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Computer assisted home range analysis of tule elk in the Diablo range of California

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COMPUTER ASSISTED HOME RANGE ANALYSIS OF TULE ELK IN THE DIABLO RANGE OF CALIFORNIA

A Thesis
Presented to
The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

By
Kathleen E. Duncan
May, 1988

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Abstract

Radiotelemetry data for 5 tule elk (*Cervus elaphus nannodes*) were analyzed for independence between consecutive observations, similarities and differences between ground and aerial data, and changes in patterns of home range utilization. These analyses were used to assess the relative value of different techniques for determining home range characteristics and were the basis for recommendations for future studies.

Current tests of independence were found to be inappropriate for these data and an alternative method for assessing independence was discussed. Changes in patterns of home range utilization were found to be important for organizing data into appropriate temporal subsets.

There was no single best technique for home range analysis. Comparisons of home range sizes for different times, habitats, and animals employed fast Fourier transform analysis of aerial data. Techniques that do not assume statistical independence (minimum polygon, minimum convex polygon, and modified minimum area method) were most appropriate for analysis of data sets containing ground observations. These findings have wide applicability for other studies with large mammals.

Acknowledgements

As I conclude this work I find there are many people I wish to acknowledge. First and foremost I would like to thank Julie Phillips and Michael Kutilek for their unfailing faith and support throughout this project and especially for making me an offer I could not refuse. Without their efforts this work would not have begun, much less have been completed.

I gratefully acknowledge the skills and patience of my committee: Drs. Michael Kutilek, Howard Shellhammer and William Bros. Their questions and comments consistently lent clarity and focus to this project. My compliments to Dr. William Bros who joined this project near its completion and brought a level of statistical, computer graphic and writing expertise that allowed me to sharpen my knowledge, understanding and skill.

I especially wish to thank Dr. Howard Shellhammer for the considerable amount of administrative detail and paperwork he has handled on my behalf and for his incredible patience when I usurped his computer and assailed him with questions on traditional ecology. He always greeted my efforts with tolerance and humor. Although sometimes received without appreciation, I recognize that his role often was to urge all involved to do more, sooner. I question whether my deadline would have been met with out his aid.

A special thanks once more to Dr. Michael Kutilek for his extensive editing of this manuscript. I look forward to submitting this work for publication with his name as second author. His role as mentor, teacher, confidant and friend will always be a cherished part of my experience at this University.

Now I must thank my many friends and colleagues. Rick Hopkins introduced me to this field many years ago. Our many conversations have enriched this project. Vicki Jennings, Dr. Vida Kenk, Julie Phillips, and William Minkel provided assistance with my teaching duties throughout this last year. Dr. Robert Fowler's support and flexibility with my ongoing studies has been indispensable. Lola Arnold provided graphics support. My collaboration with Janet Carr provided considerable insight.

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Last, but never least, my warmest thanks to my family: Laurie Mercer, Deanna Sentelik and Eric Duncan. Eric's computing and text processing skills were essential for the completion of this project. His financial and moral support for my personal and professional growth are greatly appreciated. Without his patience, understanding and support, this manuscript, indeed the last two years, would not have been possible.

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Introduction

Home range analysis is the study of how much land area is required to support an animal's daily activities and how the land is used. I will refer to the former as the home range size and the latter as the internal anatomy of the home range. Investigators may choose from numerous techniques for analyzing home range including minimum polygon (MP), minimum convex polygon (MCP), modified minimum area method (MMAM), bivariate normal (BVN), weighted bivariate normal (WBVN), harmonic mean (HMEAN) and fast Fourier transform (FFT). Recommendations of which techniques should be used to answer specific biological questions are generally not available for large mammal studies.

I discuss the practical issues that must be addressed before beginning an analysis, specifically independence between consecutive observations, similarities and differences between ground and aerial data, and changes in home range utilization during the study. Radiotelemetry data for 5 tule elk (Cervus elaphus nannodes) are analyzed for these 3 criteria and the results used to explore the relative value of each of the techniques for analyzing home ranges. While the assumptions, capabilities and limitations of the techniques are discussed here, the biological implications for this elk herd are reserved for a later publication.

