

To the Graduate Council:

I am submitting herewith a thesis written by Dinesh Raj Sharma entitled “Individual-Based Modeling: Comparing Model Outputs to Telemetry Data with Application to the Florida Panther”. I have examined the final electronic copy of this thesis for form and content and recommended that it be accepted in partial fulfillment of the requirements of the degree of Master of Science, with a major in Mathematics.

Dr. Louis J. Gross

Major Professor

We have read this thesis and recommended its acceptance:

Dr. Balram Rajput

Dr. Jan Rosinski

Accepted for the council:

Dr. Anne Mayhew

Vice Provost and Dean of
Graduate Studies

Original signatures are on file with official student records.

**Individual-Based Modeling:
Comparing Model Outputs to Telemetry
Data
with Application to the Florida panther**

A Thesis

Presented for the

Master of Science Degree

The University of Tennessee, Knoxville

Dinesh Sharma

December 2002

Acknowledgements

First, I would like to thank my Advisor, Dr. Lou Gross for all his guidance and advice while preparing this thesis. I would also like to thank Dr. Balram Rajput and Dr. Jan Rosinski for serving in my committee. Their invaluable input is greatly appreciated.

Part of this work was completed with the financial support from the Center for Information Technology Research of the University of Tennessee and I kindly appreciate this assistance.

Special thanks go to Ms. Jane Comiskey of The Institute of Environmental Modeling, The University of Tennessee, for her invaluable suggestions and help in developing codes for data analysis.

Last, but certainly not least, I would like to thank my wife Bindu for supporting and encouraging me. Thank you for all your support and patient throughout my graduate studies at The University of Tennessee.

Abstract

Mean distance of the locations of an animal from the boundaries of its home range was presented as a measure of its space-use preference. Methods for evaluating the predictive ability of an individual-based model were also presented. These methods were applied to data on the Florida panther and some interesting results were obtained.

A strong negative correlation was observed between age and home range size of the panther, indicating constrained mobility of the panther during its old age. Space-use preference was also highly dependent on age of the panther. A general trend was found for panthers, which indicates they stay away from the boundaries of their home range during old age. It was also observed that sex of the panther and season of the year do not have any effect on the space-use preference.

A random movement model was used to simulate panther movement; applicability of this model to panther data was evaluated based upon its ability to depict the animal's space-use preference and shift of activity center over time. It was concluded that comparison of modeled and observed movement data accumulated over a long period of time might give misleading results. Data should be subdivided into different age periods and the model should be tested in each period.

Contents

CHAPTER 1: BACKGROUND	1
1.1 Animal Movement in Home Range	1
1.2 Simulation of Animal Movement in Home Ranges	2
1.3 Analysis of Movement as a Random Walk	4
1.4 Individual-based Models	7
1.5 Motivation and Research Objectives	10
CHAPTER 2: METHODS	14
2.1 Home Range Analysis	14
2.2 Analysis of Space-use Preference	15
2.3 Comparison of Model and Observed Space-use Preference	17
2.4 Comparison of Model and Observed Center of Activity	18
2.4.1 Areal Moments	19
2.4.2 Comparison of Model and Observed Center of Activity	24
CHAPTER 3: APPLICATION TO THE FLORIDA PANTHER DATA	27
3.1 Background	27
3.2 The Spatially-explicit Individual-based Simulation Model for the Florida Panther	28
3.3 Data	31
3.3.1 Accuracy of Data	32
3.4 Statistical Software	33
3.5 Assumptions	34
3.6 Analysis of Space-use Preferences	34
3.6.1 Sample	34
3.6.2 Home Range Estimation and Distribution of Mean Distances	37
3.6.3 Results	39

3.7	Model Vs. Observed Space-use Preference	44
3.7.1	Theoretical Model	44
3.7.2	Sample	45
3.7.3	Distribution of Distances	47
3.7.4	Results	47
3.8	Comparison of Model and Observed Activity Centers.	51
3.9	Conclusions	57
CHAPTER 4: CONCLUSIONS AND FUTURE CONSIDERATIONS		59
4.1	Conclusions	59
4.2	Future Considerations	60
REFERENCES		66
APPENDIX		73
VITA		82

List of Figures

FIGURE 3.1: STRUCTURE OF PANTHER COMPONENT OF DEER PANTHER MODEL (ADAPTED FROM COMISKEY <i>ET AL.</i> [11])	30
FIGURE 3.2: RELATIONSHIP BETWEEN AGE AND AREA OF ANNUAL HOME RANGE (ALL PANTHERS)	40
FIGURE 3.3: MEAN NORMALIZED DISTANCE OF LOCATIONS OF PANTHERS BY AGE.	43
FIGURE 3.4: HOME RANGE OF PANTHERS (A) NUMBER 49, (B) NUMBER 78, (C) NUMBER 79.	46
FIGURE 3.5: MODEL AND OBSERVED DISTRIBUTIONS OF D_t FOR PANTHER # 78, 49, AND 79..	48
FIGURE 3.6: CONFIDENCE LIMITS OF DISTANCES BETWEEN OBSERVED AND MODEL AMC S BY NUMBER OF MOVES (PANTHER NUMBER 49).	54
FIGURE 3.7: CONFIDENCE LIMITS OF DISTANCES BETWEEN OBSERVED AND MODEL AMC S BY NUMBER OF MOVES (PANTHER NUMBER 78).	55
FIGURE 3.8: CONFIDENCE LIMITS OF DISTANCES BETWEEN OBSERVED AND MODEL AMC S BY NUMBER OF MOVES (PANTHER NUMBER 79).	56
FIGURE 4.1 DISTRIBUTION OF LOCATIONS OF TWO HYPOTHETICAL PANTHERS	61
FIGURE 4.2: DISTRIBUTIONS OF DISTANCE OF POINTS FROM THE BOUNDARY OF (A) POINT PATTERN 4.1(A) AND (B) POINT PATTERN 4.1(B)	62

List of Tables

TABLE 3.1: OUTPUTS OF KOLMOGOROV-SMIRNOV TWO SAMPLE TEST	50
TABLE 3.2: COMPARISON OF OBSERVED AND MODELED ACTIVITY CENTERS OF PANTHER # 49, 78, AND 79.	52

CHAPTER 1: Background

1.1 Animal Movement in Home Range

Burt [10] defined *home range* as “that area traversed by an individual in its normal activities of food gathering, mating, and caring for young”. A statistical translation of this biological concept is that the movement trajectory generated by the animal can be modeled as a 2-dimensional, continuous, stationary, stochastic process, which by definition, generates an associated autocorrelation function [24,62]. The home range includes the nest site, shelter, locations for resting, food gathering, mating, etc. Since home range can depend upon individual status, including life stage, accurate comparisons between individuals require more explicit definitions. One approach is to limit home range estimation to a particular time period or life stage. The term *activity range* is applied when considering movements within a certain time period. Many statistical home-range estimators have been proposed. Some of the frequently used estimators are: minimum convex polygon [51], harmonic mean [21], and 95% ellipse estimators of Jennrich and Turner [33], and Koepl *et al.* [41].

Study of animal movement patterns provides a basis for understanding their foraging decisions [6,57,5], space-use in home ranges [59,63,44], spatial distribution in populations [43,39,66], dispersal behavior [56,61,68], and community interactions [53,3,38]. Movement is a mechanistic element of these and other ecological processes at various spatial and temporal scales. To link movement behavior to its many important consequences requires a description and analysis of the process of movement. Common approaches to this problem include statistical description [1], computer simulation [59,35,47] and diffusion models [56,37]. Diffusion theory has been useful in describing continuous time movement or rate-of-spread in homogeneous environments, successfully incorporating directed movement with net bias, prey taxis, or advection terms [66,3]. Movement models have also been extended to heterogeneous landscapes by simulating movements using percolation [27,34,50] and by a diffusion-based approximation of a correlated random walk [66].

1.2 Simulation of Animal Movement in Home Ranges

Siniff and Jessen simulated movement of an animal in its home range on the basis of telemetry data for red foxes (*Vulpes fulva*), snowshoe hare (*Lepus Americana*), and raccoons (*Procyon lotor*) [59]. They analyzed their data in terms of three elemental quantities: distance of travel, relative angle and relative duration of rest and movement. They determined the distance from an initial location to the point where the next location was recorded and calculated mean speed by dividing the distance traveled by the duration of time between the two locations. The observed speed distribution may be approximately represented by the gamma distribution:

$$f(v) = \frac{1}{\beta^{\alpha+1} \Gamma(\alpha+1)} v^\alpha e^{-v/\beta}, \quad (1.1)$$

where v is speed, α and β are constants satisfying the constraints $\alpha > -1$ and $\beta > 0$, and $\Gamma(v)$ is the gamma function; and the distribution of the relative angle is approximated by the circular normal distribution:

$$f(\theta) = \frac{1}{2\pi} I_0(c) \exp\{c \cos(\theta - m)\}, \quad (1.2)$$

where $I_0(c)$ is the modified Bessel function of order zero; m is the angle of maximum probability, i.e., the modal direction; and c is the parameter of concentration of the distribution.

For computer simulation, Siniff and Jessen first tried a simple model using the distribution laws (1.1) and (1.2), and the distribution of rest and of movement as obtained from the observed values of the three fundamental quantities.

To measure the differences in animal movement patterns, Siniff and Jessen applied the method of square sampling units. The home range was partitioned into square units, and the number of individuals in the unit, n , was assumed to be approximated by the negative binomial distribution. The negative binomial distribution is given by

$$f(n) = \frac{(k+n-1)!}{(k-1)!n!} \left(\frac{m^n}{m+k} \right) \left(1 + \frac{m^{-k}}{k} \right), \quad n = 1, 2, \dots, \quad (1.3)$$

where m is the arithmetic mean and $k > 0$. Values of the dispersion parameter k were used to compare the movement pattern. Low values of k produce clumping, and high values indicate considerable randomness in the distribution.

1.3 Analysis of Movement as a Random Walk

Movement is often compared to a correlated random walk (CRW), which produces pathways in a series of discrete time steps having a net directional bias [36,67]. CRW models have the advantage of providing a general framework for making quantitative predictions about an organism's rate of spread. These models can also be used to make succinct comparisons of movement behaviors in different habitat situations. CRW models are discrete models and are appropriate when the number of steps between observations is small.

In a study of the role of small-scale vegetation heterogeneity in determining the movement characteristics of darkening beetles, Crist *et al.* [14] compared observed movement pathways of *eleodes* beetles with that obtained from simulation using a CRW. They simulated CRWs using observed mean step length (mean of distances traveled between successive time steps), variance in step length, mean turning angle (trigonometric mean of angles formed by the changes in directions between time steps), and mean vector length (a unit vector measure of the dispersion of turning angles with variation between 0.0 (uniform) to 1.0 (perfectly directional)) to parameterize the theoretical distribution used in the simulation. They used net

displacement (the straight-line distance from beginning to the end point of a path) as an overall measure to compare the simulated and observed models.

Turchin ([67], pp 247-301) presented methods for measuring rate of dispersal and analysis of movement pathways based upon individual mark recapture (IMR) data. He presented a method for analyzing IMR data as an uncorrelated random walk (i.e. there is no directional persistence, or any other kind of correlation between successive displacements). In this approach each displacement between two successive fixes are equated to a random walk move. The random walk process is characterized by the distribution of move lengths and durations (distance and time between two successive locations).

The path characteristic that is most often used in analysis is either net displacement or net squared displacement. Net displacement is defined as the straight-line distance from beginning to the end point of a path. Since net displacement is an aggregate result of movement step length and turning angle, it is often used as an overall measure of movement (e.g. see [14]). However, Turchin argued that net displacement is a poor statistic with which to compare different paths, because of its sensitiveness to path duration. A better and theoretically sounder statistic is the rate of increase in net squared displacement per unit of time ([67], pp 17-18).

Net squared displacement is often the quantity of interest in a variety of random walk formulations and associated diffusion approximations. It is the squared displacement, rather than the linear displacement that grows linearly with time (or with the number

of moves), and it provides us with a measure of spread on the population level. Thus, net squared displacement has been recognized as the most convenient and theoretically sound parameter with which to quantify dispersal [60,56,36].

Turchin suggested use of net squared displacement, \bar{R}_n^2 , as a way to test the applicability of CRW model and extended use of this quantity in the analysis of IMR data using an uncorrelated random walk model. If an animal moves according to correlated random walk (CRW) in two dimensional space, then its net squared displacement, for large n is approximately [67,60,36]:

$$\bar{R}_n^2 \approx nm_2 + 2n \frac{\psi}{1-\psi} m_1^2, \quad (1.4)$$

where subscript n indicates number of moves and the bar indicates the expectation, or alternatively an average taken over several paths, and m_1, m_2 and ψ are defined as

$$\begin{aligned} m_1 &= \frac{1}{n} \sum_{i=1}^n l_i && \text{mean move length,} \\ m_2 &= \frac{1}{n} \sum_{i=1}^n l_i^2 && \text{mean squared move length, and} \\ \psi &= \frac{1}{n-1} \sum_{i=1}^{n-1} \cos \theta_i && \text{average cosine of the turning angle.} \end{aligned} \quad (1.5)$$

In uncorrelated random walk there is no directional persistence such that $\psi = 0$.

Therefore the formula relating \bar{R}_n^2 to move attributes simply reduces to

$$\bar{R}_n^2 = nm_2. \quad (1.6)$$

That is, under the assumption of no correlations between moves, \overline{R}_n^2 increases linearly with number of moves. A plot of \overline{R}_n^2 versus n can then be used to test the applicability of the uncorrelated random walk model by checking if it increases linearly with n . If \overline{R}_n^2 increases faster than linearly (curves up), then one explanation is that there is significant directionality in the movement. This could be a result of correlation between the directions of successive moves, or because there is a directional bias. If net squared displacement curves down, then either dispersal rate is decreasing with time or there is some barrier to dispersal. For example, in movement within a home range \overline{R}_n^2 should approach a constant asymptote.

1.4 Individual-based Models

Most ecological models make assumptions that contradict two important properties of organisms. First, grouping individuals into categories violates the principle of the uniqueness of the individual. Second, by not distinguishing among the locations of the individuals, the models violate the principle that interactions are inherently local [31]. As an alternative, ecologists use models based on explicit representation of individual organisms.

Ecologists interested in movement were among the pioneers in developing individual-based models (IBMs) [59,35]. The essence of the individual-based approach is the derivation of the properties of ecological systems from the properties of the individuals that make up these systems. IBMs are bottom-up approaches that start at the bottom level of population ecology, i.e., at the individual level [26]. IBMs

have the potential to determine which individual properties and elements of an individual's performance are essential for generating the characteristic features of overall population dynamics.

The basic assumption in IBMs is that each action during the movement process (e.g., whether to stop or to continue movement, or which direction to take) is a mixture of stochastic and deterministic elements [67]. For example, whether or not an organism will stop in a certain locality could be a probabilistic process. But in some localities (for example, with abundant food) the probability of stopping might be much higher than in localities where food is absent. Therefore, every move in the model is controlled by sets of rules based upon the movement attributes of the animal. For example, the model of Florida panthers [11] includes separate sets of rules that account for *i*) search for prey, primarily white-tailed deer; these include short distance local searching for prey and intermediate scale and long-distance movement when local search for prey have failed, with the direction of search depending on the individual's past hunting history, *ii*) remaining at a kill site until the deer has been eaten or has spoiled, *iii*) activity of males in search of a mate, *iv*) dispersal of juveniles from the natal area, *v*) dispersal of adults when food availability is low, and *vi*) avoidance of high water depths. The movement rules were all based on random local neighborhood searches (for prey and mates), constrained by water depths and habitat features, with movement into an expanding range of cells around the current location if the local search was unsuccessful.

IBMs provide a very “feature-rich” framework for modeling individual movements. Death and birth events are easily incorporated within the framework. Attempting to model too many behaviors and too many individuals, however, can strain both the capacity of the computer to execute the model, and the capacity of the human brain to interpret the results [67].

