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Wolf territories in Scandinavia; sizes, variability and their relation to prey density

Kjell Johansson

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Handledare: Håkan Sand

Institutionen för naturvårdsbiologi
Grimsö forskningsstation
SLU
730 91 Riddarhyttan

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Contents

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1 Abstract

Eight annual wolf territories were estimated for six different adult wolves in south-central Sweden during 1998-2000. The wolves were followed from the ground or by aircraft using conventional radio-telemetry.

Wolf territory sizes were estimated using the Minimum Convex Polygon (MCP) and the Adaptive Kernel Method (AKM), with the average result 1259 km² (range 405-2221 km², n = 8) and 1056 km² (range 484-1849 km², n = 8) respectively. In stable territories, with a reproducing pair, the MCP-method gave 90 % territory cover estimates with 100-150 relocations evenly distributed over the year. In unstable territories, with one adult animal, 150-200 relocations were needed to cover the same proportion of the total area used by the wolves.

Scandinavian wolf territory sizes were generally larger than was North-American territories at comparable prey densities and at similar latitude. They were generally smaller than North Alaskan territories but larger than wolf territories further south in North America or in Europe. Wolf territory sizes in North America, but not in Scandinavia, were related to ungulate densities with larger territory sizes at low values of relative ungulate biomass.

1.1 Key words

adaptive kernel, area-observation curve, bootstrap, *Canis lupus*, GIS, home range, minimum convex polygon, telemetry, territory size, utilisation distribution, VHF-transmitter, wolf.

2 Introduction

Estimating animals' home ranges or territory sizes is one important part in the study of ecology. An adjacent field of interest is space requirement when animals are to be reintroduced or controlled (Bekoff & Mech 1994). This is especially important when the species of interest are endangered and in need of large areas and therefore, such as for wolves (*Canis lupus*), are in conflict with other interests. Wolves in particular, could in this sense, be regarded as a "problem" species.

2.1 Theoretical basis

A home range was defined by Burt (1943) as; "*...the area traversed by the individual in its normal activities of food gathering, mating and caring for young*", and does not include defence. A distinction between home range and territory is that home ranges are not defended, while a territory is the area defended by an individual or a group of individuals (White et al. 1996). It may even be regarded as a fixed area of exclusive or priority use, either the whole territory or part of it (Powell 2000). Territory is more appropriate when dealing with wolves, since the area used generally is defended and maintained by frequent scent-markings, like raised leg urination or feces, and by howling or direct aggression (Mech et al. 1998). A wolf territory can be formed even in the absence of neighbouring wolves (White et al. 1996).

Animals' home ranges and territories are not static entities. It is fundamental to treat an actual estimate as a brief approximation that constantly is changing over time. If not an animals use of a particular site is positively associated with length or frequency of collected data points, then all estimators poorly measure importance of space use (Harris et al. 1990). Therefore different time intervals are commonly used, and in this study I estimate the size of *annual* territories.

The term "utilisation distribution" has been used to describe a probabilistic distribution pattern (Jennrich & Turner 1969, Anderson 1982 and Seaman & Powell 1996). This term relate to the Adaptive Kernel method used here (Appendix 2). It was first presented for ecologists by Worton (1989) and is probably the best method known for estimating animal's utilisation distribution (Seaman & Powell 1996).

Numerous of factors influence the accuracy of home range estimates and their shape. The most obvious are sample size, sampling interval, and the type of sampling technique, i.e. radio-telemetry, trapping or direct observations (Sanderson 1966, Mech 1983, Bekoff & Mech 1984, Harris et al. 1990 and Powell 2000). Other important variables are social status of individuals, age, sex, reproductive condition, available food resources, the presence or absence of other conspecifics or individuals and the surrounding habitat. These variables influence space use and movement patterns and consequently even the reliability of home range estimates (Bekoff & Mech 1984 and Powell 2000).

Theoretical approaches on how to provide data on location, movement and behaviour as well as their interpretation are numerous (e.g. Mohr 1947, Jennrich and Turner 1969, Van Vinkle 1975, Anderson 1982, Harris et al. 1990, Powell 2000 and Fuller & Sievert 2001). Recently, there has been a tremendous increase in techniques on how to track animals, such as GPS and satellite technique (Fancy & Ballard 1995), but the more traditional VHF-technique is still valid (Harris et. al. 1990, Mech & Gese 1992 and Ballard et al. 1995). Telemetry data are of major importance when trying to estimate territories for species with very large territory requirements (Linnell et al. 2000). A disadvantage with traditional radio telemetry is that it normally requires high working effort and therefore is expensive.

Even though data can bee relatively easy to collect, there is no straight forward method for the interpretation of data. The adequate method depends on the questions being asked and the method of data collection (Bekoff & Mech 1984). Theoretical approaches are numerous, how to interpret data (e.g. Mohr 1947, Jennrich & Turner 1969, Van Vinkle 1975, Koeppl et al 1975, Anderson 1982, Don & Rennolls 1983, Harris et al. 1990 and Powell 2000).

2.2 The study species

Wolves use considerable areas when hunting and interacting socially among and between packs (Person & Sand 1998, Mech et al. 1998). This fact influence the effort needed when studying the ecology and behaviour of wolves. The number of relocations (fixes) taken during a time period have shown to be important to get reliable estimates of wolf territory size (Bekoff & Mech 1984, Harris et al. 1990 and Ballard et al. 1998), and are an important component affecting the costs of research and management.

Generally estimates of wolf territory size seem to increase towards an asymptotic level when the numbers of locations (sample size) increase (Jennrich & Turner 1969, Anderson 1982, Bekoff & Mech 1984, Harris et al. 1990, White et al. 1996, Powell 2000 and Fuller & Sievert 2001). Asymptotic levels are constructed in area-observation curves, which are helpful when trying to estimate the effort needed for a specific objective; in this case the number of relocations needed for a certain level of territory cover.

Bekoff & Mech (1984) performed simulations on the subject that is comparable. They reported that 100-200 relocations were needed to get reliably estimations of wolf home range areas but this is higher than figures reported elsewhere. For example Fritts and Mech (1981) reported that 79 (range 35-120) locations were necessary when following a pack more than 1.5 years. Messier (1985) suggested that 40-80 locations were needed to estimate annual territories while Ballard et al. (1998) concluded that 123 (range 55-179) locations were necessary to explain 90 % of true annual territory size.

2.3 Predictions and objectives of this study

With respect to preliminary data within the Scandinavian wolf research project (SKANDULV), annual Scandinavian wolf territories were expected to be around 1000 km^2, calculated with the MCP-method. Here I also present territory sizes calculated with the Adaptive Kernel Method (AKM).

This is the first study in Scandinavia that focus on the number locations needed to accurately describe annual wolf territory-sizes. According to earlier findings in other areas, 75-150 relocations annually were expected to define approximately 90 % of territory size.

Bekoff & Mech (1984) was the only study found on the subject of variation in simulated territory estimate. According to their result I expected variation among replicates within simulations to decrease with sample size and to be less than 10 % at sample size > 100 locations per year.

In Scandinavia a low wolf: ungulate ratio is expected, which is typical for areas where wolves newly are established or newly protected (Fritts & Mech 1981, Wydewen et al. 1995 and

Fuller & Sievert 2001). Wolves' numerical response is closely related to the availability of food recourses (Messier 1985, Fuller 1989 and Hayes & Harestad 2000). Territory sizes are generally smaller in areas with high prey density according to these studies. This postulated correlation will be further tested both within the Scandinavian population, and between different populations.

The main objectives of this study were to: (1) estimate territory sizes with two commonly used methods (Minimum Convex Polygon and Kernel) for different percentage of the total number of relocations, (2) to estimate the relationship between sample sizes of relocations and territory estimate, (3) to evaluate the relationship between sample size and the variability in area estimation, and (4) to discuss the results in terms of the general relationship between territory size, wolf density and availability of prey.

3 Materials and Methods

3.1 Study area and population

The wolf-population in Scandinavia are newly recovered and still endangered (wolves are protected in Sweden since 1966), but show a high degree of population growth, 19-30 % year^{-1} during the 1990's (Person & Sand 1998, Persson et al. 1999, Ebenhard 1999, Wabakken et al. 2001). In winter 2001/2002 population size (including mortalities) ranged between 98 and 113 in Scandinavia, with 10-11 potential breeding groups (Aronson & Wabakken 2002). The wolf population is not yet showing the dynamics and interactions, i.e. multiyear territory mosaic among established territories, that has been documented for example in Alaska (Mech et al. 1998). In Scandinavia there are gaps between territories and wolf density in the population core area still is low (on average < 1 wolf km^{-2}) compared to other comparable populations and to the ecological carrying capacity *K* (Persson & Sand 1998, Wabakken et al. 2001). Wolf densities for each territory are shown in Table 1.