Methods

In December 1980, 21 tule elk were relocated to the San Felipe ranch in the Diablo range of California by the California Department of Fish and Game. Four elk maintained functional radio-collars for the next 3 years and one other elk maintained a functional radio-collar for the next 2 years. These 5 elk were the source of the locational data used herein. From March 1981 thru February 1984 radiotelemetry data on elk locations were collected by ground and fixed-wing aircraft observers (Phillips 1985).

Aerial observations used triangulation (56%) and visual (44%) sightings to determine the UTM coordinates of the animals. Ground observations also included both visual (78%) and triangulation (22%) sightings. The number of elk observed in a single sighting varied from 1 to 23 animals. The minimum time interval between observations was 24 hours for both ground and aerial data (Phillips 1985).

The data were organized into temporal subsets. I first examined the data over 3 separate years: March 1, 1981 to February 28, 1982; March 1, 1982 to February 28, 1983; and March 1, 1983 to February 27, 1984. Each year was then organized into 4 seasons: Spring (March 1 to May 31), Summer (June 1 to August 31), Fall (September 1 to November 30), and Winter (December 1 to February 28). Two other data organizations were used: dry (April 1 to September 30) and wet (October 1 to March 31) seasons, and rutting (August 1 to October 31) and nonrutting (November 1 to July 31) seasons. The minimum sample size for all calculation techniques was 10 observations.

I tested the assumption that consecutive observations were independent by comparing the mean distance between consecutive points to the mean distance between each point and the arithmetic center of the data (Swihart and Slade 1985). Comparisons between home range areas using ground and aerial data separately were made only when the percentage difference in sample size was <33%. Comparisons were made between differences in 50% home range areas (FFT analysis) (Anderson 1982). A percentage difference was calculated as the difference between the ground and aerial areas divided by the maximum value of the ground and aerial areas times 100.

Cramer von Mises goodness of fit tests (Stephens 1974) were used to determine if data were bivariate normally or weighted bivariate normally distributed. I used nearest neighbor analysis (Diggle 1979) to evaluate whether data were uniformly distributed (Samuel and Garton 1985).

Program home range (Samuel et al. 1985) was used to perform MCP, BVN, and WBVN home range analyses, the test of independence, and the goodness of fit tests. Program AND and Micro DIXON (Timossi and Barrett 1985) were used to perform the FFT and HMEAN analyses, respectively. Graphic analysis and program MMAM developed by the author were used for the MMAM analyses. Graphic analysis identified temporal trends in home range size, using 50% home range sizes (FFT analysis) for aerial data sets and 100% home range sizes (MCP analysis) for data sets combining ground and aerial observations.

Results

Aerial data organized by years, nonrut, wet and dry seasons tended to be significantly autocorrelated. Most data organized by rutting and 4 seasons and most of the data sets (66%) for elks 282 and 360 were independent (Table 1). There was no linear relationship between sample size and independence.

Estimates of home range size based on ground data were consistently less than estimates based on aerial data for elks 240, 282 and 330. This observation was true for 77% of the data sets for elk 315 and 54% of the data sets for elk 360 (Tables 2 - 5). For data organized by years, the difference in the calculated home range size using aerial versus ground data ranged from 27 to 91% (Table 2). The range of differences were similar (17 to 88%) for data organized by rutting and nonrutting seasons (Table 3). Differences for data organized by 4 seasons ranged from 1 to 86% (Table 4). When data were organized by wet and dry seasons, differences ranged from 4 to 92% (Table 5).

Table 1. Ratios for test of independence between consecutive aerial observations for tule elk in the Diablo Range of California.