IBMs have many features that make them an attractive modeling tool for empirical ecologists. Their ability to make connections between phenomena at different levels of biological organization is a very important feature [16]. They are one of the most effective ways to investigate the mechanisms of species interaction and quantitatively associate these mechanisms with phenomena in question. They are readily testable and should be easy to validate. IBMs also offer excellent potential to examine questions of natural selection and evolution. Their value resides in the fact that the models are constructed at the level (individual) on which natural selection operates. One of the advantages of the simulation of IBMs that especially recommends their use in the context of applied work is that it is easier to communicate the system, mechanism, etc. between the biologists and the modeler than with many of the partial differential equation systems currently used [16]. The importance of IBMs has widely been noted [31,8,16,17,30,45,49] and have been frequently used by ecologists under varying conditions. As an example, a spatially-explicit individual-based simulation model for the Florida panther will be treated separately in Section 3.2.

1.5 Motivation and Research Objectives

Finding the “true” model of an animal’s movement may be impossible, as animals change their behavior patterns over time and space, and field data are typically too sparse to permit one to entertain complicated models. IBMs are supposed to be more testable than their counterparts developed using the classical approach, because they are closer to reality [54]. However, more reality means more parameters and, in turn, more effort to determine these parameters. With individual behavior in a heterogeneous, randomly fluctuating environment in particular, the number of parameters will soon exceed manageable limits. Even with the state of art technology at hand, it is almost impossible to incorporate all the parameters into the model. So there should always be a trade off between the degree of closeness of the model to reality and manageability of the parameters. Nevertheless, these models should be able to produce meaningful outputs that are within a statistically acceptable range of observed movement parameters. Therefore, the next challenge ecologists face is to compare the simulated and observed movement patterns. However, the task of judging the statistical accuracy of the simulated movement patterns, in comparison with telemetrically observed movement patterns, remains less addressed. A criterion for goodness of fit is required for such comparisons, the choice of which poses a difficult problem. The issue in question is that of pattern recognition and testing the validity of the model movement parameters.

Considering the importance of the home range in the life of animals, one might expect that animal movements within the home range have been studied in detail. In

fact little is known to us. During the 60's and 70's, studies on home range were primarily limited to the delineation of the home range itself [33,40,9]. However, in recent years ecologists have shown more interest in studying different aspects of animal movement in their home range, including space-use and habitat selection [19,64,48,65]. Study of space-use is basically focused on identifying activity centers and habitat use within the home range. Nomadic mammals like panthers can cover large areas. For example a male panther, in average, covers an area of 39,630 ha [12]. However, a little is known about the pattern of their space-use preference.

It has been well documented that animals do not use all the areas of their home range uniformly. Some portion of the home range is used more intensively than others. This portion is called the "core area", where the probability of finding the animal is higher. The method used to calculate core area is the "utilization distribution" (UD) [33] from which one estimates the smallest area that accounts for some percentage (e.g. 95%) of the space utilization. This concept is based on a bivariate probability density function that gives the probability of finding an animal at a particular location based upon space utilization. Harmonic mean center [55] is also often used to identify the focal activity center in the home range of an animal [21].

Although these measures have proven to be very useful in analyzing space utilization, they do not take into consideration the relative position of the "core area" or the center of activity with respect to the boundaries of home range. That is, they do not provide information on the locations of the animal in relation to the home range boundaries. For example, in the case of the Florida panther, it has been well

documented that during their youthful years they move vigorously and widely within and beyond the boundary of their home range, and show a territorial attitude toward defending their boundaries [46]. To reflect this tendency, a measure that would take into account the position of the animal relative to the boundary of its home range is required.

Furthermore, in studies of animal movement, statistical analysis of radio telemetry data poses special problems due to lack of independence of successive observations along the sample path. These data are typically not gathered continuously, but sampled at particular times, which adds further difficulties in analysis. James E. Dunn proposed a multivariate Ornstein-Uhlenbeck diffusion process as a workable model for analysis of telemetry data [25]. However, he assumed that data are generated by a continuous, stationary, Gaussian process. In spite of the well-recognized usefulness in providing a good database for studying animal dispersal and wide use in mammal and bird population research, the potential of radiotracking data for a quantitative analysis of movements of vertebrates has hardly been tapped.

Therefore, in general, the following issues remain open for further investigation and research.

- Methods of analysis of telemetry and other behavior data in order to assess movement differences between individuals and determine how these differences are affected by underlying habitat and spatio-temporal variation in environmental conditions.

- Methods to compare modeled movements with data in order to evaluate the reliability of the model to mimic the dynamics of movement, the trajectories of individuals as well as the spatial patterns that arise at the population level.
- Derivation from available movement data of a simplified set of rules for the model, including what environmental or habitat characteristics are essential to include and which can be ignored, under what circumstances movement is modified by location of con-specifies, potential predators, and what history-dependence occurs (e.g. what memory there is in the system).

These issues require a detailed understanding of animal behavior, extensive analysis of movement data and technical sophistication. However, for the purpose of my thesis, I focused on issues of comparing outputs of the IBM with the observed data.

The overall goal of my research was to produce appropriate statistics to compare the outputs of IBMs of an animal to data, particularly those obtained from telemetry. Specifically, my work was focused on the following three issues.

1. How to measure space-use preference of animal with respect to their tendency to stay near or away from the boundary of their home range.
2. Does the preference of the animal regarding space-use depend upon their age, sex or season of the year?
3. How well does the IBM depict the space-use preferences and movement patterns of the animal?

CHAPTER 2: Methods

2.1 Home Range Analysis

Many methods for estimating home range and utilization distribution have been developed. They have been thoroughly reviewed [69], and several of the most popular methods have been numerically compared through Monte Carlo simulations [7,70]. In a survey of home range analysis using radio tracking data, Harris *et al.* [28] found that a majority of papers (81 out of the 93 papers included in the survey) resulting from a literature search of 18 of the major journals likely to include such papers published through 1984 to 1988, used a minimum convex polygon (MCP) or modified polygon estimator. This illustrates that polygon methods are playing a central role in analysis and interpretation of home range data. The MCP is appealing to ecologists, perhaps because it is well defined and straightforward to evaluate. For the purpose of my thesis, I also used the MCP method not only because of its computational simplicity but also because one of my thesis objectives is to apply methods developed to the Florida panther data, and the home range of the Florida panther has been estimated using this method.

The area of the MCP home range can readily be estimated by [71]

$$A_{MCP} = \frac{1}{2} \sum_{j=1}^m (x_j y_{j+1} - x_{j+1} y_j), \quad (2.1)$$

where, (x_j, y_j) is the j^{th} point in anticlockwise order from a total of m points on the convex hull, and $(x_{m+1}, y_{m+1}) = (x_1, y_1)$.

Since MCP is based on the peripheral points of the data set, it is extremely sensitive to *outliers*, irrespective of the distribution of the inner points; as a result, these outer points have great influence on the home range size estimate. It is also known that the home range is highly dependent on the sample size of the data set [69]. This means that estimates calculated from the data sets with unequal sample sizes are not comparable. Gary *et al.* [69], suggested that this problem of increasing home range size with increasing sample size can be corrected by eliminating the *outliers* before the home range polygon is calculated. They suggested to rank the locations based on their contribution to the area of MCP and then to eliminate the 5% highest ranked locations to get a 95% MCP. For the purpose of my analysis, I computed 95% MPC home range based on the methods suggested by them. Hereafter in this thesis, the terms MCP and 95% MCP will be synonymously used to represent the home range computed using the 95% MCP method.

2.2 Analysis of Space-use Preference

I define space-use preference of an animal as its tendency to stay near or away from the boundaries of its home range during its daily activities. This preference is

measured by computing the mean distance of the locations of the animal from the nearest boundary of its home range.

Let $\mathbf{X}_p = (X_p, Y_p)$ ($p = 0, 1, \dots, N$) denote the position of an animal after p moves from its initial position ($p = 0$), and suppose that \mathbf{X}_i 's are independently and randomly distributed within the home range. Consider a random sample $\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n$ of n observed locations, where $\mathbf{x}_i = (x_i, y_i)$ ($i = 1, 2, \dots, n$) denotes the i^{th} observed location of the animal in its home range. Let $\mathbf{x}'_j = (x'_j, y'_j)$ ($j = 1, 2, \dots, m$) be the coordinates of the vertices of the 95% MCP based on the sample observations. If $A_j x + B_j y + C_j = 0$ represents the equation of the straight line joining the j^{th} and $(j+1)^{\text{th}}$ vertices¹ of the 95% MCP, then the linear distance between the location point \mathbf{x}_i and the line $A_j x + B_j y + C_j = 0$ is given by

$$d'_j = \frac{|A_j x_i + B_j y_i + C_j|}{\sqrt{A_j^2 + B_j^2}}, \quad (2.2)$$

provided that A_j and B_j are different from zero. Then the distance of the i^{th} location from the closest boundary of the 95% MCP will be the minimum of (2.2) over j . That is, the distance of i^{th} location from the closest boundary is given by $d_i = \min_{1 \leq j \leq m} d'_j$.

¹ Here $A_m x + B_m y + C_m = 0$ represents a line joining the vertices (x_m, y_m) and (x_1, y_1) .

If the animal spends more time near the boundary of its home range, we should expect a clustering of points along the boundary and hence get smaller d_i s. Similarly, clustering of the locations away from the boundary would yield larger d_i s. Therefore, comparison of the distribution of d_i s would allow us to compare the space-use preferences of two animals. Larger $mean(d_i)$ would indicate a greater tendency of the animal to stay away from the boundaries of home range and vice versa.

I used this statistic to test the following two hypotheses.

- a) The observed and model space-use preferences are similar; i.e., the model and the observed tendency of the animal to stay near or away from the boundary of the home range are similar.
- b) The tendency of the animal to move closer or further away from the boundary of home range does not depend upon its age, sex and season of the year. In other words, there is no age, sex and seasonal preference with respect to space-use in the home range.

2.3 Comparison of Model and Observed Space-use Preference

I used Kolmogorov-Smirnov's two-sample test to see if the observed and modeled space-use preferences are similar. The Kolmogorov-Smirnov test is a powerful alternative to the Chi-square test for testing the similarity between two frequency distributions. Technically, Kolmogorov-Smirnov requires continuously distributed

variables, but only slight errors result when the technique is applied to discrete data [20,13].

Let D_1 and D_2 be the random variables respectively representing the distances of observed and modeled locations of the animal from the closest boundary of home range. Then if the model accurately depicts the space-use preference of the animal, distributions of D_1 and D_2 should be identical. Let $F(x)$ and $G(x)$ be the distribution functions of the random variables D_1 and D_2 . Then the null hypothesis to be tested is

$$H_o : F(x) = G(x) \text{ against the alternative } H_a : F(x) \neq G(x) \quad (2.3)$$

The two-sample Kolmogorov-Smirnov statistic is defined as [20]

$$D_{n_1 n_2} = \sup_x \left| \hat{F}_{n_1}(x) - \hat{G}_{n_2}(x) \right| \quad (2.4)$$

where, \hat{F}_{n_1} and \hat{G}_{n_2} are respectively the empirical distributions and, n_1 and n_2 are the number of modeled and observed locations. The null hypothesis is then rejected at the α level of significance for large values of $D_{n_1 n_2}$, i.e., we reject H_o in favor of H_a , if $D_{n_1 n_2} \geq d_{n_1 n_2}$, where $P_{H_o} [D_{n_1 n_2} \geq d_{n_1 n_2}] = \alpha$.

2.4 Comparison of Model and Observed Center of Activity

Biologists have used different statistics as estimates of the “true center of activity”. Hayne’s center of activity, which is “a two-dimensional average of a group of points” [29], has been the most widely used, but has been criticized as lacking biological significance. Mohr and Stumpf [52] computed a median center with the

median of X values and the median of Y values as coordinates. Unfortunately, this center is not a true bivariate statistic, since its location changes as axes are rotated [42]. Dixon and Chapman [21] advocated use of the harmonic mean center as the alternative to Hayne's center of activity; they showed that unlike the arithmetic mean, the harmonic mean was usually located in areas of high activity in individual ranges. The following paragraphs give an overview of these three methods of locating the center of activity of an animal's home range.

2.4.1 Areal Moments

The major reference on areal moment is the work of Neft [55], so the following description is drawn largely from his work.

Areal moments are similar in form to ordinary statistical moments except for the fact that they are not based on reference lines or axes. However, the basic characteristic of moments is retained: the number of the moment is equal to the exponent of distance that is used. Thus the value of the n^{th} areal moment, M'_n , at a point j is defined as: $\frac{1}{P} \int_A r^n dA$, where P represents the number of observations in the population and r is the radial distance between j and the element of area, dA . In practice, since areal populations are finite and discrete, summation replaces the integration. The n^{th} moment then is

$$M'_n \text{ at } j = \frac{1}{P} \sum_{x=1}^n r_{jx}^n, \quad (2.5)$$

where r_{jx} is the distance between j and the locus of a member of the population, x . As in linear statistics, areal moments can be used to construct an integrated system of measures of central tendency. A measurement of central tendency of an areal distribution is called a *measure of average position* and represents a specific point on an area. The location of the minimum value of the n^{th} root of M'_n represents such a measure. Areal moment can also be used to indicate the dispersion of an areal population. Such measures are defined by the magnitude of the minimum value of $\sqrt[n]{M'_n}$. Thus, this one value defines both the measures of average position and dispersion [55].

Several areal moments are available as measure of average position: the *arithmetic mean center (AMC)*, the *median center (MC)*, and the *harmonic mean center (HMC)*. Biologists and geographers have also used other measures, which are not based on moments. They are *modal center* and *geometric mean center*.

a) The Arithmetic Mean Center

The *arithmetic mean center* (S_c) of an areal population is the location of the minimum value of $\sqrt{M'_2}$, or more simply, the position of the minimum value of M'_2 . This is analogous to the concept of the arithmetic mean, which also has the property that it represents the location of the minimum value of the sum of the squared deviations. This center is invariant with respect to the choice of a coordinate system. Since the second power of distance is involved, the Pythagorean Theorem is applicable. Thus, virtually all *AMCs* have been calculated as the point representing

the arithmetic mean of the X values and the arithmetic mean of the Y values, where X and Y values were a pair of orthogonal axes.

AMC has several characteristics that make it disadvantageous as a measure of average position of animal activities:

- i. *AMC* does not have to be located inside the area of animal activity.
- ii. *AMC* does not necessarily indicate any characteristics of the region in which it is located.
- iii. *AMC* is greatly affected by the extreme locations.
- iv. *AMC* is extremely sensitive. Any movement within the population causes some change in its location, although the change may be minute.

This sensitivity to internal movements makes the *AMC* a useful parameter for studying general trends in the pattern of an areal distribution over a long period of time. Most importantly, *AMC* has the advantage of possessing the majority of the valuable statistical properties of arithmetic mean. Therefore, it is not surprising that despite its disadvantageous characteristics, it is the basis for nearly all statistical methods of home range calculation for the past five decades including probability circles and probability ellipses [21].

b) The Median Center

The *median center (MC)*, denoted by MD_c , is the point that minimizes the mean distance to all other points in the activity field. Formally, it minimizes the value of

the first areal moment, M'_1 . MC is often called the point of minimum average travel or minimum aggregate travel. There is no arithmetic solution for finding MC . One cannot locate it by using the median of the X values and the median of the Y values [42]. Initially the concept of a median for areal analysis was based on the median's property of dividing a population in half. Thus, a "median point" was defined as the intersection of two orthogonal axes, each of which divides the population in half. However, the location of this intersection depends on the direction of the axis.