The study area is located in south-central Scandinavia between 59º N and 61º N. Six territories totaling eight different wolf-years are included in this study (Figure 1). The area is dominated by coniferous forest, spruce (*Picea abies*) and pine (*Pinus sylvetsris*), partly containing deciduous trees as birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*), willow (*Salix spp*.) and alder (*Alnus incana*). The area is characterized by intensive forestry with a high frequency of forest roads (average 1.5 km road km^{-2}), clear-cuts and areas with uniform young forests. The human population density is low (on average < 1 inhabitant km^{-2}) and people are gathered in small communities and villages, surrounded by some agricultural land (Wastesson 1992, Sveriges National Atlas- SNA). Lone cabins and summer houses are located at many different places in the forests, used mainly as summer residences. The area includes lots of hills, mires, lakes and rivers of different sizes, which makes the landscape variable. From December to April the ground is generally covered with snow (20-50 cm), and daily mean temperature in January is between -5° C and -8° C (SMHI).

The fauna in the area are normal for Scandinavia, with potential prey as moose (*Alces alces*), roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), badger (*Meles meles*) and different rodent species, as well as capercaillie (*Tetrao urogallos*) and black grouse (*Tetrao tetrix*). Main prey species are moose and roe deer, with average densities of 0.85 to 1.1 moose km^{-2} and 0.006 to 0.02 roe deer km^{-2} respectively in winter (H. Sand, unpublished data). Other carnivores of importance in the area are Eurasian lynx (*Lynx lynx*), bear (*Ursos arctos*), red fox (*Vulpes vulpes*), marten (*Martes martes*) and other mustelids.

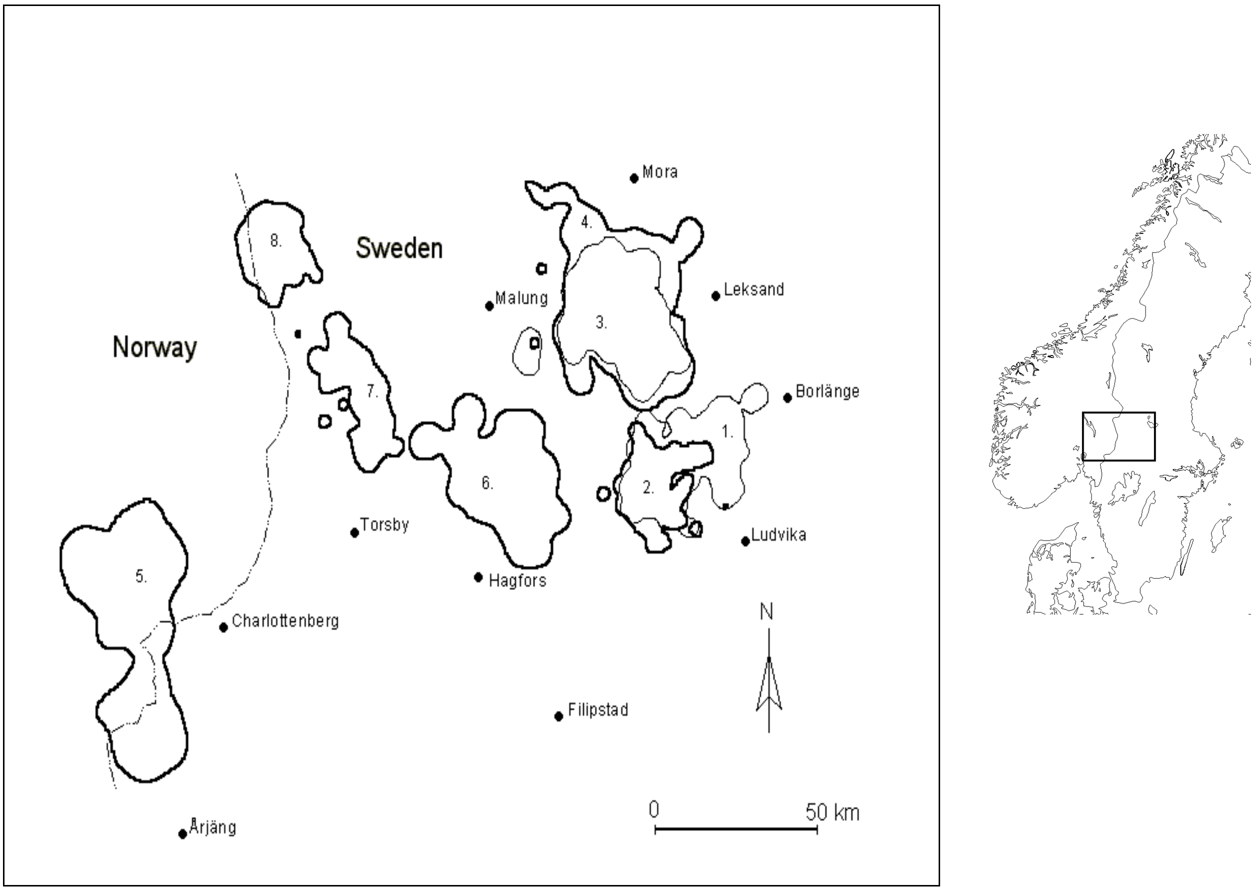

Figure 1. Study area and eight annual wolf territories, exemplified with 95 % adaptive kernel method in south-central Scandinavia 1999-2000 (thin lines) and 2000-2001 (thick lines). See table 1 and 2 for details.

3.2 Fieldwork

This study is part of the Scandinavian Wolf Research Project (Årsrapport 2000/01), from which data have been collected. Since 1998 a total of 28 wolves have been radio collared. The animals were darted from helicopter with an anaesthetic agent, captured and then lifted to a marking place. At the occasion of capture age and sex of the wolves were determined and samples of blood, hair and tissues was taken. The wolves were also weighted and measured. Finally they were equipped with ear-tags and a neck-collar containing a VHF- radio transmitter for telemetry use (Årsrapport 1999).

Wolf relocations were taken either from aircraft or from the ground. Relocations taken from the ground was done by triangulation. Three bearings (cross-bearings) were taken from different positions at 1-3 km distance to create a relocation polygon. To minimise the error in triangulation quick movements between the different positions was conducted by car. The error in triangulation is < 1 ha when the distance to the animal is < 1 km (Cederlund and Sand 1994). Normally two relocations per week were taken through out the year, but during December to March 99/00 and 00/01 more intense radio tracking was conducted in the Grangärde, Leksand and Nyskoga territory with ≥ 2 relocation's per 24 hours.

3.3 Data on studied individuals

Eight different wolf-years have been created from six different wolves for this study (Figure 1 and Table 1). A *wolf-year* was defined as the relocations evenly distributed from the first of May to the last of April the year after. Only alpha animals (i.e. individuals that reproduce and dominate pack activities) were used for the analyses. Pack size was defined as the maximum number of socially interacting wolves within a pack, including members that temporarily are dissociated from the pack. In the Grangärde territory one alpha-male 9804 was followed for two separate wolf-years, 1999/00 with his partner 0004 and in 2000/01 with his 3-4 puppies. The female partner was missed since 4 December 2000, but the same territory was maintained by the male to the end of April 2001. In the Leksand territory the alpha couple was intact until 6 February 2000, when the male was found paralysed and subsequently killed by humans due to injuries in the backside. The Leksand territory remained unchanged during the wolf-year 1999/00, but was more unstable during wolf-year 2000/01, when the alpha female (9805) increased the area used sufficiently. For all the other individuals' only one single wolf-year have been used in this analysis (Table 1).

Table 1. Data from six wolves and eight annual wolf territories in south-central Scandinavia 1999-2001. Ts is the total sample size (all available locations) while Ss is the corrected sub-sample in order to avoid autocorrelation. Wolves/1000 km^2 is calculated from MCP 100% Ts in table 2.

Wolf-Year	Id	Sex	Territory	Age	Year	Packsize[a]	No fixes Ss	No fixes Ts	Wolves/ 1000 km^2
1	9804	♂	Grangärde	1	99-00	2	287	730	1.7
2	9804	♂	Grangärde	2	00-01	4[b]	333	645	4.0
3	9805	♀	Leksand	5-6	99-00	3[c]	221	239	1.6
4	9805	♀	Leksand	6-7	00-01	1-2[d]	157	185	0.9
5	0001	♂[e]	Årjäng	5-6	00-01	6	116	120	4.0
6	0006	♂	Tyngsjö	2	00-01	2[f]	49	53	2.2
7	0007	♂[g]	Nyskoga	3	00-01	4	230	261	4.0
8	0009	♂[h]	Bograngen	5-7	00-01	3	139	143	7.4

[a] *Data from Årsrapport (1999, 2000/01) and Wabakken et al. 2001.*
[b] *Female partner missed from 4 Dec 2000.*
[c] *Stationary female and two yearling pups. Male was killed 6 Feb. 1999, due to injuries.*
[d] *Lone stationary female in former pack site, perhaps with one other wolf.*
[e] *Pair with 0002, Årjäng territory.*
[f] *Scent-marking alpha-couple.*
[g] *Mate to 0008, Nyskoga territory.*
[h] *Mate to 0011, Bograngen territory.*

3.4 Analysis

There are many different computer programs available for home-range analyses (Gallerani Lawson & Rodgers 1997). In this study I used the software ArcView 3.2B with the extension of Animal Movement, which is one of the most user-friendly programs at present (Hooge & Eichenlaub 1997).