		Elk	Collar	Frequency		
Season	Year	240	282	315	330	360
Year	1981	0.50**	0.77**	0.38**	1.28*	0.51**
Year	1982	0.25**	1.11*	0.41**	0.29**	1.79
Year	1983	0.36*	--	1.03	0.62**	0.95*
Spring	1981	1.67	2.39	0.78*	2.69	1.20
Summer	1981	0.85	2.07	2.07	2.07	2.07
Fall	1981	1.40	1.42	1.41	1.41	1.42
Spring	1982	0.44*	1.19	na	na	2.08
Summer	1982	--	--	0.55*	0.36*	1.82
Fall	1982	--	--	0.61*	na	1.76
Dry	1981	0.54**	1.58	0.48**	2.45	0.88*
Wet	1981	0.21**	0.34**	0.47**	0.33**	0.47**
Dry	1982	na	1.23	0.56**	0.57**	1.86
Wet	1982	0.58**	--	0.75*	0.29**	1.82
Dry	1983	--	--	1.59	--	1.59
Wet	1983	--	--	--	--	0.70*
Nonrutting	1981	0.65**	2.18	0.56**	2.64	0.78*
Rutting	1981	1.18	1.18	1.18	1.18	1.18
Nonrutting	1982	0.09**	0.31**	0.51**	0.42**	0.63**
Rutting	1982	--	--	0.98	0.98	2.07
Nonrutting	1983	0.43**	--	1.59	0.42**	1.55

* statistically significant autocorrelation (p < .005).
** statistically significant autocorrelation (p < .0005).
-- sample size < 10.

Table 2. Comparison of annual home range sizes for tule elk in the Diablo Range of California (fast Fourier transform analysis, 50% utilization distribution).

Elk	Year	50% Home range size (km^2) Aerial Size	Aerial n	Ground Size	Ground n	Percentage difference in home range size
240	1981	4.02	45	2.08	62	48.3
282	1981	2.52	46	1.19	58	52.8
315	1981	6.16	46	0.55	55	91.1
315	1982	4.39	43	0.87	54	80.2
330	1981	3.43	46	1.19	57	65.3
360	1981	2.42	46	1.37	62	43.4
360	1982	1.62	43	2.31	37	26.7 *

* Ground home range size > aerial.

Table 3. Comparison of rutting and nonrutting seasonal home range sizes for tule elk in the Diablo Range of California (50% utilization distribution, fast Fourier transform analysis).

Elk	Year	Season	50% Home range size (km^2) Aerial Size	Aerial n	Ground Size	Ground n	Percentage difference in home range size
240	1981	Nonrutting	7.71	20	2.55	29	66.9
282	1981	Nonrutting	1.13	20	0.55	25	51.3
315	1981	Nonrutting	2.51	20	0.30	22	88.0
315	1982	Nonrutting	3.82	34	1.99	40	47.9
315	1982	Rutting	2.23	13	0.26	16	88.3
315	1983	Nonrutting	1.78	19	6.42	16	72.3 *
330	1981	Nonrutting	2.22	20	0.47	24	78.8
330	1982	Rutting	2.23	13	0.36	20	83.9
360	1981	Nonrutting	1.20	20	0.90	29	25.0
360	1982	Nonrutting	3.11	34	2.59	33	16.7
360	1983	Nonrutting	1.40	19	5.35	14	73.8 *

* Ground home range size > aerial.

Table 4. Comparison of seasonal home range sizes for tule elk in the Diablo Range of California (50% utilization distribution, fast Fourier transform analysis).

Elk	Year	Season	50% Home range size (km^2) Aerial Size	Aerial n	Ground Size	Ground n	Percentage difference in home range size
240	1981	Spring	7.69	11	5.37	14	30.2
240	1981	Fall	0.84	13	0.83	17	1.2
282	1981	Spring	5.67	11	1.70	11	70.0
282	1981	Fall	0.79	14	0.59	17	25.3
315	1981	Fall	0.95	14	0.59	17	37.9
315	1982	Spring	3.04	12	3.63	14	16.2 *
315	1982	Summer	2.60	13	0.37	15	85.8
330	1981	Fall	0.95	14	0.59	17	37.9
330	1982	Fall	1.27	11	0.24	15	81.1
360	1981	Spring	4.53	11	4.62	14	2.0 *
360	1981	Fall	0.79	14	0.83	17	4.8 *
360	1982	Spring	1.61	12	0.40	14	75.1

* Ground home range size > aerial.

Table 5. Comparison of wet and dry seasonal home range sizes for tule elk in the Diablo Range of California (50% utilization distribution, fast Fourier transform analysis).