Another disadvantage of this measure is that large movements of the population within one quadrant will not affect the location of the median point but any movement from one quadrant to another will change its location. Because of these two features, the median point is virtually useless as a measure of average position.

c) The Harmonic Mean Center

The *harmonic mean center (HMC)*, denoted by H_c , is located at the point that minimizes the inverse of the mean of inversed distances to other points. Formally, it minimizes the inverse first areal moment $1/M'_{-1}$, where

$$\frac{1}{M'_{-1}} = \frac{P}{\sum_{j=1}^P \frac{1}{r_{jx}}}. \quad (2.6)$$

It is easier to see from the above expression that HMC is analogous to the harmonic mean for linear distributions. There are two important characteristics of HMC : it must be located within the area under consideration and it is relatively insensitive to

movement within the home range. Therefore, *HMC* cannot be used to indicate the gradual changing of an areal pattern over time. As *HMC* indicates the “hub” or true center of activity of a distribution [42,21], change in *HMC* is likely to be sudden large shift from one region of very high density to another. This property of *HMC* can be used in time series analysis to indicate when there have been shifts in the location of the center of activity

As with *MC*, there is no arithmetic solution for finding *HMC*. The inverse first moment must be computed at all points to locate the point that minimizes its value. In practice, the exact calculation of *HMC* is extremely time consuming with distributions of more than a trivial number of points. The data can be grouped into quadrants to compare an approximation [21], but the size of the grid and choice of control points seriously affects the precision of the estimate [55].

These same characteristics of *HMC* make it a promising measure of center of activity. Lair [42] evaluated the relative usefulness of the aforementioned measures in red squirrel activity in the field and concluded that *HMC* was a good estimate of focal center location, which coincided with the behavioral focal mean center. Similarly, Dixon and Chapman showed that *HMC* was usually located in areas of high activity in individual home range.

For my analysis, I used the *AMC* to evaluate the appropriateness of the model to depict movement patterns of the animal under consideration. The hypothesis was if the modeled and observed movement patterns are similar, we should expect the *AMC*

of the modeled and observed location to be close. Thus, distance between the observed and modeled *AMCs* can be used as a measure of predictive capability of the model. My choice of *AMC* as a measure of center of activity was mainly due to the following reasons:

- i.* If the home range was estimated using the convex polygon method, *AMC* would always be inside the corresponding home range.
- ii.* I wanted to study general trends in the patterns of the distribution of locations over a period of time. Because of its sensitivity, the *AMC* is a preferable measure for this purpose over its other counterparts.
- iii.* *AMC* is easy to use and easy to interpret.
- iv.* Most importantly, *AMC* possesses most of the valuable statistical properties of arithmetic mean and therefore is suitable for further statistical analysis.

2.4.2 Comparison of Model and Observed Center of Activity

Let the rectangular coordinates of the animal's i^{th} location be given by a two-dimensional state vector $\mathbf{X}_i = (X_i, Y_i)$. Assume that locations of the animals are independent and follow a normal probability surface distribution [55]. Consider a sample of p_1 observed locations, $\mathbf{x}_{1i} = (x_{1i}, y_{1i})$, ($i = 1, 2, \dots, p_1$) of an animal and let $\mathbf{x}_{2j} = (x_{2j}, y_{2j})$, ($j = 1, 2, \dots, p_2$) denotes a sample of model locations. Using the notations of Neft *et al.* [55], let $s_{c_1} = (\bar{x}_{1i}, \bar{y}_{1i})$ and $s_{c_2} = (\bar{x}_{2j}, \bar{y}_{2j})$ represent the *AMCs* of the observed and modeled locations.

The null hypothesis to be tested is that these samples were drawn from the same population, i.e., distance between the two *AMCs*, $r_{ss} = 0$.

The standard error of the distance between the two arithmetic centers is given by

$$SE_{r_{ss}} = \sqrt{\frac{(p_1 + p_2)(p_1 s_{r_1}^2 + p_2 s_{r_2}^2)}{p_1 p_2 (p_1 + p_2 - 2)}}, \quad (2.7)$$

where s_{r_1} and s_{r_2} are respectively the observed and modeled *standard distance deviations* and are defined as the square root of the second areal moments when computed about s_{c_1} and s_{c_2} respectively. Then the test statistic [55]

$$t_r = \frac{r_{ss}}{SE_{r_{ss}}}, \quad (2.8)$$

with $n = p_1 + p_2 - 2$ *d.f.* is a univariate areal counterpart of the student's t in linear statistics (one should not confuse it with one sided usual t -statistic). As in the linear case, as $n \rightarrow \infty$, t_r approaches a normal probability surface. Critical values of t_r for various *d.f.* have been calculated by Neft *et al.* [55]. The $(1 - \alpha) \times 100\%$ confidence limit for r_{ss} is then given by

$$r_{ss} < t_{r(n,\alpha)} SE_{r_{ss}}, \quad (2.9)$$

where $t_{r(n,\alpha)}$ is critical value of t_r for n *d.f.* and α level of significance.

If $p_1 = p_2 = p$ then the standard error can be rewritten as

$$SE_{r_{ss}} = \sqrt{\frac{(s_{r_1}^2 + s_{r_2}^2)}{(p-1)}}, \quad (2.10)$$

and the test statistic can be computed accordingly.

The above test is suitable for areal distribution when sphericity of earth is taken into consideration. If sphericity of the earth is ignored, the Pythagorean Theorem can be invoked and the confidence interval can be computed by replacing s_{r_i} with

$$\sqrt{s_{x_i}^2 + s_{y_i}^2}.$$

CHAPTER 3: Application to the Florida Panther Data

3.1 Background

As a part of the efforts toward restoration of the Everglade ecosystem and development of a landscape conservation strategy for panthers, extensive and ongoing radio telemetry monitoring and field studies of panthers have been conducted in Florida continuously since 1981. These provide a wealth of information about panther biology, behavior and demographics. Presently these data are being used in defining behavior rules for use in the ATLSS Deer/Panther model, an individual-based spatially-explicit model for panthers and white-tailed deer in the Everglades and Big Cypress landscapes [11,18]. The predictive capabilities of individual-based models are closely tied to the realism of the decision rules that determine how a simulated animal moves across the landscape, interacts with other individuals, and responds to their environment. The definition of these rules in turn depends upon the availability and interpretation of empirical observations of behaviors and movement patterns [12]. In this section, methods developed in Chapter 2 will be used to test the predictive capability of the movement model and to draw

inferences about the space-use preferences and movement patterns of the Florida panther.

3.2 The Spatially-explicit Individual-based Simulation Model for the Florida Panther

The Deer/Panther model was designed to be used as a management and evaluation tool to analyze the relative effects of alternative water management scenarios on long-term population dynamics of the Florida panthers and their primary prey species, white-tailed deer. The Florida panther model is one of four components of the Deer-Panther model. The other three components are hydrology, vegetation and deer. The following abstract from the work of Comiskey *et al.* [11], describes the spatially-explicit individual-based simulation model for the Florida panther constructed for application to Everglades restoration.

A spatially-explicit model is grid based, with the landscape subdivided into spatial cells. Within this spatial grid, individual-based models track the states of each individual within a population. Each individual has a state consisting of its location, gender, age, body weight, etc. Decision rules, which are a function of the states of each individual, determine how individual animals move across the landscape, interact with one another and respond to their environment.

The Florida panther sub-model offers a choice of options for defining the panther population parameters at the start of a simulation. Initial conditions can be based on empirical data for the existing population, or data for a hypothetical population with

any pre-defined set of characteristics can be used. By varying the autoecological characteristics, such as age, weight, health status, and location of the selected individuals, the viability of different reintroduction scenarios can be evaluated. The panther sub-model is coupled to the hydrology sub-model, which provides water depth, to the vegetation sub-model, which provides cover, and to the individual-based deer sub-model, which provides the prey (Figure 3.1). Panther behavior and physiology are simulated on a daily time step. Each panther is assigned a state which includes individual characteristics, such as age, gender and weight; predation information such as number of days at a deer kill site and number of days since the last deer kill; and several gender specific variables which describe each individual's reproductive status.

Panthers move daily on the landscape at the 500 m. scale of resolution, based on behavior rules, which specify:

- ❑ search for prey, which are primarily white-tailed deer. These include short distance local searching for prey and intermediate scale and long-distance movement when local searches for prey have failed, with the direction of search depending on the individual's past hunting history,
- ❑ remaining at a kill site until the deer has been eaten or has spoiled,
- ❑ activity of males in search of a mate,
- ❑ dispersal of juveniles from the natal area,

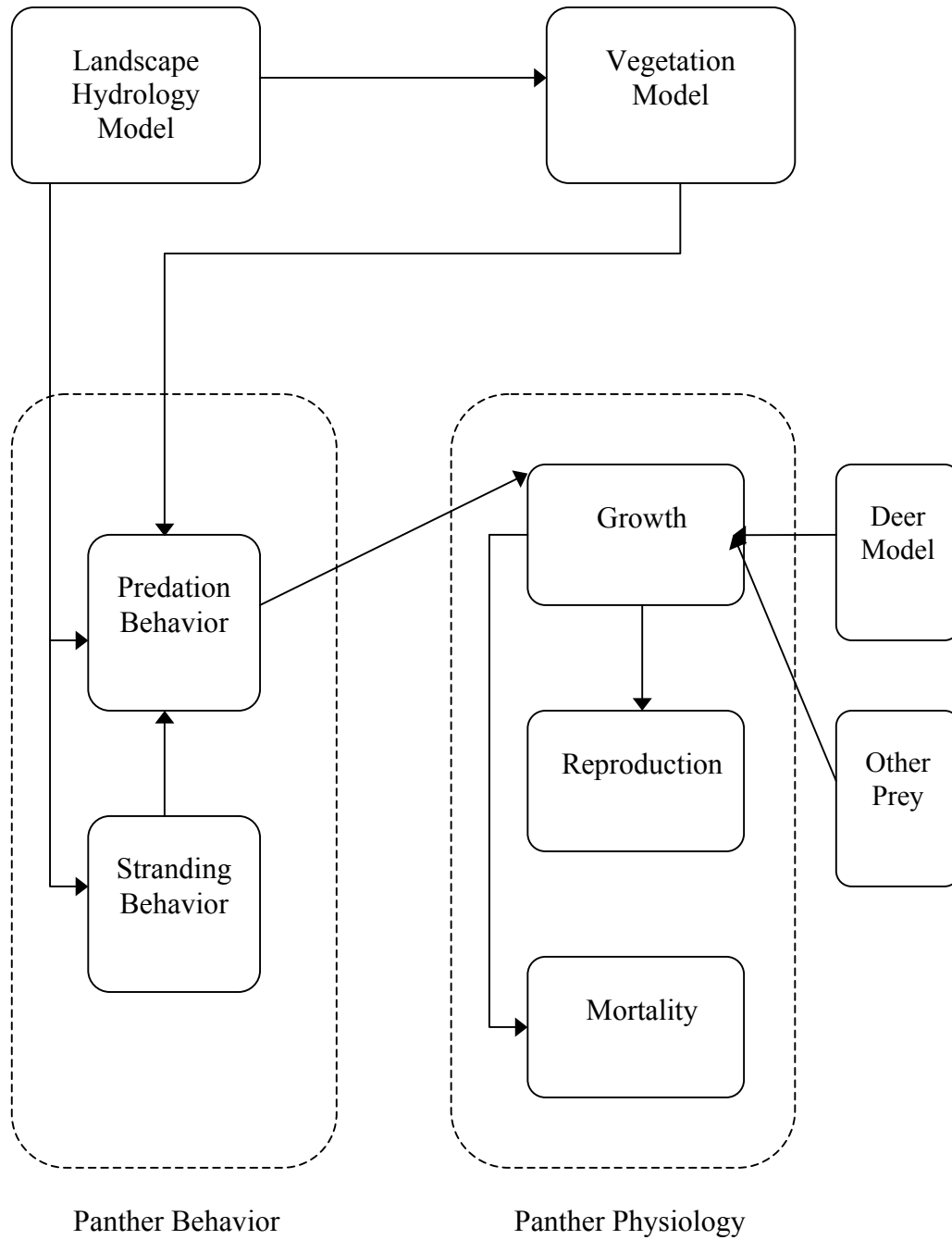


Figure 3.1: Structure of Panther Component of Deer Panther Model (Adapted from Comiskey *et al.* [11])

- ❑ dispersal of adults when food availability is low, and
- ❑ avoidance of high water depths.

To incorporate a panther's awareness of the presence and status of other panthers in the model, each panther marks spatial cells with its unique ID, so that other panthers encountering this mark can identify its gender and reproductive status from the mark. Movement and behavior of each panther is then mediated by the presence or absence of foreign markers. Marks are dated and decrease in potency over time.

In simulating predation behavior, the model assumes that individual panthers know where they have been and where they hunted successfully. By recording for each panther the N-S and E-W offsets from its starting point or center and the location and date of deer settings and kills, the information needed to incorporate this memory of locality into movement behavior is made available. Panther mortality occurs in the model due to starvation, intra-species aggression, accidents, and other factors, such as chemical toxicity and disease.

3.3 Data

Panther telemetry data have been collected by three different groups from two agencies: Florida Fish and Wildlife Conservation Commission (FWC), and National Park Services (NPS). Over the monitoring period of February 22, 1981 to December 2001, 115 panthers have been monitored.

Location records of radio-collared panthers are collected using a fixed-wing airplane flying at an altitude of about 200 meters. Except for daily monitoring of panthers in Everglades National Park (ENP) for the period 1986-1991, flights have been conducted three days per week. Directional antennae mounted on either side of the aircraft are used to identify the general locations of individual panthers by sighting along an antenna to the point on the ground where the radio signal is strongest. The radio collar of each monitored panther emits a unique frequency that allows its signal to be distinguished from those of other collared panthers. A point is plotted as accurately as possible by hand on a 1:24,000-scale topographic map, and the date, time, panther number, and habitat type are recorded. A straightedge is subsequently used to measure the Universe Transverse Mercator (UTM) coordinates for each panther location as determined from the topographic map to the nearest 100 meters. BCNP and ENP use similar techniques to determine panther locations.

The primary database consisted of UTM coordinates specifying location of individual panthers along with date when the location was measured and demographic and other information such as: sex, age and date on which the cat was radio-collared, date and cause of death, date on which independent home range started, etc. These data sets were further refined for specific analysis.

3.3.1 Accuracy of Data

Accuracy of these data is affected by a number of variables, including equipment used, collection and reporting protocols, and the experience and expertise of operators. Belden *et al.* (1988) [4] reported that radio-telemetry locations collected

using the techniques mentioned above were accurate to 230 m. Dees *et al.* (2001) [19] collected radio-telemetry data on some of the same panthers being monitored by FWC between 1994-1998 using similar techniques, but their observations also included an on-board global positioning system to determine coordinates. They also tested the accuracy of their locations by placing test transmitters in known locations in the field, plotting transmitter locations from the air, and then determining the error of actual versus observed locations. They reported that the mean distance between estimated and actual locations was 77 m. and 95% of estimated locations were within 200 m. of the actual location. However, Dees *et al.* (2001) [19] and Janis *et al.* (1999) [32] reported mean error between recorded and actual locations to be 204 and 247 m. for FWC and NPS, respectively, with 95% of locations occurring within 489 and 485 m., respectively.

3.4 Statistical Software

All of the statistical analyses were done using the statistical software JMP 4 (SAS Institute Inc.) and Microsoft Excel. JMP is a software tool for interactive statistical graphics and includes a broad range of graphical and statistical methods for data analysis and an extensive design of experiments module. Simulation of panther location, estimation and analysis of home range, data visualization, and other computational works were done in PV-WAVE (Visual Data Analysis Software by Visual Numerics), a software application for visualization, representation and analysis of data.

3.5 Assumptions

Three basic assumptions were made about the panther movement data.

1. Patterns of daytime activities and habitat use were representative of nighttime patterns as well.
2. Panther location data are statistically independent. This assumption was based on the hypothesis that as the difference between the two times becomes greater, the probability that the second location can be known, given the first, becomes small. Therefore, if the interval between recordings of two consecutive sample locations is sufficient, then the observations can be considered independent. An interval of 48 hours between recordings of two sample locations was assumed to be sufficient for the statistical independence of the panther data.
3. The last assumption was that sample data have a bivariate normal distribution, which was a prerequisite for the methods used in Section 3.8.

3.6 Analysis of Space-use Preferences

3.6.1 Sample

Analysis of space-use preference was done at two different levels: composite home range and yearly home range level. Accordingly, two different samples were selected. For both samples, selection of the panthers and location observations was a multistage process, in which observations were filtered at various stages according to

some predefined criteria. The following paragraphs describe the processes of selecting sample observations for these two analyses.

