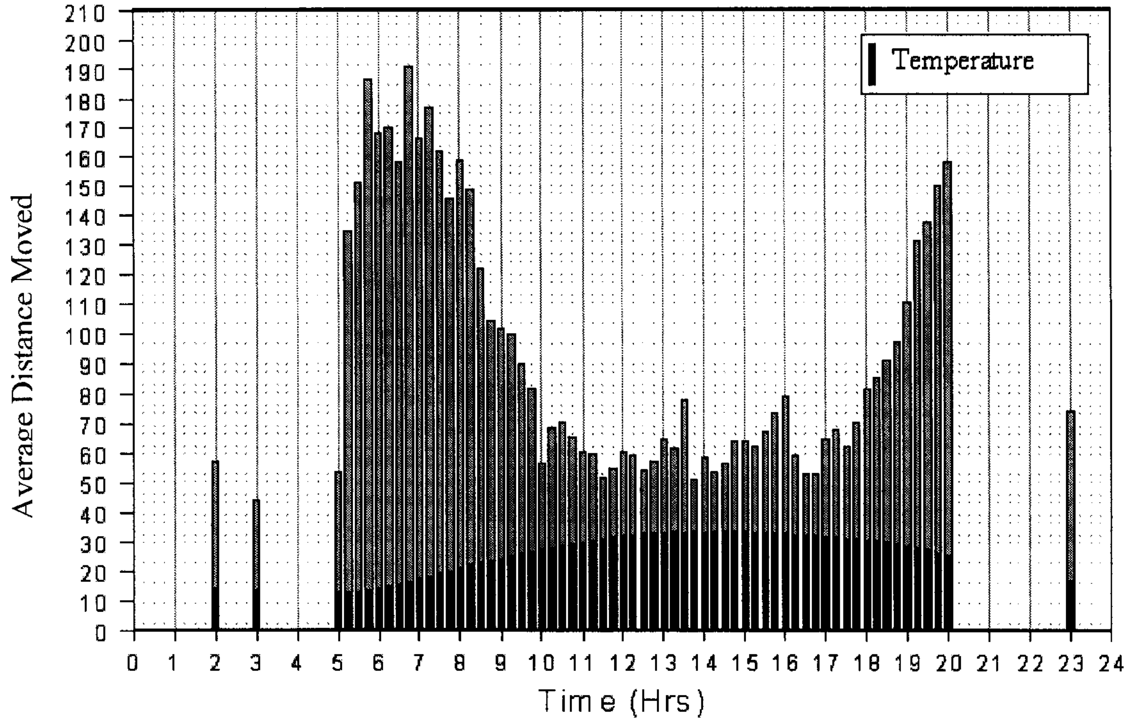

Figure 4.2 Average distance traveled between 15-minute GPS telemetry point locations for 12 woodland caribou between August 3 - 12, 1998 expressed as a 24 hour period

Examination of the B matrices showed that all caribou had a strong tendency to move "ahead" and a much weaker tendency to move "backward". Caribou 506 (Table 4.5) in particular had a strong tendency to move ahead in comparison to other individuals, a condition that would be required to produce the widely distributed point locations evident in the data.

Differences between individuals were also apparent from the HMMs. For example observing long relocating bouts was more likely in the case of caribou 502 (Table 4.4) and 506 (Table 4.5) compared to caribou 508 (Table 4.6) and 509 (Table 4.7). This is interesting when considered in the light of how point locations of each individual are distributed spatially (Fig. 4.1); individuals with long relocating bouts associated with relatively shorter distances should present comparatively more clustered point locations than those with long relocating bout lengths associated with longer distances.

Bout lengths, transition and state dependent observation probabilities permitted detailed interpretation of individual caribou behavior. For example, given "relocating" in the current time step, the model predicted caribou 508 (Table 4.6) would most likely continue relocating (p=0.69) in the next time step and would do so for relatively long periods. Although movements were most likely directionally ahead (p(Ahead/R)= 0.50), this animal was more likely than the others to move backward (p(Backward/R)= 0.22). In addition, relocating distances were most likely to be short (p(Short/R)=0.85) and quite unlikely to be long (p(Short/R)=0.04). In the event that caribou 508 stopped relocating, it did so in favor of a long bedding bout (p(B|R)=0.21 and p(B|B)=0.68). Finally, in the situation that caribou 508 suspended a bedding bout, it did so in preference for a relatively short foraging bout (p(F|B)=0.29 and p(F|F)=0.28). In summary, our model indicates that this animal was bedded for long periods, relocated short distances ahead, quite likely reversed direction and foraged for short periods.

In contrast to the well-localized point location pattern exhibited by caribou 508, caribou 506 (Table 4.5) presented a widely distributed point location pattern. Both animals (508 and 506), however, share some common behaviors: for example, given relocating, our models indicate that both caribou would most likely continue relocating for a relatively long periods. Movements were also most likely ahead. In the event that caribou 506 stopped relocating, the model indicates that, like caribou 508, it would do so in favor of a long bedding bout (p(B|R)=0.14 and p(B|B)=0.87). Unlike caribou 508, however, caribou 506 was least likely to move backward (p(Backward/R)= 0.08), and, in addition, relocating distances were likely to be long (p(Long/R)=0.38) and unlikely to be short (p(Short/R)=0.04). Generally, our model indicates that caribou 506 bedded and relocated for long periods, relocation distances were long and directionally ahead, backward movements were unlikely and foraging bouts were short.

Important distinctions between these two animals remain; caribou 508 apparently embarked upon short-distance relocating bouts and with some tendency to reverse direction (resulting in clustered point locations; a condition evident from Figure 4.1) and caribou 506 undertook long- distance relocating bouts with almost no tendency to reverse direction (resulting in more widely distributed point locations (Figure 4.1)).

Table 4.4 Multiple Observation HMM for caribou 502

A: State transitions

	State 1 (B)	State 2 (F)	State 3 Markov
State 1 (B)	0.89	0.11	0.00
State 2 (F)	0.00	0.00	1.00
State 3 (R)	0.21	0.00	0.79

B1: Distance between locations

	Stationary	Short	Medium	Long
State 1 (B)	0.94	0.05	0.01	0.00
State 2 (F)	0.00	0.70	0.26	0.05
State 3 (R)	0.00	0.34	0.33	0.33

B2: Turn Angle

	Stationary	Ahead	Right	Left	Backward
State 1 (B)	1.00	0.00	0.00	0.00	0.00
State 2 (F)	0.00	1.00	0.00	0.00	0.00
State 3 (R)	0.00	0.39	0.26	0.19	0.16

Figure 4.3 summarizes model simulations for caribou 502, 506, 508 and 509. Simulations clearly demonstrated the aggregated nature of point locations displayed by caribou 508 as well as the wandering quality of those displayed by caribou 506. HMMs are capable of simulating different land-use strategies of each animal.

Table 4.5 Multiple Observation HMM for caribou 506

A: State transitions

	State 1 (B)	State 2 (F)	State 3 (R)
State 1 (B)	0.87	0.037	0.09
State 2 (F)	0.90	0.04	0.06
State 3 (R)	0.14	0.02	0.84

B1: Distance between locations

	Stationary	Short	Medium	Long
State 1 (B)	0.97	0.03	0.01	0.00
State 2 (F)	0.52	0.46	0.02	0.00
State 3 (R)	0.00	0.42	0.20	0.38

B2: Turn Angle

	Stationary	Ahead	Right	Left	Backward
State 1 (B)	1.00	0.00	0.00	0.00	0.00
State 2 (F)	0.91	0.01	0.02	0.00	0.06
State 3 (R)	0.00	0.60	0.15	0.18	0.08

Table 4.6 Multiple Observation HMM for caribou 508

A: State transitions

	State 1 (B)	State 2 (F)	State 3 Markov
State 1 (B)	0.68	0.29	0.02
State 2 (F)	0.69	0.28	0.03
State 3 (R)	0.21	0.10	0.69

B1: Distance between locations

	Stationary	Short	Medium	Long
State 1 (B)	0.99	0.01	0.00	0.00
State 2 (F)	0.91	0.09	0.00	0.00
State 3 (R)	0.00	0.85	0.11	0.04