3.4.1 Territory estimation

Individual annual territory sizes were calculated with the minimum convex polygon method-MCP (White and Garrot 1990, Appendix 2), which connects the outermost locations of each individual during chosen time period. This was done both for all available locations (= total sample, Ts) and for a corrected subsample (Ss) to avoid autocorrelation (only using relocations > six hours apart and not more than two per 24 hours, Appendix 2). Estimations of annual territory sizes for the total sample and the sub sample were conducted by the MCP-method using 100 %, 95 %, 75 % and 50 % of relocations. The removal of fixes was done by procedure of outlier removal (Appendix 2). The adaptive kernel method (AKM) (Appendix 2) was used to create annual utilisation distribution curves at the levels of 95 %, 75 % and 50 % for Ts and Ss respectively. Least square cross validation (LSCV) was the method used for calculating the smoothing parameter H, a parameter that regulates the coarseness of the raster (Hooge & Eichenlaub 1997).

3.4.2 Influence of sample size on area estimation

The relationship between the number of relocations and territory size was studied, in order to create a general guideline that would be useful for field researchers interested in space use patterns. To be able to compare data from different territories the frequencies of relocations used for estimating territory size were sampled evenly in time intervals in the analyses. This was done by applying the bootstrapping technique in the Animal Movement Extension of ArcView 3.2 (Hooge & Eichenlaub 1997). The selected intervals were evenly and randomly distributed over the wolf-year (Appendix 1). The program allows the user to do many simulations of an area for each interval and produce results in terms of MCP-mean area, standard error (SE) and standard deviation (SD) (Appendix 1).

Asymptotic area-observation curves were created for every single wolf-year from which analysis of territory cover was conducted. These analyses make it possible to estimate the number of relocations needed for any chosen percentages of territory cover. Here the total area generated from all available positions (Ts) accumulated during one year were used, when calculating the number of positions needed to cover 90 %, 85 %, 80 %, 75 % and 50 % of that total territory area (Table 3).

3.4.3 Variability in area estimation

Depending on which relocations that are selected for creating a certain sample interval, the calculated mean territory area can vary considerably in size. This aspect is seldom analysed in earlier publications, but see Bekoff and Mech (1984). Since the program that was used simulated the area estimate 100 times at each interval, it was possible to calculate the coefficient of variation (CV = SD*100/meanarea) at different sample sizes. CV was calculated and plotted against sample size. This treatment makes it possible to evaluate how the mean area estimate is affected by different constellations of fixes in the simulations.

3.4.4 Territory size versus prey availability

Data from several studies on prey densities were reviewed and plotted against territory size. The relationship was tested with Spearman Rank Correlation Coefficient, r_s (Fowler & Cohen 1997). ANCOVA was used to test for the partial effect of prey biomass on territory size between Scandinavia and North American wolf territories. The software used for analyses was Statwiev 5.1.

4 Results

4.1 Territory sizes

Wolves in south-central Scandinavia have on average annual territory sizes of 1247 (range 405-2209) km², when the MCP-method was applied on the subsample (Ss) for eight different wolf-years (Table 2). The annual average territory size was not significantly larger 1259 (range 405-2221) km² when all available positions (Ts) were used (paired t-test; df =14, t = 0,200, P > 0.10). When the unstable wolf-year for wolf 9805 (00/01) was excluded the

*Table 2. Territory areas estimated with the MCP- and Kernel methods for eight wolf years in south-central Scandinavia between 1999-2001. Datasets on non-corrected total sample size is **ts**, while **ss** is the corrected subsample due to avoidance of autocorrelation (i.e. all fixes closer than six hours in time are removed randomly). The 95%-, 75%- and 50% MCP areas are calculated by outlier removal in ArcView, where the points to remove are selected by their largest harmonic mean value (Hooge and Eichenlaub 1997). The kernel method used calculates a fixed kernel home range utilisation distribution (at 95%, 75% and 50% levels), using the least squares cross validation (LSCV) to estimate smoothing parameter (H). Different H-values for both **ts** and **ss** are automatically chosen by the program and are showed in the table within parentheses. The kernel estimates are based on 100% ts and 100% ss respectively.*

Territory estimate (km²)

	MCP								KERNEL							
	100%		95%		75%		50%		95%		75%		50%			
Wolf (year)	ts (n)	ss (n)	ts (n)	ss (n)	ts (n)	ss (n)	ts (n)	ss (n)	ts	ss	ts	ss	ts	ss	H_{ts}	H_{ss}
9804 (99-00)	1175 (730)	1160 (287)	946 (694)	963 (273)	548 (548)	612 (216)	216 (365)	347 (144)	781	1123	240	468	67	74	0,20	0,25
9804 (00-01)	999 (645)	928 (333)	632 (613)	552 (317)	407 (515)	320 (250)	232 (411)	146 (167)	587	549	181	150	66	74	0,16	0,17
9805 (99-00)	1887 (230)	1887 (221)	1064 (228)	1051 (210)	687 (180)	651 (166)	344 (120)	318 (111)	1213	1190	559	519	205	176	0,28	0,28
9805 (00-01)	2221 (185)	2209 (157)	1346 (176)	1480 (150)	941 (139)	925 (118)	526 (93)	530 (79)	1849	1806	945	785	300	226	0,35	0,36
0001 (00-01)	1498 (120)	1498 (116)	1454 (114)	1454 (111)	917 (90)	917 (87)	318 (60)	329 (58)	1766	1776	945	921	330	314	0,45	0,46
0006 (00-01)	894 (53)	894 (49)	773 (51)	695 (45)	475 (40)	475 (37)	247 (27)	257 (25)	1217	1273	452	532	121	154	0,35	0,35
0007 (00-01)	996 (261)	996 (230)	639 (248)	650 (219)	321 (196)	331 (173)	152 (131)	149 (115)	578	613	214	220	82	78	0,22	0,22
0009 (00-01)	405 (143)	405 (139)	361 (136)	346 (133)	249 (108)	242 (105)	163 (72)	162 (70)	484	484	153	166	41	47	0,18	0,18
Mean	1259	1247	902	899	568	559	275	280	1019	1056	432	454	137	138		
Range	405- 2221	405- 2209	361- 1454	346- 1480	246- 941	242- 925	125- 526	139- 530	484- 1849	484- 1806	153- 945	150- 921	41- 330	40- 314		

corresponding figures were lower; 971 (range 405-1887) km² for subsample and 981 (range 405-1887) km² for total sample. An annual weighted 95 % distribution curve calculated with the Adaptive Kernel method gave on average a mean territory area at 1019 (range 484-1849) km² for the total sample, while corresponding figure for sub sample was 1056 (range 484-1806) km² (table 2) (no significant difference between Ss and Ts in estimates; paired t-test, df =14, t = 0.372, P > 0.10). Ss-values in table 2 were sometimes larger than corresponding Ts-values. This is probably due to the weighted choice of smoothing parameter in the Adaptive Kernel method (Appendix 2).

4.2 The number of relocations needed

Area-observation curves with the number of locations plotted versus the area and percent of total area covered was constructed (Figure 2 and 3) to settle the number of fixes that was required to describe 90 %, 85 %, 80 %, 75 % and 50 % of territory cover (Table 3). According to these results approximately 150-200 positions are enough to define 90 % of annual territory sizes in Scandinavian wolf territories. This corresponds to approximately three relocations per week during one wolf-year.

