

Methods for monitoring
European large carnivores
- A worldwide review of
relevant experience

John D.C. Linnell
Jon E. Swenson
Arild Landa
Tor Kvam

NINA•NIKUs publikasjoner

NINA•NIKU utgir følgende faste publikasjoner:

NINA Fagrapport NIKU Fagrapport

Her publiseres resultater av NINA og NIKUs eget forskningsarbeid, problemoversikter, kartlegging av kunnskapsnivået innen et emne, og litteraturstudier. Rapporter utgis også som et alternativ eller et supplement til internasjonal publisering, der tidsaspekt, materialets art, målgruppe m.m. gjør dette nødvendig. Opplag: Normalt 300-500

NINA Oppdragsmelding NIKU Oppdragsmelding

Dette er det minimum av rapportering som NINA og NIKU gir til oppdragsgiver etter fullført forsknings- eller utredningsprosjekt. I tillegg til de emner som dekkes av fagrapportene, vil oppdragsmeldingene også omfatte befaringsrapporter, seminar- og konferanseforedrag, års-rapporter fra overvåkningsprogrammer, o.a. Opplaget er begrenset. (Normalt 50-100)

NINA•NIKU Project Report

Serien presenterer resultater fra begge instituttene prosjekter når resultatene må gjøres tilgjengelig på engelsk. Serien omfatter original egenforskning, litteraturstudier, analyser av spesielle problemer eller tema, etc.

Opplaget varierer avhengig av behov og målgrupper

Temahefter

Disse behandler spesielle tema og utarbeides etter behov bl.a. for å informere om viktige problemstillinger i samfunnet. Målgruppen er "allmennheten" eller særskilte grupper, f.eks. landbruket, fylkesmennes miljøvern-avdelinger, turist- og friluftlivskretser o.l. De gis derfor en mer populærfaglig form og med mer bruk av illustrasjoner enn ovennevnte publikasjoner.

Opplag: Varierer

Fakta-ark

Hensikten med disse er å gjøre de viktigste resultatene av NINA og NIKUs faglige virksomhet, og som er publisert andre steder, tilgjengelig for et større publikum (presse, ideelle organisasjoner, naturforvaltningen på ulike nivåer, politikere og interesserte enkeltpersoner).

Opplag: 1200-1800

I tillegg publiserer NINA- og NIKU-ansatte sine forskningsresultater i internasjonale vitenskapelige journaler, gjennom populærfaglige tidsskrifter og aviser.

Linnell, J.D.C., Swenson, J.E., Landa, A. & Kvam, T. 1998. Methods for monitoring European large carnivores - A worldwide review of relevant experience. - NINA Oppdragsmelding 549: 1-38.

Trondheim, juli 1998

ISSN 0802-4103

ISBN 82-426-0951-9

Forvaltningsområde:

Naturovervåking

Management area:

Nature monitoring

Rettighetshaver ©:

NINA•NIKU

Stiftelsen for naturforskning og kulturminneforskning

Publikasjonen kan siteres fritt med kildeangivelse

Redaksjon:

Kjetil Bevanger og Lill Lorck Olden

Montering og layout:

Lill Lorck Olden

Sats: NINA•NIKU

Kopiering: Norservice

Opplag: 500

Kontaktadresse:

NINA•NIKU

Tungasletta 2

N-7005 Trondheim

Telefon: 73 80 14 00

Telefax: 73 80 14 01

Tilgjengelighet: Åpen

Prosjekt nr.: 12305

Ansvarlig signatur:



Oppdragsgiver:

Direktoratet for naturforvaltning (DN)

Abstract

Linnell, J.D.C., Swenson, J.E., Landa, A. & Kvam, T. 1998. Methods for monitoring European large carnivores - A worldwide review of relevant experience. - NINA Oppdragsmelding 549: 1-38.

Against a background of recovering large carnivore populations in Norway, and many other areas of Europe, it is becoming increasingly important to develop methods to monitor their populations. A variety of parameters can be monitored depending on objectives. These parameters include; presence/absence, distribution, population trend indices, minimum counts, statistical estimates of population size, reproductive parameters and health/condition. Three broad categories of monitoring technique can be recognised, each with increasing levels of fieldwork required. The first category includes those techniques that do not require original fieldwork. The second category involves fieldwork, but where individually recognisable carnivores are not available. The third category includes methods where fieldwork has recognisable individuals available. Different methods tend to have been used for different species, mainly because of limitations imposed by the different species' ecology. The most precise estimates of population size have been obtained in research projects with relatively small study sites and with the help of radio-telemetry. However, it may be difficult, or impossible, to apply these methods over large monitoring areas. Therefore, in terms of practical management, a combination of minimum counts, supported by an independent index may be more useful than statistical population estimates. All methods should be subject to a careful design process, and power analysis should be conducted to determine the sensitivity of the method to detect changes.

Based on the review of over 200 papers and reports we recommend a package of complementary monitoring methods for brown bear, wolverine, lynx and wolf in Norway. These include the use of observations from the public and reports of predation on livestock to determine broad patterns of distribution, and an index based on hunter observations per hunting day, for all four species. Minimum counts of reproductive units, natal dens, family groups, and packs, should be obtained from snow-tracking for wolverines, lynx and wolves respectively. In addition a track-count index should be obtained for wolverines and lynx. As much data as possible should be obtained lynx and wolverines killed in the annual harvest. Brown bears will be difficult to monitor without the use of radio-telemetry, therefore they may require periodic telemetry based, mark-recapture studies. Such a program can easily be constructed within existing central and regional wildlife management structures, but will require extensive involvement from hunters.

Keywords: Carnivore – monitoring – census – bear – lynx – wolf – wolverine

John D C Linnell, Jon E Swenson, Arild Landa & Tor Kvam, Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway.

Foreword

Against a background of increasing conflicts caused by recovering large carnivore populations, it has become increasingly vital to develop effective and robust methods to monitor the development of brown bear, wolf, lynx and wolverine populations in Norway. This literature review attempts to examine worldwide experience and recommend which methods, or combinations of methods, hold promise for application to the Norwegian situation. It is not a "cookbook" with detailed instructions on how to apply each method. Before any given method can be applied in a routine manner in Norway it will require development to adapt it to local conditions and specific objectives. Although the review was written with a view to developing a large carnivore monitoring program in Norway, the methods should be relevant to most areas in Europe. In order for this document to be of use to as many people as possible it has been written in both English and Norwegian.

Funding was provided by the Norwegian Directorate for Nature Management. Reidar Andersen (NTNU), David Garshelis (Minnesota Department of Natural Resources), Lee Fitzhugh (University of California), Harley Shaw (formerly with Arizona Department of Fish and Game), Luke Hunter (University of Pretoria), Peter Jackson (IUCN- Cat Specialist Group), Joe Fox (University of Tromsø), H el ene Jolicoeur (Minsitry of Environment, Quebec), Olav Strand (NINA), Erling Johan Solberg (NINA), Lee Allen (Department of Natural Resources, Queensland, Australia) & Scott Brainerd (NJFF) have all provided valuable information, discussion, and literature. Conversations with Arne Mortensen, Petter Wabakken, Erling Maartmann, Hans Haagenrud, H akon Solvang, Jan Solberg, Erling Ness and other hunters and managers at the local level in Hedmark, Oppland and Troms counties have greatly helped develop our ideas of what is practical and what is not in the real world. Eli Kvingedal took care of the translation into Norwegian at very short notice. We are grateful to you all.

Trondheim, July 1998

John D. C. Linnell, Jon E. Swenson, Arild Landa and Tor Kvam

Contents

Abstract	3	7.2 Resources available	23
Foreword	3	7.3 The management context	23
1 Introduction	5	7.4 Recommended monitoring system	24
1.1 Defining goals and information needs	5	7.4.1 All species	24
1.2 Some basic concepts: parameters suitable for monitoring	6	7.4.2 Lynx	25
1.2.1 Distribution	6	7.4.3 Wolf	25
1.2.2 Population indices	6	7.4.4 Wolverine	26
1.2.3 Population minimum counts	6	7.4.5 Bears	26
1.2.4 Population density estimates	6	7.4.6 Structure	26
1.2.5 Reproductive parameters	7	7.5 Incentives for public involvement	27
1.2.6 Health	7	7.6 Co-operation with existing or future moni- toring programs	27
2 Monitoring without original fieldwork	7	8 Research and education needs	27
2.1 Questionnaires and observations from the public	7	9 References	28
2.2 Damage reports	8	Appendix	38
2.3 Analysis of harvest data	8		
2.4 Habitat evaluation	8		
3 Monitoring with fieldwork, but without recognis- able individuals	9		
3.1 Presence - absence	9		
3.2 Indices	10		
3.2.1 Scent stations	10		
3.2.2 Sign surveys	10		
3.2.3 Finnish triangles	11		
3.2.4 Hunter observations	11		
3.2.5 Aerial surveys	11		
3.2.6 Extrapolation of indices to density: assumptions	12		
3.3 Minimum counts	12		
3.3.1 Howling surveys	12		
3.3.2 Aerial Reconnaissance Surveys (ARS)	12		
3.3.3 Ground snow-tracking surveys (GTS)	13		
3.3.4 Genetic methods	13		
3.3.5 Den counts	13		
3.3.6 Unduplicated counts of reproduc- tive units	13		
3.3.7 Ensuring that a minimum count really is a minimum	14		
3.4 Population estimates	14		
3.4.1 Line transects	14		
3.4.2 Track Intercept Probability Estima- tor (TIP)	15		
4 Monitoring with fieldwork, and with recognis- able individuals	15		
4.1 Minimum counts	15		
4.1.1 Sum of "known" individuals	15		
4.1.2 Identification of individuals from tracks	16		
4.2 Population estimates using mark-recap- ture methods	16		
4.2.1 Capture - mark - recapture	16		
4.2.2 Capture - mark - resight	17		
4.2.3 Camera traps	17		
4.2.4 Tracks and sign	17		
4.2.5 Radioactive tracers	17		
4.2.6 Tetracycline	17		
4.3 Reproductive and survival data	18		
5 Summary of methods	18		
6 Statistical issues	21		
6.1 Sampling scale	21		
6.2 Distribution of sampling sites	21		
6.3 Power analysis	21		
7 Case study – recommendations for Norway	22		
7.1 Methods in current use in Norway	22		

1 Introduction

Large carnivores probably attract more conservation interest from the public than any other group of wildlife. Tigers, wolves, bears, pandas and lions have become species of household interest throughout the world. They are also probably the most difficult (and expensive) group of animals to conserve in our modern and over-crowded world. Among the many questions of conservation interest, none attracts more interest and debate than population estimates. Politicians, the public and wildlife managers constantly demand to know "how many wolves (or tigers, or pandas etc.) are there left?". Having methods to monitor the size and trend of large carnivore populations is crucial for at least 6 reasons;

- (a) The size of the population is important to determine the appropriate level of protection that should be afforded it.
- (b) Repeated estimates of population size, or of an index, are vital to determine if the population is decreasing, increasing or stable.
- (c) Such estimates are vital to measure the success or failure of management strategies.
- (d) Interpreting research results without an estimate of population density is difficult.
- (e) Where large carnivores are harvested it is vital to set hunting quotas that can be supported by the population.
- (f) Where large carnivores cause conflict with livestock, measures of presence/absence and relative density may be important to ensure fair payment of compensation.