B2: Turn Angle

	Stationary	Ahead	Right	Left	Backward
State 1 (B)	1.00	0.00	0.00	0.00	0.00
State 2 (F)	1.00	0.00	0.00	0.00	0.00
State 3 (R)	0.00	0.50	0.11	0.17	0.22

Table 4.7 Multiple Observation HMM for caribou 509

A: State transitions

	State 1 (B)	State 2 (F)	State 3 Markov
State 1 (B)	0.87	0.03	0.10
State 2 (F)	0.33	0.02	0.65
State 3 (R)	0.21	0.02	0.77

B1: Distance between locations

	Stationary	Short	Medium	Long
State 1 (B)	0.95	0.04	0.01	0.00
State 2 (F)	0.81	0.19	0.00	0.00
State 3 (R)	0.00	0.54	0.30	0.16

B2: Turn Angle

	Stationary	Ahead	Right	Left	Backward
State 1 (B)	1.00	0.00	0.00	0.00	0.00
State 2 (F)	0.91	0.09	0.00	0.00	0.00
State 3 (R)	0.00	0.47	0.21	0.20	0.12

4.4 Discussion

I successfully applied discrete state, multiple observation HMMs as a predictive modeling technique for animal behavior, assessed the degree to which state and observation components can encapsulate use of space. Although I selected only 3 states and proposed that they corresponded to bedding, foraging and relocating, obviously they do not describe all possible caribou behavior and were merely inferred from the data. In addition, the underlying cause of these apparently different resource-use strategies remains unknown but might be related to factors such as landscape grain, degree of disturbance or some feature operating as an anchor. For example, a calf (Rettie and Messier 2001) or well-localized (fine grain) resources may anchor an individual to a particular location for a period of time. On the other hand, widely distributed resources (coarse grain) would result in relocation bouts of longer duration and distance in order for that individual to meet its resource requirements.

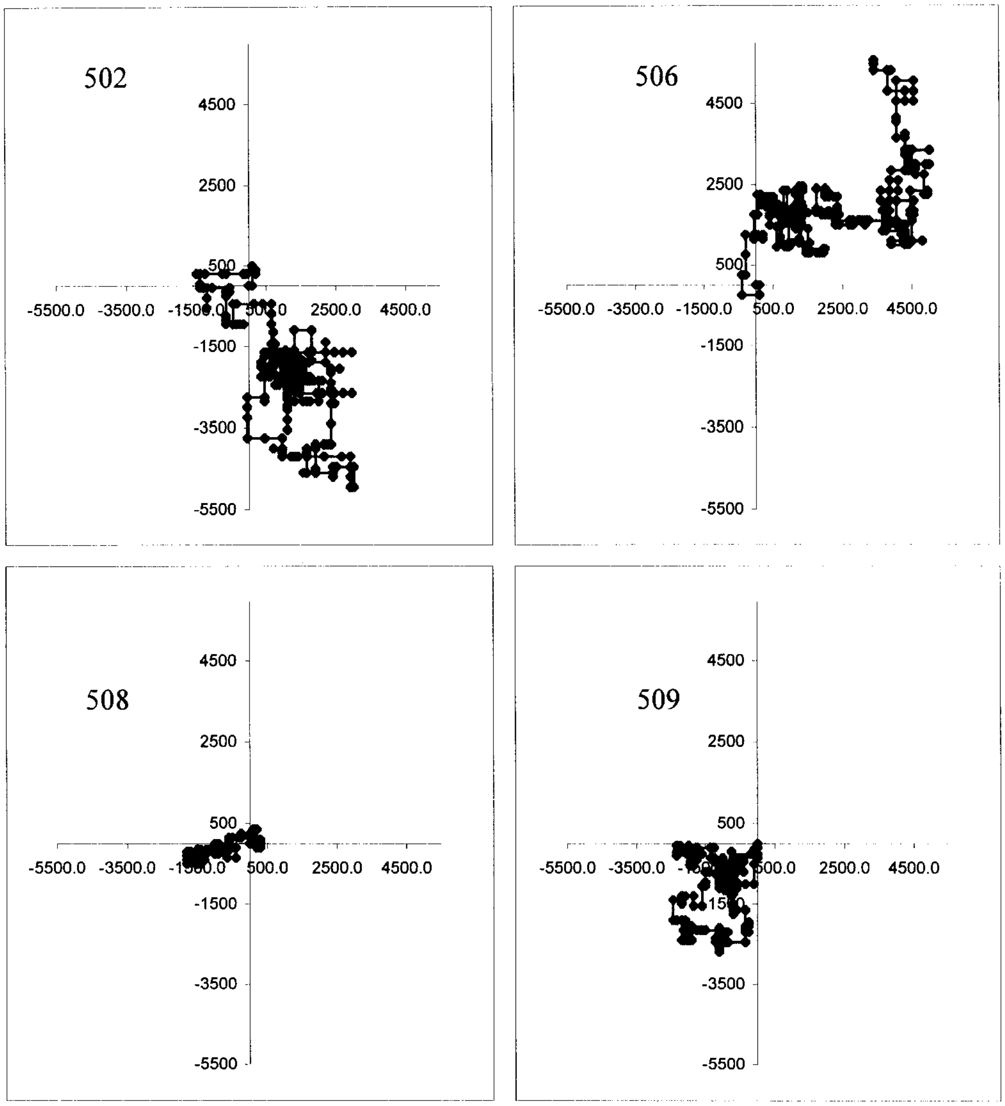

Figure 4.3 HMM simulations predicting use of space for caribou 502, 506, 508, and 509.

Furthermore, collared animals repeatedly disturbed by humans, predators or insects should show a propensity to exhibit widely distributed point location patterns. All of these factors are important to biologists studying ways to reverse the decline in caribou numbers throughout the boreal zone of Western Canada.

Resource selection is widely applied in wildlife management to maintain habitat or evaluate impacts of human activity, but despite its widespread use, conventional phenomenological analyses reveal disappointing predictability. The difficulty seems related to scale and to problems inherent in averaging behaviors of individual animals.

Resource selection is scale-dependent in both spatial (resolution and extent) and temporal dimensions, but analysis between scales (landscapes, stands and sites) is seldom performed (Senft et al 1987). This approach improves predictability of behavior but, by avoiding integration across ecological scales, fails to address population-level processes or predict impacts of human activity on wildlife. In addition, individual animals likely have distinctive resource selection strategies, which are lost when results are pooled for a population.

In this study, for example, caribou 506 bedded for long periods, relocated over long distances, seldom reversed direction, likely foraged for short periods within sub-patches of about 18 hectares (fine spatial scale) from a total of approximately 14500 ha (MCP) and moved between them approximately on a daily basis (fine temporal scale) over the entire 10 days (coarse temporal) of data collection. On the other hand, caribou 508 remained bedded for long periods, relocated short distances ahead, quite likely reversed direction and foraged for short periods within a 19-hectare patch (spatial) for the entire 10 days (fine temporal scale); if data were collected for a longer period of time, it is possible that caribou 508 may have moved to another 19 ha patch (spatial) for another 10 days (coarse temporal).

Habitat selection studies routinely use an analysis that involves "use" (time spent in a location, number of GPS fixes or distance moved in a habitat type) as a function of "availability" to infer differential use of specific habitat by individuals. The assumption is that selection of, or preference for, superior habitat relates to the fitness of an individual and hence to population growth or stability. Indices of preference, however, are frequently established by pooling the data from many individuals, which potentially obscures individual selection of resources that are truly related to fitness and also accounts for resources used by individuals that have no bearing on fitness. In addition, the spatial extent and arrangement of resources (i.e. landscape context) varies by individual home ranges to the point that transitions between behavioral states (bout lengths) will likely also vary by individual. This would also be the case if landscapes were suddenly altered; an individual obliged to accommodate to relatively rapid changes in the spatial extent and arrangement of resources (e.g. fire or logging) should exhibit concurrent behavioral changes in bout length and transitions between behaviors. Individuals would be compelled to quickly gain knowledge of the "recent renovations" or its decisions (and indecisions) may, in fact, make it more vulnerable to predation or energetic deficit.

For example, caribou residing in forested uplands may be at reduced predation risk from wolves simply because diminished accessibility concomitantly diminishes the probability of wolf-caribou encounters. Abrupt changes to the landscape (e.g. fire, logging or seismic lines) leading to improved accessibility by wolves (and other predators) would likely increase the odds of wolves encountering resident caribou. It logically follows that the probability of survival due to available resources (cover in the case of the caribou and travel routes in the case of the wolves) should shift away from the caribou toward the wolves in more accessible landscapes.