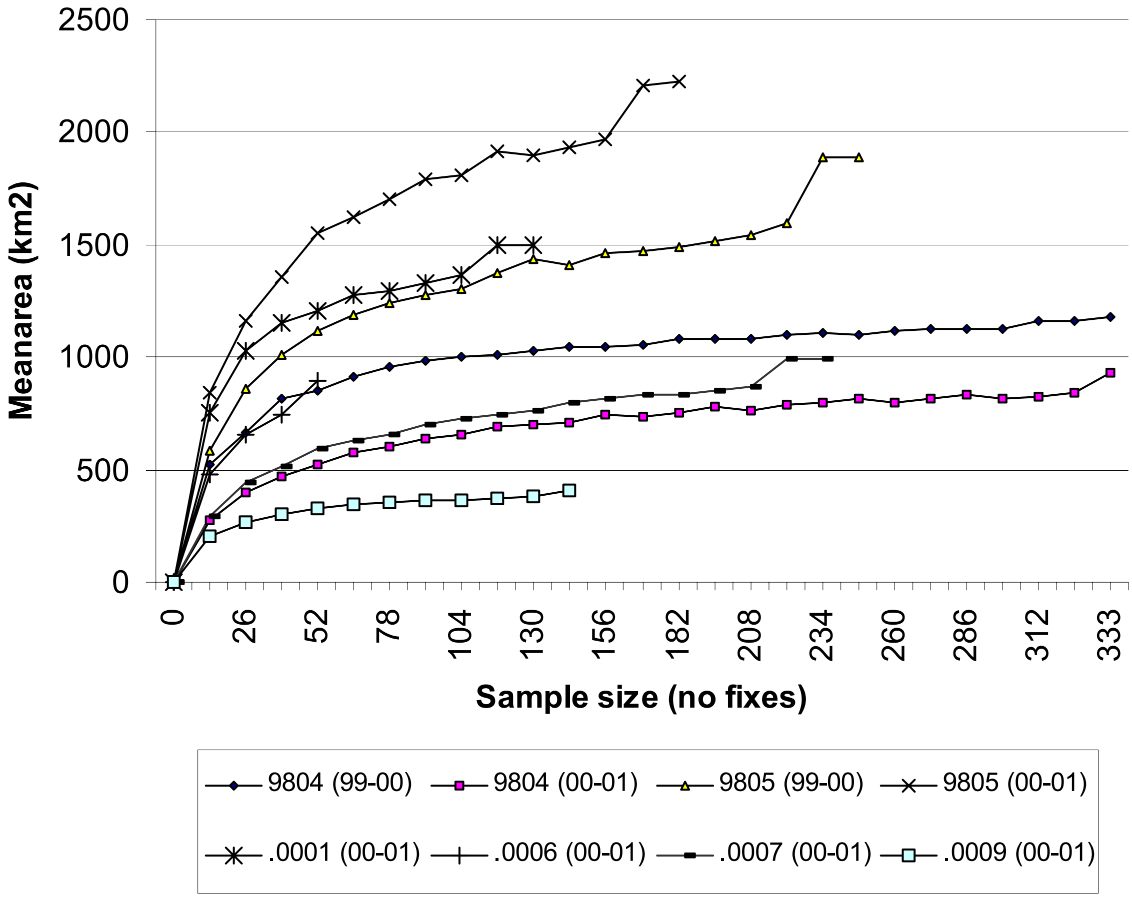

Figure 2. Area-observation curves (the relationship of randomly selected relocations and area estimates, see Appendix 1) for eight annual wolf territories 1999-2001 in south-central Scandinavia. The y-axis show mean areas for different sample intervals and the last two points in each curve represent the maximum areas for subsample (Ss) and total sample (Ts) respectively. Those points differ clearly from the calculated mean areas which make the curve look somewhat unsmoothed at the ends. In some cases Ts are sufficiently larger than Ss. This is shown in Appendix 1. Interval; 26 positions =2 /month, 52 positions = 1/week etc.

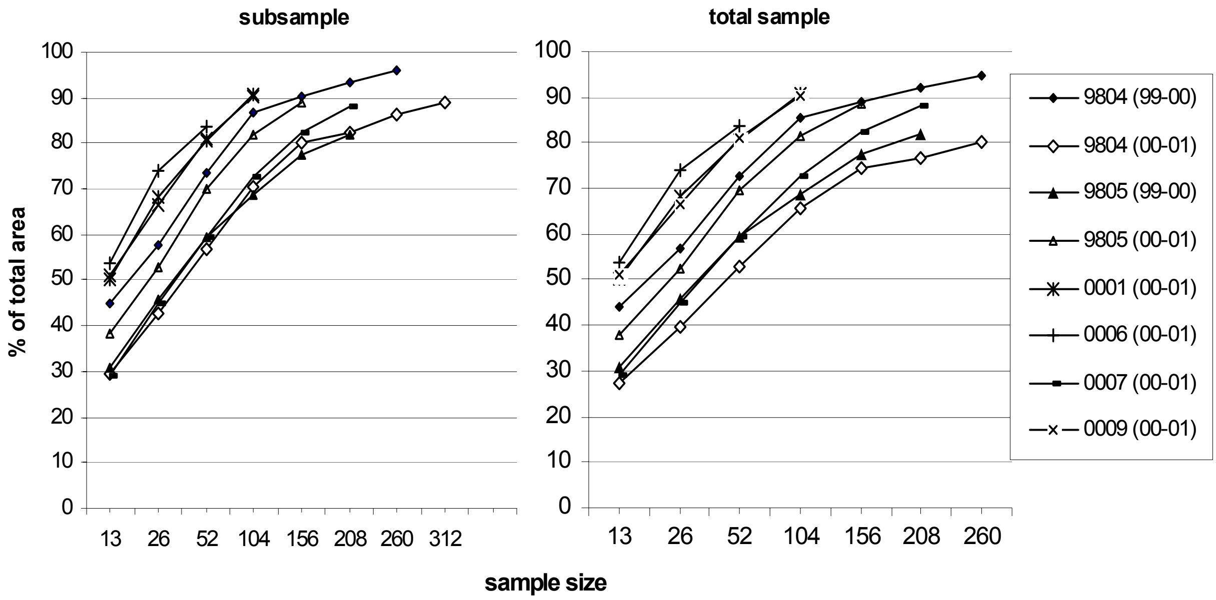

Figure 3. Area-observation curves where the territory mean areas are shown as percent area of total territory size for each sample interval. The figure is based on the same data as in figure 2 and shows at which sample interval 90 %-, 85 %-, 80 %-,75 %- and 50 % of the territory are encompassed by the fixes (Table 3). Intervall; 26 positions =2 /month, 52 positions = 1/week etc.

Table 3. Number of locations needed for different percentages of territory cover for sub sample (Ss) and total sample (Ts) respectively. The results are illustrated graphically in figure 3. Eight wolf-years in south-central Scandinavia 1999-2001.

	Cover									
Individual	**90%**		**85%**		**80%**		**75%**		**50%**	
	Ss	Ts	Ss	Ts	Ss	Ts	Ss	Ts	Ss	Ts
9804 (99-00)	-	166	98	101	78	82	64	64	18	18
9804 (00-01)	350	-	239	-	156	257	124	170	39	44
9805 (99-00)	-	-	-	-	188	186	140	140	33	37
9805 (00-01)	175	170	124	127	97	96	72	91	24	37
0001 (00-01)	100	98	72	74	50	51	40	40	12	12
0006 (00-01)	-	-	65	60	45	42	28	30	11	12
0007 (00-01)	-	260	182	181	143	143	115	115	33	35
0009 (00-01)	102	101	72	74	51	50	40	42	12	13
Average	182	159	121	103	101	113	78	87	23	26
Range	100-350	98-260	65-239	60-181	45-188	42-257	28-140	30-170	11-39	12-44
n	4	5	7	6	8	8	8	8	8	8

4.3 Variability in area estimation

Initially there was a rapid increase in mean area as the sample size increased. As expected, the bootstrap simulations of territory size with different sets of sample size of relocations showed increased coefficient of variation (CV) at smaller sample sizes (Figure 4). Generally the coefficient of variation was < 15 % for samples sizes of >100 relocations and ranged from 10 to 36 % for sample sizes < 50 relocations. Four of the eight wolf territories had CV at only 10 % level already with 52 relocations (Figure 4).

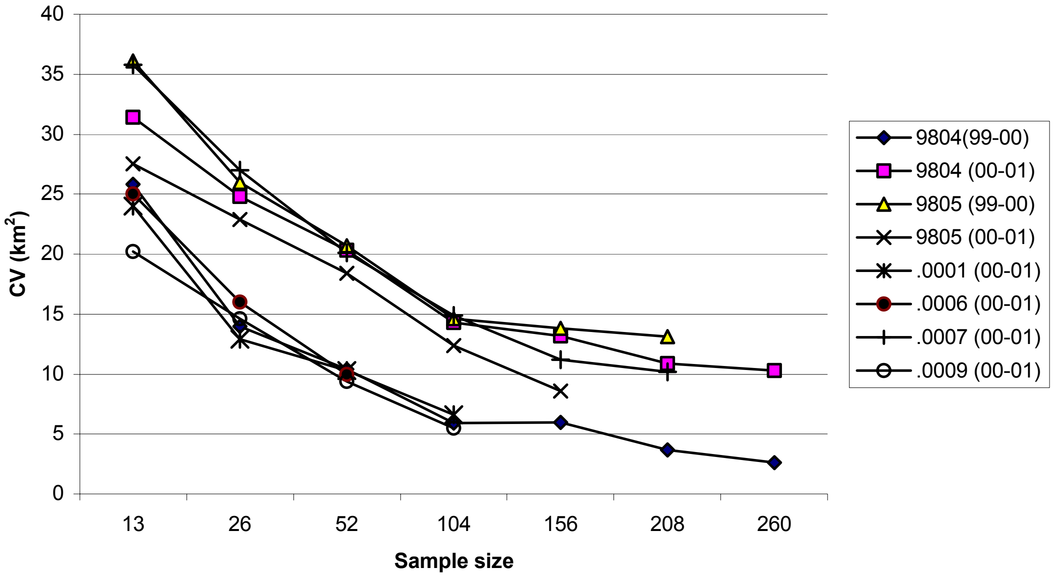

Figure 4. Variation (CV) among bootstrap simulations of territory size versus sample size for eight wolf territories in south-central Scandinavia. Interval; 26 positions =2 /month, 52 positions = 1/week etc.