Composite home range Analysis:

As of December 2001, the panther database contained information on 115 panthers. Since the primary objective was analysis of movement of panthers in home ranges, only those panthers that were reported to be monitored for dispersal behavior and home range establishment activities were selected at the first stage. As such, a total of 85 panthers were selected. A total of 53,589 observations had been recorded on these panthers during February 1981 to December 2001.

Selection at the second stage was based on consistency in data recording. Frequency of recording locations of panthers was not consistent over time and between the agencies involved in data collection. Although a *three times per week* recording pattern was generally used, panther locations in ENP were also recorded on a daily basis during the period of 1986 to 1991. In a few cases when special monitoring of the panther was required, data were also collected more than once a day. Such inconsistencies in recording locations of panthers introduce measurement errors into the space-use preference analysis. One way of minimizing these errors is to exclude such inconsistent observations from the analysis. Therefore, observations that did not fit the standard *three times per week* pattern were identified for each panther, and panthers with 10 percent or more such inconsistent observations were excluded from the sample. From the remaining 56 panthers, those with a threshold of less than 1.5

years of residence in a home range were further excluded. The resulting sample consisted of 25,483 observations on 40 panthers.

Annual Home Range Analysis:

For yearly analysis, the sample selection process was started with the 85 panthers that were monitored for dispersal behavior and home range establishment activities. Observations on these panthers were further categorized by age of the panthers² (hereafter, these age categories will be referred to as *cases*.) In total, there were 407 such *cases* for 85 panthers. These *cases* served as sampling units for the second round of selection.

At the second stage, the number of observations that did not fit the standard *three times per week* pattern was determined for each *case*, and *cases* with 10 percent or more such inconsistent observations were excluded from the sample. To ensure sufficient number of observations for home range analysis, *cases* with the number of observations less than 50 were further omitted from the subset obtained at second stage of selection. The resulting sample consisted of 34,096 observations in 258 *cases* of 69 panthers. This sample was used to construct the 95% MCP home ranges for all ages of each panther. Consequently, 258 such home ranges were constructed.

Construction of 95% MCP home ranges was, in a sense, removal of so-called *outliers* from the data set. It was observed that removal of these *outliers* resulted in considerable decrease in the number of observations in some of the 95% MCP home ranges. Therefore, to be on safe side, home ranges with fewer than 50 observations

² Approximate age of the panther at time of recording its location.

(ensuring at least four months of residence in the home range) were excluded from the final sample. The final sample thus consisted of a total of 30,238 observations in 239 cases of 66 panthers.

3.6.2 Home Range Estimation and Distribution of Mean Distances

Home ranges for each of the sample panthers were estimated using the Minimum Convex Polygon (MCP) method [69]. I computed two types of home ranges for sample panthers: *i*) home range computed based upon all the locations accumulated throughout the life span of the panther, which will be termed the “composite home range”, and *ii*) the home range computed for each age of the panther (termed “annual home range”). In other words, the composite home range is the area used by a panther throughout its lifespan. For the computation of annual home range, observations were categorized according to the age of the panther and home range for each age was estimated. These home ranges, which are sometimes also referred to as *activity ranges*, are therefore the areas the panther has used at various ages during its lifespan. For the purpose of computation of home ranges, I used codes developed by the ATLSS modeling group at The Institute of Environmental Modeling, University of Tennessee. These codes were written in the PV-WAVE application package.

Boundaries of the home ranges were determined and distance (d_i) of each of the locations inside the 95% MCP from the nearest boundary of the corresponding home range was computed using the methods described in Section 2.2. These distances were used to analyze the space-use preference of the panthers. For example, equality

of mean distances of two groups of panthers indicates similarity in the tendency of the panthers in those groups to stay near or away from the boundary of the home range. This tendency is indicative of the space-use preference of the panthers.

There was a strong positive linear co-relationship between mean distances ($mean(d_i)$) and square root of area of the 95%MCP home range ($r = 0.905, p < 0.001$) (Annex 1). A panther with large home range is also expected to have a larger $mean(d_i)$ than the panther with smaller home range. Because of this dependency of $mean(d_i)$ on size of the home range, space-use preferences of panthers with different home ranges cannot be compared based upon the distance statistic. Therefore, meaningful comparisons of space-use preferences of two groups of panther requires normalization of the effect of home range size on the mean distance, which in turn requires selection of an appropriate normalization factor.

It was also noticed that the rates at which $mean(d_i)$ increased with square root of area were almost equal for female (slope of best-fit line = 149.12) and male (slope of best-fit line = 157.2) panthers. This relationship of home range size with $mean(d_i)$ makes it a strong candidate of normalization factor. I divided each d_i by the square root of the area of the corresponding 95% MCP to get normalized distances, $norm(d_i)$. Distributions of these normalized distances were used to compare the dependence of space-use preference of the panthers on their age, sex and season of the year.

For the analysis of age-adjusted annual home range, the 95% MCP home range and the distribution of $norm(d_i)$ were constructed for each *case* separately using the aforementioned methods.

3.6.3 Results

Comparison of composite home ranges of male and female panthers indicates that the mean home range size for females (218.6 sq. km.) was significantly smaller than the mean for males (518.2 sq. km.) ($p < 0.0001$). It also indicates a wide difference between the variation in the home range sizes of male and female panthers (Annex 2). Female panthers in the sample had home ranges ranging from 61 sq. km. to 390 sq. km. (sd. = 105.2 sq. km.) while this range was from 204 sq. km. to 1268 sq. km. (sd. = 215.7 sq. km.) for male panthers.

Size of the home ranges is often related to an animal's energetic costs. That is, the larger the home range the more energy expended in searching for various life requisites [69]. Accordingly, area of home range is expected to have an inverse relationship with age. Results of analysis of age-adjusted annual home ranges were consistent with this hypothesis (Figure 3.2). Area of annual home range adjusted for age had a unimodal distribution with peak around the age seven. Home ranges became smaller as panthers grew older. Adult panthers of age from 7 to 8 years seem to occupy the largest area (mean = 234.2 sq. km., maximum = 1873 Sq. Km). During old age, their home range areas become very small (mean = 111.1 sq. km.).

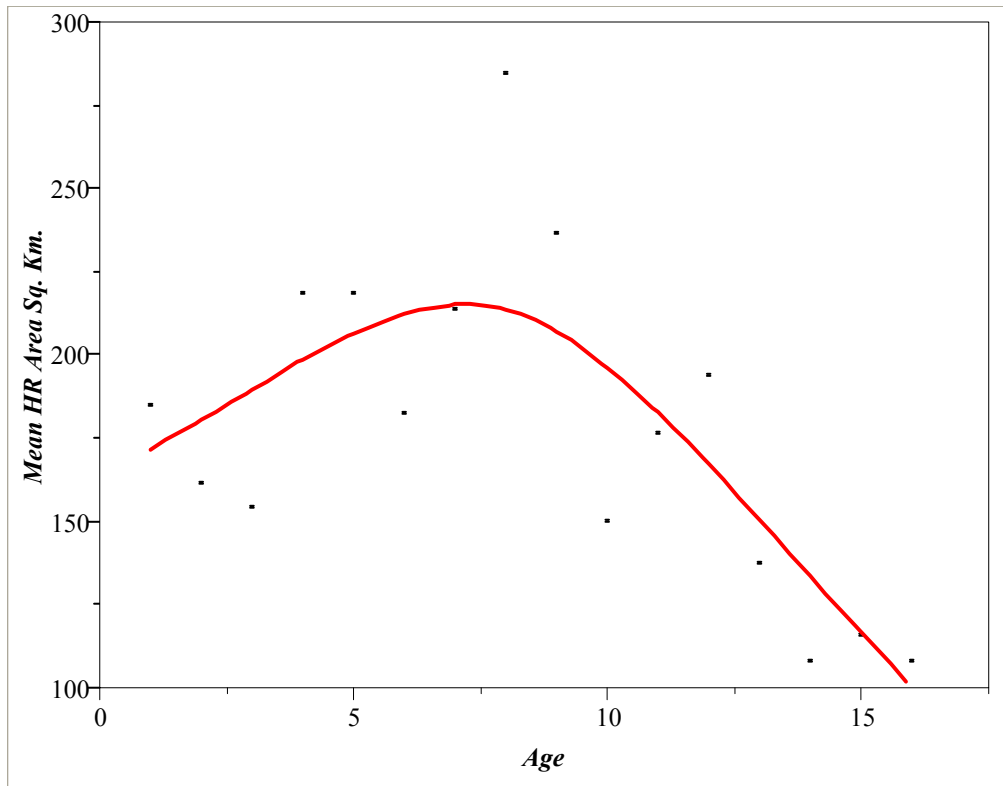


Figure 3.2: Relationship Between Age and Area of Annual Home Range (All Panthers)

Panthers who prefer to stay deep inside their home ranges are expected to have larger $norm(d_i)$ than those who utilize each section of the home range uniformly or those who preferentially utilize area near the boundary of the home range. Based on this hypothesis, I compared the space-use preferences of panthers of different genders and ages and at different seasons of the year. My analysis showed that the difference between the mean normalized distances of male (mean = 179.3) and female panthers (mean = 167.8) was not significant ($p = 0.097$) (Annex 4), indicating similar space-use preferences of both sexes. However, age of the panther seems to have great influence on their space-use preference. This is clear from the following analysis.

Relationship between mean $norm(d_i)$ and age of the panther was somewhat erratic in nature (Annex 5). In the age interval 1 to 10 years, the relationship was approximately parabolic with local minima around year five. After age 10, the mean $norm(d_i)$ decreased sharply with age. The graph clearly shows a clustering of points around the ages 12 to 14 years. Means of d_i s for these ages were noticeably lower than that of age 11. This observation contradicts the prevailing hypothesis that as panthers grow older their movement becomes restricted to a smaller area, resulting in larger mean distance of their locations from the boundaries of the home range. There are two possible explanations for this unexpected drop off of the mean $norm(d_i)$ after age 11: *i)* the panthers in the sample with these ages have unusual and unexpected movement patterns or *ii)* the annual home range of older panthers shrinks towards one sub-area of the composite home range.

Further analysis revealed that six sample panthers have reached the age of 12 to 15 years. Among them, only two (ID # 31 and 32) have passed age 13 and only one has passed ages 14 and 15 (ID # 32). This indicates possible sampling bias due to the low representation of panthers from the age group 13 to 15. Drawing any inferences about the population of panthers in that age group based upon the behavior of only one or two panthers would not be practically meaningful. Because of such a low representation of panthers from ages 13 to 16 in the sample, it was desirable to restrict the analysis to age below 13 years. Furthermore, plots of $norm(d_i)$ against age for these six panthers clearly reveal that panther # 26 had somewhat irregular and unexpected low mean $norm(d_i)$ at the age of 12 years (Annex 6). This mean value

was quite different from the means at other ages of this panther and was a principle contributor in lowering overall mean $norm(d_i)$ for age 12. Therefore, for the purpose of my analysis of age dependence of space-use preference, I considered this panther as an *outlier* and excluded it from analysis.

With the aforementioned adjustment in the sample, I re-examined the relationship between $norm(d_i)$ and age of the panther. It was observed that initially mean $norm(d_i)$ was decreasing with age, reached a minimum around age 5 and then started increasing again (Figure 3.3).

As expected, mean $norm(d_i)$ was significantly different between different ages of panthers ($p < 0.001$). Based upon the clustering of points in Figure 3.3, I categorized the panthers into four age categories: juveniles (1 to 4 years), younger adults (5 to 7 years), adults (8 to 10 years), and older adults (11 and 12 years). Results based on Tukey's test for comparison of means revealed that younger adults (age 5 to 7) had significantly different space-use preference than panthers in other age groups ($\alpha = 0.05$) (Annex 7). Panthers at this age tend to stay closer to the boundary of their home range (mean $norm(d_i) = 171.8$) than panthers in any other age group. Panthers in the remaining age groups had similar space-use preferences.

The current occupied range of the Florida panther constitutes approximately 8,000 sq. km. of the landscape of South Florida, consisting of a mosaic of vegetation types including swamps, marshlands, water conservation areas swamp forests etc. The

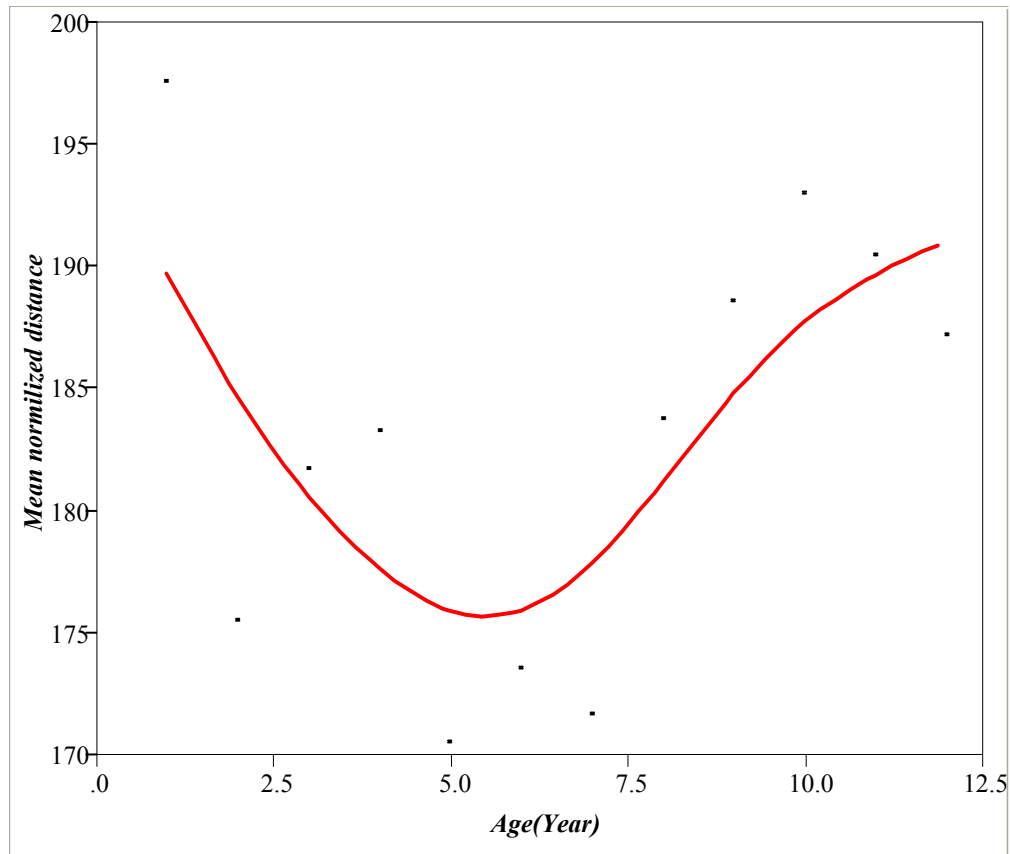


Figure 3.3: Mean Normalized Distance of Locations of Panthers by Age.

hydrology of the conservation area, therefore, is expected to play an important role in the space-use preferences of the Florida panthers. For example as water level rises during the wet season (May to October), panther movement is expected to be confined in upland areas. My findings however did not support this hypothesis. Based on the date of collection, I divided the observations into two categories: wet (May to October) and dry (November to April) seasons. Difference between the mean $norm(d_i)$ for these two seasons was not significant ($p = 0.55$, Annex 8), indicating no significant effect of seasonality on the space-use preferences of panthers.

3.7 Model Vs. Observed Space-use Preference

One of the objectives of this thesis was to test the predictive capability of an individual-based model by comparing the observed and simulated movement patterns. The panther model was meant to serve as a test model. Since it was still under development and was not available for use, I considered a random movement model to simulate panther movement within its home range. The only significance of this model is its role as a test model to demonstrate how the methods developed in this thesis can be used to compare model and simulated movement patterns.