In other words, I allow that different individuals use different locations, in different amounts at different times, in different amounts. If, as it appears, resource selection is individually based, then grouping similar bouts of activities that occur at similar spatial and temporal scales may allow researchers to appropriately aggregate resource selection data between individuals and decrease the ambiguity common to resource selection studies. For example, combining a vegetation-coverage at scales meaningful to individuals may identify behavior specific resources that are more important than is suggested by time spent (number of locations) there.

In fact, the 15-minute interval at which the data were collected may be too coarse to appropriately study turning angle in foraging bouts. The Markov chains often indicate that the probability of foraging in the next time step given foraging in the current time step to be very low or even zero. The interpretation is that foraging bout lengths are seldom longer than 15 minutes and almost certainly never longer than 30 minutes. It follows then that the occurrence of three consecutive time-steps (the minimum required to calculate a turning angle) during a foraging bout are very rare. The implication of this is that foraging behavior/resource selection may be occurring at very localized spatial scales that are currently not measured either temporally (high frequency GPS point locations) or spatially (high resolution remote sensed data). In addition, the 15 minute interval may be too coarse only during summer months when individuals are disturbed by biting insects; such differences could easily be examined by studying bout length and state transitions between seasons.

4.5 Conclusion

Using distance and turning angle between locations to reflect behavioral states, I have shown that Hidden Markov Models can be used to describe and predict the complexities of animal movement and decision-making behavior. Model parameters allowed me to estimate expected behavioral states (bedding, feeding and relocating), their relative bout length and transitions, as well as the most likely behavioral state sequence. By combining distance-traveled with turn angle information, I have described a space-time-action system for woodland caribou. Although I have decomposed individual caribou movement data into simple observations of distance traveled and turning angle, the determinants of these simple observations remain unspecified; individual site selection and the decision to move between or remain within a site is likely related to factors such habitat quality and quantity, landscape grain, degree of disturbance or some other feature operating as an anchor. These determinants are critical to the maintenance of habitat and the evaluation of environmental impacts due to resource extraction activity.

The behavioral states offered here were only inferred from the data and remain unknown. I address this issue in the next Chapter by taking advantage of a unique data set in which the state is known and, thus, offers the opportunity to test the efficacy of this modeling approach to correctly discover the state. Briefly, 3 wolves in separate packs were monitored concurrently using GPS radio collars and aerial relocation. In this instance, the time and location of wolf kill-sites (state) is known from aerial relocation. I will derive data meaningful to the construction of HMMs from the GPS radio collars in order to predict the kill-sites. The presence of an HMM-predicted kill-site will then to be compared to the presence of a kill-site recorded by an observer during aerial re-location.

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CHAPTER 5: PREDICTION OF WOLF *(CANIS LUPUS)* KILL-SITES USING HIDDEN MARKOV MODELS

5.1 Introduction

The calculation of predator kill-rates is important for gaining insight into dynamics and management of predator-prey communities. Unfortunately, estimating kill rates in large carnivores has been hampered by logistics. The advent of global positioning system (GPS) technology has presented managers and scientists with the opportunity to collect data for the purpose of estimating kill-rates. Analytical methods that are able to discern kill-sites from GPS data are therefore required. The object of this chapter is to determine if hidden Markov models are able to predict moose kill-sites solely from radio-collared wolves.

Contemporary investigation of the effects of wolf predation on moose has focused on estimating the functional and numerical responses of wolves to moose (Hayes and Harestad 2000, Messier 1994, Dale et al. 1994, Messier 1991). The numerical response is defined as the trend in predator numbers as a function of prey density. Factors such as dispersal and territoriality (Ballard et al. 1987, Fuller 1989) make the numerical response particularly difficult to characterize: as a result, it is often assumed to have the same slope as functional response. The functional response (killing rate per predator per unit time) is influenced by factors such as capture efficiency, prey abundance and handling time and, it is usually expressed as a function of prey density.

Theoretical characterization of the dynamics of predator-prey systems vary with the shape of the functional response curve which take of one of three forms (Type I, II, or III). A Type I functional response assumes that predators search randomly for prey, have an unlimited appetite and, spend a constant amount of time searching for prey. This results in a linear function where the number of prey killed per predator per unit time increases directly with prey density. The assumptions of a Type I functional response are generally unrealistic from a biological perspective; for example, appetite is not unlimited and search time usually varies. A Type II response is asymptotic at higher prey densities, thus constraining consumption. A Type III response is sigmoidal and reflects a relatively low feeding rate per predator per unit time at low prey densities: feeding rate increases steadily with prey density to an asymptote that reflects the limit on appetite. Thus, a Type III functional response can reflect biological mechanisms such as search image development, prey switching, and satiation.

Debate has centered on whether or not wolves regulate moose populations. By itself, a type III functional response is purported to provide evidence for regulation (Oaten and Murdoch 1975, Messier 1994). Alternately, the presence of a type II functional response accompanied by a density-dependent numerical response is also evidence of type III regulation. The nature of type II or III responses can be obscured by alternate prey (Pimlott *et al.* 1969, Carbyn 1975, 1983, Potvin 1988), the density of the predators (Vucetich *et al.* 2002), phase dependence (Post *et al.* 2002), presence of other predators and kill-rate sample size (Marshall and Boutin 1999).

Vucetich *et al.* (2002) present compelling evidence that kill-rates are related not only to density of prey but also to the density of predators. In their long-term observational study of wolf-moose dynamics on Isle Royale National Park (Michigan, USA), wolf-density explained 36% of the variation in kill rate compared to 17% for prey density. It appears that kill rate may also be phase-dependent. Given similar moose densities, Post *et al.* (2002) reported that the daily number of wolf-killed moose was greater during the increase phase of the Isle Royal wolf population than it was for the decline phase. To address the sample size issue, Messier (1994) undertook a meta-analysis of 27 studies, but reported that use of a type III functional response did not improve model fit when compared a type II model. More recently, Hayes and Harestad (1999) augmented Messier's (1994) wolf predation model with data from a rapidly growing moose population in the east-central Yukon. However, based on the available moose density distribution and parsimony, they too suggested that a Type II response explained wolf-moose dynamics most appropriately. Marshall and Boutin (1999) reported that sample size must be large in order to statistically differentiate between type II and type III functional responses. Thus, Marshall and Boutin (1999) suggest that more effort be committed to directly measuring the proportion of moose in a population that are killed rather than attempting to determine the shape of the functional response.

Ecologists interested in modeling kill-rate (kills per predator per unit time) generally consider variables such as capture efficiency, prey abundance, and handling time. In turn, these variables encompass consumption time and rate, capture time and search time (Hollings 1959). Search time *per se* is related to a predator's ability to move through the landscape and therefore, movement behavior of predators is likely an important determinant of predation risk and must contribute to the form of the functional response. Wolves travel widely to locate prey. Several authors have recorded wolf travel distances as much as 30-50 kilometers per day during moose hunts (Mech 1966, Peterson 1977, Mech et al. 1998). Musiani et al. (1998) reported that wolves could travel 3.8 kilometers per hour (km/hr) in forested landscapes during winter and Mech (1966, 1994) reported rates of travel as high as 8-9 km/hr in winter and summer. Linear features, too, exacerbate rates of travel; for example, James (1999) reported winter travel rates could be as much as 2.8 times faster on linear features than in forests. Kuzyk (2002) reported that on average travel rates were significantly lower when near kill sites (45 m/hr) than when away from kill sites (190 m/hr).

Consumption time varies according to prey size: given similar numbers of predators, large prey species are expected to take longer to consume than smaller prey species (Hollings 1959). Mech (1966) reported that wolves were close to moose kills for 21 of 31 days. Furthermore, moose kills are usually handled (time taken to subdue, kill, eat and digest) within 24-48 hours (Peterson 1977, Ballard et al. 1987, Mech et al. 1998, Hayes et al. 2000); while it appears that deer (*Odocoileus* spp.) are usually handled in less than 24 hours. Deer fawns are generally handled in very short time periods (Fuller 1989). If wolves select large and abundant prey and, spend 24-48 hours at or near a kill site, predation risk to alternate prey species such as caribou (*Rangifer tarandus*) may be reduced.