			50% Home range size (km^2)				Percentage difference in home range size
			Aerial		Ground		
Elk	Year	Season	Size	n	Size	n	
240	1981	Wet	1.99	21	1.83	19	8.0
282	1981	Dry	1.58	25	0.54	35	65.8
282	1981	Wet	3.81	22	1.85	19	51.4
315	1981	Dry	1.70	25	0.58	32	65.9
315	1981	Wet	3.70	22	2.16	22	41.6
315	1982	Dry	3.96	25	0.39	34	90.1
315	1982	Wet	1.77	16	2.32	17	23.7 *
330	1981	Dry	2.59	25	0.71	34	72.6
330	1981	Wet	6.41	22	1.85	19	71.1
330	1982	Dry	9.89	25	0.81	17	91.8
360	1981	Wet	3.70	22	2.16	22	41.6
360	1982	Dry	1.28	25	1.34	22	4.5 *
360	1982	Wet	1.15	16	4.80	12	76.0 *

* Ground home range size > aerial.

The home range sizes based on aerial data for 4 elk showed consistent annual decreases ranging from 29 to 79%. Elk 330 aerial data showed a nearly 5-fold increase between the first and second years, followed by a 48% decrease between the second and third years. Seasonal trends of aerial data showed an initial decrease (86 to 98%) in home range size for all elk between spring and summer of the first year. For the second year, elks 315 and 360 showed a seasonal peak in home range size during spring with a decline in size during summer and fall. Four elk had the same home range size (0.43 km^2) for the first summer. Aerial data organized into wet and dry seasons showed an increase (54 to 68%) in home range sizes between the 1981 dry and wet seasons for 4 elk. There was a consistent peak in home range size during the second nonrutting season (Table 6 and 7).

All elk showed a consistent annual decrease (17 to 79%) in home range size when aerial and ground observations were combined. First year seasonal trends for all 5 elk revealed a decrease in home range size for the summer and fall as compared to the spring and winter. Four elk had approximately the same home range size (2.3 km^2) for the first summer. All elk had approximately the same home range size (5.3 km^2) for the first fall. When aerial and ground data were combined and organized by wet and dry seasons,

Table 6. Home range size (km^2) based on tule elk aerial observations in the Diablo Range of California (50% utilization distribution, fast Fourier transform analysis).

		Elk Collar Frequency				
Season	Year	240	282	315	330	360
Year	1981	4.02	2.52	6.16	3.43	2.42
Year	1982	0.86	1.71	4.39	15.56	1.62
Year	1983	0.36	--	3.17	8.08	1.15
Spring	1981	7.69	5.67	11.43	17.37	4.59
Summer	1981	1.11	0.43	0.43	0.43	0.43
Fall	1981	0.84	0.79	0.95	0.95	0.79
Spring	1982	1.24	5.02	3.04	na	1.61
Summer	1982	--	--	2.60	19.36	1.15
Fall	1982	--	--	1.82	1.27	0.31
Dry	1981	3.22	1.58	1.70	2.59	1.20
Wet	1981	1.99	3.81	3.70	6.41	3.70
Dry	1982	na	1.81	3.96	9.89	1.28
Wet	1982	1.53	--	1.77	4.69	1.15
Dry	1983	--	--	2.03	--	2.03
Wet	1983	--	--	--	--	0.32
Nonrutting	1981	7.71	1.13	2.51	2.22	1.20
Rutting	1981	1.95	1.95	1.24	1.24	1.95
Nonrutting	1982	4.64	8.78	3.82	17.11	3.11
Rutting	1982	--	--	2.23	2.23	0.79
Nonrutting	1983	0.56	--	1.78	6.29	1.40

-- sample size < 10.

Table 7. Percentage change in home range size (km^2) between consecutive seasons; based on tule elk aerial observations in the Diablo Range of California (50% utilization distribution, fast Fourier transform analysis).