3.7.1 Theoretical Model

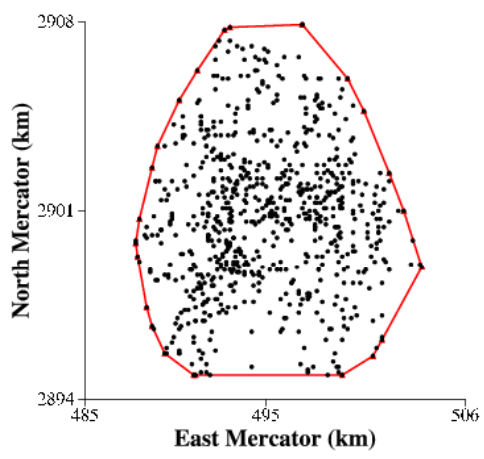
Panthers can cover a large distance in a single movement vector. My calculations showed that the maximum linear distance between two consecutive locations was 80 km. for male and 75 km. for female panthers. It has also been noted that panthers move freely within large home ranges. Therefore, ignoring effects of factors like spatial heterogeneity of the landscape, prey availability, age etc., which affect movement of the panthers, it can be reasonably assumed that successive moves of panthers are random in nature. Based upon this assumption I considered a model, which assumes that panthers can move randomly and without any restrictions within their home ranges, and that their movement within the boundaries of home ranges are independent. Under the random movement assumption, simulated location points are distributed randomly and uniformly within the boundaries of the home range. This means that each section of the home range is used with equal frequency. Moreover, distribution of the locations of panthers simulated by such a model is a

spatial Poisson process. It is a very naïve model that may have no practical significance, other than to generate a movement pattern with which observed location patterns can be compared using the techniques proposed in this thesis. The idea was to demonstrate how these methods could be used to compare observed and model movements.

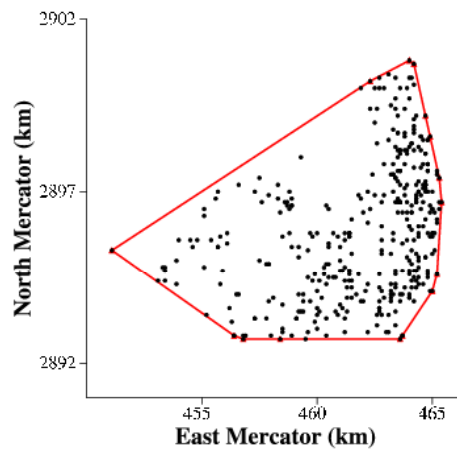
Simulation of location points using the random movement model was a straightforward process. For simulation purposes, 95% MCP home range of each of the sample panthers was estimated and the home range boundaries were determined. The RANUNI function of PV-WAVE was used to simulate random location points within each of the home ranges. The number of locations generated in a particular home range was equal to the number of observed locations within the corresponding 95% MCP.

3.7.2 Sample

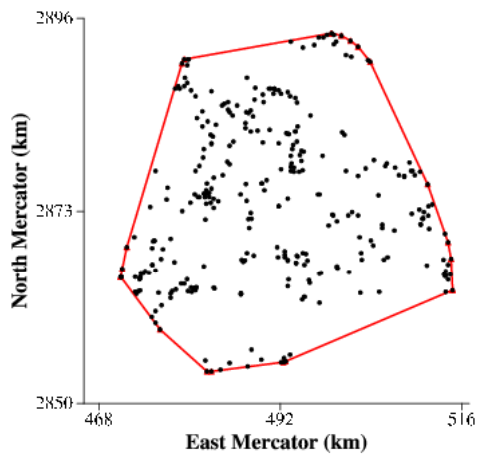
I compared model and observed distributions of d_i for three panthers. Number 49 was a female of age 11 years (as of December 2001). She was radio collared at the age of 2 years. She was resident in her home range for 9.85 years and was still living as of December 2001. Number 78, another female panther was also selected for comparison. As of December 2001, she was about 5 years old, and had been resident in her home range for 2.87 years. Number 79, a male panther, was born in September 1995. He was radio collared at the age of 3.5 years and resided in his home range for 2.33 years before his death in a vehicular accident in February 2000. These panthers were selected because of their distinct movement patterns (Figure 3.4). For example,



(a)



(b)



(c)

Figure 3.4: Home Range of Panthers (a) Number 49, (b) Number 78, (c) Number 79.

distribution of location points of number 49 showed a tendency to stay more towards the center of the home range; location points of number 78 were concentrated near the boundary; and number 79 seemed to move freely in his home range, resulting in randomly distributed locations.

3.7.3 Distribution of Distances

For each of the above panthers, coordinates of the vertices of the 95% MCP home range were computed. These vertices were then used to draw boundaries of the home range. Model location points within the boundaries of the observed home range were then generated using the random movement model. Distances of these modeled location points as well as the observed location points from the nearest boundary were computed using the methods described in Section 2.2.

Although distribution of d_i s depends on the shape as well as size of the home range, normalization of the effect of size of home range is not necessary for comparing model and observed distributions of d_i s. Because the model and observed distribution of d_i s for a particular panther were based on the same home range, comparisons were not made between two different panthers. Histograms of the model and observed distributions for this panthers were constructed for comparisons (Figure 3.5).

3.7.4 Results

Mean distance of the locations of number 49 from the boundary of its home range was 3007.11 meters, which was significantly larger than the mean of the distances of its simulated locations (mean = 2059.51 meters, $p < 0.0001$ (one sided)).

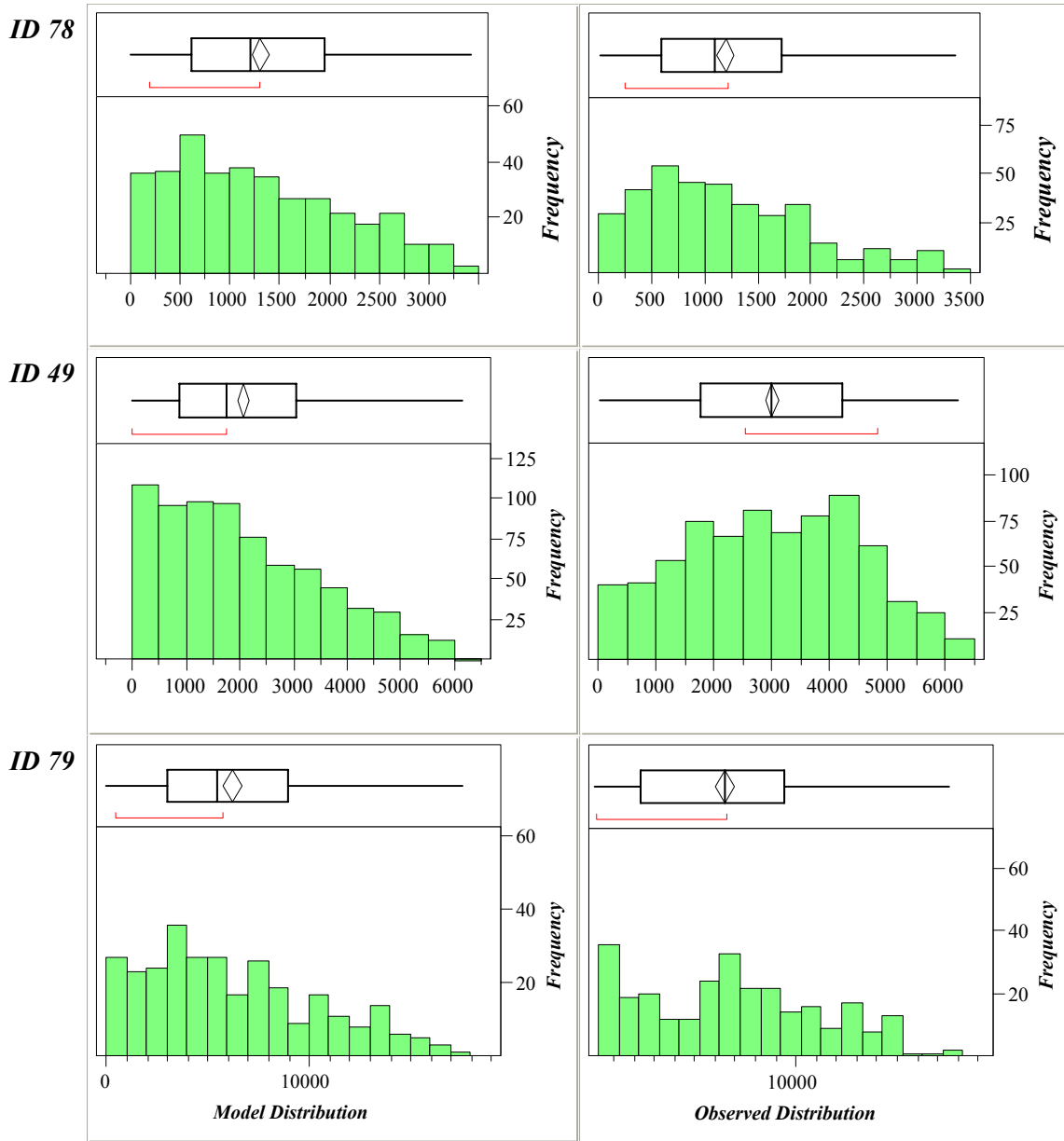


Figure 3.5: Model and Observed Distributions of d_i for Panther # 78, 49, and 79..

This supports the preliminary claim that locations of number 49 were not distributed randomly; they were, on average, located at a greater distance from the boundary of the home range as compared to the simulated locations. The hypothesis of no difference, however, could not be rejected at 1% level of significance for number 78 and 79 (number 78: model mean = 1303.50 m., observed mean = 1198.64 m., $p = 0.04$; number 79: model mean = 6217.15 m., observed mean = 6480.86 m., $p = 0.2297$ (one sided test)). This suggests that simulated locations for these two panthers were located, on average, at the same distance from the boundary as the observed locations.

It was interesting to note that locations of number 78 were not distributed randomly; they were concentrated along the eastern boundary of its home range (Figure 3.4). Yet, based on the outcome of the t-test we fail to reject the hypothesis of no difference of $mean(d_i)$ for this panther. Failing to reject the hypothesis of no difference means only that, on average, the modeled and observed locations were at the same distance from the boundary of the home range. Under no circumstances does this imply identical clustering of points or similar point patterns of the two distributions being compared. This explains why the difference between the mean distance of the observed locations, which were highly concentrated along the boundary, and model locations, which were distributed randomly, was not significant for number 78.

Though t -tests are sensitive to differences between the means of the two distributions being compared, they may not detect differences of other types, such as differences

in variances. Therefore, the next step was to see if the modeled and observed distributions of the distances were similar. I used the Kolmogorov-Smirnov two-sample statistic to test if the empirical distribution functions of observed and simulated distances were identical.

Table 3.1 summarizes outputs of the Kolmogorov-Smirnov test. Distributions of the observed and simulated d_i s were found to be identical for panther numbers 78 and 79, but were not in the case of number 49 ($\alpha = .01$). These results suggest that the random movement model failed to predict the space-use preferences of number 49, while it worked well in the cases of panthers 78 and 79. It should be noted that, even though the distribution of the locations of number 78 was not quite random, distribution of distances of these locations was found to be identical to the distribution of the distances of randomly simulated locations. Arguments similar to those presented in the previous paragraph can be used to explain this not so counter intuitive result

Table 3.1: Outputs of Kolmogorov-Smirnov Two Sample Test

ID	Smirnov Statistic T	Number of Observations		$\sqrt{\frac{m+n}{mn}}$	0.99 Quantiles ³
		Model (m)	Observed (n)		
49	0.28159	728	728	0.05241	0.116192
78	0.09115	373	373	0.07323	0.162326
79	0.12	300	300	0.08165	0.181001

³ Quantiles are based on asymptotic distribution of the Kolmogorov-Smirnov Statistic T for large sample size.

3.8 Comparison of Model and Observed Activity Centers.

I used *arithmetic mean center (AMC)* to evaluate the ability of the model to depict movement patterns of an animal. Tests developed in Section 2.4.2 were based on the simple hypothesis that if the modeled movement pattern is close to the observed pattern then the *AMCs* of the modeled and observed locations should also be close. Two types of comparisons were made in this respect. First, the *AMCs* of the observed and modeled locations of the sample panthers in their composite home range were compared. Secondly, *AMC* of cumulative locations at each time step was computed and significant tests were carried out for the departure of modeled *AMC* from the observed *AMC* with time.

Results of the significance tests for comparing modeled and observed *AMC* are presented in table Table 3.2. The hypothesis to be tested was that the two sets of locations were drawn from the same population. Distances between modeled and observed *AMCs* (r_{ss}) of the selected panthers are listed in column three. The fourth column contains values of the test statistic (t_r), computed by dividing r_{ss} by the corresponding standard error. Critical values of the test statistic were computed at $\alpha = 0.01$, based upon the asymptotic distribution t_r for large sample [55].

AMC simulated by the random movement model was found to be acceptably close to the observed *AMC* of number 79. These findings further support the initial observation made about the randomness of the distribution of locations of this panther. However distances between the modeled and *AMCs* of number 49 and 78

Table 3.2: Comparison of Observed and Modeled Activity Centers of Panther # 49, 78, and 79.

ID	$SE_{r_{ss}}$	r_{ss}	$t_r = \frac{r_{ss}}{SE_{r_{ss}}}$	Critical value of t_r for $\alpha = .01$
49	121.90553	325.2012	2.667649	
78	134.92519	1472.678	10.91478	2.146
79	590.27752	1069.517	1.811889	

were both significantly large at $\alpha = 0.01$. Therefore, there was room for doubt of the appropriateness of the random movement model to simulate the movement patterns of these two panthers.

The above test compared *AMCs* of locations accumulated over the life span of panthers. Their use of area within their composite home range changes consistently [46], and therefore occasional shifts in their activity areas is not unusual. *AMC* is very sensitive to these types of internal movements. Any change in the locations of the panther causes some change in its location, although the change may be minute. Analysis of the shift in the *AMC* with subsequent moves of a panther can, therefore, reveal much about its overall movement pattern.

I computed *AMC* of the first 75 locations for each of the sample panthers. With *three times per week* recording pattern, 75 records would ensure location recording for approximately six months. This *AMC* is therefore, the activity center of the animal during the first six months in its observed home range. *AMC* of the locations at each successive move after the first 75 moves was then computed. That means each move after the first 75 moves would result a new arithmetic center based on the set of

locations accumulated up to that point. Simply speaking, the *AMC* corresponding to the n^{th} move was calculated using the first n locations. For each successive move, distance between the observed and modeled *AMCs* and the 99% confidence limit for this distance were computed. These confidence limits and the distances between observed and modeled *AMCs* panthers 49, 78 and 79 were then plotted against number of moves (Figure 3.6, 3.7 and 3.8 respectively).

Up to approximately 400 moves, modeled *AMC* of number 49 differed noticeably from its observed *AMC*. After this point, except for a slight departure around move # 500 and at the end of the recording period, modeled and observed *AMC* were acceptably close. This indicates that the random movement model was reasonable accurate in approximating the movement patterns of this panther after move # 400. Some mixed results were observed in the case of number 79. Except for a few short intervals, the model and observed activity centers of this panther were significantly different from each other. The longest interval when the distance between these two centers was not significant was between the 45th and 85th moves. The random movement model, however, appeared to fail completely to depict the movement pattern of number 78. This is evident from the consistently wide departure of model and observed *AMCs* of this panther with time.