Although, observational studies of wolves have provided keen insight into their hunting behavior (Carbyn and Trottier 1988, Mech 1997), unfavorable weather conditions for flying small aircraft often limit thorough aerial relocation of radio-collared wolf packs (Mech 1995). Consequently, we need alternative techniques that can identify potential kills and provide quantitative information that illustrates the activities of wolves at and away from kill sites. This is particularly important in summer and in forested landscapes where wolf behavior and kill sites are difficult to detect from the air.

In this study, I explore hidden Markov model (HMMs) as a predictive modeling technique and assess the degree to which the model encapsulates movement and killing behavior in 3 wolf packs in west central Alberta, Canada. HMMs have been used successfully to infer use of space by individual woodland caribou (Franke *et al.* in press). However, in that study the actual behavioral states remained hidden and were assumed to be bedding, foraging and relocating. In this study, global positioning satellite (GPS) technology allowed me to derive wolf movement data (distance between locations, turning angle and travel rate) meaningful to hidden Markov modeling techniques and aerial relocation allowed confirmation of wolf kill site locations (i.e. the states were known). The first objective of our study was to evaluate whether HMMs could predict observer-confirmed kill sites solely from the GPS wolf relocation data (correctly discover the hidden states). Secondly, I predicted that the Markov structure inherent in the HMMs would provide insight into wolf behavior in terms of bout (time period) length and transitions. Finally, as wolves travel up to several kilometers from a kill to rest (Mech 1970), I estimated this distance using confirmed field observations and GPS data in conjunction with HMMs.

HMMs are unique compared to other behavioral models because they infer optimal hidden states from observation sequences. Time series models, on the other hand, predict observations from past observations. These are quite different problems as time series' simply query temporal correlations in the data while HMMs pose the question of optimal inference of a causal model (Markov Chain) generated from the data. Assuming the states (behavior for example) are known, the advantage of HMMs over other modeling techniques is that HMMs are able to provide the optimal state (in this case behavioral) sequence from observed data (Rabiner 1989).

The most common HMM structure is a doubly stochastic, first order (unit time lag) model for representing time-varying systems (such as animals moving across a landscape). Assuming a finite number of observations, hidden states and time periods, discrete HMMs can be defined by three basic components: (1) a vector containing the prior probability of each hidden state (π), (2) the state transition probabilities (A matrix: the first-order Markov assumption) and, (3) the probability of the observations given a state (Bl matrices). More formally, a discrete[5] HMM, λ is defined by:

$$\lambda = \{\pi, A, B\} \tag{5.1}$$

where

$$\pi = p(S_i); A = p(S_j(t+1)/S_i(t)); B_l = p(O_k^l / S_i) \tag{5.2}$$

for states (S_{ij}), independent observation variables, *l*, with observations, *k*.

Given suitable estimates of these quantities, solutions (Rabiner 1989) are well known for: (1) predicting observation and state sequences from the model by Monte Carlo sampling methods; (2) determining the most likely behavioral "state" sequence given the model and an observation sequence (the Viterbi algorithm); (3) updating the model estimate given new observations (the Baum Welch algorithm). I do not present details of the Viterbi or Baum Welch solutions here (see Rabiner 1989); however, these techniques have been widely employed in speech recognition (Levinson *et al.* 1983, Rabiner 1989), automated cartographic applications (Caelli *et al.* 2001a), genetics (Henderson *et al.* 1997) and human movement production (Caelli *et al.* 2001b). In accord with the HMM formulation, transitions between the same or different behavioral states can be predicted from the state transition matrix (the model Markov matrix, A) and the state-dependent observation matrices (model B matrices). The latter defines the context sensitive nature of the behavioral states and can be quantified using Bayes rule. The π vector refers to the (aggregated or steady state) likelihood of each state.

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[5] Continuous HMMs are not conceptually different from the discrete case except for

5.2 Methods

During the period March 2-15, 2000, 3 wolves in 3 separate packs (1 wolf/pack), named for their home range (Simmonette, Prairie Creek and Cutbank) were concurrently monitored in west central Alberta using GPS radio-collars and twice daily aerial relocation. Given that locations of pack members are generally spatially auto-correlated (Legendre 1993), one wolf from each pack was instrumented with a radio-collar programmed to record its location every 60 minutes [see Kuzyk (2002) for details on wolf captures and radio tracking]. GPS data were differentially corrected using N4Win Version 2.40 (Lotek Engineering 2000).

The issues related to developing HMMs for each pack involved determining a set of interpretable states, the behaviors to which they corresponded, and the type of observations to make. I developed 3-state HMMs for each pack to examine the possibility that at least one state corresponded to the behavior associated with kill sites. I assumed that distance-between-location (DBL), turn-angle (TA) and travel rate per hour (TR) were suitable observations to predict observer-confirmed kill sites solely from the GPS wolf relocation data and to encapsulate movement behavior and use of space. DBL, TA and TR were all calculated from UTM coordinates and resulting observation sequences were used to train models for the three wolf packs.

5.2.1 Distance-between-locations

Where locations were not acquired, DBL was standardized by dividing total distance traveled by the number of elapsed location intervals. DBL data were subsequently clustered, resulting in six discrete observations; distances between locations of 20m or less were considered equal to zero (the pack was stationary: O=1), those greater than 20m and less than or equal to 200m were considered " very short" (O=2), those greater than 200m and less than 500m were considered "short" (O=3), those greater than 500m and less than 1000m were considered "medium" (O=4), those greater than 1000m and less than 2500m were considered "long" (O=5) and, finally those greater than 2500m were considered "very long" (O=6) (see summary in Table 5.1).

5.2.2 Turn-angle

Turning angles were clustered in the following manner: 316° through 45°, 46° through 135°, 136° through 225°, 226° through 315° were assigned "ahead" (O=2), "right" (O=3), "back" (O=5) and "left" (O=4), respectively. If a wolf remained stationary (according to the distance between location calculation) between fixes, the assigned observation was "stationary" (O=1).

Table 5.1 Distance-between-location bin widths

DBL	Observation	Bin
Stationary	1	$\leq$ 20m
Very short	2	> 20m and $\leq$ 200m
Short	3	> 200m and $\leq$ 500m
Medium	4	> 500m and $\leq$ 1000m
Long	5	> 1000m and $\leq$ 2500m
Very long	6	> 2500m

5.2.3 Travel rate

Kuzyk (2002) reported a median travel rate of 190 m per hour when the Simmonette, Prairie Creek and Cutbank packs were away from kill sites. I used this finding to assign O=1 when wolf successive hourly locations were less than 190m apart or O=2 when successive locations were equal to or greater than 190m apart.

HMMs for each pack were estimated using the Baum Welch procedure (Rabiner 1989) and commonly used measures (Proportion Correct: PC and the Average Absolute Difference: AAD) were used to determine the degree of association between observation sequences predicted by HMMs and the data for each pack. I trained, estimated and evaluated models using the full data set for each pack. I examined estimated model parameters for differences in relative bout length, transition and state-dependent observation probabilities. The most likely behavioral "state" sequence given the model and an observation sequence was determined using the Viterbi procedure. Finally, by combining DBL, TA and TR in the form of multiple-observation HMMs, I predicted typical space-time-action systems for each wolf pack using Monte Carlo sampling methods.

During aerial relocations, observers recorded wolf pack size and searched the surrounding area for ungulate carcasses. When a carcass or the pack was not immediately apparent, wolf trails were backtracked until either a carcass was discovered or the search was abandoned (Hayes *et al.* 2000). Ungulate kills were distinguished from scavenging if bloodstained snow, a disarticulated carcass and/or chase trails were clearly obvious (Hayes *et al.* 2000). Kill-site locations were recorded from the aircraft using a GPS receiver. Carcasses were categorized by species, gender and age from the aircraft or ground-inspected when identification from the air was not possible.

I used the wolf relocation data and carcass location to identify 4 distinct situations: 1) wolves were stationary and close to a carcass; 2) periods when the wolves were stationary and relatively far from a carcass cases; 3) periods when successive wolf locations were relatively far apart and; 4) periods when the wolves were stationary and very far from a carcass.