However, as this review will hopefully make clear, estimating the density, and monitoring the trend, of large carnivore populations is not easy - in fact it must be one of the most difficult tasks that a wildlife biologist or manager can undertake! In some cases it may be impossible to produce estimates that fall within less than an order of magnitude of the true population size. In other cases accurate methods exist, but they require large amounts of fieldwork, high costs, and invasive methods like radio-collaring animals. Why is it so difficult to count large carnivores? The answer lies within the very nature of the biology of large carnivores.

By definition, large carnivores are very high, or on top of, the food chain. This greatly limits their potential densities. Usual densities in temperate areas are in the order of 1 to 20 individuals per 1000 km². To make matters worse, persecution and habitat degradation may have brought populations to even lower levels, or else subdivided a large population into small fragments. This implies that in any survey, most sample units will not contain any individuals, or signs left by an individual, at the time of the survey. In other words there will be many zero values and low absolute values, factors that introduce large variances into any statistical analysis. Large carnivores

are also generally very hard to observe, as they are often nocturnal or occupy dense habitats, implying that many survey methods may not detect the presence of carnivores which are present. Density may also vary greatly across relatively small distances, for example across an expansion front (Swenson et al. 1998), making the choice of sampling area crucial (Smallwood & Schonewald 1996, Smallwood 1997).

To make matters even worse, large carnivore populations generally have slow growth rates, a factor which means that failure to detect a real decline in population density could be very serious. Many decades may be needed for the population to recover. Because of these problems, many diverse methods have been used to estimate the size of large carnivore populations, and to monitor their distribution and development, in all possible habitats from tundra to rain forests. In contrast to other groups of species, like seabirds (Anker-Nilssen et al. 1996, Lorentsen 1997), there are no internationally recognised standard methods. In this review we try to describe those which are relevant to European conditions. As a result most examples are chosen from European and North American species and study sites, although we have included examples from Africa and Asia where appropriate to illustrate points. Methods that seem promising are given more space than those which are inappropriate. This is *not* a detailed "cookbook" or methodological manual for counting large carnivores. Rather, it is an overview of the methods that have been tried, and the concepts underlying them. For any reader interested in putting a particular method to use, it is essential that they read some of the primary literature referred to here, and that they adapt it to their own conditions and requirements (statistical, logistical, political and ecological).

1.1 Defining goals and information needs

Before a monitoring program for a particular species can be designed and put into effect, there is one question that needs to be answered - *what is the goal, or objective, of the monitoring program?* (Goldsmith 1991, Hellowell 1991, Noss & Coperrider 1994). A related question is - *what degrees of accuracy and precision are required?* Without knowing why you are monitoring, and what the information is going to be used for, there is absolutely no point in monitoring. The answers to these questions obviously depend on the context. However, the importance of these questions cannot be overstated, as the choice of methodology to be adopted depends largely on what answers are required.

Generally, where large carnivores are being harvested throughout their distribution there is a need for much more precise information than where they are effectively protected. This stems largely from the oft-demonstrated ability of hunters to dramatically reduce large carnivore populations to the edge of extinction (Brown 1985, 1992,

Swenson et al. 1994, Boitani 1995, Breitenmoser 1998). Large carnivore harvest therefore requires careful monitoring if quotas are to be sustainable. Effective quota setting (hunting quotas or determination of maximum allowable mortality) can be achieved in two ways. Firstly, if precise population estimates exist, and the population dynamics are understood such that the harvestable proportion of the population can be calculated, an appropriate harvestable quota can be calculated. Secondly, if population estimates are lacking, an acceptable quota can be set through a process of trial and error by monitoring the response of an abundance index to various quotas. Preferably, both methods would be used to support each other. As our knowledge of large carnivore population dynamics and resilience is limited (Weaver et al. 1996) we must always use caution. The closer a quota is set to the maximum that is possible, the more accurate information is required to prevent over-harvest.

The precision required from monitoring methods decreases greatly if effective refuge areas exist (with little or no harvest). Animals can disperse from these areas to recolonise areas that might have been over-harvested. Refuge areas have been advocated on a theoretical basis in recent years (McCullough 1996), and are commonly used for managing black bears in some parts of North America (e.g. Powell et al. 1996). The problem with most large carnivores is that because of their large home ranges and low densities these refuges need to be very large.

1.2 Some basic concepts: parameters suitable for monitoring

The next question is to determine the population parameters that should be measured. Again this depends largely on the goals and objectives of the program.

1.2.1 Distribution

The most basic information about a species status is its distribution. Surveys of animal distribution are widely used in the production of mammal and bird atlases (Harding 1991, Gjershaug et al. 1994, Løvdal et al. 1998) and typically record the presence or absence of a species within a given area. In the context of large carnivores it is vital to separate between the distribution of *reproducing individuals* and the *total distribution*, because males of most species can have very long dispersal distances and unstable home ranges before establishment (Wabakken & Maartman 1994, Swenson et al. 1994). This can lead to the occasional presence of individuals in a large area where no reproduction occurs. Provided data collection is systematic, distribution surveys have value as a monitoring tool and are especially vital to place the results of more detailed studies (of more limited areas) into context.

1.2.2 Population indices

As well as knowing the distribution of a species, it is possible to record its relative abundance in different areas, even without estimating numbers. For example given a standard search technique, such as counting tracks in snow along transects, it is typical to say that if area A has a higher frequency of tracks as compared to area B there must be more animals in area B, even if we don't know the exact numbers in either area. Similar logic is used to compare relative abundance in the same area over time. However, although a linear relationship is assumed between the index and actual density, indices have rarely been validated for most groups of animals (Van Dyke et al. 1986, Swenson 1991). Indices are becoming more commonly used in many management contexts largely because of the problems associated with obtaining precise counts or estimates of population size (Swenson 1991, Vincent et al. 1991, 1996, Cederlund et al. 1998, Solberg et al. submitted).

1.2.3 Population minimum counts

Traditional methods of monitoring large carnivore populations have often relied on so-called minimum counts, or unduplicated counts. Using a variety of methods, the location of individual carnivores are detected and recorded. Then using a variety of field protocols and "rules", these are added up, attempting to avoid counting the same individuals twice (Knight et al. 1995), somewhat similar to the territory mapping method used for songbirds (Baillie 1991). A variation on this method is to try and identify, or mark all individuals that are seen or captured (Gros et al. 1996, Maddock & Mills 1994, Mills et al. 1996). Either way one determines that there were at least a minimum number of individuals in the surveyed area. Whereas this result may be robust, the problem is that there is no objective way of knowing that there was not really 2 or 3 times that number of individuals, whose presence was not detected. No statistical measure of this error can be obtained, and it is very hard to statistically detect changes in the population density (Yoccoz et al. 1993, Mattson 1997). Alternatively, there may be wrong assumptions made during the process of producing the "minimum" number, and some animals may have been counted at least twice.

1.2.4 Population density estimates

Rather than trying to count all individuals present within a study area, population estimators attempt to sub-sample the population and calculate the proportion of individuals that are not counted. Methods such as mark-recapture or probability sampling come into this category (Seber 1986). Such methods generally produce an estimate of statistical error that can be expressed as a confidence interval. Whereas this allows the quality of the estimate to be evaluated, there are often problems when applied to small populations, as the error tends to be quite large purely as an artefact of the small sample size.

1.2.5 Reproductive parameters

Apart from monitoring the number of individuals within a population, it is desirable to know how well the population is reproducing, and how the sexes or ages are structured. Such data can be collected either during the process of sampling in the field, or with some difficulty may be estimated from harvest material. When combined with estimates of mortality rates (for example from a sample of radio-collared animals) the population trend can be estimated by population modelling, even without estimating population size (Eberhardt et al. 1994).

1.2.6 Health

Because diseases and parasites may have large effects on large carnivore populations, the health and condition of individuals within a population may also be an important part of a monitoring program (Nowell & Jackson 1996). Such data can be obtained from individuals killed in harvests, or from those live-captured in research projects, or indirectly from scats.

Determining *which* parameters to monitor and *why* are the first steps. The next important step is to determine *how* to collect these data in a manner that is statistically robust and economically affordable. We have ordered the options under three categories, which involve increasing amounts of fieldwork and increasingly invasive techniques (Harris 1986).

2 Monitoring without original fieldwork

Some of the cheapest methods for monitoring large carnivores are those that involve no original fieldwork. Whereas this may seem attractive at first, the accuracy and precision of such methods leave much to be desired.

2.1 Questionnaires and observations from the public

The most simple level of data collection is to send out questionnaires to local contact people, asking about either the presence or number of large carnivores in a given area with which they are familiar, or to solicit observations from members of the public. These methods have been widely used in Europe and North America (e.g. Bjärvall 1978, Heggberget & Myrberget 1979, Berg et al. 1983, Kolstad et al. 1984, 1986, Jakubiec 1990, Fuller et al. 1992, Blanco et al. 1993, Ionescu 1993, Vila et al. 1993, Mertzanis 1994). Although tempting in their simplicity, there are many problems, which may cause under-, or over-estimation of the true numbers;

- (a) Many people misidentify tracks, signs and even sightings through lack of experience (e.g. Elgmork et al. 1976, Van Dyke & Brocke 1987a,b, Smallwood & Fitzhugh 1989).
- (b) Even experienced observers have no chance of accurately estimating true numbers (Elgmork 1988, 1996, Swenson et al. 1995).
- (c) As many segments of the public may have vested interests in over- or under-representing carnivore numbers, the honesty of informants cannot be assumed.
- (d) Despite the fact that large carnivores are large, their presence may sometimes go unnoticed, or unreported. Therefore, the absence of reports is not the same as an absence of carnivores.
- (e) People may be more likely to report sightings in areas where carnivores are not common (novelty value). Therefore the frequency of reporting may not reflect the frequency of occurrence (Finn Sandegren, unpublished data).

However, such surveys can produce an approximate picture of carnivore distribution, which may be of interest when it detects the presence of very low density or newly colonised populations. The error resulting from (a) and (c) can be greatly reduced if experienced personnel control every report or sighting (Van Dyke & Brocke 1987b). Certainly information from the public provides a starting point to plan more intensive studies, and confirmed observations should be recorded. In general, such surveys need to be carefully planned, interpreted and controlled in order to produce meaningful results. If a large number of controlled observations can be regularly

collected, it may be possible to produce minimum counts provided strict rules are applied (see below, Knight et al. 1995, Kvam 1997).

2.2 Damage reports

Where large carnivores occur together with free-ranging livestock, like domestic sheep, goats, cattle, horses or semi-domestic reindeer, predation will occur (Kaczensky 1996, Aanes et al. 1996, Linnell et al. 1996). It is nearly always possible to determine which carnivore species is responsible for a predation event if a trained person carefully examines a freshly killed carcass. As most European countries pay compensation for livestock and require that cause of death be verified, this should be a widely applicable method for gathering data (Kaczensky 1996). Therefore, if all reports of predation on livestock are recorded, a picture of carnivore distribution will appear. Large changes in the distribution and number of depredation events can be used to gain a first approximation of changes in carnivore numbers (Aune 1991, Torres et al. 1996). However, it is a totally different issue to extrapolate the number of dead livestock to the number of carnivores present. The relationship is unverified, and may depend more on husbandry methods being used (Kaczensky 1996) and the numbers of livestock present (Gudvangen et al. 1998). In addition the existence of problem individuals that kill disproportionate numbers of livestock within a carnivore population is a much debated theme (Linnell et al. 1996). If such individuals exist it will severely bias these data.