4.4 Comparison to other wolf populations and effects of ungulate density

A comparison of territory sizes between different wolf populations with the MCP-method show that annual Scandinavian wolf territories are comparable in size to North American territories in areas of the same latitude (Table 4). In North America higher wolf density and smaller wolf territories are found further south, while territory sizes are much larger in the north-east of Alaska. In Europe, e.g. Poland and Italy and further south in Israel, wolf territories are generally much smaller (Table 4).

Table 4. Annual territory sizes in different wolf populations in North America, Europe and Israel.

Site	Latitude	Range (km2)	Average (km2)	Reference
N.E Alaska	65-68°N	1572-8079	3750	(Ballard et al. 1998)
Brooks Range, N.E Alaska	65°N	1610-2126	1868	(Ballard et al. 1997)
Denali, S Alaska	62°N	560-4300	1500	(Mech et al. 1998)
S.C Scandinavia	60°N	405-2209	1247	(This study)
Poland, Europe	52°N	173- 279	212	(Okarma 1998)
Minnesota, N USA	47°N	50- 223	116	(Fuller 1995)
Italy, Europe	45°N	197[1]	197	(Ciucci et al- 1997)
Israel, Middle East	33°N	5,3- 37,5	22	(Hefner & Geffen 1999)

[1] *Only one territory present.*

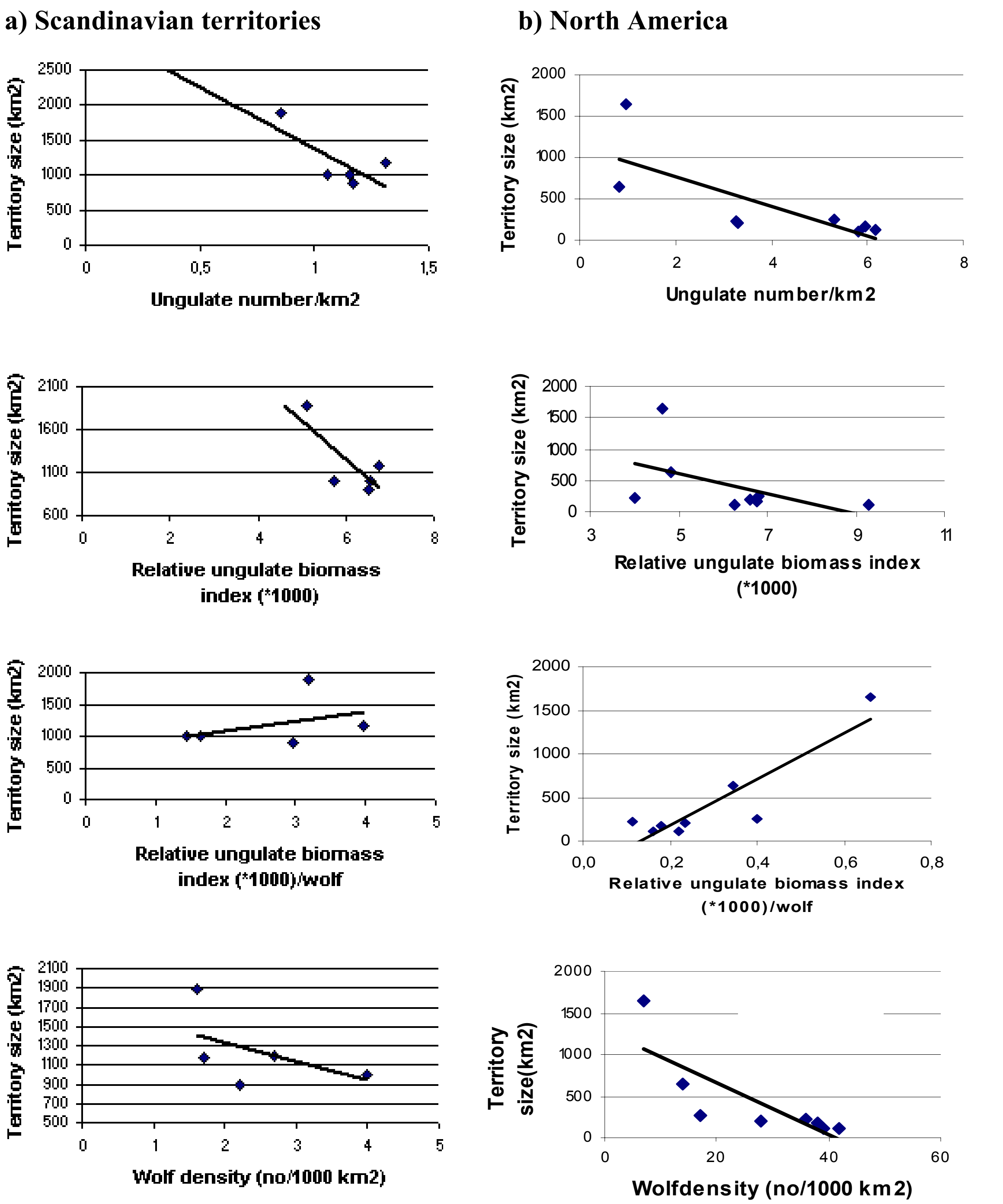

Figure 5. Territory sizes in relation to four other factors. Ungulates in Scandinavia are moose and roe deer, with relative biomass values at 6 and 0.4 respectively. In North America ungulates are deer, moose and caribou, with relative biomass values at 1, 6 and 2 respectively. Details are presented in Table 5.

Table 5. Territory size, ungulate and wolf densities and relative ungulate biomass index during winter in Scandinavia 1999-2001 (this study) and at different locations in North America 1969-2002 (modified from Fuller et al. In press). In this study ungulate densities are based on faecal pellet group counts (H. Sand, unpublished data). SC = south central, NW = north west, EC = east central, S = south, NC = north central and NE = north east.

SCANDINAVIA (This study)

Territory	Year	MCP-area (km²)	Wolf-density[2] (no/1000 km²)	Ung. density (no/km²)	Moose (no/1000 km²)	Roe deer (no/1000 km²)	Caribou (no/1000 km²)	Relative ungulate[1] biomass index	Relative ungulate[1] biomass index/wolf
Leksand	1999	1887	1,6	0,9	851	6		5108	3192
Grangärde	2000	1175	1,7	1,3	1109	201		6734	3961
Grangärde	2001	999	4	1,1	950	106		5742	1436
Nyskoga	2001	996	4	1,2	1086	66		6542	1636
Tyngsjö	2002	894	2,2	1,2	1082	89		6528	2967
Average		1190	2,7	1,1	1016	94		6131	2638

NORTH AMERICA

Territory	Year	MCP-area (km²)	Wolf-density[2] (no/1000 km²)	Ung. density (no/km²)	Moose (no/1000 km²)	Roe deer (no/1000 km²)	Caribou (no/1000 km²)	Relative ungulate[1] biomass index	Relative ungulate[1] biomass index/wolf	Reference
SC Alaska	1975-1982	1645	7	1,0	665		311	4612	659	Ballard et al. 1987
Kenai Peninsula	1976-1981	638	14	0,8	800		13	4826	345	Peterson et al. 1984
NW Minnesota	1972-1977	260	17	5,3	300	5000		6800	400	Fritts and Mech 1981
Algonquin Park	1969	224	36	3,3	154	3100		4021	112	Kolenosky 1972
S Quebec	1980-1984	199	28	3,3	600	3000		6600	236	Potvin 1988
EC Ontario	1958-1965	175	38	5,9	146	5769		6783	179	Pimlott et al. 1969
NC Minnesota	1980-1986	116	39	6,2	20	6160		6280	161	Fuller 1989
NE Minnesota	1970-1971	110	42	5,8	800	5100		9300	221	Van Ballenberghe et al.1975
Average		421	28	3,9	436	4688	162	6153	289	

[1] Calculated for both prey types with different relative biomass values for; moose 6, roe deer 0.4, deer 1 and caribou 2 (Fuller et al. In press).