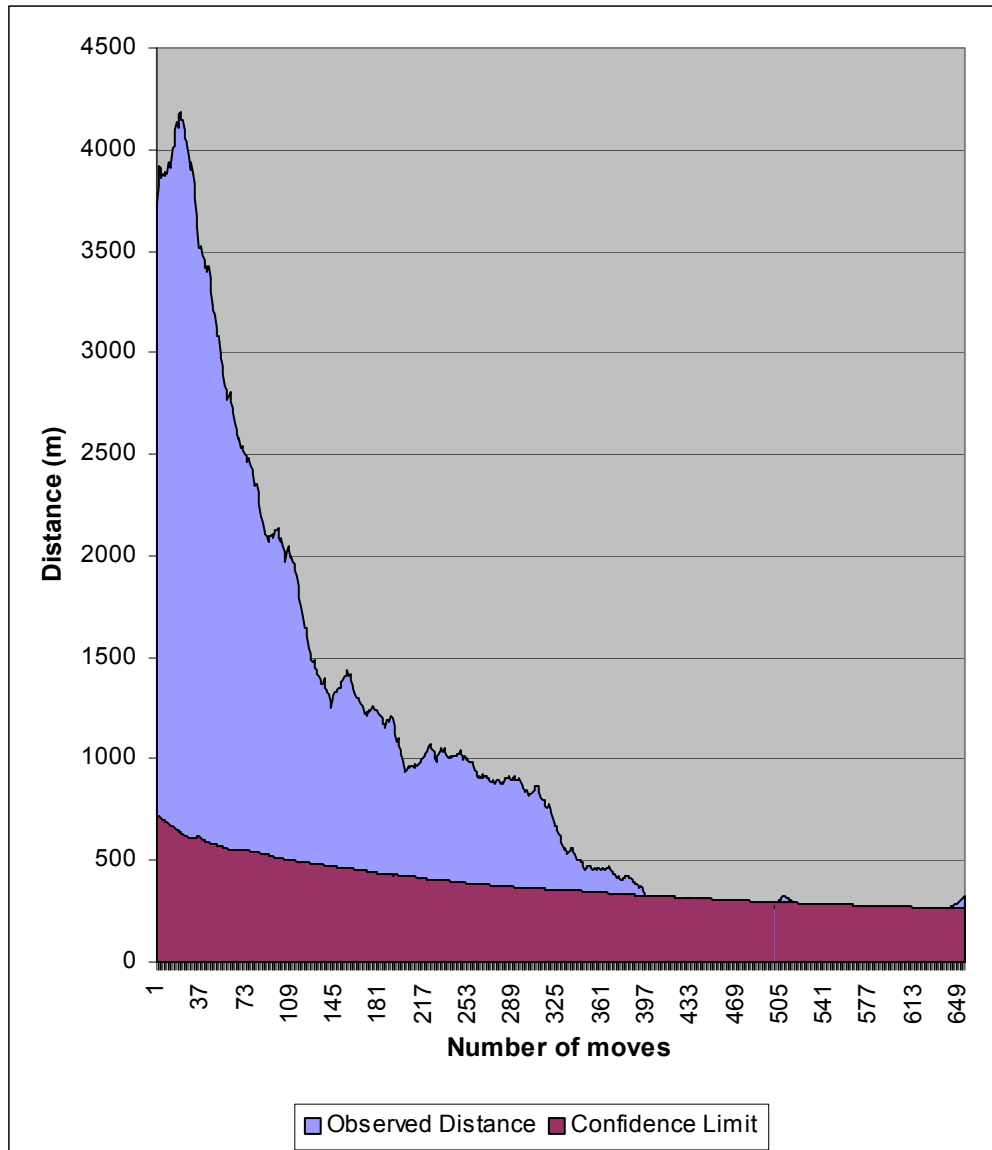


Figure 3.6: Confidence Limits of Distances between Observed and Model *AMC* s by Number of Moves (Panther Number 49).

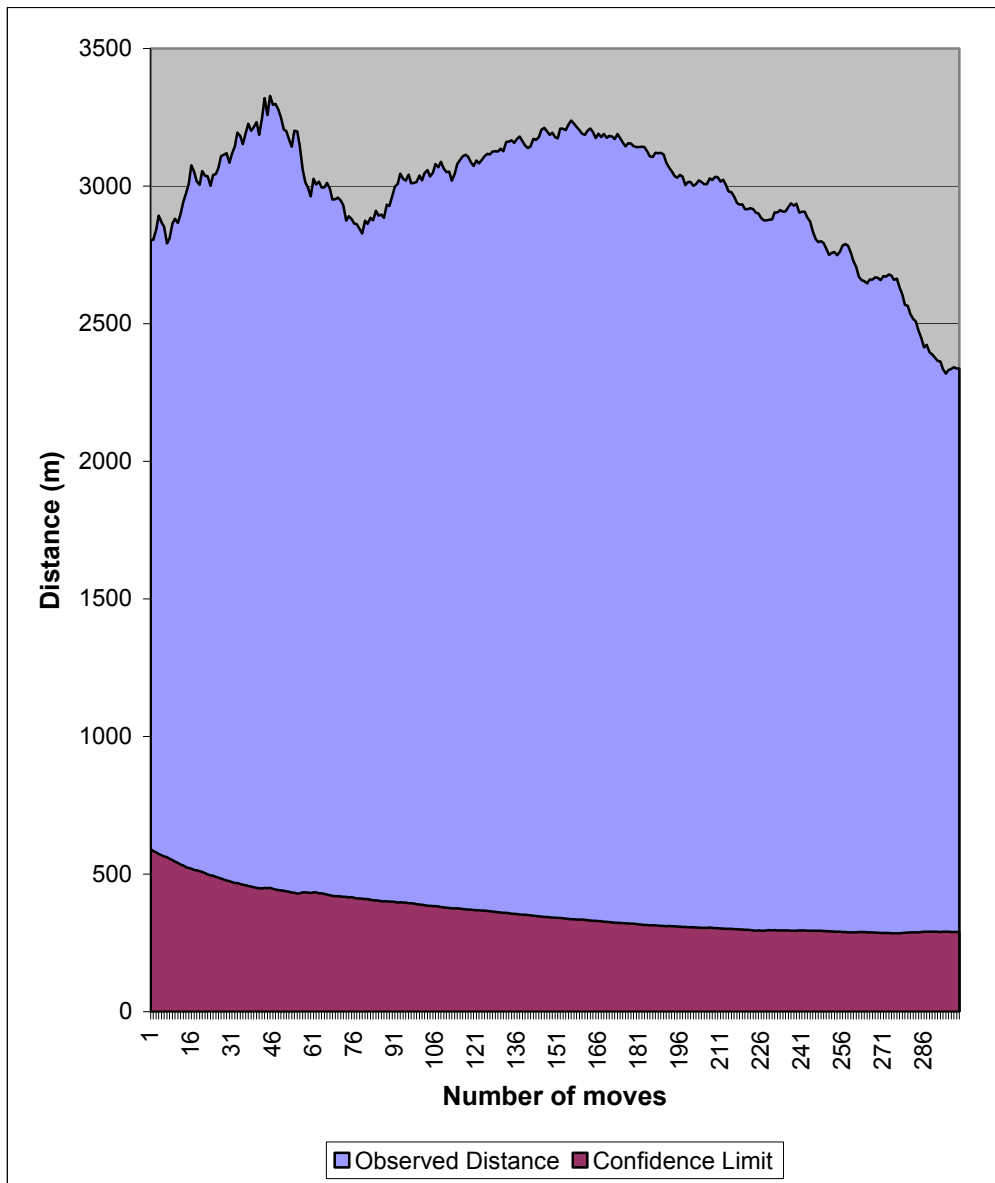


Figure 3.7: Confidence Limits of Distances between Observed and Model *AMC* s by Number of Moves (Panther Number 78).

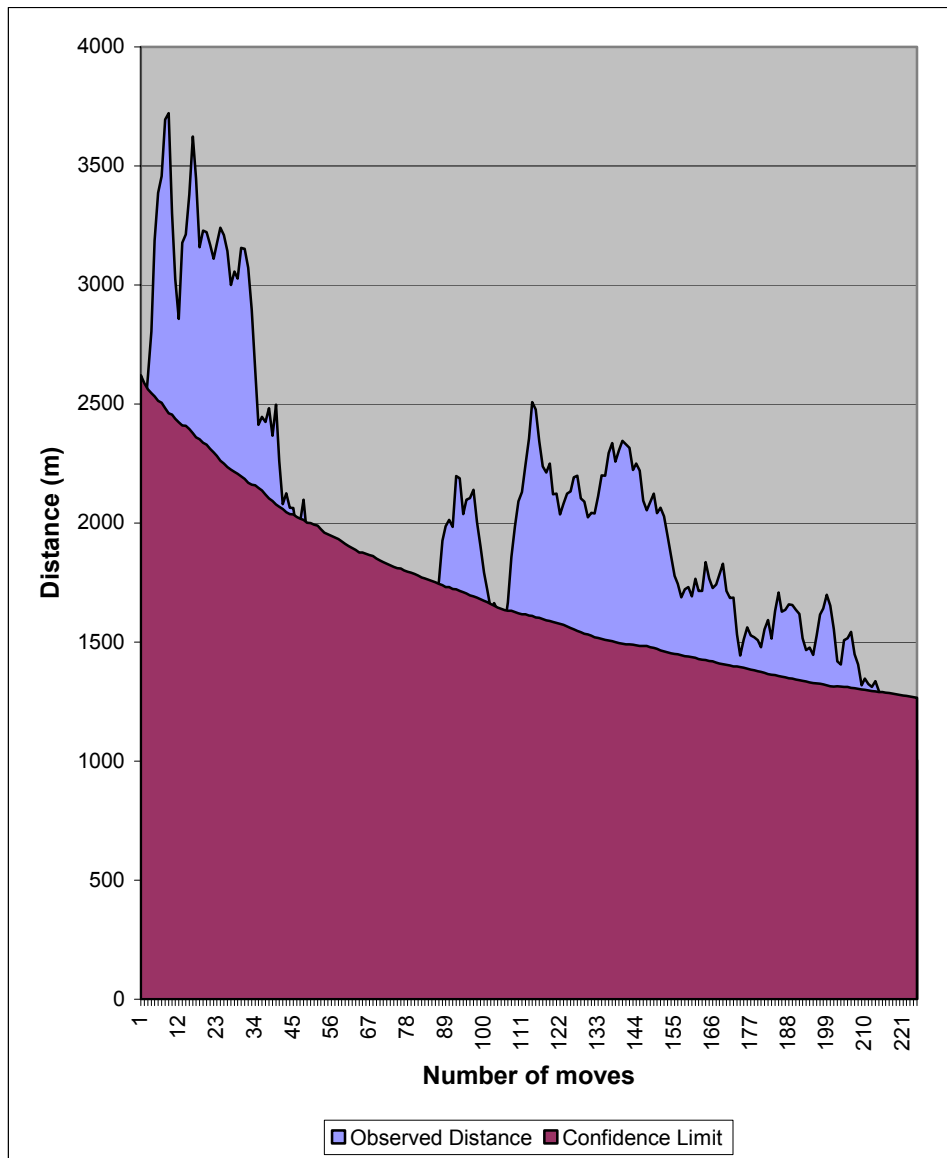


Figure 3.8: Confidence Limits of Distances between Observed and Model *AMC* s by Number of Moves (Panther Number 79).

3.9 Conclusions

Panthers are top carnivores requiring abundant large prey and large home ranges. An adult panther's home range is an area of extensive habitual use, providing resting and denning sites, travel routes, hunting grounds and areas where habitat requirements of their prey are met. Male panthers occupy ranges covering, on average, 518 sq. km., while female home ranges are significantly smaller (219 sq. km.) (Annex 3). In general, home range size depends upon age of the panther. While adult panthers can occupy area as large as 976 sq. km. (mean = 207 sq. km.) in their yearly activity, during old age their activities are confined within an area of 111 sq. km. This is as expected, because as panthers age they may become less energetic and hence less able to defend their home range boundaries.

Age also appeared to be a determining factor affecting the space-use preferences of the panthers. Younger adults prefer to visit areas near their home range boundaries more frequently than panthers in any other age group. These observations can be explained in light of the territorial characteristics of the panther at this age. Adult male panthers regularly indicate their presence along game trails, swamp buggy trails, old logging trams, and forest edges via scrapes containing feces or urine. Adult males maintain primary breeding rights with females in their home ranges [46]. Therefore, it is not surprising that they travel widely to protect their home range from invasion by other male panthers.

As the Panther Model was not available to simulate movement patterns, a random movement model was used. Comparisons of space-use preferences based upon

simulated and observed movement patterns indicate that the random movement model seems to reasonably depict the overall space-use preferences for number 78 and 79, in their composite home ranges. However, slightly different results were obtained when model and observed center of activities were compared. The simulated center of activity of number 78 was significantly different from the observed center throughout the period of comparison. In the case of number 49, these centers of activity were significantly different for a long period at the beginning and then came acceptably closer. This indicates that movement patterns of panthers change over time. Therefore, comparisons based upon movement patterns accumulated over a long period of time might be misleading. Data should be subdivided into different age periods, and the model should be tested in each period.

CHAPTER 4: Conclusions and Future Considerations

4.1 Conclusions

In this thesis, mean distance of the locations of an animal from the nearest boundary of the home range was presented as a simple but useful measure of space-use preferences of the animal under study. Methods based on the distance statistic were applied to the movement data of the Florida panther and the results obtained from the analysis were quite encouraging. The tests based upon the distance statistic revealed an interesting space-use preference pattern, which was strongly associated with the age of the panther. These patterns were consistent with the observations made by ecologists about the vigorous and wide-ranging movement behavior and the protective attitude of the animal towards its home range during its younger years.

Mean distance of the locations from the boundary of home range was also used to compare the modeled and observed space-use preferences of panthers. Selection of panthers number 49, 78 and 79 for comparison was quite purposeful. Distribution of their locations on their corresponding composite home ranges suggested different

space-use preferences. For example, location points of number 49 were more focused towards the center of the home range, and those of number 78 were clustered along the boundaries of its home range. On the other hand, observed locations of number 79 did not reveal any observable space-use preferences, as they were distributed randomly over the entire home range. I used a random movement model to simulate the space-use preferences of these three panthers. Test results confirmed similarity of modeled and observed space-use preferences of numbers 78 and 79. However, tests were unable to detect differences between the patterns of distribution of locations.

Limitations of these methods should be given due consideration during analysis. These limitations are discussed and possible solutions are suggested in the following sections.

4.2 Future Considerations

The following improvements and considerations are recommended to enhance analysis based upon the distance statistic.

1. Pattern Analysis

By definition, the distance statistic measures only distance of the locations from the nearest boundary of home range. It does not, however, take into account the quadrant or the section of the home range in which the points are located. It is quite possible for the point pattern of the observed locations to be completely different from the point pattern of the modeled locations, but yet the means of the observed and

modeled distributions are not significantly different. This can be explained with the help of the following example.

Suppose the rectangles in Figure 4.1a and Figure 4.1b represent home ranges of two different animals and the dots in the rectangle represent their locations at different times. The difference between the distribution patterns of the points in Figure 4.1a and Figure 4.1b is quite visible. In fact, Figure 4.1b was obtained by overlapping the points in the right half and the mirror image of the points in left half of the rectangle in Figure 4.1a. Figure 4.2 presents the identical histograms of the distribution of the distances of these points from the closest side of the corresponding rectangle. In this case if a significance test were conducted, the hypothesis of no difference would not be rejected.