2.3 Analysis of harvest data

Where large carnivores are harvested, or regularly killed in response to depredation on livestock or nuisance behaviour, the bodies can provide valuable information. Changes in hunter success can reflect changes in the population, although it is important to control for confounding factors such as quota size, weather and the economic value of the species (Myrberget 1988). In addition, a measurement of hunter effort is very important to correctly interpret results. Some basic sex, age and allometric parameters can be collected by the hunter immediately after making a kill. Additionally, carcasses can be sexed (Mano 1995) and examined for reproductive history (Coy & Garshelis 1992) if the whole carcass, or at least some teeth and reproductive organs, can be collected for laboratory analysis and age determination (Kvam 1984). Many attempts have been made to model population structure and trend of black, brown and polar bears from harvest data (Paloheimo & Fraser 1981, Fraser et al. 1982, Fraser 1984, Kolenosky 1986, Aoi 1987, Harris & Metzgar 1987, Mano 1987, 1995, Miller 1990, Kvam 1991, Lee & Taylor 1994, Rossel & Litvaitis 1994, Godfrey et al. 1998). The methods used have become increasingly complex, involving detailed demographic models and are beyond the scope of this review. However, there are several problems that are frequently encountered;

- (a) Sample sizes are often too small.
- (b) The different age, sex and reproductive classes are rarely equally vulnerable to harvest or capture (Miller 1990, Landa & Skogland 1995, Huber et al. 1996). There may even be important individual differences in vulnerability (Noyce et al. 1998). Therefore the sample is not random with respect to the population. This problem especially confounds the use of life table analysis.
- (c) Any given harvest structure can often be interpreted in many different ways (Miller & Miller 1990, Garshelis 1990, 1993).

Despite these problems, harvested animals provide much hard data about the extent and location of human caused mortality, and at least in broad terms can provide coarse data on population structure and reproductive parameters. Also, constant monitoring of harvest allows changes in the composition of the harvest to be detected (Jordhøy et al. 1996, Solberg et al. 1997) which can be used to indicate that changes may be occurring in the population structure. However, further research is desperately required to find ways to utilise more information from harvest data - especially promising are ways to combine harvest data with independent estimates of population trend, and the use of harvest data to determine the spatial structure and distribution of the population (Swenson et al. 1998).

2.4 Habitat evaluation

Large scale habitat evaluation has become possible during the last decade due to the development of satellite based remote sensing techniques, increased attempts to inventory habitat distribution from the ground, and the availability of Geographic Information System (GIS) computer programs to analyse such data. Following detailed analysis of carnivore habitat selection in research areas (e.g. Clark et al. 1993), attempts have been made to use map data to predict the suitability of large areas as black bear or wolf habitat (Rudis & Tansey 1995, Mladenoff et al. 1995, Mladenoff & Sickley 1998). These examples, have used the method largely as a tool for planning carnivore recovery and evaluating the relative suitability of recovery areas. Similar studies have tried, often successfully, to find relationships between prey density (an important component of habitat quality) and carnivore density (e.g. Fuller 1989, Messier 1995, Gros et al. 1996, but see Mills & Gorman 1997 for an important exception). Sequential surveys can also be used to monitor the changing quality of carnivore habitat with time. As such, habitat evaluation is a vital step in the formulation of carnivore management plans, especially when potential sources of conflict are also included as negative factors to balance the positive habitat attributes (Mladenoff et al. 1995, Clevenger et al. 1997).

However, other studies have attempted to use habitat suitability or prey density as a method for estimating the number of carnivores present within a region (Gros et al.

1996). For example, managers attempted to estimate the number of grizzly bears present in the Canadian provinces of British Columbia and Alberta by extrapolating a density estimates from research areas to the other areas with similar habitat across the provinces (Nagy & Gunson 1990, Gunson & Markham 1993, Banci et al. 1994). Fuller et al. (1992) attempted to estimate the number of wolves present in Minnesota by extrapolating their documented relationship between wolf density and prey density to unsurveyed areas where they just had an estimate of prey density. Other studies have just assumed that estimates of carnivore density from research sites can be extrapolated across the whole distribution of the species (e.g. Schaller et al. 1988, Theberge 1991, Rabinowitz 1993), or else extrapolated with subjective adjustments (Ross et al. 1996). This approach is simply *not valid* for evaluating the status or numbers of a carnivore species. It provides an estimate of the *potential* numbers that *could* be present if it was only prey density or habitat quality that determined carnivore abundance. Most (all?) large carnivore species are exposed to varying degrees of legal and/or illegal harvest (e.g. Knight et al. 1988, Kenney et al. 1995, Nowell & Jackson 1996, Powell et al. 1996, Andersen et al. 1998). Therefore, knowing that an area has the capacity to support a high density of a carnivore species is not the same as saying that it actually does. Finally, research areas are almost never picked at random, instead they are generally chosen because they contain relatively dense populations of carnivores (Fitzhugh & Smallwood 1989, Schonewald-Cox et al. 1991). Therefore, density estimates obtained from research areas are not suitable for general extrapolation (Blackburn & Gaston 1996, Smallwood & Schonewald 1996, Smallwood 1997) without some form of sample stratification or correction. One of the few cases where such extrapolation has been justified is a brown bear density estimate for Sweden. Swenson et al. (1994) used research area density estimates to calibrate a nationwide index of bear density (harvest rate). The result was an "as accurate as possible" estimate of the number of bears in Sweden.

3 Monitoring with fieldwork, but without recognisable individuals

Clearly, there are limits to what can be achieved without fieldwork. This section reviews the different methods that have been used to produce population abundance indices or estimates based on fieldwork, but under circumstances where no individuals can be recognised. Surveys can be designed to collect data on three different levels, presence/absence, an abundance index, and an estimate of population density.

3.1 Presence - absence

The most basic methodology for monitoring a species in the field is to determine if it is present or not within a given area. Accepting the difficulties with determining population density over large areas and their poor state of knowledge about carnivore distribution patterns in the western United States, Zielinski & Kucera (1995) developed a standard set of methods to be applied throughout the region to detect the presence of wolverine, Canadian lynx, American marten and fisher. They recommended minimum systematic sampling intensities for the use of snow-tracking, camera stations, or track-plate surveys (see later). Similar methodology could be applied to any species, in any area, as long as the technique guaranteed a high chance of detecting the presence of carnivores that actually are present. It is logical that the sampling units should be about the same size as an individual's home range (usually in the order of hundreds of km²). However the major drawback is in the low sensitivity of presence-absence methods to changes in population density.

Virtually all of the methods listed in the previous and following sections can provide data on distribution, or the presence or absence of a species in a study area. While some methods that involve fieldwork may be relatively systematic, others like questionnaire and observations provided by the public are only really good for first investigations of an area. *One fundamental issue is the separation between continual presence in an area indicative of resident and reproducing animals and the occasional presence of dispersing or transient individuals.* For example, the continuous finding of signs and observations of bears in a small area over many years allowed Camarra & Dubarry (1997) to conclude that a small relict bear population still exists in the French Pyrennes. However, the occasional finding of very few signs and observations in several areas of Norway was falsely interpreted as being due to relict populations when in fact it was due to transient individuals covering very large areas (Elgmork 1996).

3.2 Indices

The principle behind the use of population indices is that it is possible to record the frequency of some parameters (such as a number of tracks, scats or observations), and that the frequency of these parameters will reflect the density of the population. The methods produce an index such as the number of tracks found per kilometre of transect, which hopefully reflects population density, but does not tell you anything directly about the number of individuals. Generally, indices are used to detect changes over time (Kendall et al. 1992, Beier & Cunningham 1995), or across space (Fox et al. 1991, Van Dyke et al. 1986, Smallwood & Fitzhugh 1995, McCarthy & Munkhtsog 1997). Repeated measures, or replicates, allow statistical comparison between samples. The various methods that are commonly used to collect observations of individual carnivores or their sign are outlined below.

3.2.1 Scent stations

Scent stations depend on using an attractant (food, urine, chemicals, Harrison 1997) to attract a carnivore to a point, where its visit is recorded. For example, the attractant may be hung in a tree or on a pole surrounded by sand which would record an impression of a footprint (Lindzey et al. 1977, Conner et al. 1983, Diefenbach et al. 1994, Allen et al. 1996), or placed in a box such that the carnivore has to cross a surface treated with material to record a track (track-plate box, Bull et al. 1992, Zielinski & Kucera 1995, Zielinski & Stauffer 1996). These methods assume that the tracks made can be identified to species level (Zielinski & Truex 1995). Other methods involve the use of a camera that reacts to the presence of a moving animal (Bull et al. 1992, Zielinski & Kucera 1995). One of the most commonly used scent station methods for black bears in North America is the "sardine-tin method" (Garshelis 1990, 1993, Powell et al. 1996). A perforated tin of sardines is nailed up a tree at a height that only a bear can reach. Signs of claw marks from a climbing bear, or bear hairs, are visible if a bear visits a station. The proportion of tins visited within a given number of nights is the index.

Regardless of the specific method used, the principle is that stations will be visited by carnivores that exist in the area so the method will at least detect presence-absence (Zielinski & Kucera 1995), and a higher density of carnivores should result in higher visitation rates. Although several studies have found that visitation rates broadly reflect changes or differences in density (Conner et al. 1983, Diefenbach et al. 1994, Powell et al. 1996), there are clearly problems in detecting small changes in population density. Large numbers of stations, and replicated surveys may be needed to have any chance of detecting changes in population size in the order of 10-20 % (Diefenbach et al. 1994). This problem will be especially acute when applied to European large carnivores which typically occur at much lower densities than the abundant

medium to large sized carnivores (bobcat, black bear) that the method is commonly used on in North America. This will result in a very high proportion of zero values, greatly reducing the power of the test to detect changes in population density. Further variation caused by seasonal, and possible annual, changes in response to the bait (Lindzey et al. 1977) need to be taken into account. This leads to an uncertain form of the relationship between the visitation frequency and real density. Only one study has attempted this comparison, and found fairly good agreement between the index and actual density (Diefenbach et al. 1994). Whereas scavengers like wolverines and bears may investigate attractants, it is uncertain if carnivores like wolves and lynx will be attracted to a chemical or meat bait, especially in areas where they have been hunted and are wary of human scent.

3.2.2 Sign surveys

Sign surveys are probably the most commonly used method for monitoring large carnivores (Kutilek et al. 1983, Van Dyke et al. 1986, Jackson & Hunter 1995, Smallwood & Fitzhugh 1995). Transects are searched for tracks, scats, scrape marks or any other sign of a passing carnivore. The principle is that a higher carnivore density will result in more signs, on a higher proportion of transects.