Instances of Situation 1 were established by determining cases where the distance between a wolf pack and the associated carcass (W-C) was less than 200m (Kuzyk 2002) plus the distance between successive wolf locations (W-W) was less than 200m; all instances that met these two criteria were assumed "At Kill". Cases where W-W was less than 200m, but W-C was greater than 200m were assumed "Bedded Away" (Situation 2). Cases where W-C and W-W were both greater than 200m were assumed "Relocating" (Situation 3). In cases where W-C was greater than 3000m, but W-W was less than 200m, I assumed a kill had been made but remained undetected during aerial relocation; I coded these situations "Missed Kill" (Situation 4). This resulted in a simplified data series (see Table 5.2 for an example) describing wolf activity over time.

Having estimated the HMMs, I studied the B matrices for evidence suggesting that a pack was associated with a kill. Accordingly, I assumed that state 1 was consistent with bedding, State 2 with localized activity and, State 3 with relocating behavior. I determined the most likely behavioral "state" sequences for each pack (given the model and an observation sequence) using the Viterbi procedure and collapsed States 1 and 2 into a single new state called "Kill"; State 3 remained on its own and was recoded "No Kill" (Table 5.2).

This left two data series each describing the behavior of the wolf packs. One set was derived from examining the GPS data (W-W) in conjunction with the carcass data (W-C) and, the other was derived from the HMM analysis. Field observations identified when packs were associated with kills. I was then able to compare the known kill site observations with those derived from our wolf-wolf / wolf-carcass derivations and the HMM analysis. In addition, using the wolf-wolf / wolf-carcass derivations I assembled all the observations that were categorized as either "At Kill" or "Bedded Away" and calculated the average distance and standard deviation for each situation.

Table 5.2 Example showing Situations 1 – 4, 3 state and collapsed 2 state models.

GPS derived wolf and carcass location data			HMM derived states	
W-C(m)	W-W(m)	Situation 1 - 4	3 State Full Model	Collapsed 2 State Model
68	39	At Kill	Locally Active	Kill
88	25	At Kill	Locally Active	Kill
109	21	At Kill	Locally Active	Kill
413	469	Relocating	Relocating	No Kill
433	23	Bedded Away	Locally Active	Kill
1874	1441	Relocating	Relocating	No Kill
5299	3428	Relocating	Relocating	No Kill
7354	2277	Relocating	Relocating	No Kill
7507	284	Relocating	Relocating	No Kill
7506	1	Missed Kill	bedding	Kill
7510	7	Missed Kill	bedding	Kill
7511	11	Missed Kill	bedding	Kill

Finally, I used the HMMs constructed for each pack to simulate the presence of kill sites on a three dimensional grid. Given the most likely state sequence (Viterbi procedure), I sampled (Monte Carlo) the underlying HMM distribution for TA and DT observations. This left us with a time series where each time step could be described by an observation for TA and DT. Using these attributes, I generated random distances and turn angles according to the bin widths selected for initial HMM construction and mapped the time series according to distance traveled and turn angle.

5.3 Results

Correspondence (Proportion Correct) between models trained and estimated using the full data set (FDS) are summarized in Table 5.3. Proportion Correct (PC) values ranged from 0.74 to 0.77 for the 3 packs.

Such scores indicate that the underlying models could, on average (using Monte Carlo sampling) predict the correct observation at the correct time-step between 74% and 77% of the time. This is significant given that sequences of between 144 and 176 observations were being predicted.

Table 5.3 Model-data correspondence using full data set (FDS)

Model	Proportion Correct	Absolute Average Distance
PRCK	0.74	0.43
CTBK	0.75	0.42
SIMM	0.77	0.40

Observer reported sightings of packs "associated" with and "not associated" with carcasses are reported in Table 14. Models were consistently able to detect occasions (22 of the 23) when packs were associated with carcasses. Of the 21 occasions packs were observed "not associated" with a carcass, models agreed with 16 instances; on the remaining 5 occasions, field observations failed to detect a kill-site yet, our models indicated that one existed.

Estimated multiple observation HMM parameters for the Cutbank, Prairie Creek and Simmonette packs are shown in Tables 5.5, 5.6 and 5.7, respectively. The A matrices report state transition probabilities and the B matrices report the state dependent observation probability distributions.

The summary data for the "At Kill" and "Bedded Away" distances (i.e. associated with a kill) are reported in Table 18. On average, packs were located 81 ± 37m from the carcass when "At Kill" and were located 1473 ± 840m from the carcass when "Bedded Away".

Figure 5.1 illustrates the comparison of known kill site observations with those derived from our wolf-wolf-carcass derivations and the HMM analysis. Occasions when packs were associated with a carcass (black spike) are compared to occasions when packs were not associated with a carcass (white space). Each set of four graphs (column wise, left to right) refer to the Cutbank, Prairie Creek and Simmonette packs respectively. Each set of three graphs (row wise, top to bottom) refers to observer recorded classifier, 1500m W-C classifier and, HMM classifier.

Figure 5.2 shows actual GPS locations for the Prairie Creek pack (A) and demonstrates a Monte Carlo movement simulation (B) also for the Prairie Creek pack. Counts are indicative of time spent in a given location.

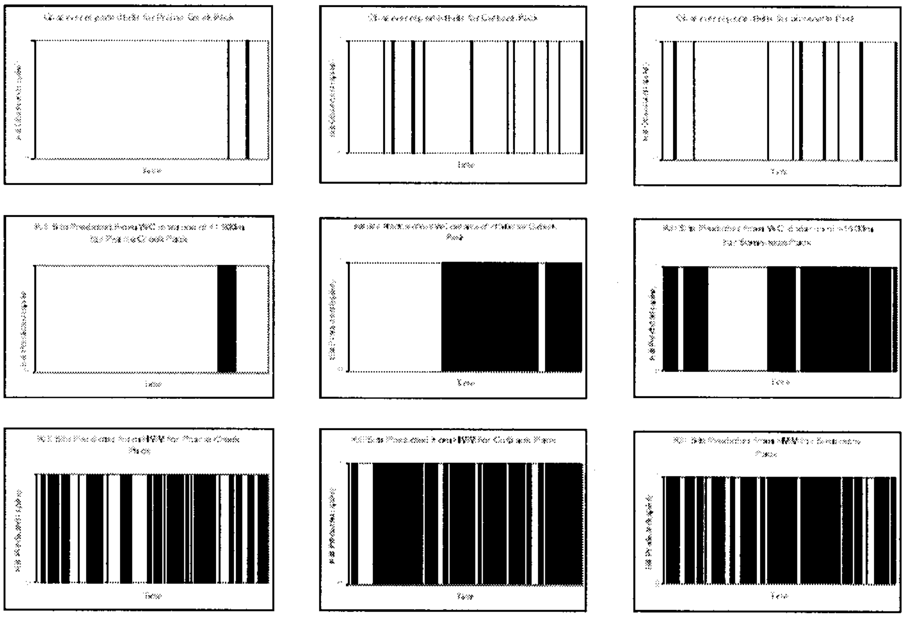

Figure 5.1 Occasions packs were associated with a carcass (black spike) compared to occasions when packs were not associated with a carcass (white spike). Each set of three graphs (column wise, left to right) refer to the Cutbank, Prairie Creek and Simmonette packs respectively. Each set of three graphs (row wise, top to bottom) refers to observer recorded classifier, 1500m W-C classifier and, HMM classifier.