[2] Wolf densities are not directly comparable between Scandinavia and North America, since it is measured within territory in Scandinavia and in a larger area in North America.

A comparison of several studies in North America and with data from this study indicate that wolf territory sizes gets smaller at higher levels of ungulate density (Figure 5). In Scandinavia there was no significant correlation between territory size and pack size (df=8, r_s=0.39, P=0.69). Neither were there any significant correlation between territory size and wolf ungulate density (r_s= -0,36, P=0,47), relative ungulate biomass (r_s= -0,30, P=0,54), ungulate biomass:wolf ratio (r_s0=0,50, P=0,32), or wolf density (r_s= -0,67, P=0,18) (Figure 5a). In North America mean territory size from the eight different areas was significantly correlated to ungulate density (r_s= -0,83, P=0,023), wolf density (r_s= -0,97, P=0,01) and almost significant to relative ungulate biomass:wolf ratio (r_s=0,67, P=0,078) but not to relative ungulate biomass (r_s= -0,57, P=0,13) (Figure 5b). To test weather the level of relationship between prey biomass index and territory size differed between Scandinavia and North America an ANCOVA was performed with area as an independent factor and relative ungulate biomass:wolf as a covariate variable. Both area ($F=5.75$, $P=0.0.04$) and ungulate biomass:wolf index ($F=16.1$, $P=0.003$) showed significant effects on territory size of wolves, as did the interaction term between these independent variables ($F=12.8$, $P=0.006$).

5 Discussion

Reasons for maintaining territories may be numerous including fluctuation in food production, the ability to hunt large ungulates may require a large pack size, which call for an area large enough to support them all. There may also be a demand of large areas around a denning place, to safely breed the puppies so defending territories may be an insurance to keep other wolves away and thereby enhance the fitness of the own pack members.

5.1 Territory sizes

First I conclude that there is not a large difference in area estimate between the subsample and the total sample. There is probably no need for a correction due to autocorrelation, which is in accordance with the findings of De Solla et al. (1999). The maximal territory sizes calculated with the total samples size (Ts) were in some territories somewhat larger compared to the asymptotic mean territory size conducted in the bootstrap procedure (the latter two points of each curve in Figure 2). This may be explained by the method used (MCP), which is sensitive to extraterritorial excursions that may occur occasionally. Asymptotic territories (section 4.2) are based on simulations of subsets of relocations (Appendix 1) and may show a territory size without one or more extraterritorial excursions. Interesting is that the asymptotic levels in the curves are similar to the 95 % adaptive kernel method in table 2. If the MCP-method is used, and if extraterritorial forays are to be eliminated the most appropriate level is 95 %, because these figures are closest to the asymptotic level (Table 2). However, what is the "real" territory size is a matter of choice. Figures in Table 2 should be used with caution depending on what question that is asked. The total area used may be of interest, but sometimes you want to exclude the extraterritorial excursions. If some core area is of interest, then of course a smaller percentage is a better choice.

5.2 The number of relocations needed for adequate area estimation

There are indications that traditional VHF radio telemetry data does not provide a correct result of annual territories as compared to satellite based telemetry (Ballard et al. 1998). In this study I examined the relation between sample size of relocations and territory size (Figure 2, Appendix 1), to evaluate the number of relocations needed for a reliable estimation of territory size with conventional VHF-technique.

The overall result was that approximately 100-150 fixes were needed for 80-90% estimation of the total area used in stable territories (territories with a reproducing pair), while unstable territories (lone wolves) needed 150-200 fixes. The curves in figure 2 are based on 100 randomly selected simulations and resulted in an asymptote in all cases except two, 9805 and 0006 during 00/01. For wolf 9805 this may be explained by the fact that she was a single adult wolf, resulting in an unstable territory and wide extraterritorial excursions. Estimates of territory size for wolf 0006 was based on a rather few number of relocations (49/53 for ss and ts respectively). In the latter case, the positions were unevenly distributed during the year. The MCP-method is sensitive to these kinds of factors. Harris et al. (1990) reports that transient adults, dispersing sub adults, range shifts or inappropriate time interval could give rise to this kind of problems for estimations of territory size.

The results of this study corresponds to the results presented by Bekoff and Mech (1984), who suggest 100-200 locations when thoroughly investigating the number of locations needed in computer simulations whereas Ballard et al. (1998) recommended 123 positions to correctly describe annually territories in Alaska.

Calculations revealed that 90 % cover of the total areas was approximately equal to the asymptotic mean areas developed in the computer simulations (Figure 3 and Table 3). According to this a 90 % level of all available positions is relevant (for n >150) when outliers ought to be excluded representing extraterritorial forays, dispersal or migratory movements.

In conclusion, the annual number of relocations needed for adequately describe 90 % of the actual territory size of Scandinavian wolves, is approximately 100-150 for stable territories and 100-200 for unstable territories. Consequently, this requires at least 2-3 relocations per week year around. New GPS-technique in combination with telecommunication will reduce fieldwork and thereby reduce costs and enhance the precision when relocating wolves.

5.3 Variability in area estimation

As sample size increased, variability decreased among the territory estimates generated by multiple simulations for each interval of locations. Evidently it is less important which specific relocations that are chosen the greater the sample size there is (Figure 4). At sample sizes < 50 (Figure 4), variation in the estimates of territory size may be large and depend on specific locations used. Biological systems in general are stable at coefficient of variation (CV) < 10 % (Bekoff & Mech 1984). This level of stability was used here when trying to evaluate the degree of reliability in wolf territory size estimation. CV was < 10 % already at 52 relocations in four annual wolf territories in this study (Figure 4). They all represent stable packs or alpha-couples, while the other annual wolf territories are known to be affected by, low number of fixes (wolf 0006), loss of mate (wolf 9805), or being a newly established territory (wolf 9804). Still the latter ones had CV < 15 % at approximately 100 relocations.

5.4 Influence of ungulate density on territory size

Wolf population dynamics is largely dominated by four factors; wolf density, ungulate density, human exploitation and ungulate vulnerability (Fuller 1989). Territory size and pack size are related to these factors. Several studies have documented that wolf territory sizes are correlated to pack size, resulting in smaller territory sizes with decreased pack size (Messier 1985, White et al. 1996, and Peterson et al 1984). This is often the case in harvested wolf populations, where the general prediction is small packs, a high number of packs per area and high total number of pups (Peterson et al. 1984). Pup survival and growth (Fuller 1989, Messier 1987 and Fuller & Sievert 2001) as well as adult survival are enhanced where prey biomass is high (Fuller & Sievert 2001). If prey is scarce there may be an increase of wolf extraterritorial excursions in order to find more food (Messier 1985 and Fuller 1989), hence larger areas are used. Therefore low prey availability is thought to result in increased movements and area use, including dispersal and transient behaviour (Fuller & Sievert 2001). There is however a risk of higher mortality when wolves visit unknown areas (Pettersson et al. 1984, Messier 1985 and Mech et al. 1998), for example due to intraspecific strife among wolves (Mech 1994).

A comparison of several studies in North America with data from this study indicate that wolf territory sizes gets smaller at high levels of ungulate density (Figure 5). In Scandinavia where only five territories were available, there was no correlation between territory size and pack size. According to Figure 5a, however, there was no significant relationship between territory size and wolf density, ungulate density, relative ungulate biomass, or ungulate biomass:wolf ratio. For North American wolf territories size was tested significantly correlated to ungulate density, wolf density, and almost significant to biomass:wolf ratio (Figure 5b). These results are in accordance with the findings by Fuller et al. (in press). Together with this factors prey type, prey vulnerability and habitat type affect territory size in a complex manner (Fuller et al. In press). In this study there was also a significant effect of study area independent of ungulate biomass:wolf ratio indicating that Scandinavian wolf territories were larger than found in North America at comparable levels ungulate biomass per wolf.

Biologists in Scandinavia are challenged with the important task to accurately estimate the ungulate density to be able to estimate the biological carrying capacity, which is fundamental when to control the wolf population in relation to decided levels of the ungulate harvest. Availability of prey do affect wolf pup survival and general wolf density, which also are related to territory size and the overall pack dynamics. The wolf:ungulate relationship may be altered not only by poor estimates of carnivores or their prey, but also by time-lags in wolfs demographic response to differences in prey density, competition with other carnivore species and mortality due to diseases, inbreeding depression or acceptance among humans (Fuller & Sievert 2001). Harvest and illegal killing of wolfs might result in unstable small packs and increased total number of pups and packs per area unit. Therefore the issue of harvesting a wolf population is to be considered carefully. Further long term studies on the wolf:ungulate dynamics in relation to human management actions should be conducted here in Scandinavia and in comparison with other areas.