One of the best developed forms is the track survey used for monitoring cougar populations in the western United States (Van Dyke et al. 1986, Shaw et al. 1988, Smallwood & Fitzhugh 1995, Beier & Cunningham 1996). Transects along sandy, dusty or snow-covered roads or trails are made on foot, horseback or from a motorcycle, and the incidence of footprints and/or scats and scrapes are recorded; usually as the number of tracks per kilometre per day of accumulation. Consistent methodology has been proposed to maximise the detectability and recording of tracks and signs (Fitzhugh & Gorenzel 1985, Galentine & Fitzhugh 1989, Smallwood & Fitzhugh 1989, 1991, 1993, 1995, Smallwood 1997). Four studies have found clear variation between regions based on track density (Van Dyke et al. 1986, Shaw 1988, Cunningham et al. 1995, Smallwood & Fitzhugh 1995). In the case of Van Dyke et al.'s (1986) study, this variation was closely related to real differences in density as determined by radio-telemetry.

Similar methods have been used throughout central Asia (Pakistan, India, Nepal, Mongolia) to detect regional variation in snow leopard abundance (Fox et al. 1991, Ahmad et al. 1997, Fox & Chundawat 1997, McCarthy & Munkhtsog 1997). Short-transects (< 1 km) are walked in areas most likely to be passed by snow leopards, and all scats, paw-prints and scrapes are recorded (Ahlborn & Jackson 1988, Jackson & Hunter 1995). The widespread application of this simple, but standard technique represents the most extensive, international large carnivore monitoring system anywhere (Jackson et al.

1997). Track and sign surveys have also been used for monitoring black bear, grizzly bear, wolf and coyote populations in North America (Pelton 1972, Messier & Crête 1985, Kendall et al. 1992, Rose & Polis 1998), brown bear in Spain (Clevenger & Purroy 1996) and preliminary attempts have been made to use it for wolverines and Eurasian lynx in Norway (Fox et al. 1990, Mortensen 1996) and for mountain mammals in northern Sweden (Björvall & Lindström 1984, 1991).

However, because large carnivores typically occur at very low densities, tracks and signs are not found on many transects (Clevenger & Purroy 1996). Therefore a large number of transects are required to increase the power of statistics to detect changes in the index. As carnivores almost always use the available habitat in a non-random fashion and favour certain travel routes, the probability of detecting carnivore presence can be increased by placing transects in areas where they are most likely to pass (Ahlborn & Jackson 1988, Jackson & Hunter 1995, Smallwood & Fitzhugh 1995, Beier & Cunningham 1996). Whereas this method may increase the number of tracks detected, it makes the comparison between regions more difficult, although if the same transects are used each year, it should not affect the ability of the method to detect temporal changes within a region. Finally, the skill of the field worker to see tracks and sign may greatly influence the results, especially on substrates other than snow.

Power tests of existing data sets consistently confirm the inability of sign surveys to detect small annual changes, however they confirm the ability of the methods to detect larger changes (Kendall et al. 1992, Beier & Cunningham 1996, Clevenger & Purroy 1996). It is therefore vital to carry out a pilot study within a proposed study area to determine which density and configuration of transects will be required to provide adequate power for the area specific management purposes. Finally, it is important to remember that the relationship between the index and real density is largely untested and may depend on habitat, climate, track/sign detectability, time of year, prey density and social structure of the carnivore population (e.g. Thompson et al. 1989).

3.2.3 Finnish triangles

The world's most intensive and systematic form of track survey index sampling is probably the Finnish Game Triangle network. Almost 1500 4 x 4 x 4 km triangles cover Finland. Each is skied during mid-winter following recent snowfall and all mammal tracks crossing it are counted (Lindén et al. 1996). The index is calculated as the number of tracks/km/day since snowfall. The results can be used to detect variation in numbers between areas and in the same area over time (Danilov et al. 1996, Helle et al. 1996). Furthermore, data on species-specific habitat selection can be obtained if the index data is combined with habitat maps (Helle & Nikula 1996). One advantage of this system is that it covers all

winter-active mammalian species and therefore gives more benefit per unit effort. However, the efficiency of the triangle transect configuration for detecting wide-ranging species, like large carnivores is unclear.

3.2.4 Hunter observations

The main problem with using observations from the public as an index of abundance lies in the fact that the search effort behind each observation is unknown. This problem can be overcome if a group of observers can be asked to systematically record the time spent in the field as well as the number of observations. Organised hunters have often been used to record observations of ungulates. For example, throughout Scandinavia an index of moose-observations per hunter-day is widely used to follow trends in the moose population (Solberg et al., submitted). Early attempts were made in Norway and Sweden to use moose hunters to also record observations of bears and bear sign (Elgmork 1991, 1992, 1997, Mysterud 1991). Despite a low number of observations (over 1000 hunter days per observation) the data gave a broad picture of differences in density between areas. Similar methods are also used in Quebec, Canada, for wolf and black bear monitoring (Messier & Crête 1985, Crête & Messier 1987, Jolicoeur pers. comm.). In the Quebec study the number of wolves seen, the number of wolf scats seen, and the number of nights when wolf howls were heard were all used to form indices (Crête & Messier 1987). A recent attempt has been made to evaluate similar methods in Sweden (Swenson and Sandegren unpublished data) and moose hunters will be asked to note all observations of brown bear, wolf, wolverine and lynx beginning in 1998. Although the number of observations will always be low, the possibility of using the technique to monitor trends is clearly deserving of further research as it makes use of existing management structures, and taps into the enormous man-power resource of hunters. Swenson & Sandegren (1996) also investigated the ability of Swedish hunters to correctly identify the trend (increasing or decreasing) of the bear population. They found that hunters were generally correct, but that there was a time lag in the order of a decade. These methods require that a large number of hunters are distributed throughout the area in question and that a well organised system exists for collecting their observations.

3.2.5 Aerial surveys

Although large carnivores are often difficult to observe directly because of their low density and often cryptic behaviour, a number of attempts have been made to spot them from low flying aircraft or helicopters. Apart from using these observations to make minimum counts (see later), the number seen per hour of flying can also be used as an index of abundance. Examples include polar bears off Alaska, and wolves in the forest-tundra of northern Canada (Amstrup et al. 1986, Carbyn et al. 1993). Numbers of tracks in snow seen per 100 km of

flying has also been used in Alaska for wolverine and lynx population monitoring (Golden 1993, Golden et al. 1993). The method is only likely to be of use in open landscapes, but may be a useful compliment to line-transect or minimum count methods.

3.2.6 Extrapolation of indices to density: assumptions

In many cases, researchers and managers attempt to extrapolate from an index to a real density using correction factors (Smallwood & Fitzhugh 1991, Högmander & Penttinen 1996). In some cases this is based on comparison between areas for which both an index value and an actual density are known, and then extrapolating to another area for which only an index value exists (e.g. Messier 1985, Swenson et al. 1994). In other cases, data about animal movement patterns (for example distance moved per day) are used to convert index data into a real density (Danilov et al. 1996). However, there are a number of assumptions that need to be made, and which have rarely been tested. These generally concern the shape of the relationship between index density and population density, which is generally assumed to be linear. However, this is unlikely to be true in all real life situations. For example in one study, when snowshoe hare density decreased, Canada lynx density decreased, but their movement rate increased (Ward & Krebs 1985). Thus, track count indices underestimated the degree of population decline (Stephenson & Karczmarczyk 1989). Similar effects could be expected to occur if variation in density effects social interactions, home range patrolling and marking behaviour. As age and sex often effect carnivore movement patterns, the population structure is likely to affect the rate of track accumulation. The conclusion is that while indices may be robust, their relationship with density needs to be documented carefully.

3.3 Minimum counts

The most widespread methods for estimating carnivore density in study areas have come under the categories of minimum counts. These methods attempt to count individual large carnivores through either direct observation, or by isolating their location using tracks. Using various decision-making rules to avoid counting the same individual twice, a minimum number of individuals within the surveyed area is determined. The methods make no effort to calculate the number of animals that were present but not detected by the survey, and no statistical measure of error is produced. However, the problems associated with the reality of counting large carnivores mean that good minimum counts are often the best measures that we are able to obtain.

For example, the Yellowstone Ecosystem in the Rocky Mountains of North America contains one of the most studied grizzly bear populations in the world. However, from the very beginning of the bear studies initiated after

the grizzly bear was protected in 1975, it was realised that obtaining statistical estimates of population size would be impossible without a massive radio-collaring effort. As such the Interagency Grizzly Bear Study Team decided to concentrate on using a minimum count of reproductive females (Knight et al. 1995, Eberhardt & Knight 1996) and the collection of demographic data.

3.3.1 Howling surveys

Many species of social carnivore like wolves, coyotes, jackals and spotted hyenas use sound as a means of communication (Laundre 1981, Harrington & Mech 1982, Jaeger et al. 1996, Mills 1996, Rose & Polis 1998). In many cases a response can be elicited by either broadcasting a recorded howl, or simulating it using the human voice. Such a response indicates the presence of a group of the respective carnivore. Factors such as time of year, time of day, and group composition will affect the natural frequency of howling and therefore the response rate (Harrington & Mech 1982, Jaeger et al. 1996). A variant is to broadcast attractive sounds and record the numbers of animals that approach (Mills 1996). The distance that sound can carry, and the ability of human hearing to detect a reply varies with many environmental factors, with usual limits being around 3 km (Harrington & Mech 1982, Mills 1996). This requires a large number of broadcast sites if an area is to be completely covered. Although the method has been used with some success to survey spotted hyenas over large areas in Africa (Mills 1996). A test with a known population of wolves in Minnesota found that the method gave a poor estimate of population size, with wide confidence intervals Fuller & Samson (1988). At best the method probably only reliably gives a minimum count for a limited sampling area for European wolves. Species such as lynx, wolverine and bear do not reply to broadcast sound.

3.3.2 Aerial Reconnaissance Surveys (ARS)

The Aerial Reconnaissance Survey has long been the most widespread method used to census wolves in northern North America (e.g. Peterson 1977, 1995, Gasaway et al. 1983, Bergerud & Elliot 1986, Boertje et al. 1996). The principle is that a study area is surveyed by aircraft when snow-tracking conditions are optimal. All encountered wolf tracks are followed until the pack is located, and the number of animals in the pack counted. The process is repeated again and again until it is felt that the entire study area has been covered and that all packs present have been detected. The process requires good tracking conditions and experienced observers and pilots to be able to follow a wolf track from the air. Problems can occur when high ungulate densities can leave tracks that obscure the wolf tracks. One main disadvantage with the method is that single wolves are rarely detected. This will be especially important on dispersal fronts where the colonising individuals will be of disproportionate interest.