Consecutive Seasons				Elk Collar Frequency				
Season	Year	Season	Year	240	282	315	330	360
Year	1981	Year	1982	-78.6	-32.1	-28.7	78.0	-33.1
Year	1982	Year	1983	-58.1	--	-28.8	-48.1	-29.0
Spring	1981	Summer	1981	-85.6	-92.4	-96.2	-97.5	-90.6
Summer	1981	Fall	1981	-24.3	45.6	54.7	54.7	45.6
Spring	1982	Summer	1982	--	--	-14.5	na	-28.6
Summer	1982	Fall	1982	--	--	-30.0	-93.4	-73.0
Dry	1981	Wet	1981	-37.9	58.5	54.0	59.6	67.6
Wet	1981	Dry	1982	na	-52.5	6.6	35.2	-65.4
Dry	1982	Wet	1982	na	--	-55.3	-52.6	-10.2
Wet	1982	Dry	1983	--	--	12.8	--	43.3
Dry	1983	Wet	1983	--	--	--	--	-84.2
Nonrutting	1981	Rutting	1981	-74.7	42.0	-50.6	-44.1	38.5
Rutting	1981	Nonrutting	1982	58.0	77.8	67.5	92.7	37.3
Nonrutting	1982	Rutting	1982	--	--	-41.6	-87.0	-74.6
Rutting	1983	Nonrutting	1983	--	--	-20.2	64.5	43.6

-- sample size < 10.

4 elk showed an initial increase (23 to 71%) in home range size between the 1981 dry and wet seasons. This was followed by a dramatic decrease (52 to 89%) for the 1982 dry season for 3 of these elk. Trend analysis of ground and aerial data for rutting and nonrutting seasons revealed a repeated cycle of marked decrease (54 to 93%) in home range size during periods of rutting. All elk had approximately the same home range size (5.5 km^2) during the first rutting season (Table 8 and 9).

The following descriptions are preliminary findings for elks 315 and 360. Home ranges were consistently leptokurtic regardless of how the data were organized. Yearly home ranges were bimodal with no consistent shape. Home ranges for short time periods spanning 3 or 4 months (spring, summer, fall, winter and rut seasons) were generally unimodal and elliptical. Many of the data sets for these home ranges fit a bivariate and/or weighted bivariate normal distribution. Home ranges for longer time spans (wet, dry and nonrut seasons) were not consistently bimodal or unimodal. When these home ranges were unimodal, they also tended to be elliptical.

Discussion and recommendations

In choosing the appropriate analysis, a researcher must consider the underlying assumptions and basic capabilities of each technique (Appendix 1). If an underlying assumption

Table 8. Home range size (km^2) based on tule elk combined aerial and ground observations in the Diablo Range of California (100% utilization distribution, minimum convex polygon analysis).

		Elk Collar Frequency				
Season	Year	240	282	315	330	360
Year	1981	82.92	67.23	83.93	181.18	57.61
Year	1982	18.97	14.21	44.59	149.57	16.95
Year	1983	23.38	--	14.29	57.15	14.29
Spring	1981	17.73	20.31	38.07	71.26	17.89
Summer	1981	13.41	2.31	2.34	2.34	2.34
Fall	1981	5.25	5.34	5.34	5.34	5.34
Winter	1981	33.78	56.85	21.25	70.17	21.25
Spring	1982	7.84	10.81	16.89	33.79	3.98
Summer	1982	--	--	17.31	88.67	12.10
Fall	1982	--	--	11.52	20.70	3.74
Winter	1982	--	--	2.47	--	2.47
Summer	1983	--	--	6.09	--	6.09
Dry	1981	23.36	22.14	47.87	71.26	22.32
Wet	1981	62.88	75.83	33.69	92.56	33.69
Dry	1982	6.76	14.21	43.33	101.37	16.32
Wet	1982	11.60	--	13.69	88.85	11.10
Dry	1983	--	--	8.72	--	8.72
Wet	1983	--	--	--	--	2.98
Nonrutting	1981	20.75	20.31	40.36	71.26	20.64
Rutting	1981	5.47	5.56	5.56	5.56	5.47
Nonrutting	1982	76.22	100.91	34.38	121.63	33.48
Rutting	1982	--	--	15.96	15.96	8.29
Nonrutting	1983	11.60	--	16.27	106.51	16.27
Nonrutting	1984	--	--	--	--	1.43

-- sample size < 10.