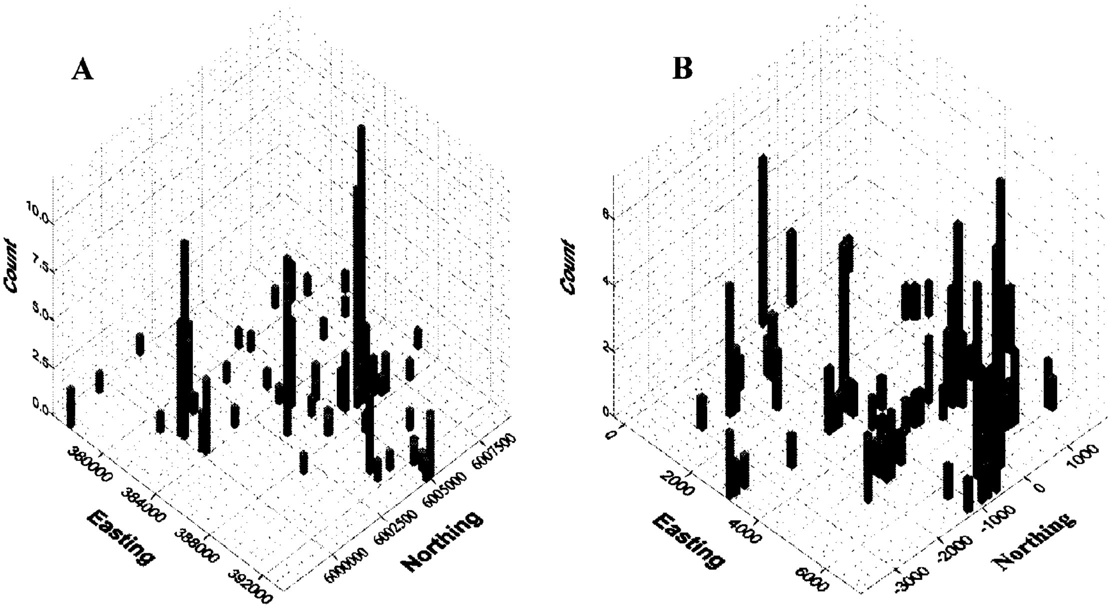

Figure 5.2 Prairie Prairie Creek GPS locations (A) and Monte Carlo simulated Prairie Creek data. Counts are indicative of time spent in a given location.

Table 5.4 Ungulate kills between March 2 – 15, 2000 (* denotes ground inspection). S = snow, W = wind, R = rain. M, E, D denotes moose, elk, deer respectively. Subscript A or C denotes adult or calf respectively.

Pack Name	Observation (Spp)	Date Observed	a.m./p.m.	Model Detected
Prairie Creek Pack	No Kill	Mar 02	a.m.	No Kill
	No Kill	Mar 02	p.m.	Kill
	No Kill	Mar 03	a.m.	No Kill
	No Kill	Mar 03	p.m.	Kill
	No Kill	Mar 04	p.m.	No Kill
	No Kill	Mar 05	p.m.	No Kill
	No Kill	Mar 06	a.m.	Kill
	No Kill	Mar 07	a.m.	Kill
	No Kill	Mar 07	p.m.	No Kill
	No Kill	Mar 08	a.m.	No Kill
	1 (E_A^*)	Mar 08	p.m.	Kill
	No fly (W)	Mar 09	a.m.	Kill
	No Kill	Mar 10	a.m.	No Kill
Cutbank Pack	No Kill	Mar 02	a.m.	No Kill
	No Kill	Mar 02	p.m.	No Kill
	1 (M_C^*)	Mar 03	a.m.	Kill
	1 (M_C^*)	Mar 03	p.m.	Kill
	1 (M_C^*)	Mar 04	a.m.	Kill
	1 (M_C^*)	Mar 04	p.m.	Kill
	No Kill	Mar 05	a.m.	No Kill
	No Kill (S)	Mar 05	p.m.	Kill
	1 (M_A^*)	Mar 06	a.m.	Kill
	No fly (W)	Mar 06	p.m.	Kill
	1 (M_A^*)	Mar 07	a.m.	Kill
	1 (M_A^*)	Mar 07	p.m.	Kill
	1 (M_A^*)	Mar 08	a.m.	No Kill
	No Kill	Mar 08	p.m.	No Kill
	1 (M_A^*)	Mar 10	a.m.	Kill
	1 (M_A^*)	Mar 10	p.m.	Kill
	1 (M_A^*)	Mar 11	a.m.	Kill
Simmonette Pack	1 (M_A)	Mar 02	a.m.	Kill
	1 (M_A)	Mar 02	p.m.	Kill
	1 (M_A)	Mar 03	a.m.	Kill
	No Kill	Mar 03	p.m.	No Kill
	No Kill	Mar 04	a.m.	No Kill
	No Kill	Mar 04	p.m.	No Kill
	No Kill	Mar 05	a.m.	No Kill
	1 (M_A^*)	Mar 05	p.m.	Kill
	1 (M_A^*)	Mar 06	a.m	Kill
	No Kill	Mar 07	a.m.	Kill
	1 (M_A^*)(R)	Mar 07	p.m.	Kill
	1 (M_A^*)	Mar 08	a.m.	Kill
	No Kill	Mar 08	p.m.	No Kill
	No fly (W)	Mar 09	a.m.	Unknown
	2 (D_A^*)	Mar 09	p.m.	Kill
	2 (D_A^*)	Mar 10	a.m.	Kill
	1 ($M_{C\&A}^*$)	Mar 12	a.m.	Kill
	1 ($M_{C\&A}^*$)	Mar 13	a.m.	Kill

Table 5.5 Multiple Observation HMM for Cutbank wolf pack

A: State transitions						
	State 1 (B)	State 2 (L)	State 3 (R)			
State 1 (B)	0.68	0.25	0.068			
State 2 (L)	0.22	0.65	0.13			
State 3 (R)	0.07	0.25	0.68			
B1: Proximity to kill						
State 1 (B)	0.99	0.01				
State 2 (L)	0.98	0.02				
State 3 (R)	0.01	0.99				
B2: Turn Angle						
	Stationary	Ahead	Right	Left	Backward	
State 1 (B)	1.00	0.00	0.00	0.00	0.00	
State 2 (L)	0.00	0.33	0.19	0.23	0.25	
State 3 (R)	0.00	0.27	0.23	0.18	0.32	
B3: Distance between locations						
	Stationary	V. Short	Short	Medium	Long	Very Long
State 1 (B)	0.90	0.10	0.00	0.00	0.00	0.00
State 2 (L)	0.00	1.00	0.00	0.00	0.00	0.00
State 3 (R)	0.00	0.03	0.27	0.29	0.25	0.16

Table 5.6 Multiple Observation HMM for Prairie Creek wolf pack

A: State transitions						
	State 1 (B)	State 2 (L)	State 3 (R)			
State 1 (B)	0.55	0.26	0.18			
State 2 (L)	0.22	0.49	0.29			
State 3 (R)	0.12	0.22	0.67			
B1: Proximity to kill						
State 1 (B)	0.99	0.01				
State 2 (L)	0.99	0.01				
State 3 (R)	0.01	0.99				
B2: Turn Angle						
	Stationary	Ahead	Right	Left	Backward	
State 1 (B)	1.00	0.00	0.00	0.00	0.00	
State 2 (L)	0.00	0.60	0.13	0.15	0.11	
State 3 (R)	0.00	0.38	0.0.25	0.15	0.23	
B3: Distance between locations						
	Stationary	V. Short	Short	Medium	Long	Very Long
State 1 (B)	1.00	0.00	0.00	0.00	0.00	0.00
State 2 (L)	0.00	1.00	0.00	0.00	0.00	0.00
State 3 (R)	0.00	0.00	0.16	0.26	0.43	0.15

Table 5.7 Multiple Observation HMM for Simmonette wolf pack

A: State transitions			
	State 1 (B)	State 2 (L)	State 3 (R)
State 1 (B)	0.73	0.16	0.12
State 2 (L)	0.35	0.40	0.25
State 3 (R)	0.17	0.31	0.52

B1: Proximity to kill		
State 1 (B)	0.99	0.01
State 2 (L)	0.99	0.01
State 3 (R)	0.01	0.99

B2: Turn Angle					
	Stationary	Ahead	Right	Left	Backward
State 1 (B)	1.00	0.00	0.00	0.00	0.00
State 2 (L)	0.00	0.37	0.22	0.07	0.34
State 3 (R)	0.02	0.29	0.26	0.21	0.21

B3: Distance between locations						
	Stationary	V. Short	Short	Medium	Long	Very Long
State 1 (B)	0.86	0.14	0.00	0.00	0.00	0.00
State 2 (L)	0.00	1.00	0.00	0.00	0.00	0.00
State 3 (R)	0.00	0.05	0.38	0.10	0.31	0.17

Table 5.8 Summary data for distances during which packs were associated with and not associated with carcasses.