3.3.3 Ground snow-tracking surveys (GTS)

A variation of the above method is to search for tracks in the snow on the ground using a network of roads, paths or transects. Double counting is avoided by either back-tracking all tracks encountered or by ensuring that one or more transects without tracks lie between two transects where tracks are found. The method has mainly been used in Eurasia for estimating the density of wolves (Jedrzejewska et al. 1996, Smietana & Wajda 1997), lynx (Liberg & Glöersen 1995, Jedrzejewska et al. 1996, Mortensen 1996), tigers (Smirnov & Miquelle 1998), brown bears (Swenson & Wikan 1996) and wolverines (e.g. Kvam et al. 1987, Landa et al. 1998). The assumptions are that all carnivores present have a high probability of being detected and that double counting can be avoided. This clearly represents a trade off, as with increasing numbers of days after snowfall the carnivores are likely to travel further and therefore be easier to detect, but the abundance of tracks will also make the back-tracking and separation of individuals harder. It will also be harder to determine accurate minimum numbers at higher densities as the greater number of tracks will complicate interpretation. In order to use resources most effectively, it may be best to concentrate on identifying the number of reproductive units, rather than total numbers. This will limit the number of animals to backtrack, and remove that segment of the population for which it is hardest to develop movement rules (a single animal could be stable, resident male or a widely travelling, dispersing juvenile).

3.3.4 Genetic methods

In very small populations where snow-tracking is not possible, for example for bears that sleep for most of the winter, minimum population counts may be obtained through the use of genetic analysis. Using PCR techniques, DNA can be extracted from hairs and scats (Taberlet & Bouvet 1992, Wasser et al. 1997), both of which can be found by searching a study area. This allows both the determination of sex (Taberlet et al. 1993) and individual identity (Taberlet & Bouvet 1992). Disadvantages are the cost, and the fact that the method is only really suitable for very small populations living in small areas. In addition, recent concerns about genotyping errors may require the use of even more expensive methods (Taberlet & Waits 1998).

3.3.5 Den counts

Rather than counting individual carnivores or their tracks, it is often possible to count dens. Bears can be back-tracked to their dens if they emerge before snow-melt (Harris 1986), although this may seriously underestimate population size for females with cubs-of-the-year (COY), as they usually emerge later than males, often after snow has melted. Wolverines dig natal dens where they give birth in spring. As this is usually before snow-melt, careful searching of suitable and traditional sites can result in the

finding of dens. Although care is needed to separate between primary and secondary dens (to avoid double counting), den counting provides an effective technique to obtain a minimum count of the number of breeding females within a population (Bergström et al. 1994). Landa et al. (1998) have used the method to obtain minimum counts of the number of breeding wolverine females in Scandinavia, and were also able to produce an estimate of the minimum total population size using assumed population structures. Although wolves often dig dens, or enlarge fox dens, for their cubs, they are too cryptic to find systematically in forest habitat (Peterson 1995). Felids like lynx and cougars do not dig natal dens, or modify natural cavities in any recognisable manner.

3.3.6 Unduplicated counts of reproductive units

Rather than trying to cover a large area simultaneously to produce a minimum count with the ARS and GTS survey methods, it may be possible to accumulate observation (of individuals or tracks) over an extended period. By using data on home range size, movement rate and social organisation, a minimum estimate of the number of individuals responsible for these observations can be obtained. In most applications of these methods, the effort concentrates on reproductive units (family groups, usually an adult female with dependent young) because their movement patterns are more conservative. The collection of unduplicated observations of female grizzly bears with cubs-of-the-year (COY) has been a standard method for monitoring the status of the Yellowstone population since 1976 (Knight et al. 1995, Eberhardt et al. 1986, Eberhardt & Knight 1996). Observations of females with COY are collected from all sources during the whole summer period, with the date, location, and number of cubs noted. Extensive telemetry data (Blanchard & Knight 1991) allowed a set of conservative rules to be developed to determine if two observations belonged to the same family or not. For example, all observation separated by twice the mean home range diameter were regarded as being from different families. Within this distance, observations needed to be made simultaneously in two different places, or to be separated by major topographical features, or to contain a different number of COY to be regarded as distinct (Knight et al. 1995). Although the method has been criticised for not controlling for search effort and between year differences in bear visibility (Mattson 1997), and therefore being unsuitable for producing unbiased trends, it does produce a robust minimum estimate that can be used to document that the population is at least at or above a given level (McCullough 1986). A similar method has also been used for monitoring the isolated brown bear population in the Corillera Cantabrica region of northern Spain since 1982 (Wiegand et al. 1998).

Similar methods are also used in Norway and Sweden to estimate the number of family groups of lynx that are present each winter. Data on home range diameter and maximum movement rates are used to separate between

distinct groups which are localised from tracks left in snow (Kvam 1997, Östergren & Segerström 1998, Bergström et al. 1998). The fact that adult female lynx with kittens are almost always territorial, or at least have low levels of overlap also helps to separate between distinct groups (Breitenmoser et al. 1993, Schmidt et al. 1997, Andersen et al. 1998). A final issue is the problem of failing to detect the presence of a reproductive group. This can happen when observations of animals or their tracks fail to reveal the juveniles. For example, lynx kittens often walk in their mother's foot-steps in deep snow so as to conserve energy. Alternatively, juveniles may not join their mother on hunts, but wait for her to make a kill and lead them to it (Barnhurst & Lindzey 1989). In both cases, casual observation would report the presence of a single animal where a reproductive group actually existed.

3.3.7 Ensuring that a minimum count really is a minimum

The most important aspect of minimum counts is that they really should reflect a minimum, i.e. double counting must not occur. The rules used to separate distinct groups based on distance and time need to be based on telemetry data representative for the area being counted. This is one of the advantages with using family groups as they have smaller, and more consistent movement patterns (Blanchard & Knight 1991, Breitenmoser et al. 1993, Schmidt et al. 1997, Andersen et al. 1998). Single animals could either represent resident adult males, non-reproductive females or transient individuals of either sex. Because of the wide-ranging and irregular movement patterns of transients, it is not possible to determine rules for separating observations of single animals based on movement pattern.

It cannot be assumed that all observations and reports are correct, and therefore only verified or documented observations from the public, and those made by trained or experienced personnel should be used (Van Dyke & Brocke 1987a,b). Bear numbers in Norway in the early 1980's were massively overestimated because both normal home range sizes and dispersal movements were underestimated by at least an order of magnitude (Kolstad et al. 1984, 1986, Elgmork 1988, 1996, Swenson et al. 1995, 1996). Similarly, many lynx sightings in Austria were found to be wrong, leading to inflated estimates (Kaczensky pers. comm.).

With ARS or GTS surveys an assumption is made that tracks can be attributed to different individuals when there is no connection between sets of tracks. This assumes that all tracks are visible and that all are detected. Neither of these assumptions need be true. Tracks can often be destroyed by wind, snow falling from trees, or the passage of a large ungulate. In addition, many carnivores choose to walk in ungulate tracks, along ploughed roads, on the most compact snow under dense canopy cover or on ice covered rivers and streams.

Finally, it is very easy to miss a track entering or leaving a ploughed road, where snow is banked on the sides. Because of this it is desirable to set a rule that more than one transect between observations should fail to detect tracks in order for them to be regarded as distinct (Liberg & Glöersen 1995). As tracks are hard to see when travelling at speed in a car, especially on ploughed roads where compacted snow forms banks on the sides, we recommend that cars should not be used for track searches. Snow scooters driven slowly may be acceptable, but the very best methodology is to use skis or snowshoes, preferably while moving up the slope.

When collating observations over long periods of time in an effort to count unduplicated reproductive units it is vital that the rules used to separate between units are correct. In the Yellowstone example the rules presented by Knight et al. (1995) are based on extensive telemetry data (Blanchard & Knight 1991) and are all based on verified sightings by park and project staff. Therefore, even though the extent to which the data can be used may be open to discussion (Mattson 1997), it at least provides a robust minimum count. However, in the Spanish example (Wiegand et al. 1998), there is not enough information presented in the paper to evaluate the rules used, and the fact that almost half of the observations accepted were apparently made by the public, opens the question of whether their data is even a robust minimum. Finally, rules made for one area may not apply across all areas where a species occur. The results of lynx family groups counts using rules presented by Östergren & Segerström (1998) appear to have worked in the northern part of the range, but the results from central Sweden (Bergström et al. 1997) appear somewhat open to question.

3.4 Population estimates

There are clearly weaknesses with minimum counts due to the lack of a statistical estimate of error. This becomes especially important when trying to determine the accuracy of an estimate of trend. There are really only two methods that can do this with accuracy when marked or recognisable individuals are not available.

3.4.1 Line transects

Line transect estimators are frequently used for censusing bird or ungulate populations (Seber 1986, Van Hensbergen & White 1995, Gill et al. 1997). Individuals seen from a transect are counted, and the distance from the transect is estimated. The problem when applied to large carnivores is that they are usually not detectable under forest canopy, and even if they are, their low density means that very long transects are needed to obtain enough observations. Double counting has been used to correct for the problem of detectability in several studies (Dean 1987, Crête et al. 1991), however no study of which we are aware has used formal line-transect methodology. Rather, they have performed corrected

minimum-counts over certain zones of habitat. The only applications where line-transects methods might work would be for polar bears, or tundra dwelling grizzly bears.

3.4.2 Track Intercept Probability Estimator (TIP)

The TIP estimator must be one of the very few methods which has been especially developed for large carnivores. The method was developed in Alaska for use with Canadian lynx and wolverines (Schwartz & Becker 1988, Schwartz et al. 1988, Hundertmark et al. 1989). The principle is that a series of parallel linear transects (consisting of a set of randomly spaced transects with replicates) are flown (or skied) when snow-tracking conditions are good. All tracks intercepted are counted and both back-tracked to where the movement began before the last snow-fall, and forward-tracked to present location. This allows the minimum number of animals detected to be determined. Furthermore the distance moved by the tracked animals perpendicular to the orientation of the transect lines allows the calculation of the probability that some animals have gone undetected (Becker 1991). As a result an estimate with statistical error is obtained for that population. Present field applications have included wolf, Canadian lynx and wolverine (Becker 1991, Ballard et al. 1995), and simulations have modelled its suitability for cougars (Van Sickle & Lindzey 1991). Assumptions include the detectability of all tracks that cross a transect and that they can be both back-, and forward-tracked.

4 Monitoring with field-work, and with recognisable individuals

By far the most accurate methods of estimating the density of large carnivore populations is where individuals can be recognised either through natural markings or through the use of ear-tags or radio-collars. Entirely different statistical methods can be used which provide greater precision and accuracy.

4.1 Minimum counts

Even in cases where individuals can be recognised, many research projects only report a minimum count rather than a statistical estimate (Garshelis 1990, 1993).

4.1.1 Sum of “known” individuals

Over a period of time researchers begin to accumulate an overview of the number of individuals animals that inhabit a study area. As more and more animals become recognisable or radio-collared, it becomes possible to determine if there are any unmarked, or unrecognisable individuals present. Such a picture is much easier to construct when animals are territorial, and a “hole” is known to exist in the territorial mosaic of recognisable animals, but evidence exists that this hole is occupied by an unknown animal (Mech 1986, Garshelis 1993). The population estimate becomes the sum of all marked/recognisable individuals plus those unmarked animals that are known to exist. Although such methodology is very difficult to evaluate (Yoccoz et al. 1993), it is very widely used in telemetry based research projects for species like black bears (Lindzey et al. 1986), grizzly bear (Reynolds & Garner 1987, McLellan 1989), wolves (Mech 1986, Adams et al. 1995, Ballard et al. 1997), bobcats (Knick 1990), cougars (Maehr et al. 1991, Lindzey et al. 1994, Beier 1995, Logan et al. 1996), and Eurasian lynx (Breitenmoser et al. 1993, Jedrzejewski et al. 1996). However, many research projects have used such intensive trapping methods and conducted such intensive field activity, that these estimates are probably the most reliable available.