Table 9. Percentage change in home range size (km^2) between consecutive seasons; based on tule elk combined aerial and ground observations in the Diablo Range of California (50% utilization distribution, minimum convex polygon analysis).

Consecutive Seasons				Elk Collar Frequency				
Season	Year	Season	Year	240	282	315	330	360
Year	1981	Year	1982	-77.1	-78.9	-46.9	-17.4	-70.6
Year	1982	Year	1983	18.9	--	-67.9	-61.8	-15.7
Spring	1981	Summer	1981	-24.4	-88.6	-93.8	-96.7	-86.9
Summer	1981	Fall	1981	-60.8	56.7	56.2	56.2	55.4
Fall	1981	Winter	1981	84.3	90.6	74.9	92.4	75.3
Winter	1981	Spring	1982	-76.5	-81.0	-20.5	-51.8	-81.3
Spring	1982	Summer	1982	--	--	2.4	61.9	67.1
Summer	1982	Fall	1982	--	--	-33.4	-76.6	-69.1
Fall	1982	Winter	1982	--	--	-78.6	--	-34.0
Dry	1981	Wet	1981	62.8	70.8	-29.6	23.0	33.7
Wet	1981	Dry	1982	-89.2	-81.3	22.2	8.7	-51.6
Dry	1982	Wet	1982	41.7	--	-68.4	-12.3	-32.0
Wet	1982	Dry	1983	--	--	-36.3	--	-21.4
Dry	1983	Wet	1983	--	--	--	--	-65.8
Nonrutting	1981	Rutting	1981	-73.6	-72.6	-86.2	-92.2	-73.5
Rutting	1981	Nonrutting	1982	92.8	94.5	83.8	95.4	83.7
Nonrutting	1982	Rutting	1982	--	--	-53.6	-86.9	-75.2
Rutting	1983	Nonrutting	1983	--	--	1.9	85.0	49.0

-- sample size < 10.

is violated, it is uncertain whether the result reflects the violation or a biological phenomenon. All techniques of home range analysis assume that the probability of observing an animal at a specific location is proportional to the time that animal spends at that location and that the pattern of home range utilization does not change during the study period. Hence, all techniques require random sampling and consideration of environmental and behavioral factors that may alter patterns of use.

Attempts to provide a mathematical structure for the intuitive concept of home range have generally followed 1 of 3 approaches: nonstatistical, parametric and nonparametric statistical techniques (Worton 1987). Nonstatistical techniques utilize the outer perimeter points of observation and, therefore, do not provide any information concerning the internal anatomy of the home range. The major advantage of these techniques is the simplicity of calculation and the minimal assumption that the home range shape is a polygon. The major disadvantages are that these methods are sensitive to sample size bias and the method of connecting perimeter points is often subjective. Because of this subjectivity, results are often not reproducible and comparison between studies is difficult. Methods most commonly used for nonstatistical analysis are the minimum polygon (MP) (Clutton-Brock, et al. 1982), minimum convex polygon (MCP)

(Mohr 1947) and modified minimum area method (MMAM) (Harvey and Barbour 1965). MMAM analysis allows for consideration of locations that represent single explorations by an animal rather than daily activity. These locations are considered outliers and are excluded from the area calculations.

Statistical techniques attempt to incorporate information from the entire set of observations. The location sightings are used to estimate a two dimensional relative frequency distribution, the utilization distribution (UD) (Van Winkle 1975), that can then be used to calculate the size and define the internal characteristics of the home range. Estimation of the UD employs either parametric or nonparametric techniques. Both methods assume independence between observations. In addition, parametric estimation makes assumptions concerning the shape of the home range. The bivariate normal (BVN) (Jennrich and Turner 1969) and weighted bivariate normal (WBVN) (Samuel and Garton 1985) parametric techniques assume an elliptical home range. Nonparametric estimation does not make this assumption, but requires a larger minimum sample size.

The most common nonparametric statistical techniques are harmonic mean analysis (HM) (Dixon and Chapman 1980, Samuel et al. 1985, Spencer and Barrett 1984) and fast Fourier transform analysis (FFT) (Anderson 1982). Both of these methods attempt to "smooth" the observed UD. Harmonic mean analysis does this by using inverse moments while FFT analysis eliminates low frequency observations. With both techniques, outlier effects are minimized. Another advantage of HM and FFT is that the internal anatomy of the home range can be studied by the identification of core areas, which are the more extensively used portions of the home range.