	Associated with known carcass		Not associated with known carcass
	At Kill	Bedded Away	Relocating
Mean (m)	81	1473	5752
SD (m)	37	840	4491
High (m)	199	2665	17335
Low (m)	3	221	249

5.4 Discussion

In general, HMMs are useful as they infer optimal hidden states from observation sequences. As discussed above, the resulting state dependent observation probability distributions (B matrices) allowed us to infer behaviors that correspond to each state. Accordingly, I proposed that state 1 was consistent with bedding given that the probability of state 1 given an observation of stationary is 0.99. I further suggest that state 2 is consistent with localized activity given the probability of state 2 given short distance moves is 1.0 and the probability of turn-angle is approximately evenly distributed (suggesting multi-directionality). Finally, I suggest state 3 is consistent with relocating behavior given that the probability of distance-between-location is biased to long distance moves.

I found that identification of kill sites (states) can be based purely on the B matrices. This is useful because it indicates that kill-sites can be detected on the basis of easily calculated data that describe distance between locations. However, such information is less informative of pack behavior (bout lengths and transitions) which can only be achieved using the additional Markov conditions. Although the distance-between-location observations clearly distinguish between states, turn angle is not so clear and neither gives an indication of the temporal aspects of a wolf pack's behavior. That is, the Markov structure (A matrices) permits interpretation of state transitions (the likelihood that a pack will remain in the same state or change states) and relative bout lengths. For example, in the case of Cutbank pack (Table 5.5), the model indicates the probability is 0.68 that the pack will bed (state 1) in the next time step given bedded (state 1) in the current time step. Similarly, given relocating (state 3) in the current time step, the likelihood is 0.07 that the next state will be bedding. The model describing the relative bout length indicated that the Simmonette pack (Table 5.7: "A" matrix) had the long stationary bouts (0.73). This aspect of the model is consistent with field observations that indicate the Simmonette pack was known to prey on moose which reportedly take between 24 and 48 hours to consume (Peterson 1977, Hayes *et al.* 2000).

Cells aligned along the principal diagonal of a transition matrix indicate relative, behavior-specific bout lengths. In general, models indicated that wolf packs exhibit stable, periodic behavior; state 1 is most likely to be followed by state 2, which is most likely to be followed by state 3, which is most likely followed by state 2, finally returning to state 1. In other words, stationary (e.g. resting) behavior is most likely to be followed by local activity which should be followed by relocating, followed by local activity and finally returning to stationary behavior. This type of transitional behavior has been documented in several canid species including wolves (Mech 1970). This pattern of behavior is consistent with our "At Kill" and Bedded Away" calculations (Table 5.8); as the actual carcass is a focal point for conflict, wolves typically tend to avoid the carcass *per se* by removing pieces from it and moving to private locations to feed.

The 3 packs were equally likely to make "very long" (>2500m per hour) movements. However, interesting differences among the packs exist. The Prairie Creek pack, for example, was much more likely to make "long" moves (0.43) than either the Cutbank (0.25) or the Simmonette (0.31) packs and, in addition, it showed the greatest tendency than either Cutbank (0.27) or Simmonette (0.29) packs to move ahead (0.38). Furthermore, the Prairie Creek pack (Table 4: "A" matrix) had the shortest bouts of stationary behavior (0.55), which is consistent with smaller prey species requiring less handling time (Fuller 1989). The Prairie Creek pack was observed at only one successful hunt (cow elk) over 10 days of repeated aerial monitoring. The Prairie Creek model, however, predicted the presence of a kill-site in spite of the fact that none were seen during aerial back-tracking. Interestingly, of the 5 occasions that models detected the presence of behavior reminiscent of a kill-site (in spite of field observations that failed to discover a kill-site), 4 were associated with the Prairie Creek pack. In addition, on three occasions models predicted the presence of a kill-site at times that occurred between flights that were generally less than 12 hours. Such observations are consistent with smaller prey species such as deer that are consumed very quickly and almost entirely (Fuller 1989). It is also possible that these instances (that were classified as kill-sites) were actually examples of sleeping behavior and no kill was present: in this case aerial relocation and backtracking were correct, however, the Prairie Creek pack was observed on several occasions in close proximity to deer (Kuzyk 2002). The remaining instance (March 7, a.m.) in which models detected a kill-site that was not observed during aerial relocation occurred while the Simmonette pack was "relocating" (according the model). Field observation confirmed that although the pack had in fact relocated some distance away from their last kill, they were observed sleeping in close proximity to at least 3 other moose (one of which was believed to have been tested); although no kill was confirmed, our models perceived such behavior as that associated with a kill-site. It is possible too that the pack had killed a deer that remained unobserved during aerial relocation. The pack returned to the remains of the moose-kill made 2 days earlier; an event that was correctly categorized by the model. Although further calibration of the technique is required, HMM signatures could potentially be used to estimate the number of kills per unit time, given the model detected 22 kill-site associations of a possible 23 observed kill-site associations (i.e. true positives).

There are several potential advantages of using this modeling technique to study wolf-prey systems given our ability detect moose kills. Field conditions such as inclement weather and night-fall often hamper gathering of wolf kill-rate data (Mech 1995); this results in small sample size and poor statistical power (Marshall and Boutin 1999). In addition, tracking of wolves in summer is difficult because the absence of snow and tree canopy cover interfere with detection. I suggest that inferring kill sites from frequent relocation data combined with HMM analysis may complement existing methods to increase sample size in general and could provide additional insight into wolf behavior during the summer.

Moose kill-sites detected using this technique could easily be integrated with natural and anthropogenic landscape coverages in a geographical information system. Such an approach would be useful to land managers who, for example, are interested in the response of wolves to anthropogenic linear features or forest harvest procedures. This technique is not necessarily limited to wolf-moose interactions; it could potentially be used by wildlife managers to explore any predator-prey system. For example, if wolf packs habitually select for large, abundant prey and spend from 24-48 hours at or near a kill site, predation risk to alternate prey species such as woodland caribou (*Rangifer tarandus*) may be relaxed.

A next step in this area of wildlife research should be a calibration of the technique in conjunction with aerial reconnaissance which could potentially serve as an observer error model. For example, remotely downloadable GPS data retrieved relatively frequently could be used to predict kill sites. An observer would then be sent to the model-predicted locations. The number of kill sites discovered by this method could be compared to those discovered by an independent observer searching for kill sites without the assistance of the model predicted locations.

5.5 Conclusion

Using distance between locations, turning angle and travel rate to reflect behavioral states, I have shown that hidden Markov models can be used to predict wolf-killed moose carcasses. In addition, model parameters allowed me to estimate expected behavioral states (bedding, feeding and relocating), their relative bout length and transitions, as well as the most likely behavioral state sequence.

Based upon GPS data used in this study, I suggest that wolves on average were located 1.5 km (and as far as 2.5 km) from a kill site. The development of procedures outlined in this analysis may be used to identify prey species and provide improved understanding of handling and search time that should increase the statistical power in predation studies where low sample-size is a constant criticism.

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CHAPTER 6: WHERE TO BE, WHAT TO EAT, AND WHAT TO DO!

6.1 A Brief Synopsis

The focus of this thesis has been the development and evaluation of hidden Markov models to the study of animal actions in time and space. The framework has demonstrated success and is distinguished from traditional wildlife modeling techniques by characterizing underlying states from the data rather simply characterizing the data *per se*. Aside from the inclusion of variability, the dynamic nature inherent in the model structure and, the ability to predict states from observations, perhaps the most important aspect of this modeling technique is it's generalizability to other complex systems as well as the integration of complex systems. This type of analysis has allowed me to probe behaviors specific to wildlife and, by extending the use of HMMs to the study of wildlife, has drawn together the fields of Computing Science and Ecology in a novel and practical manner.

In Chapter IV, I used multiple observation HMMs to describe and predict the complexities of woodland caribou movement and decision-making behavior. Using distance and turning angle between locations, model parameters allowed me to estimate expected behavioral states (bedding, feeding and relocating), relative bout length, state transitions, the most likely behavioral state sequence and, in addition, I was able simulate individual use of space over time. However, two major issues remained unaddressed; the states remained unknown and, the determinants of these simple observations (distance traveled and turning angle) remained unspecified. I addressed these two issues in Chapter V by taking advantage of a unique situation where 3 wolves in separate packs were monitored concurrently using GPS radio collars and aerial relocation. In this instance, the states (wolf kill-sites) were known and, thus, offered the opportunity to test the efficacy and ability of HMMs to correctly discover these hidden states.