A variation on the use of radio-collaring is to use photographs of unmarked animals and to use natural markings to identify them. Large surveys using these methods have been made for African wild dogs (Maddock & Mills 1994, Woodroffe et al. 1997), cheetahs (Caro 1994, Gros et al. 1996) and lions (Hanby et al. 1995, Woodroffe et al. 1997). Although effective in open savannah habitats, such methods are difficult to apply to cryptic, forest dwelling European carnivores, unless animals concentrate at natural or anthropomorphic food sources.

4.1.2 Identification of individuals from tracks

In many studies researchers have claimed to be able to identify animals as individuals or as being from a given sex and age class, based on track size and shape. Such methods have been used to produce minimum counts of population size (Støen 1994), population age structure (Hornocker 1969, Spreadbury et al. 1996, Gula & Frackowiak 1996) or as aids in separating the number of animals responsible for tracks found during GTS surveys (Smirnov & Miquelle 1998). For more than 2 decades, tiger censuses in the Project Tiger reserves in India have been based on identification of individuals from tracings of track imprints in sand or mud (Karanth 1989, 1995, Støen 1994). However, experimental control of the ability of trackers to differentiate tracings from captive animals lead Karanth (1989) to question the reliability of these methods. Similar criticism has been aimed at attempts to identify individual black and brown bears (Klein 1959, Smith et al. 1998) from tracks. The only study which has managed to demonstrate reliable individual differentiation based on track shape has used multiple group discriminant analysis on cougar tracks, measured on good substrate in a standard manner (Fjelline & Mansfield 1989, Galentine & Fitzhugh 1989, Smallwood & Fitzhugh 1993). Accordingly, serious doubts must be raised about all estimates based on individual track recognition where complex statistical analysis has not been carried out, unless an individual track has some dramatic morphological characteristic such as a missing toe.

The ability to tell the age or sex of an animal from its track is another issue. As foot size may actually vary between the different age and sex classes of a species, especially in those that show high rates of sexual dimorphism, there is a biological reason to expect differences in track size to reflect differences in age/sex of the animal making the tracks. There are however, two problems. Firstly, the range of foot sizes for each age and sex class needs to be calibrated against animals of known sex and age. This is rarely done, making it hard to evaluate studies. Although adult males and young may be distinct, there is likely to be much overlap between adult females and sub-adult males (Gula & Frackowiak 1996). For species like Eurasian lynx which have large and flexible feet, the same foot may make very different sized imprints depending on snow conditions. Clearly the method needs to be validated for each species, and in some cases for each population if large variation in body size exists (Zielinski & Kucera 1995).

The second problem lies with the measurement of tracks. The speed of movement of the animal, the gait, and the substrate need to be considered (Zielinski & Kucera 1995). Substrates like sand and mud may offer reasonable imprints that do not vary after being deposited. However, tracks made in snow can change dramatically, either due to snow drifting into the hole, the snow subsiding, or from the track melting out in sunlight.

All these factors can cause significant distortion to the track and need to be taken into account (Camarra 1992). Finally, the observer effect can be large (Fjelline & Mansfield 1989) as different sections of the track may be measured by different people. As the track sinks deeper into the substrate there will be more of a slope on the side of the impression, such that there may be no clear-cut method of defining the edge. Track measurement needs to be very clearly explained to different observers if erroneous results are to be avoided.

4.2 Population estimates using mark-recapture methods

The real benefit of using marked (or recognisable) animals lies in the possibility of using mark-recapture methods to statistically estimate population size. The underlying principle lies in marking a representative proportion of the population, and then recapturing individuals (both marked and unmarked). The assumption is that the proportion of marked animals in the recaptured sample is equal to its proportion in the population as a whole. Therefore if you know how many animals are marked, you can estimate how many are in the population (Seber 1986, White & Garrott 1990, Van Hensbergen & White 1995). Repeated recapture sessions allow errors and confidence intervals to be calculated. Several statistical assumptions underlie the various methods of analysis. However, the main issues of concern are the degree of population closure (can animals marked inside the study area, be outside the area when recapturing occurs) and the biases involved in capturing animals (Garshelis 1992, 1993). The latter issue is quite important as many studies have documented that various age and sex groups, and even individuals within a population may have different degrees of vulnerability to capture (e.g. Garshelis 1993, Huber et al. 1996, Noyce et al. 1998). This latter problem may be overcome using different methods for the first capture (when individuals are marked) and the "recapture". The available methods of analysis are diverse and need to be carefully evaluated (e.g. Pollock et al. 1990, Lebreton & North 1993). They are beyond the scope of this review.

4.2.1 Capture - mark - recapture

The original applications of mark-recapture methods used the same recapture methods as those used for the original capture (e.g. Schweinsburg et al. 1982). Black bears are readily trapped in foot snares or barrel traps. Long term projects such as that in the Smoky Mountains National Park of Tennessee have made 1239 captures of 605 individuals between 1973 and 1989. Despite these very impressive (by large carnivore research standards) capture rates, the resulting population estimates had very large confidence intervals (McLean & Pelton 1994). This illustrates the problems of obtaining adequate observations with using physical capture as the recapture method.

4.2.2 Capture - mark - resight

Effective methods have been developed using resighting as a means of "recapture". Miller et al. (1997) present data from 15 brown bear and 3 black bear studies in Alaska. In each study bears were radio-collared over a period of years using either traps or helicopters. This premarking reduces the biases associated with adult females with COY, which are hard to capture. In other words, in order to have a representative sample of individuals including adult females with COY available when resighting, it is necessary to capture some at least the year before. When sufficient individuals were collared, aerial transects were flown over the area in search of bears. All bears seen were categorised as being marked or unmarked. These searches were replicated 2-9 times. The result was a series of population estimates with relatively tight confidence intervals. The two main advantages of the method were (1) resighting allowed a larger sample of recaptures to be made, and overcomes the bias associated with using the same method for capture and recapture, and (2) radio-tracking of the bears' locations after the search allowed the degree of closure to be determined.

A variant that has been used in areas where resighting is harder due to dense forest cover is to determine the proportion of marked vs. unmarked females that were located with radio-collared males during the mating season (Swenson et al. 1994, Garshelis et al. 1998).

4.2.3 Camera traps

Camera-traps (self activating cameras placed close to a bait or other attractant or on a frequently used path) have often been used to detect presence-absence of species or to collect an index of abundance for difficult to see species (Seyback 1984, Griffiths & Van Schaik 1993, Zielinski & Kucera 1995). Where aerial resighting is difficult, camera-traps can also be used to provide recapture observations. Extensive efforts have been used to estimate grizzly bear populations using these methods in the Swan Mountains of Montana (Mace et al. 1990, 1994a, 1994b, Mace & Waller 1997). From 27-42 cameras were deployed throughout the 800 km² study site to obtain acceptable rates of recapture. Bears were radio-collared, which provided a visual mark that was visible in photographs, and also allowed estimates of the catchment area from which observations were drawn (Mace et al. 1994a). Similar methods have been used with tigers in India, however, here the natural stripe patterns were used to identify individuals (Karanth 1995). The first time an individual was observed was the first capture, the second observation was the recapture. Although it produced a usable estimate of the number of tigers present, the absence of telemetry data meant it was difficult to determine the catchment area, and therefore the density (Karanth 1995).

4.2.4 Tracks and sign

If transect surveys can be combined with radio-tracking of animals known to be present in an area, such that the tracks found can be attributed to a marked or unmarked animal, a simple mark-recapture estimate can be produced (Swenson et al. 1994, Cunningham et al. 1995). Care needs to be taken when choosing the criteria used to attribute tracks to the marked animals though. If individuals bears can be identified using genetical techniques it is possible to design a mark-recapture set-up using hair traps (sticky plates or rough wire which traps hair when a bear rubs against it).

4.2.5 Radioactive tracers

The problem of attributing a given sign to a marked or unmarked individual can be avoided if the marked individuals are injected with a radioactive tracer element. Intra-muscular injection, or subcutaneous implantation of a radio-active element will lead to the slow release of the element in the faeces of the animal for periods of months, without exposing the animal to dangerously high levels of radiation (Kennedy et al. 1993, Jolicoeur et al. 1993). The proportion of radioactive vs. non-radioactive scats recovered along tracks, trails and roads allows mark-recapture statistics to be used. To date the method has been used on badgers, European otters, racoons, coyotes, and black bears (Pelton & Marcum 1977, Kruuk et al. 1980, Conner & Labisky 1985, Crabtree et al. 1989, Jolicoeur 1993, Kruuk 1995). A refinement was developed for North American otters by injecting each individual with a unique combination of elements, such that the individual responsible for each scat could be determined (Testa et al. 1994).

4.2.6 Tetracycline

Tetracycline can also be used as a bio-marker because it binds to bone and teeth tissue within an animal, and is visible under ultraviolet light for several years after being administered. The disadvantage is that the animal must be dead before it can be examined. The methodology has been tested in both black and polar bears (Taylor & Lee 1994, Garshelis & Visser 1997). In both cases the tetracycline was administered remotely, thus avoiding the need for immobilising the bears. The polar bears received the dose by remote injection from a helicopter, whereas the black bears obtained theirs by consuming baits placed throughout large areas of habitat. Hunters were asked to return teeth and bones from animals shot during normal hunting seasons. The major prerequisite is that a large number of dead animals are needed for an accurate population estimate. Therefore the method is only practical for species which are being intensively harvested.

4.3 Reproductive and survival data

When the main objective is to determine the trend of a population, rather than its specific density at a given time (Eberhardt et al. 1986, Eberhardt & Knight 1996), it may be more suitable to monitor reproductive and survival rates of radio-collared individuals. Although this requires much effort and invasive techniques, the resulting data will identify trend, and will be able to identify causes of mortality. Such approaches have been used widely for bear populations (Garshelis 1990, Eberhardt et al. 1994, Wieglus & Bunnell 1994, Hovey & McLellan 1996, Sæther et al. 1997, 1998), perhaps because bear populations are so hard to enumerate using other methods. The major problem is that these methods usually require access to data from radio-collared individuals, which imposes economical and logistical limits on the amount of data that can be collected. When variation caused by age and food availability is taken into account, it may require many years of data to accurately determine population trend.

Harvest material may also be analysed in order to produce data on reproduction and survival (e.g. Kvam 1990). However, there are many biases associated with harvest data that make its analysis rather complex. Most important of these is the fact that the different age and sex classes may differ in vulnerability to harvest. Another important factor is that the main reproductive parameters that can be measured from carcasses are either ovulation rate or the number of embryos. While these provide evidence that animals are mating and that fertilization is achieved, they provide no data on the levels of juvenile survival or recruitment.