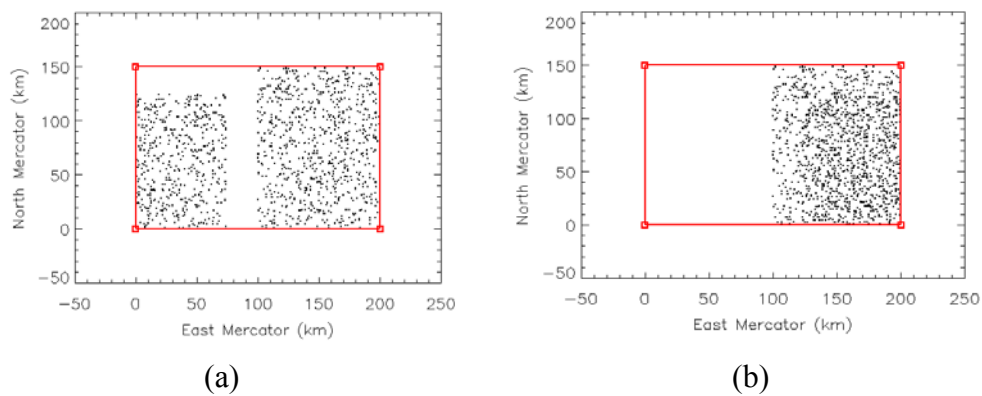


Figure 4.1 Distribution of Locations of Two Hypothetical Panthers

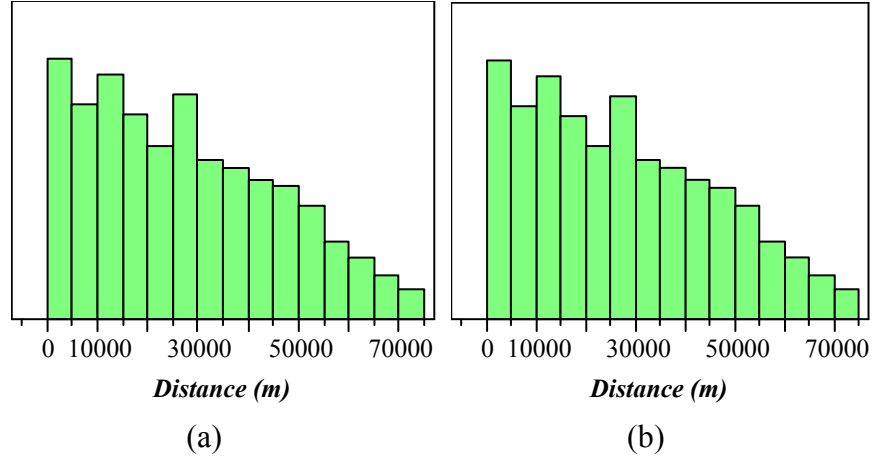


Figure 4.2: Distributions of Distance of Points from the Boundary of (a) Point Pattern 4.1(a) and (b) Point Pattern 4.1(b)

Therefore, care should be taken when interpreting the results of tests based upon the distance statistic. Rejection of the hypothesis of no difference means only that the average distance of the locations from the nearest boundary of the home range for observed and modeled movement patterns were not significantly different. Equality of mean distances should not be interpreted as similarity of movement patterns.

Usefulness and applicability of the distance statistic can be significantly improved if used in association with methods developed for pattern analysis. Some of the methods that can be used to analyze point patterns are the quadrant method, kernel estimation and the nearest neighbor distance method. Further references on these methods can be found in Dale *et al.* [15] and Bailey *et al.* [2].

2. Independence of Observations

Methods discussed in this thesis require that the input data (i.e. locations of panther) be statistically independent. It was assumed that each location contributes as much information as every other location. If two locations are not independent, the sum of the information contributed by the two data points is not 2 units but less than 2 units, because one of the locations can be used to make a reasonable estimate of the other. Since tracking data are three dimensional, the closer in time two locations are taken, the less likely they are to be statistically independent. In other words, given the animal's location at time t , the expected change in location would be small for a small increase in time, $t+\Delta t$. As the interval between two times becomes greater, the probability that the second location can be known, given the first, becomes small. In the presence of auto correlation, the statistical estimate for a sample will be biased. Tests of independence and methods for resampling data should be applied to avoid this problem. To ensure temporal independence of the locations, ecologists often fix an independence interval based on the attributes of the ranging behavior of the animal, and then resample the locations using that interval. In this research, I assumed that a 48-hour interval between two consecutive observations would be sufficient to ensure temporal independence of the observations. However, fixing independent intervals in this way was subjective and, therefore, use of some functionally correct method of estimating independent intervals would be appropriate.

Reliability and statistical validity of the results can be improved by ensuring statistical independence of the observations. Although the independence of activity data is particularly hard to assess, as it is not set by any fixed parameter, some sophisticated methods for testing the independence of the locations [22,23] and estimating the independence interval [58] are available and can be used to evaluate panther data.

3. Selection of Normalization Factor

To normalize the effect of home range size on the distribution of d_i s distance, each location was divided by the square root of the area of the corresponding home range. This approach assumes that mean distance is directly proportional to square root of the area of the home range, which may not be equally true in all cases, especially for home ranges that have the shape of an elongated polygon (length is considerably greater than width). Therefore, other normalization factors, e.g. maximum of d_i s, should also be considered and their relative advantages should be compared.

4. Sampling of Locations

One of the criteria for selecting samples for this analysis was to exclude panthers with 10 percent or more inconsistent observations (observations that did not fit the standard *three times per week* pattern). Therefore, the sample used in this research did not represent the entire monitored panther population. This sampling error should be minimized by using resampling techniques, ensuring that sample locations are equally spaced in time.

5. Data Sufficiency

It is widely recognized that panthers exhibit distinct daily patterns in activities and habitat use. During non-daylight hours, they roam widely across the mosaic of habitats within their home range, with peaks of activity around dusk and dawn. Panthers are typically at rest in dense cover during the day, when monitoring flights are made [46]. The telemetry data are therefore not representative of 24-hour activity patterns; rather they represent the pattern of resting sites of the panther within its home range. Analysis presented herein uses these telemetry locations to delineate the general boundary of home ranges and activity areas and to evaluate and compare patterns of daytime resting sites of panthers.

References

- [1] Angevine, M.W., and S.N. Handel. 1986. Invasion of forest floor space, clonal architecture and population growth in the perennial herb *clintonia borealis*. *Journal of Ecology* **74**: 547-560.
- [2] Bailey, C.T., Gatrell A.C. 1995. *Interactive Spatial Data Analysis*. Longman Group Limited, Essex, UK.
- [3] Banks, H.T., P.M. Karevia, and K. Murphy. 1987. Parameter estimation techniques for interaction and redistribution models: a predator-prey example. *Oecologia* **74**: 356-362.
- [4] Belden, R.C., W. Frankenberger, R.T. Mc Bird, and T.S. Schwikert. 1988. Panther habitat use in southern Florida. *Journal of Wildlife Management* **57**: 388-397.
- [5] Bell, W.J. 1991. *Searching Behaviour: The Behavioural Ecology of Finding Resources*. Chapman and Hall, London.
- [6] Bond, A.B. 1980. Optimal foraging in a uniform habitat: the search mechanism of the green lacewing. *Animal Behaviour* **28**: 10-19
- [7] Boulanger, J.G., and G.C White. A comparison of home range estimators using Monte Carlo simulation. *Journal of Wildlife Management* **54**: 310-315.
- [8] Breckling, B., and H. Reuter. 1996. The use of individual-based models to study the interaction of different levels of organization to ecological systems. *Senckenbergiana maritima*, **27**(3/6): 195-205.
- [9] Brown, L.E. 1962. Home range in small animal communities. *Survey of Biological Progress* (ed. B. Glass) **4**: 131-179. Academic Press, New York, NY.
- [10] Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mamalogy* **24**: 346-352.
- [11] Comiskey, E. J., L. J. Gross, D. M. Fleming, M. A. Huston, O. L. Bass, Jr., H. K. Luh and Y. Wu. 1994. A Spatially-explicit individual-based simulation model for Florida panther and white-tailed deer in the Everglades and Big Cypress landscapes. *Proceedings of the Florida Panther Conference* (ed. Dennis Jordan) pp. 494-503. U. S. Fish and Wildlife Service, Ft. Myers, FL.
- [12] Comiskey, E. J., O.L. Bass, Jr., L.J. Gross, R.T. McBride, and R.A. Salinas. 2002. Panthers and forests in South Florida: an Ecological Perspective. *Conservation Ecology* **18**. [online] URL: <http://www.consecol.org/Journal/vol6/iss1/art18/manuscript.html>

- [13] Conover, W.J. 1980. *Practical Nonparametric Statistics*. John Wiley & Sons, Inc. New York, NY.
- [14] Crist, T.O., D. S. Guertin, J. A. Wiens, B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* **6**: 536-544.
- [15] Dale, Mark R.T. 1998. *Spatial Pattern Analysis in Plant Ecology*. University Press Cambridge, UK.
- [16] DeAngelis, D., and L. Gross, editors. 1992. *Individual-Based Models and Approaches in Ecology: Populations, Communications and Ecosystems*. Chapman and Hall, New York, NY.
- [17] DeAngelis, D., K. Rose, and M. Huston. 1994. Individual-oriented approaches to modeling ecological populations and communities. *Frontiers in Mathematical Biology* (ed. S. Levin), pp. 390-414. Springer-Verlag, Berlin.
- [18] DeAngelis, D., L. J. Gross, M. A. Huston, W. F. Wolff, D. M. Fleming, E. J. Comiskey, and S. M. Sylvester. 1998. Landscape modeling for Everglades ecosystem restoration. *Ecosystems* **1**:64-75.
- [19] Dees, C. S., J. D. Clark, and F. T. Van Manen. 2001. Florida panther habitat use in response to prescribed fire. *Journal of Wildlife Management*, **65**:141-147.
- [20] Dickinson, G.J. 1976. *Nonparametric Statistics*. Holt, Rinehart and Winston. New York, NY.
- [21] Dixon, K.R., and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* **61**:1040-1044.
- [22] Dunn J.E. 1978. Computer programs for the analysis of radio telemetry data in the study of home range. *Stat. Lab. Tech. Rep. No. 7*. University of Arkansas, Fayetteville, AK.
- [23] Dunn, J. E. and P.S. Brisbin, Jr. 1982. Characterization of the multivariate Ornstein-Uhlenbeck diffusion process in the context of home range analysis. *Stat. Lab. Tech. Rep. No. 16*. University of Arkansas, Fayetteville, AK.
- [24] Dunn, J. E., and P. Gipson. 1977. Analysis of radio telemetry data in studies of home range. *Biometrics* **33**:85-101.
- [25] Dunn, J.E. 1977. Analysis of radio telemetry data in studies of home range. *Biometrika* **33**: 85-101.

- [26] Fahse, L., C. Wissel, and V. Grimm. 1998. Reconciling classical and Individual-Based approaches in theoretical population ecology: a protocol for extracting population parameters from Individual-Based Models. *The American Naturalist* **152**: 838-852.
- [27] Gardener, R.H., R.V. O'Neill, M.G. Turner, and V.H. Dale. (1989) Quantifying scale- dependent effects of animal movement with simple percolation models. *Landscape Ecology* **3**:217-227.
- [28] Harris, S., W.J. Cresswell, P.J. Forde, W.J. Trehwella, T. Woollard, and S. Wray. 1990. Home range analysis using radio-tracking data - a review of problems and techniques particularly as applied to study of mammals. *Mammal Review* **20**: 97-123.
- [29] Hayne, D.W. 1949. Calculation of size of home range. *Journal of Mammalogy* **30**:1-18.
- [30] Hogweg P., and B. Hesper. 1990. Individual-oriented modeling in ecology. *Mathematical Computational Modeling*, **13**(6): 83-90.
- [31] Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *Biosciences* **38**:682-691.
- [32] Janis, M.W. 1999. *The effects of recreational deer and hog hunting on the behavior of Florida panthers*. M. S. Thesis. University of Tennessee, Knoxville, TN.
- [33] Jennrich, R.I., and F.B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* **22**:227-237.
- [34] Johnson, A.R., B.T. Milne, and J.A. Wiens. 1992. Diffusion in fractal landscapes: simulation and experimental studies of tenebrionid beetle movements. *Ecology* **73**: 1968-1983.
- [35] Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **49**: 629-642.
- [36] Kareiva P.M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* **56**:234-238.
- [37] Kareiva, P.M. 1982. Experimental and mathematical analysis of herbivore movements: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52**:261-282.

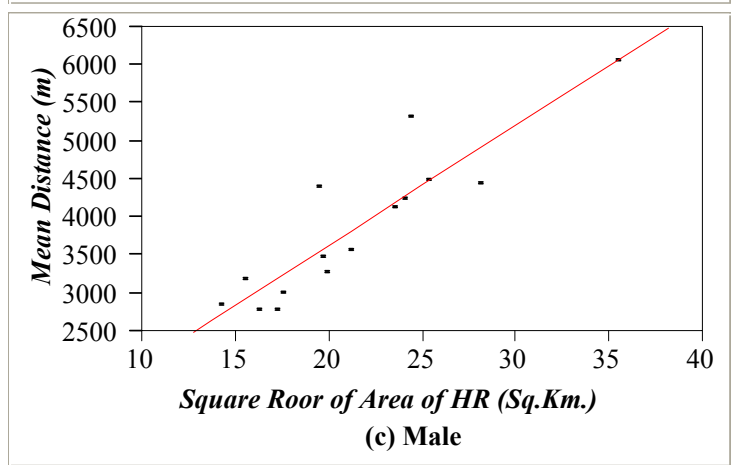
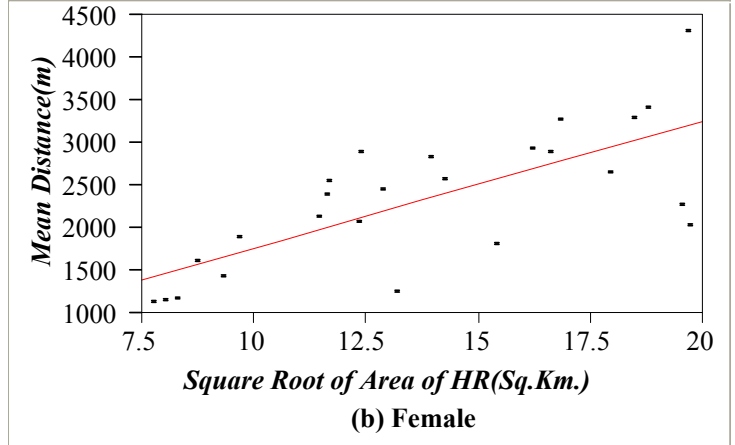
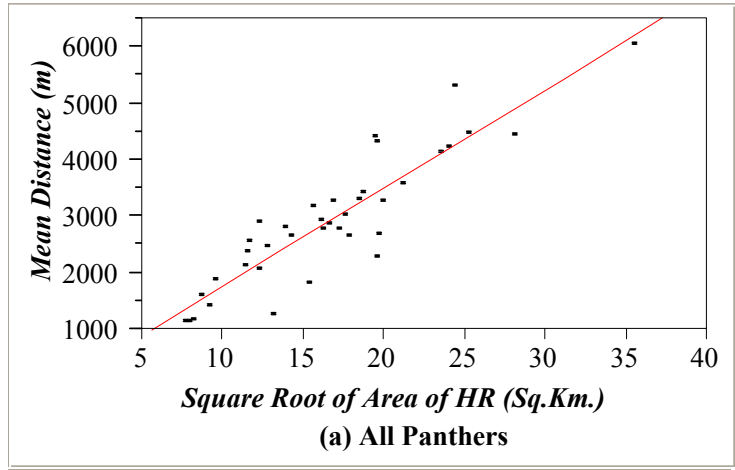
- [38] Kareiva, P.M., and G. Odell. 1987. Swarm of predators exhibit prey taxis if individual predators use area restricted search. *American Naturalist* **130**: 233-270.
- [39] Kareiva, P.M.1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London B* **330**: 175-190.
- [40] Koepl, J. W., N. A. Slade, and R. S. Hoffmann. 1977. Distance between observations as an index of average home range size. *American Midland Naturalist* **98**: 476-482.
- [41] Koepl, J.W., N.A. Slade, and R.S. Hoffman. A bivariate home range model with possible application to ethological data analysis. *Journal of Mammalogy* **56**:81-90
- [42] Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology* **68**: 1092-1101.
- [43] Levin, S.A. 1974. Dispersion and population interactions. *American Naturalist* **108**: 207-228.
- [44] Loehle, C. 1990. Home range: a fractal approach. *Landscape Ecology* **5**: 39-52.
- [45] Lomnicki A. 1988. *Population Ecology of Individuals*. Princeton University Press, Princeton, NJ.
- [46] Maehr, S.D. 1998. *The Florida Panther: Life and Death of a Vanishing Carnivore*. Island Press, Washington D.C.
- [47] McCulloch, C.E., M.L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. *Ecology* **70**: 383-388.
- [48] McIntyre, N.E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes Hispilabris* (Coleoptera: Tenebrionidae) (in notes and discussion). *American Midland Naturalist* **138**: 230-235.
- [49] Metz, J.A, and O. Diekmann, editors. 1986. *The dynamics of Physiologically Structured Populations*. Springer-Verlag, Berlin.
- [50] Milne, B.T., M.G. Turner, J.A. Wiens, and A.R. Johnson. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology* **41**:337-353.