5.5 Conclusions

- Scandinavian wolf territory sizes are generally larger than North-American territories at sites with comparable prey densities and at the same latitude. They are generally smaller than North Alaskan territories but larger than territories further south in North America or other European territories.

- There was no significant difference if the total sample or corrected sub sample was used for the territory size estimate; correction with respect to autocorrelation was not necessary.

- Researchers should use at least 100 relocations evenly distributed over the year to cover 80-90 % of the true annual wolf territory area, when using the MCP-method. In unstable territories probably 150-200 relocations are needed.

- As sample size increased, variability decreased among the territory estimates generated by multiple simulations for each interval of locations. The coefficients of variation (CV) ranged from 10-36 % for N < 50 locations, and were < 10 % already at 52 positions in four cases. Obviously the set of randomly chosen relocations are insignificant for the territory estimate at sample size > 100 relocations.

- Variation in territory sizes between sites was related to the variation in ungulate density among areas in North America with smaller territories in areas with a high density or biomass of ungulates, but larger territories in areas with a high biomass:wolf ratio suggesting that pack size and wolf density is also affecting this relationship.

- If the goal to secure a viable wolf-population on a national plan is to be achieved, then the wolf population dynamics in space use and numbers within years and among years as a response to prey availability and human management actions are important issues for future studies.

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Appendix 1.

*Bootstrap result and territory cover at different sample intervals for eight wolves in south-central Scandinavia 1999-2001. The bootstrap intervals is constructed in Animal Movement (se Methods for details) and all mean territory areas are estimated by the 100 % minimum convex polygon method (MCP 100) with 100 simulations (N) for each interval (except for 9804 (99-00) where 50 simulations is used). The mean areas should be compared with the maximal asymptotic territory size, either Ss (sub sample where autocorrelated fixes are deleted) or Ts (all available fixes are used). Coefficient of variation (CV) is calculated as SD*100/mean area.*
Sample size intervals is to compare with 1 fix/month (13), 2 fixes/month (26), and then 1-6 fixes/week (52/104/156/208/260/312) evenly distributed over the wolf year.

ID	**METHOD**	**SAMSIZE**	**MEANAREA**	**STDERR**	**STDDEV**	**CV**	**N**	**Territory cover**	
		(intervall)	(km2)	(SE)	(km2)		(sim)	(% of Ss)	(% of Ts)
9804 (99-00)	MCP 100	13	519.3	37.2	134.1	25.8	50	44.8	44.2
	MCP 100	26	666.7	18.2	93.0	14.0	50	57.5	56.8
	MCP 100	52	851.6	12.3	88.5	10.4	50	73.4	72.5
	MCP 100	104	1004.4	5.8	58.9	5.9	50	86.6	85.5
	MCP 100	156	1047.6	5.1	63.2	6.0	50	90.3	89.2
	MCP 100	208	1083.6	2.8	40.4	3.7	50	93.5	92.2
	MCP 100	260	1114.3	1.8	28.5	2.6	50	96.1	94.9
	Ss	287	1159.5						
	Ts	730	1174.7						
9804 (00-01)	MCP 100	13	272.4	23.7	85.6	31.4	100	29.4	27.3
	MCP 100	26	395.5	19.3	98.2	24.8	100	42.6	39.6
	MCP 100	52	526.4	14.8	106.7	20.3	100	56.7	52.7
	MCP 100	104	654.5	9.2	93.4	14.3	100	70.5	65.5
	MCP 100	156	742.2	7.8	97.7	13.2	100	80.0	74.3
	MCP 100	208	764.5	5.8	83.0	10.9	100	82.4	76.5
	MCP 100	260	801.6	5.1	82.4	10.3	100	86.4	80.2
	MCP 100	312	825.3	4.5	80.0	9.7	100	88.9	82.6
	Ss	333	927.9						
	Ts	645	999.0						
9805 (99-00)	MCP 100	13	585.3	58.6	211.3	36.1	100	31.0	31.0
	MCP 100	26	861.0	43.9	223.7	26.0	100	45.6	45.6
	MCP 100	52	1119.5	32.2	232.3	20.7	100	59.3	59.3
	MCP 100	104	1299.9	18.6	189.3	14.6	100	68.9	68.9
	MCP 100	156	1460.9	16.2	202.3	13.8	100	77.4	77.4
	MCP 100	208	1545.2	14.1	203.1	13.1	100	81.9	81.9
	Ss	221	1887.2						
	Ts	239	1887.2						
9805 (00-01)	MCP 100	13	844.6	64.4	232.1	27.5	100	38.2	38.0
	MCP 100	26	1164.1	52.3	266.6	22.9	100	52.7	52.4
	MCP 100	52	1551.1	39.6	285.9	18.4	100	70.2	69.8
	MCP 100	104	1811.6	22.0	223.9	12.4	100	82.0	81.6
	MCP 100	156	1965.7	13.5	168.7	8.6	100	89.0	88.5
	Ss	157	2208.9						
	Ts	185	2220.8						

ID	METHOD	SAMSIZE	MEANAREA	STDERR	STDDEV	CV	N	Territory cover	
		(interval)	(km2)	(SE)	(km2)		(sim)	(% of Ss)	(% of Ts)
.**0001** (00-01)	MCP 100	13	753.9	50.2	180.8	24.0	100	50.3	50.3
	MCP 100	26	1026.5	25.9	131.9	12.9	100	68.5	68.5
	MCP 100	52	1207.5	17.3	125.0	10.3	100	80.6	80.6
	MCP 100	104	1361.9	8.9	90.3	6.6	100	90.9	90.9
	Ss	116	1498.3						
	Ts	120	1498.3						
.**0006** (00-01)	MCP 100	13	481.9	33.4	120.4	25.0	100	53.9	53.9
	MCP 100	26	660.0	20.7	105.3	16.0	100	73.9	73.9
	MCP 100	39	749.1	12.0	74.7	10.0	100	83.8	83.8
	Ss	49	893.5						
	Ts	53	893.5						
.**0007** (00-01)	MCP 100	13	288.6	28.7	103.4	35.8	100	29.1	29.1
	MCP 100	26	447.7	23.7	121.0	27.0	100	45.1	45.1
	MCP 100	52	589.8	16.4	118.4	20.1	100	59.4	59.4
	MCP 100	104	722.7	10.6	107.7	14.9	100	72.8	72.8
	MCP 100	156	815.9	7.3	91.1	11.2	100	82.2	82.2
	MCP 100	208	873.1	6.2	88.9	10.2	100	87.9	87.9
	Ss	214	992.8						
	Ts	230	992.8						
.**0009** (00-01)	MCP 100	13	206.1	11.5	41.5	20.2	100	50.9	50.9
	MCP 100	26	270.0	7.7	39.3	14.6	100	66.7	66.7
	MCP 100	52	328.9	4.3	31.1	9.4	100	81.2	81.2
	MCP 100	104	365.8	2.0	20.2	5.5	100	90.3	90.3
	Ss	139	404.9						
	Ts	143	404.9						

Appendix 2.

Territory estimators

Any chosen model for calculating territory size should quantify the probability to find the animal studied at different places and how important a specific area is to the animal (Powell 2000). Problems with estimation to keep in mind is; *i/* estimators do not reveal 3D-pictures of the territory, *ii/* positions of an animal is only part of its real distribution area and *iii/* utilisation distribution is rarely appropriate for statistical methods.

There is no intention to review all the estimators that has passed through the years in this study, but I list some references on methods that are useful for anyone interested; the bivariate normal method (Jenrich & Turner 1969 and Koeppl et al. 1975), two-dimensional relative frequency distribution (Van Vinkle 1975), the harmonic mean method (Dixon & Chapman 1980), the fourier transform method (Andersson 1982), the kernel method (Worton 1989) and the minimum convex polygon, MCP (White & Garrot 1990). Useful rewievs are Anderson (1982), Bowman (1985), Silverman (1986), Worton (1987), Harris et al (1990), Powell (2000). Tests by means of Monte Carlo simulations are done by Boulanger and White (1990) and Worton (1995). Their results show that the kernel method is least biased followed by the harmonic mean method.

The methods used here is the minimum convex polygon -MCP (White & Garrot 1990), the kernel method (Worton 1989) and the harmonic mean method (Dixon and Chapman, 1980). The latter is here used only to do the outlier removal when using different percentages of MCP. Methods are either non-parametric or parametric, where the latter is based on probabilistic areal distributions that describe an arithmetic mean centre of activity. MCP, the kernel method and the harmonic mean method are all non-parametric. The choice of such methods are natural, since it is important that statistical methods do not make unrealistic assumptions when dealing with natural wildlife (Worton 1995).