5 Summary of methods

There is clearly a diverse range of methods available for detecting presence/absence, indices of abundance, minimum counts or statistical population estimates. Most of these methods have been developed for use in research contexts, i.e. for estimating the population density of individuals within a given study site of limited area. **Table 1** summarises the methods used in several studies of temperate zone large carnivores (cougars, Eurasian lynx, wolves, brown bears and black bears). Different methods tend to have found favour within different species. While part of this may be due to tradition, a large part of the choice of method is due to the ecological conditions that the species occupy. Minimum counts appear to have been the most favoured methods used on all species except for bears, where population estimates have been most common.

In general there is a trade-off to be made between the accuracy and precision of an estimate and the size of the area to be surveyed. There is no doubt that "mark-recapture" methods provide the best and most robust statistical estimates of population size (e.g. Garshelis 1992, Miller et al. 1997), yet they can clearly only be applied after intensive field work within a limited area. TIP and ARS methods can also only be applied to limited areas. Even when tracks can be followed from the air, the area that can be effectively covered is unlikely to be larger than several thousand square kilometres (Becker 1991, Ballard et al. 1995). GTS methods are also only suitable for small to medium sample areas (Smietana & Wajda 1997), unless massive amount of resources can be mobilised (e.g. Liberg & Gløersen 1995). Sum of known individual methods generally depend on the use of telemetry, which makes them unsuitable for standard monitoring. Track count indices are probably the cheapest methods, and can be applied to both small (Allen et al. 1996, Rose & Polis 1998) and large areas (Carbyn et al. 1993, Jackson & Hunter 1995). Although the use of indices is becoming more common in research and management they do not provide any estimate of absolute population size, and data from several years is required before useful results can be obtained.

Unduplicated counts of reproductive units occupy an intermediate status, in that they can be applied over relatively large areas (Smirnov & Miquelle 1998, Knight et al. 1995, Kvam 1997, Bergström et al. 1997), but the result is that you only achieve a minimum count, with no estimate of the number of units that were not detected. The overall implication is that accurate and statistically robust estimates can generally only be obtained from smaller areas because of logistical and economic reasons. In order to meet these logistical constraints, a lot of statistical robustness must be sacrificed. Although minimum counts are not ideal (Yocuz et al. 1993, Mattson 1997) they are often all that can be obtained under the logistical constraints that are inherent in

Table 1 Methods used for counting and estimating the size of large carnivore populations in European and North American research projects. Note that most study sites are restricted in area, and that different techniques tend to be most commonly used for different species. Most of these studies utilised radio-telemetry as a research technique.

I = Index, MC = Minimum Count, PE = Population Estimate, T = Telemetry used, GTS = Ground Tracking Survey, ARS = Aerial Reconnaissance Survey, TIP = Track Intercept Probability estimator, Sum = Sum of known individuals.

Study area	Type	Method	Reference
Cougars			
4500 km ² – Utah	MC	Sum (T)	Lindzey et al. 1994
5040 km ² – Florida	MC	Sum (T)	Maehr et al. 1991
925 km ² – Wyoming	MC	Sum (T)	Logan et al. 1986
520 km ² - Idaho	MC	Sum (T)	Seidensticker et al. 1973
780 km ² – Alberta	MC	Sum (T)	Ross & Jalkotzy 1992
540 km ² – British Columbia	MC	Sum (T + Track measurement)	Spreadbury et al. 1996
2070 km ² - California	MC	Sum (T)	Beier 1995
550 km ² – California	MC	Sum (T)	Hopkins 1990
2059 km ² - New Mexico	MC	Sum (T)	Logan et al. 1996
406 km ² – Arizona	MC	Sum (T)	Shaw 1977
3120 km ² - Colorado	PE	Extrapolation of home range size to study site (T)	Anderson et al. 1992
4035 km ² - Arizona	PE	Mark-resight (using tracks) (T)	Cunningham et al. 1995
360 km ² – Utah	PE	TIP (T)	Van Sicke & Lindzey 1991
Eurasian lynx			
744 km ² – Switzerland	MC	Sum (T)	Breitenmoser et al. 1993
1500 km ² - Poland	MC	Sum + GTS (T)	Jedrzejewski et al. 1996
Sweden	MC	GTS	Liberg & Glöersen 1995
Wolverines			
4400 km ² - Norway	MC	GTS	Landa et al. 1998
1800 km ² - Yukon	MC	Sum (T)	Banci & Harestad 1990
1300 km ² - Montana	MC	Sum (T)	Hornocker & Hash 1981
1870 km ² - Alaska	MC	TIP	Becker 1991
Wolves			
10000 km ² - Alaska	MC	Sum (T)	Adams et al. 1995
520 km ² – Poland	MC	GTS	Smietana & Wajda 1997
1500 km ² - Poland	MC	GTS	Jedrzejewska et al. 1996
17060 km ² - Alaska	MC	ARS	Gasaway et al. 1983
13000 km ² - Alaska	MC	ARS + Sum (T)	Gasaway et al. 1992
839 km ² – Minnesota	MC	ARS (T)	Fuller 1989
61600 km ² - Alaska	MC	Sum + extrapolation of home range size to study area (T)	Ballard et al. 1987
26600 km ² - Alaska	MC	Sum (T)	Peterson et al. 1984
12280 km ² - Alaska	MC	Sum + ARS + extrapolation of home range size (T)	Ballard et al. 1997
2700 km ² - Minnesota	MC	Sum (T)	Fritts & Mech 1981
30000 km ² - Alaska	MC	Sum (T)	Dale et al. 1994
1667 km ² – Quebec	MC	Sum (T)	Potvin 1987
6400 km ² – Quebec	MC	Sum (T)	Messier 1985
? km ² – Montana	MC	Sum (T)	Pletscher et al. 1997
7571 km ² – Ontario	MC	Sum (T)	Forbes & Theberge 1996
25000 km ² - Alberta	MC	Sum + extrapolation of home range size (T)	Fuller & Keith 1980
? km ² – British Columbia	MC	ARS	Bergerud & Elliot 1986
17000 km ² - Alaska	MC	Sum + ARS (T)	Boertje et al. 1996
520 km ² – Michigan	MC	ARS	Peterson 1977
2060 km ² – Minnesota	MC	Sum + ARS (T)	Mech 1986
9000 km ² – Alberta	MC/I	Extrapolation of home range size + Number of wolves seen per hour of flying (T)	Carbyn et al. 1993
6464 km ² – Alaska	PE	TIP (T)	Ballard et al. 1995
5011 km ² – Alaska	PE	TIP (T)	Ballard et al. 1995

Continue table 1

Study area	Type	Method	Reference
Brown bears			
14 populations - up to 2200 km ² - Alaska	PE	Capture - Mark - Resight (T + Aerial resighting)	Miller et al. 1997
2500 km ² - Alaska	PE	Aerial surveys with correction	Dean 1987
817 km ² - Montana	PE	Capture - Mark - Resight (T + Camera traps)	Mace et al. 1994
15500 km ² - Northwest Territories	MC/PE	Sum (T)/Capture - Mark - Recapture	Clarkson & Liepins 1994
20000 km ² - Yellowstone	MC	Counts of females with COY	Knight et al. 1995
868 km ² - Alberta	MC	Sum (T)	Wielgus & Bunnell 1994
727 km ² - Poland	MC	GTS + Track measurement	Gula & Frackowick 1996
2060 km ² - Norway	MC	GTS	Swenson & Wikan 1996
5000 km ² - Spain	MC	Counts of females with COY	Wiegand et al. 1998
5000 km ² - Spain	I	Sign survey	Clevenger & Purroy 1996
3 populations - up to 9800 km ² - Alaska	MC	Sum (T)	Reynolds & Garner 1987
264 km ² - Montana	MC	Sum (T)	McLellan 1989
40000 km ² - Montana	I	Sign surveys	Kendall et al. 1992
Black bear			
3 populations - up to 530 km ² - Alaska	PE	Capture - Mark - Resight (T)	Miller et al. 1997
126000 km ² - Michigan/Minnesota	PE	Capture - Mark - Harvest (Tetracycline)	Garshelis & Visser 1997
218 km ² - Alberta	PE	Capture - Mark - Recapture (T)	Young & Ruff 1982
700 km ² - Tennessee	PE	Capture - Mark - Recapture (T)	McLean & Pelton 1994
4 populaions - up to 375 km ² - Quebec	PE	Capture - Mark - "Recapture" (Radioactive tracers in scats)	Jolicoeur et al. 1993
500 km ² - Tennessee	PE	Capture - Mark - "Recapture" (Radioactive tracers in scats)	Pelton & Marcum 1977
21 km ² - Washington	MC/I	Sum/Scent station	Lindzey et al. 1977, 1986
200 km ² - North Carolina	I	Scent station (sardine tin)	Powell et al. 1996

monitoring large carnivores. However, if they are counts of family groups or reproductive units they do provide an indication of the size of the most important component of the population. Despite the lack of statistical robustness, management based on minimum counts will always be conservative (McCullough 1986).

While research projects generally survey limited areas, many countries, states or provinces produce status reports, with so-called population estimates. Questionnaires sent out to local hunters or forest workers asking for precise numbers of individuals are commonly used for bears (Spiridonov & Spassov 1990, Jakubiec 1990, Mertzanis 1990, 1994) and wolves (Bobek et al. 1993, Ionescu 1993, Adamakopoulos & Adamakopoulos 1993, Vila et al. 1993). Similarly, extrapolation from study areas to the area of distribution is commonly used (Nagy & Gunson 1990, Theberge 1991, Fuller et al. 1992, Gunson & Markham 1993, Rabinowitz 1993, Banci et al. 1994). As we have discussed earlier (sections 2.1 & 2.4), questionnaires are totally unsuitable for estimating *numbers* of carnivores, while extrapolation from study areas to total area is flawed unless study areas are chosen at random (Smallwood 1997). Therefore, these are at best only

educated guesses of the potential number of individuals that could be present. These methods are insensitive and unsuitable for monitoring anything more than the very broad pattern of distribution and abundance of large carnivores. The challenge for a large carnivore monitoring program is to take the sensitivity and accuracy of the methods used in research areas, and to apply them over areas large enough to include a significant proportion of the total area in question.

There is no magical crystal-ball technique that will easily provide all the answers. Given the wide range of habitats occupied by large carnivores, and the diversity of their ecology, there is no method that is best for all species, in all habitats and for all information requirements. All methods have some weaknesses and disadvantages. The best monitoring system may therefore consist of a package of methods that support each other. For example, minimum counts may be much more useful for detecting trends if they are supported by an independent index. An index (such as a track count index) will provide a robust indication of the trend of the population, while the supporting minimum count (perhaps of family groups or natal dens) will provide an indication of the actual number of individuals. Although some indices may be

weak, or have a large degree of variation, if several such indices all indicate the same trend, it is likely that the trend is real.

While both managers and the public are addicted to real (absolute) numbers, good data on population trend from either the use of indices (Smallwood 1994, Smallwood & Fitzhugh 1995), or from the collection of survival and reproductive data (Eberhardt et al. 1994) may be more important. Eberhardt & Knight (1995) summarised the dilemma; “estimating total population size of an endangered or threatened species should be secondary to measuring essential population parameters, but nonetheless may be necessary to avoid misunderstandings”. In other words, the “how many are there ?” question is less important than the “is the population increasing or decreasing ?” and “which parameters are responsible for the observed trend ?” questions. In other words, an optimal large carnivore monitoring system should probably consist of several independent measures that can be used to reinforce each other (e.g. a larger scale of the rational used by Rose & Polis 1998, and Eberhardt & Knight 1996). Robust indices of population trend, together with minimum counts to define the approximate absolute level of the population, will therefore probably be more useful than statistical population estimates for monitoring large carnivore populations. Reproductive and mortality data from either radio-collared animals or harvest data provides the final level of detail required to understand the processes behind the trends.