- [51] Mohr, C.O. 1947. Table of Equivalent populations of North American mammals. *American Midland Naturalist* **37**: 223-249.
- [52] Mohr, C.O., and W.A. Stumpf. 1966. Comparison of methods for calculating areas of animal activity. *Journal of Wildlife Management* **30**:293-304.
- [53] Murdie, G., and M.P. Hassel. 1973. Food distribution, searching success, and predator-prey models. *The Mathematical Theory of the Dynamics of Biological Populations* (eds. M.S. Barlett, and R.W. Hiorns), pp. 87-101. Academic Press, London.
- [54] Murdoch, W.W., E. McCauley, R.M. Nisbet, W.S.C. Gurney, and A.M. de Roos. 1992. Individual-based models: combining testability and generality. *Individual-Based Models and Approaches in Ecology* (eds. D. DeAngelis and L. Gross) pp. 18-35. Chapman and Hall, New York, NY.
- [55] Neft, D.S. 1966. Statistical analysis for areal distributions. *Monograph Series Number 2*. Regional Science Research Institute, Philadelphia, Pennsylvania, USA.
- [56] Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York.
- [57] Pyke, G.H. 1984. Animal movements: an optimal foraging approach. *The Ecology of Animal Movement* (eds. I.R. Swingland, and P.J. Greenwood), pp. 7-31. Clarendon Press, Oxford.
- [58] Salvatori, V., A.K. Skidmore, F. Corsi, and F. van der Meer. 1999. Estimating temporal independence of radio-telemetry data on animal activity. *Journal of Theoretical Biology* **198**: 567-574.
- [59] Siniff, D.B., and C.R. Jessen. 1969. A simulation model of animal movement patterns. *Advance Ecological Research*, **6**:185-217.
- [60] Skellam, J.G. 1973. The formulation and interpretation of mathematical models of diffusory processes in population biology. *The Mathematical Theory of the Dynamics of Biological Populations* (ed. M.S. Bartlett, and R.W. Hiorns), pp 63-85. Academic Press, London.
- [61] Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effect of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* **129**: 533-552.
- [62] Swihart, R.K., and J.H. Torrie. 1960. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management* **49**:1019-1025.

- [63] Swihart, R.K., N.A. Slade, and Bergstrom, B.J. 1988. Relating body size to the rate of home range use in mammals. *Ecology* **69**: 393-399.
- [64] Thomas, S.C. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri forest, Zaire. *Biotropica* **23**: 68-83.
- [65] Tufto, J.R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small Cervid: the roe deer. *Journal of Animal Ecology* **65**: 715-724.
- [66] Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**: 1253-1266.
- [67] Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associated Press, Inc. Publishers, MA.
- [68] Weiss S.B., and D.D. Murphy. 1988. Fractal Geometry and caterpillar dispersal: or how many inches can inchworms inch? *Functional Ecology* **2**: 116-118.
- [69] White, G.C., and R.A. Garrott. 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, Inc. San Diago, Ca.
- [70] Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* **59**: 794-800.
- [71] Worton, B.J. 1995. A convex hull-based estimator of home-range size. *Biometrics* **51**: 1206-1215.

Appendix

ANNEX 1: Relationship Between Area of 95% MCP HR and Mean Distance of Locations from the Nearest Boundary



ANNEX 2: One-way Analysis of 95% MCP Area (sq. km.) By Sex

Summary of Fit

<i>Rsquare</i>	0.465261
<i>Adj Rsquare</i>	0.46524
<i>Root Mean Square Error</i>	153.0893
<i>Mean of Response</i>	323.023
<i>Observations (or Sum Wgts)</i>	25483

t-Test

	<i>Difference</i>	<i>t-Test</i>	<i>DF</i>	<i>Prob > t </i>
<i>Estimate</i>	-299.66	-148.897	25481	0.0000
<i>Std Error</i>	2.01			
<i>Lower 95%</i>	-303.60			
<i>Upper 95%</i>	-295.71			

Assuming equal variances

Analysis of Variance

<i>Source</i>	<i>DF</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>F Ratio</i>	<i>Prob > F</i>
<i>Sex</i>	1	519590431	519590431	22170.31	0.0000
<i>Error</i>	25481	597180835	23436.319		
<i>C. Total</i>	25482	1116771265			

Means for Oneway Anova

<i>Level</i>	<i>Number</i>	<i>Mean</i>	<i>Std Error</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
<i>Female</i>	16600	218.568	1.1882	216.24	220.90
<i>Male</i>	8883	518.223	1.6243	515.04	521.41

Std Error uses a pooled estimate of error variance

Means and Std Deviations

<i>Level</i>	<i>Number</i>	<i>Mean</i>	<i>Std Dev</i>	<i>Maximum</i>	<i>Minimum</i>	<i>Std Err Mean</i>
<i>Female</i>	16600	218.568	105.217	390	61	0.8166
<i>Male</i>	8883	518.223	215.745	1268	204	2.2891

ANNEX 3: Summary Statistics of 95% Home Range Sizes by Age and Sex

<i>Characteristics</i>	<i>Frequency</i>	<i>95% MCP Home Range Size</i>			
		<i>Mean</i>	<i>SD</i>	<i>Minimum</i>	<i>Maximum</i>
<i>Sex</i>					
<i>Female</i>	<i>25</i>	<i>206.08</i>	<i>110.9</i>	<i>61</i>	<i>390</i>
<i>Male</i>	<i>15</i>	<i>493.27</i>	<i>272.4</i>	<i>204</i>	<i>1268</i>
<i>Age</i>					
<i>Less than 5</i>	<i>85</i>	<i>178.5</i>	<i>143.26</i>	<i>25</i>	<i>1104</i>
<i>5 to 7</i>	<i>67</i>	<i>206.9</i>	<i>160.59</i>	<i>12</i>	<i>976</i>
<i>8 to 10</i>	<i>51</i>	<i>234.2</i>	<i>298.01</i>	<i>30</i>	<i>1873</i>
<i>11 to 13</i>	<i>24</i>	<i>171.9</i>	<i>126.53</i>	<i>49</i>	<i>533</i>
<i>14 and above</i>	<i>8</i>	<i>111.1</i>	<i>25.95</i>	<i>78</i>	<i>136</i>

ANNEX 4: One-way Analysis of Normalized Distance By Sex

Summary of Fit

<i>Rsquare</i>	<i>0.000108</i>
<i>Adj Rsquare</i>	<i>0.000069</i>
<i>Root Mean Square Error</i>	<i>111.3805</i>
<i>Mean of Response</i>	<i>177.7026</i>
<i>Observations (or Sum Wgts)</i>	<i>25483</i>

t-Test

	<i>Difference</i>	<i>t-Test</i>	<i>DF</i>	<i>Prob > t </i>
<i>Estimate</i>	<i>-2.4296</i>	<i>-1.659</i>	<i>25481</i>	<i>0.0971</i>
<i>Std Error</i>	<i>1.4642</i>			
<i>Lower 95%</i>	<i>-5.2995</i>			
<i>Upper 95%</i>	<i>0.4403</i>			

Assuming equal variances

Analysis of Variance

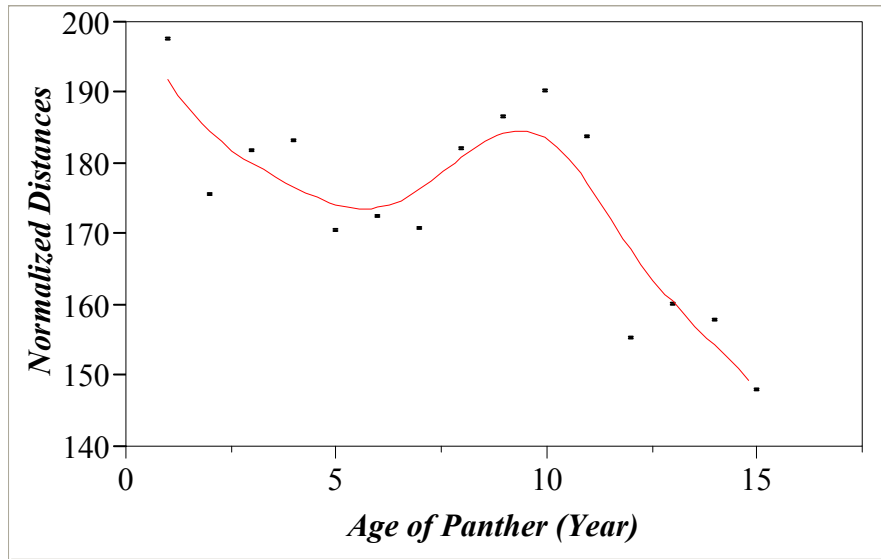
<i>Source</i>	<i>DF</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>F Ratio</i>	<i>Prob > F</i>
<i>Sex</i>	<i>1</i>	<i>34158</i>	<i>34158.4</i>	<i>2.7535</i>	<i>0.0971</i>
<i>Error</i>	<i>25481</i>	<i>316107255</i>	<i>12405.6</i>		
<i>C. Total</i>	<i>25482</i>	<i>316141413</i>			

Means for One-way ANOVA

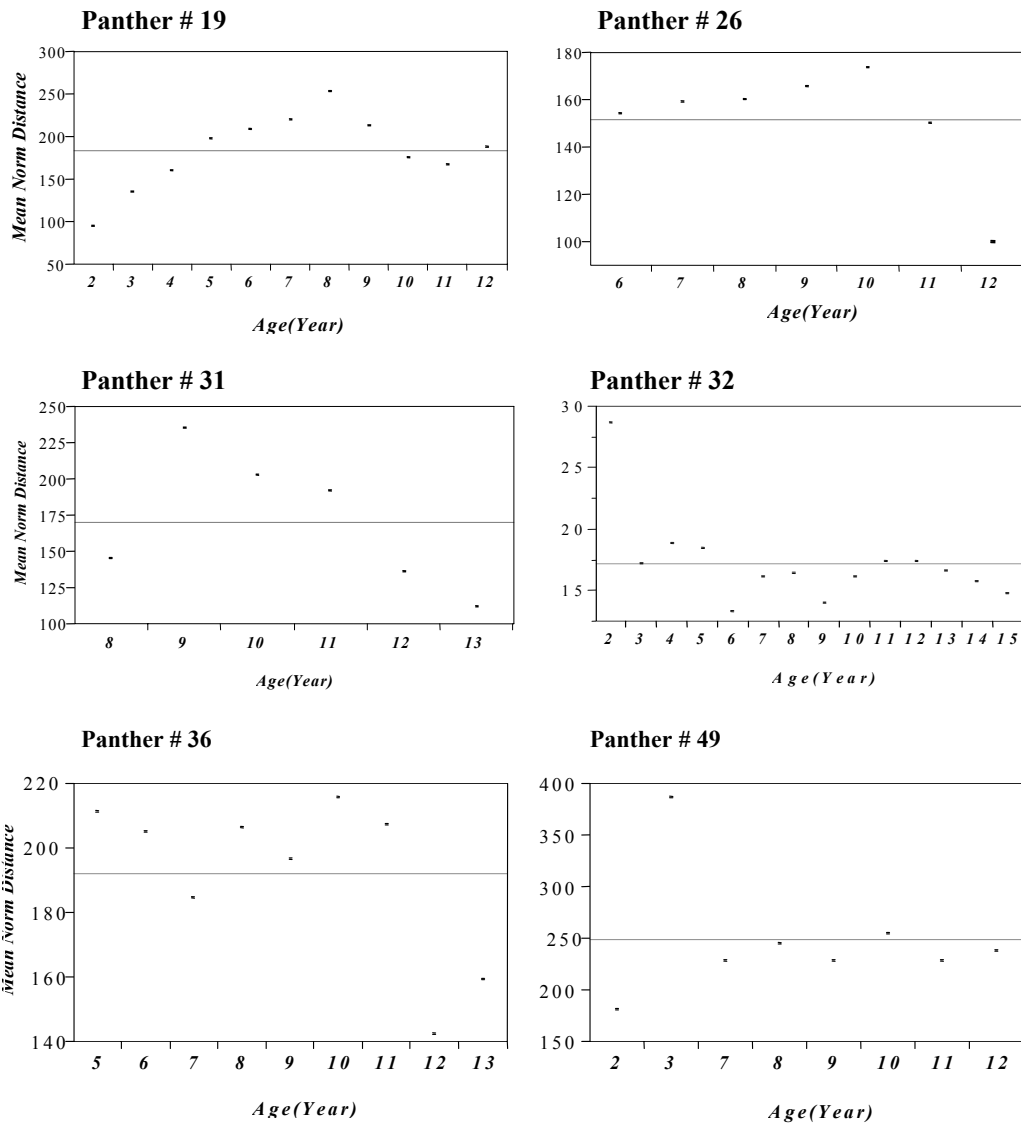
<i>Level</i>	<i>Number</i>	<i>Mean</i>	<i>Std Error</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
<i>Female</i>	<i>16600</i>	<i>176.856</i>	<i>0.8645</i>	<i>175.16</i>	<i>178.55</i>
<i>Male</i>	<i>8883</i>	<i>179.285</i>	<i>1.1818</i>	<i>176.97</i>	<i>181.60</i>

Std Error uses a pooled estimate of error variance

ANNEX 5: Relationship Between Age of Panther and Normalized Distances



ANNEX 6: Mean Normalized Distances by Age of Panthers # 19, 26, 31, 32, 36 and 49



ANNEX 7: Comparison of Mean $norm(d_j)$ for All Age-group Pairs using Tukey's test.

Comparisons for all pairs using Tukey-Kramer HSD

q*
2.56921

<i>Abs(Dif)-LSD</i>	4	3	1	2
4	-13.776	-8.134	-1.653	7.696
3	-8.134	-6.038	0.842	10.140
1	-1.653	0.842	-4.125	5.146
2	7.696	10.140	5.146	-4.387

Positive values show pairs of means that are significantly different at 5% level of significance.

ANNEX 8: One-Way Analysis of Normalized Distances by Season.

Summary of Fit

<i>Rsquare</i>	<i>0.000014</i>
<i>Adj Rsquare</i>	<i>-0.00003</i>
<i>Root Mean Square Error</i>	<i>111.3857</i>
<i>Mean of Response</i>	<i>177.7026</i>
<i>Observations (or Sum Wgts)</i>	<i>25483</i>

t-Test

	Difference	t-Test	DF	Prob > t
<i>Estimate</i>	<i>-0.8299</i>	<i>-0.594</i>	<i>25481</i>	<i>0.5522</i>
<i>Std Error</i>	<i>1.3962</i>			
<i>Lower 95%</i>	<i>-3.5664</i>			
<i>Upper 95%</i>	<i>1.9067</i>			

Assuming equal variances

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
<i>Season</i>	<i>1</i>	<i>4384</i>	<i>4383.5</i>	<i>0.3533</i>	<i>0.5522</i>
<i>Error</i>	<i>25481</i>	<i>316137030</i>	<i>12406.8</i>		
<i>C. Total</i>	<i>25482</i>	<i>316141413</i>			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
<i>Dry</i>	<i>12355</i>	<i>177.275</i>	<i>1.0021</i>	<i>175.31</i>	<i>179.24</i>
<i>Wet</i>	<i>13128</i>	<i>178.105</i>	<i>0.9721</i>	<i>176.20</i>	<i>180.01</i>

Std Error uses a pooled estimate of error variance

Vita

Dinesh Sharma graduated in 1990 from HNB Garhwal University, India with a Master of Science degree in Statistics. Following completion of his master's, Dinesh returned to his home country, Nepal, to teach Statistics at Tribhuban University in Kathmandu, where he served as a Lecturer of Statistics for 10 years.

In August 2000, he entered the Master's Program in Applied Mathematics at the University of Tennessee and graduated in August 2002. Currently he is pursuing a Ph. D. degree in Statistics at the Florida State University, Tallahassee.