6.2 The Issue of Scale

When studying aspects of how animals make decisions with regard to where to be, what to eat and, what to do, consideration must be given to the spatial and temporal resolution of the data. Although animals such as wolves and caribou tend to move non-randomly, it is customary to restrict a sampling regime or, sub-sample an auto-correlated sampling scheme in order to construct a truncated data set that favors randomness, and therefore, statistical independence. Independence has traditionally been advocated because lack of independence between observations increases the probability of committing a type 1 error (due to inflation in the degrees of freedom). Contemporary analysis of independent relocation data is often performed in conjunction with a geographic information system and, the pattern of locations is subsequently analyzed in relation to some feature on the landscape. For example, caribou locations have been studied with regard to their density relative to linear features (Dyer 1999). The emerging pattern allowed researchers to show strong evidence that caribou use locations further away from linear features significantly more than locations nearer to linear features. However, the danger of eliminating data points in order to avoid auto-correlation from what are essentially non-independent phenomena (such as animal movement) is the loss of important biological information. For example, De Solla *et al.* (1991) reported that the accuracy and precision of home range estimates improved at shorter time intervals despite the increase in autocorrelation among the observations. Autocorrelated data that provide an indication of the movement trajectory of individual caribou could clarify questions with regard to changes in velocity and direction relative to these same linear features. The resulting behavioral information may be more indicative of the process underlying the patterns of use. In order to collect data that are informative of variables such as velocity and turn angle, managers and scientists need to program collars to collect relocation data that reflect relatively smooth movement trajectories.

In addition, researchers should as much as possible match the spatial resolution of the data they collect with temporal aspects of behavior. I suggest that the two are currently discordant and it is partially this discord that increases the variability in analyses such as resource selection. If habitat specific behavior occurs at a relatively fine scale, then analyses performed at relatively course scales will likely produce erroneous results.

6.3 The importance of predicting states not data

For many questions of interest to biologists, the ability to simply predict data is interesting and sufficient. For example, one may be interested in the abundance of a population of a certain species over time and the factors that are associated with increases and declines in the abundance of individuals in that population. Given suitable estimates of fecundity and survivorship, a simple Leslie matrix can account for the distribution of age and gender within the population. In addition, a population viability analysis can forecast the likelihood that the population will persist for a given period of time. However, analytical techniques such as these provide little insight into likelihood of transitions from stable conditions to unstable ones between meaningful time-steps.

6.4 HMMs as a tool for monitoring states

HMMs may offer an opportunity to researchers to monitor states rather than observations. Using the population abundance example described in the previous section, one could potentially describe the underlying stability of populations (states) based on abundance data (observations) and, may offer a description of the likelihood of transition from a stable state to an unstable one. In addition, the HMM may well inform managers and researches of change in the transition matrix between time steps that indicate an increasing likelihood of transition to an unstable state. For example, although there may be an increase in the probability of transition to an unstable state, the increase may in fact be meaningless (i.e. the transition probability of stable at t_{l+1} given stable at t_l remains high). However, the transition matrix may report a sudden (threshold) dramatic increase in the likelihood of transition to an unstable state (i.e. the transition probability of unstable at t_{l+1} given stable at t_l suddenly increases).

6.5 Future Research Applications

6.5.1 Meaningful time periods

In both studies presented in this thesis, data were collected and analyzed over short periods; 10 and 12 days for the caribou and wolf studies respectively. Although much information with regard to individual behavior can be discovered over short periods, it would be useful to collect data over longer periods such as seasons or annual cycles (e.g. migration). Currently GPS fix frequency is limited by battery power and the subsequent size of GPS radio collars that animals can tolerate. Recent advances in telemetry, however, have shown reductions in size and weight with a concomitant increase in battery longevity. These longer-term data could clarify the appropriate time scales at which to study phases within life cycles. I suspect that the probabilities aligned along the diagonal aspect of transition matrices are likely to shift between phases of a life cycle. For example, one should observe increased proportions of time associated with "relocating" behavior during migratory phases of a life cycle compared to non-migratory phases such as is observed in migratory caribou at calving grounds. The point at which the calving ground HMM no-longer recognizes the data would identify the transition to a new phase in the life cycle. I believe that it would then be beneficial to examine the data at a finer temporal scale in order to discover the HMM within the specific phase of the life-cycle. The development of this type of procedure may be used to identify prey species and provide improved understanding of handling and search time that should increase the statistical power in predation studies where low sample-size is a constant criticism.

6.5.2 HMM analysis of cumulative landscape effects

The cumulative effect of multiple anthropogenic disturbances has been identified as a major threat to wildlife in many regions of the world. In Alberta, Canada, for example, the combined influence of the energy, agricultural and forest industries has resulted in considerable loss and fragmentation of wildlife habitat (Schneider 2003). Hidden Markov modeling could be used to examine behavioral changes immediately undertaken by individuals as a result of industrial activity. Furthermore, it may be possible to determine the period over which the original behavior (the null model) is restored.

6.5.3 HMM analysis of physiological stress

Physiological and behavioral responses of wildlife to human induced stressors associated with common management practices have become increasingly important in recent times (Bonacic 2000). For example, the effects of capture, captivity and handling of wildlife could be evaluated using HMMs and physiological data collected remotely. In this case, blood parameters would serve as observations and behavior or well-being (comfort, safety, welfare) as the states. Typical (non-stressed) transition matrices could serve as null models to which we could compare transition matrices under management practices often considered stressful. The time taken to return to the baseline or null model could be used to ascertain when animals were no-longer subjected to the negative effects of the stressful management practice.

6.5.4 HMM applications to traditional knowledge

An integrated relationship between traditional knowledge and computing science for the purpose of conserving biodiversity should be examined. For example, tracking of wildlife involves the recognition and interpretation of natural signs. A tracker constructs hypothetical "mind models" of animal behavior that explain the underlying cause of the signs. Trackers such as the San hunter-gatherers of the Kalahari have an understanding of animal behavior that is inferred from tracks and signs. These "remotely sensed" observations, especially on the behavior of rare and nocturnal species, could be recorded by San trackers using the CyberTracker™ (Froment 2002) field computer and HMMs could be constructed that explicitly and objectively quantify the "mind models" formulated by the San trackers providing a clear link between traditional local knowledge and traditional western analytical techniques.

6.5.5 HMM applications to agent-based models

Agent based modeling (see Wilensky 1999 for example) simulates the behavior of mobile agents (animals, vehicles, people) in a spatially explicit environment. Behavior is governed by transition rules; for example, minimizing travel distance using some form of the traveling salesman algorithm or setting "preferences" for a specific type of space (e.g. habitat type). Agent based transition rules are generally applied equally across all agents. For example, the movement behavior of all agents could be modeled as a correlated random walk (CRW). However, not only is animal movement unlikely to be represented by the rules of a CRW, applying a rule such as a CRW across all agents does not allow for the likelihood that real individuals may adopt different movement rules that depend on the context (environment) in which the individuals are placed. Context sensitive transition matrices such as those produced in the construction of HMMs could be used to govern the behavior of agents.

6.5.6 Other forms of future remotely sensed data

Wildlife science should take advantage of the development of nanotechnology in much the same way that it did with the development of VHF, satellite and GPS technology. The potential exists to collect data on individual animals remotely that relay information on their physiological well-being. For example, data on the blood hormone status of individuals can indicate if that individual is lactating, stressed or whether it is immediately post-parturient. From data such as these we will likely be able to infer meaningful aspects of the reproductive state of the individual.

6.6 Conclusion

A conceptual framework to the study of space-time-actions systems in woodland caribou and wolves based upon Bayesian underpinnings has been offered in the work presented here. However, debate still rages with regard to appropriate methodologies for building reliable knowledge in wildlife research. Some argue for a commitment to the scientific method with strict adherence to hypothesis testing, while others argue that the questions asked of ecologists and biologist are simply too complex to be solved through falsification and the reductionist approach and profess support for a dynamical systems approach. Regardless of the researcher's philosophy, it is critical that ecologists pursue analytical techniques and study designs that attempt to reveal underlying biological mechanisms rather than simply describing patterns associated with the distribution and abundance of organisms. Multiple observation HMMs could easily be applied to interactions of individuals of the same or different species. For example, multiple-observation HMMs describing the behavior and decision-making strategies of wolves, moose and caribou may provide additional insight into the much-discussed spatial separation hypothesis (Bergerud and Page 1987).

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