Unlike the nonstatistical techniques, HM and FFT tend to underestimate the size of the home range. In fact, a major limitation of FFT is that accuracy of the estimated home range size declines dramatically for areas greater than 50% of the total home range. Simulation studies have shown that the size of the 95% home range may be 40% less than the true area; while the 50% home range is consistently more accurate than all other techniques, even with small sample sizes ($\underline{n} > 10$) (Worton 1987). Hence, FFT is the most appropriate technique for making comparisons but does not represent the classic definition of home range, i.e., total area used by the animal.

The major disadvantage of the harmonic mean method developed by Samuel et al. (1985) is that the results are dependent on the map scale. Modifications by Spencer and Barrett (1984) appear to have corrected this, however, simulation studies are needed to evaluate the accuracy of this technique.

A major advantage of HM is that it allows greater definition of the internal anatomy of the home range. Specifically, kurtosis, skewness and relative dispersion may all be evaluated. Kurtosis provides a measure of clumping or uniformity and can be used to describe usage patterns in core areas. Platykurtic home ranges (kurtosis values < 2) have a flat UD reflecting a uniform or repulsed use pattern. At the other extreme, a highly leptokurtic home range has a high concentration of observations in one part of the home range and at the perimeter, reflecting a nonrandom or clumped use pattern. Skewness describes the general location of core areas with respect to the rest of the home range. An unskewed home range (skewness values < 1) has core areas in the center of the home range. Relative dispersion defines the relative size of the core area. Low relative dispersion indicates a small core area (a peak in the UD); high relative dispersion a large core area (a plateau in the UD). A major limitation of HM is that it is not appropriate for home ranges that are linear, multimodal, or leptokurtic (Neft 1966, Spencer and Barrett 1984, Worton 1987).

For the tule elk study that generated these data, the ground observer consistently began her search at the elks' previous locations in order to maximize the potential for making direct observations. As a result, consecutive observations were not independent. Limited access, rugged terrain and poor roads prevented complete sampling by the ground observer. As a result, all 5 elk were not located during each observation. Hence animals in areas close to previous sightings were more frequently located than animals that traveled longer distances. This resulted in nonrandom sampling and a tendency towards autocorrelation between consecutive observations. Previous aerial sightings were used to select areas for ground observations. Therefore, ground and aerial data were not independent. Only those techniques that do not assume statistical independence (MP, MCP and MMAM) should be used to analyze data sets containing ground observations collected in this manner.

The test for independence has an underlying assumption of a constant time interval between consecutive observations. The observed autocorrelation in aerial data sets may be an artifact of violating this assumption. Longer time spans may include changes in utilization patterns which may increase the mean distance between each point and the arithmetic center. Since longer time spans generally included more observations, this may be reflected in the results as a sample size effect. A correlation analysis between the test statistic and sample size should be conducted to determine if the observed patterns of autocorrelation in aerial data result from a sample size effect. The other tests of independence currently available share these problems and hence, should not be used. Instead, in future studies a simulation analysis conducted prior to data collection may be useful to determine the minimum time interval required to ensure independence between consecutive observations. A minimum sample size that ensures both accurate and precise results could also be determined for each technique by simulation analysis.

Comparison of ground and aerial home ranges suggest that, in most cases, ground data represent a subset of the aerial data, possibly defining a core area. Detailed graphic analysis may verify this observation. Ground data are generally believed to have greater locational accuracy than aerial data. If the independence issues for ground data can be resolved, it may be possible to perform a 2 step analyses for many large mammal studies in which aerial data provide a coarse estimate of the home range size and internal anatomy, and ground data provide detailed information on the internal anatomy of the home range.

An underlying assumption for all analysis techniques is that the home range utilization does not change during the study period. Therefore, an accurate analysis of how animals use their available space requires careful consideration of several behavioral and environmental factors. Newly relocated elk in this study initially had a period of wandering (Phillips 1985) demonstrated by a decrease in annual home range size between the first and second years. The bimodal distribution of annual home ranges suggested the existence of additional shifts in use patterns. Analysis of annual data organized into 3 month periods revealed large fluctuations in home range size supporting this hypothesis.