The minimum convex polygon method- MCP

MCP is a non-parametric method that links the outermost positions together to a convex polygon (Figure 6). It is therefore a function of sample size, since the longer you collect positions the greater polygon you get. MCP does not take in account any centre of activity, hence there is low precision in the estimate, and it is highly influenced by peripheral fixes like extraterritorial forays. Moreover there can be large bias in the estimate, especially when large “holes” in the data set is present, e.g. lakes or other areas that not are in use by the animal (Boulanger and White 1990). Advantages are that MCP is simple and are directly comparable between studies and therefore have been frequently used.

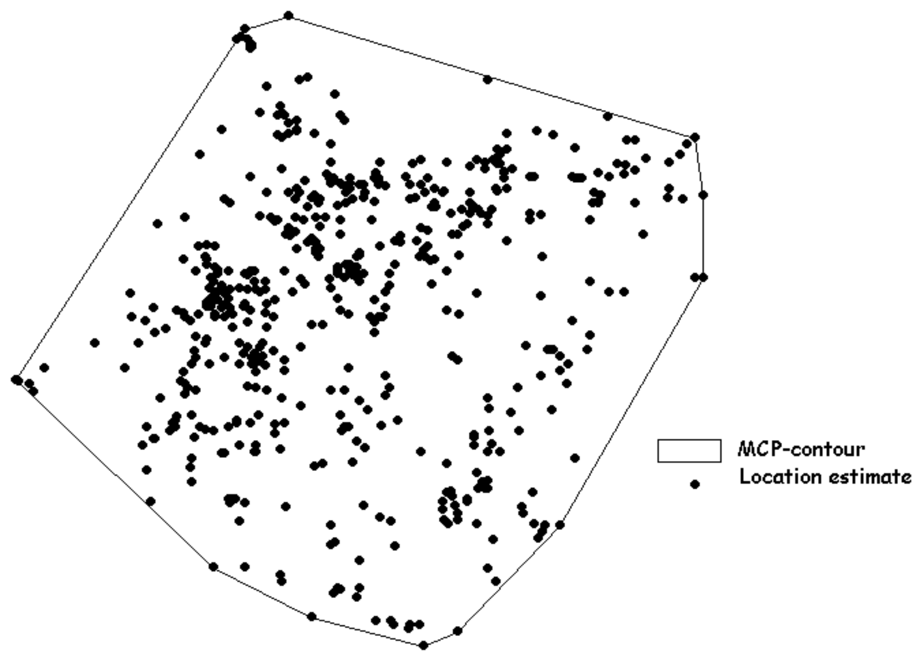

Figure 6. Example of MCP-contour for a male wolf, 9804, Grangärde territory year 00-01. MCP links the outermost locations to a minimum convex polygon, 95 % MCP, 632 km² (n=613).

The Kernel method

The Kernel method is a non-parametric model that converts the utilisation distribution of the animal into probability contours (Figure 6). Probability contours will be made with higher density where there is a higher concentration of points. Each kernel is a density in itself and is therefore a true probability density function that shows the minimum area in which an animal has some specified probability (e.g. 95 %) of being located. The percentage of territory cover used is due to the question being asked. You might be interested in the total area (100 % of fixes) that ever has been used by the animal or it may be some core area, i.e. attraction points of frequent use (Don & Rennolls 1983). If for example 95 % (the smallest area with a probability of use equal to 0.95) is used, it will exclude the outermost 5 % of relocations, which may contribute to occasional sallies (Powell 2000), i.e. extraterritorial excursions. But, there is no logic biological reason why precisely 5 % should be excluded.

Two ways of choosing smoothing parameter, H (a chosen value that controls the amount of variation in each component of the estimate), characterise the two types of kernel methods: 1) fixed kernel and 2) adaptive kernel. In the fixed kernel method the smoothing parameter are of fixed value over the plane, while H is varied in the adaptive kernel method. If a small value of H is used, the fine details of the data are revealed, while a larger H value only show the most prominent features. The most objective way of choosing H is by least squares cross validation (LSCV), since it provides H-values that minimise discrepancy between the estimate and true density. ArcView are automatically calculating the LSCV-values used in this study. More discussion about the most optimum choice of H is done by Worton (1987, 1989 and 1995).

The advantages with the Kernel method compared to other estimators are the ability to draw weighted probabilistic contours, even from a small number of data points, and that it is free from parametric assumptions. Just any form of territory can be described, thus the method are very flexible. A true picture of where to find the studied animal with highest probability is revealed.

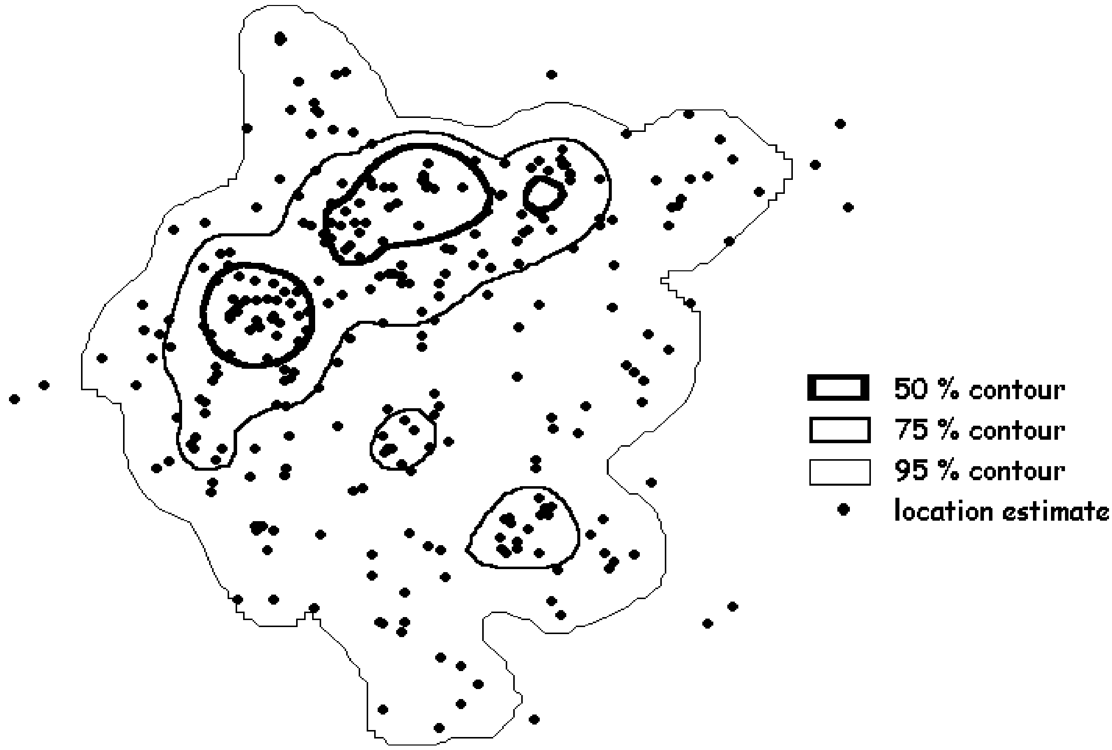

Figure 7. Example of weighted probabilistic contours for a male wolf, 9804, Grangärde territory year 00-01. Kernel method (LSCV), with different probability levels for an animal to be in any part of the territory. 95 % contour encompasses 549 km^2, while 75 %- and 50 % contours correspond to 150 km^2 and 40 km^2 respectively. If all available points are encompassed by a minimum convex polygon (MCP) the area is 928 km^2 for this actual annual wolf territory.

The harmonic mean method

This method is only used here to choose which points to delete when the outlier removal is done in ArcView. In this version you enter the percentage of points to remove and then the program removes points by their largest harmonic mean value (Hooge & Eichenlaub 1997). Generally, the harmonic mean method is based on activity centres of the animal and creates a grid gradually weighted in relation to where the animal mostly is situated. The representation of range use is done by isopleths within which a proportion of all fixes lie (Spencer 1984 and Dixon & Chapman 1990).

Autocorrelation

There is some disagreement on how autocorrelated data (i.e. relocations that are dependent of one and other in time) influence the home range estimate. Swihart and Slade (1985a and b) found that autocorrelation underestimated home range size, when keeping the sample size constant while the sampling time intervals was proportional to the intervals between observations. Contra dictionary, De Solla et al (1999) found that the home range estimate least biased and most precise when autocorrelated data was used. Here I present two values of territory sizes for each method: one where the maximal available locations are used and a second sub sample where autocorrelated data points are deleted.

Autocorrelation occurs when current position of the animal is influenced by its former position, i.e. when sampling interval is to short (Swihart & Slade 1985a and b). Time to independence between data points is proportional to the rate of home range use. Dominating wolves do traverse their territory in short time. They have the capacity to move from one boarder to the opposite within a few hours. For example Mech (1994) reported travel speed of 8.7 km h^{-1}. Therefore the recommendation, made by Swihart & Slade (1985a and b), of one or two locations > six hours apart per 24 hours for each individual was practiced in this study.

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SLU
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