In general, seasonal changes in temperature and precipitation alter the quality and quantity of available forage which may alter home range utilization. In this study, analysis of data organized into 6 month wet and dry seasons did not reveal repeated seasonal patterns of change in home range size. I suggest that this is due to variability in the amount of climatic difference between consecutive seasons. This hypothesis is supported by the observation that, during this study, the greatest difference in precipitation (98%) occurred between the 1981 dry and wet seasons (Santa Clara Water District unpubl. data) when the only consistent pattern of change in home range size occurred.

Behavioral activities of large mammals also vary throughout the year and may alter home range utilization. With tule elk in the Diablo range rutting behavior was accompanied by increased herding behavior and decreased dispersal throughout the available home range (Phillips 1985). Analysis of data organized into rutting and nonrutting seasons revealed a corresponding decrease in home range size. However, the nonrutting season was 9 months long, while the rutting season was only 3 months long. The 3-fold difference in time span resulted in a difference in sample size making the MCP analysis of combined aerial and ground data suspect. The presence of a nonrutting peak in the FFT analysis of aerial data suggested that rutting behavior did decrease home range size but had a more subtle effect than indicated by MCP analysis.

I conclude that both climatic and rutting behavior influence the pattern of home range use. Climatic conditions vary greatly from year to year. Standard wet and dry seasons did not reflect this variability. Further, rutting seasons are based on general information and may not have accurately reflected this herd's behavior. For future studies I recommend examining the locational data sequentially to identify changes in use pattern. I believe that data organized on this basis will be unimodal and more amenable to accurate analysis by the techniques that are currently available.

There was no single best technique for home range analysis with these tule elk data. Rather, a combination of techniques was needed to completely interpret locational data. For aerial data FFT analysis was best for comparing home range sizes for different times, habitats and animals. The elliptical nature of the elk data may lend itself to more powerful analysis by BVN or WBVN analysis. Ground data should be collected with more care to ensure that there is random sampling and independence between consecutive observations. In lieu of this, the analysis of ground data should use nonstatistical techniques (MP, MCP or MMAM). I believe the findings of this report may be applied to any analysis of locational data for mammals with home range sizes of equal or greater magnitude.

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Appendix 1. Attributes of different techniques of home range analysis.

	Nonstatistical techniques			Statistical techniques			
				Parametric		Nonparametric	
	MP	MCP	MMAM	BVN	WBVN	HMEAN[1]	FFT[2]
Assumptions:							
Independence	-	-	-	+	+	+	+
Shape of home range	+	+	+	+	+	-	-
Capabilities:							
Estimates 100% of area	+	+	+	-	-	-	-
Estimates 95% of area	-	-	-	+	+	+	-
Estimates 50% of area	-	-	-	+	+	+	+
Defines a core area	-	-	-	-	-	+	+
Evaluates internal anatomy	-	-	-	-	-	+	+
Problems:							
Sample size bias	+	+	+	-	-	-	-
Outlier effect	?	+	-	+	-	-	-
Recommended sample size	>30	>30	>30	30-50	30-50	30-100	30-100

Abbreviations and references:

MP	Minimum polygon	Clutton-Brock, et al. 1982
MCP	Minimum convex polygon	Mohr 1947
MMAM	Modified minimum area method	Harvey and Barbour 1965
BVN	Bivariate normal	Jennrich and Turner 1969
WBVN	Weighted bivariate normal	Samuel and Garton 1985
HMEAN	Harmonic mean	Dixon and Chapman 1980 Samuel, et al. 1985 Spencer and Barrett 1984
FFT	Fast Fourier transform	Anderson 1982

[1] not applicable for data that are linear, multimodal, or leptokurtic (Spencer and Barrett 1984).

[2] consistently provides the most accurate estimate for 50% of the total home range area (Worton 1987).

+ attribute characteristic of a particular technique.
- attribute not characteristic of a particular technique.
? unknown.