If correctly designed it should be possible to use all available information in several ways, and provide robust data on population distribution, size and trend. However, we cannot stress enough that monitoring and management are interactive processes, and that monitoring depends on the goals of management, while management must take into account the limits of the monitoring methods.

6 Statistical issues

6.1 Sampling scale

A monitoring program for large carnivores must occur at the correct scale. There is no point sampling lynx density within a 10 km² area when each individual lynx home range uses 100s of square kilometres (Andersen et al. 1998). A sample area (even for presence absence surveys) needs to completely contain at least a few home ranges, otherwise you are studying individual habitat selection rather than monitoring populations. As most laymen (including hunters) greatly underestimate the size of areas used by individual large carnivores this point cannot be overemphasised when setting up a monitoring program in the field. Generally speaking, for most temperate and northern areas, sample units will have to be in the region of 1000-5000 km². Because there is a relationship between sample area size and population density estimates (Blackburn & Gaston 1996, Smallwood & Schonewald 1996, Smallwood 1997) sample units need to be of approximately similar size in order to be comparable.

6.2 Distribution of sampling sites

In some cases it may be possible to sample the entire area in question, if the species in question has a high detectability. However, in many cases only smaller areas can be accurately monitored. Therefore, thought needs to be given to how these areas should be distributed. If an estimate of population density is required for the total area of distribution, these sample areas will need to be distributed at random (or at least stratified). The implication is that many sample areas will contain no, or very few, large carnivores, while others contain many (Smallwood 1997). This will increase the variation in the sample (making it difficult to detect changes over time), but will provide a more robust estimate for the total areas. On the other hand, if the goal is just to monitor changes over time, it may be wiser to place sample areas in areas where carnivore density is known to be higher. This will decrease the variation and make it easier to detect temporal changes, but will make it impossible to extrapolate to the total area (Smallwood 1997) without further, area specific information (Swenson et al. 1994).

6.3 Power analysis

A third aspect is that when some preliminary data becomes available it is crucial to conduct a power analysis to determine how sensitive the method is to changes in population density (Kendall et al. 1992, Taylor & Gerrudette 1993, Zielinski & Stauffer 1996, Beier & Cunningham 1996, Clevenger & Purroy 1996, Rice et al. 1998). The results of such an analysis will allow adjustment of the sampling protocol or of the adaptive

management feedback procedure, so that the sensitivity of data available corresponds to that required.

7 Case study – recommendations for Norway

7.1 Methods in current use in Norway

A variety of methods for surveying and censusing large carnivore populations are in use in Norway today. The only common method for all species is the organised documentation of the carnivore-specific cause of death of livestock (sheep and semi-domestic reindeer). These data are collected into a common database (ROVBASEN), and are used to monitor changes in carnivore distribution (e.g. Aanes et al. 1996), and help determine where compensation payments should be made.

Lynx are primarily monitored through counts of family groups on winter snow, which produce a minimum population estimate of the number of reproductive units (Kvam 1997). Extrapolation from the number of family groups to a minimum total (all age and sex classes) population size has been attempted, but the numbers used are unverified. Although quotas are set approximately as a proportion of the minimum number of lynx available, there is no robust analysis in existence of what percentage of the population can be harvested. Carcasses are collected for age and sex determination, but there is as yet no established link between these data and harvest management. Ground tracking (GTS) surveys have been conducted in some areas (e.g. Solvang 1998), however poor organisation and a lack of scientific rigour make the results difficult to interpret.

Wolverines are primarily monitored through counts of natal dens throughout their distribution (Landa et al. 1998). These den counts produce a relatively robust minimum count of the number of reproductive units that exist, and extrapolation to a minimum total population size includes an estimate of error due to variation in population structure. As of yet there is no estimate of the error in locating dens in an area. Carcasses of animals shot in the annual hunt are also processed for age and sex. As yet the link between monitoring and management is rather vague. Track count indices were obtained in some areas during the 1980's, but were not continued (Kvam & Sørensen 1983, Fox et al. 1990). GTS surveys have been conducted in the Snøhetta core conservation area at irregular intervals since 1980 (Landa et al. 1998).

Wolf pairs and family groups are counted on winter snow. A combination of all observations from the winter and GTS type surveys is used to produce an overview of distribution, and a minimum number of stationary animals (Sørensen et al. 1986, Wabakken et al. 1982, 1984, 1996, Wabakken 1993, Wabakken & Maartman 1997, Solvang

1998). Where wolves are known to exist, volunteers and local carnivore contacts snow-track the wolves to determine numbers and reproductive status. Because there are so few resident wolves, and those that are known to exist have a high detectability, these minimum counts are likely to be very close to the true total.

Bears are not monitored in any systematic manner. Tracks on spring snow are used to find dens and to determine minimum numbers. However, apart from in some areas like Pasvik where work is intensive (Swenson & Wikan 1996) many bears are not detected. Mark-resight estimates were made in Hedmark during the early 1990's (Swenson et al. 1994, 1995) using radio-collared bears. Attempts during the 1980's to estimate bear numbers using observations provided by newspapers and the public led to massive over-estimation of bear numbers (Kolstad et al. 1986, Elgmork 1987, 1996, Swenson et al. 1994, 1995).

7.2 Resources available

Monitoring large carnivores in a country as large and diverse as Norway is a very difficult task, however there are a number of resources available that make it easier. These include;

Snowy winters. Most parts of Norway, especially where large carnivore populations exist, receive snow during winter. Snow is easily the best substrate for detecting and following tracks. Without snow, most of the proposed methods would not be possible.

Extensive sheep farming. The very high rates of predation on free-ranging domestic sheep in many regions of Norway could provide an effective method for documenting the distribution of large carnivores.

Hunters. The large numbers of hunters that are active in forest and mountain habitats represent an enormous resource. Norwegian hunter's are generally knowledgeable and have a tradition of being involved in research and management. Everything possible should be done to involve them in large carnivore monitoring. In fact, a successful monitoring program will be dependent on their involvement.

Highly accessible wild-lands. The high density of forest roads, and the dispersed human population make it likely that resident carnivores are detected. There are very few forested areas, if any, where a carnivore home range will not contain roads or houses in Norway.

Carnivore contacts. Because of the need to verify claims of depredation on domestic sheep, each county has a network of local contacts that are employed by the environmental protection office of each county. These contacts are trained in recognising carnivore tracks and other signs, and are generally experienced in the field.

Their duties could be expanded to include much of the monitoring of large carnivores that we outline below.

7.3 The management context

Clear objectives for carnivore management in Norway have been laid out in a government paper (Miljøverndepartement 1996-97). The main objectives call for;

- (1) Bears to be mainly confined to a series of five core conservation areas along the borders with Sweden, Russia and Finland. When 5-10 breeding females exist in each core area, the possibility for licensed harvest exists. Control permits are issued for bears that kill livestock, especially outside the core areas.
- (2) Wolverines should be mainly confined to a core conservation area in south Norway, but should be found in viable numbers throughout large areas of north Norway. License hunting will be used to regulate density.
- (3) Lynx should be widespread throughout all of Norway apart from a few areas where the potential conflict with livestock has been judged to be too high. Quota hunting will be open where densities allow. In the areas where lynx are not meant to colonise (the south-west, some northern islands and areas of Finnmark county), there will be no restriction on the numbers shot (open quota) within the normal hunting season.
- (4) A small number of wolf packs will be tolerated in south Norway. When 8-10 packs exist in Scandinavia, the possibility for a restricted harvest in Norway exists.

The objectives call for a difficult balancing act between conserving demographically viable populations of these carnivore species (Miljøverndepartement 1996-97) and minimising the high depredation rates on domestic sheep and semi-domestic reindeer that are experienced in many regions (Mysterud & Mysterud 1995). In this context an effective monitoring system for large-carnivores in Norway is required for the following reasons;

- (1) Knowledge of distribution and relative densities of each species is important to assist in the fair distribution of compensation payments for livestock losses.
- (2) Regulating the hunter harvest of lynx (quota hunting) and wolverines (licensed hunting) requires estimates of population size and trend. The setting of management goals and harvest quotas for these species should be based upon good estimates of population size and trend, and evaluated within the context of socioeconomic "tolerance factors".
- (3) The impact of possible licensed hunting, or control actions following depredation on livestock, on the carnivore populations needs to be determined.

- (4) Research efforts into factors affecting large carnivore populations almost always require population estimates.
- (5) The management actions currently being used to achieve stated goals of carnivore population size and distribution (Miljøverndepartement 1996-97) need to be evaluated.

7.4 Recommended monitoring system

Given the scenarios mentioned above, we have developed a recommended package of monitoring methods in the following section, that should provide an acceptable compromise between scientific rigour and practicality (table 2). No other country has a nationwide monitoring system for large carnivores. This means that these recommendations are based on our evaluation of the various methods that we have reviewed, rather than on the experience of other similar systems. Ideally, for each species we should have good data on distribution (both total distribution and the distribution of the reproductive portion of the population), a repeated index to measure population trend, and a minimum count (or estimate). We believe that this can be practically achieved for lynx, and possibly wolverines, on an annual basis. Close monitoring of the harvest will also allow additional information on reproductive parameters to be obtained. Given present management scenarios and the high conflicts that exist with livestock, wolves will not be allowed to reach levels where indices or population estimates are really appropriate. Annual estimates of distribution and minimum counts (especially of breeding packs) will need to suffice. However, should attitudes change in the future and wolf populations be allowed to increase, it should be possible to monitor wolves in the same ways as lynx. Although bears are technically difficult to monitor we believe that distribution estimates and indices can be obtained annually, and perhaps

minimum counts of females with COY. However, because of the uncertainty with bears, periodic estimates involving radio-telemetry will be required.

None of the monitoring methods that we recommend here will stand alone. Instead, we believe that they depend on each other, and that only when combined will a scientifically defensible monitoring system be achieved. To increase the return from the expended effort it might be possible to survey other species at the same time, using the same methods. For example, golden eagles or other birds of prey could be included on the hunter observation sheets, while tracks of red foxes, pine martens and other mustelids could be recorded on transects.

7.4.1 All species

The general pattern of distribution of species throughout Norway should be monitored using all available sources of information. Foremost among these are observations from the public and records of livestock (mainly sheep, semi-domestic reindeer and hunting dogs) predation or bee-hive destruction.

Observations from the public. Hunters, forest-workers, tourists etc. represent an enormous network of potential informants distributed throughout the country. However, rigid criteria for evaluating observations from the general public should be observed so that only confirmed reports are accepted. A reporting system should be established such that observations are gathered into a common, central database. Although such a system would be popular with the public and would allow the detection of large carnivores colonising new areas, the data is very limited and cannot be used to determine numbers or trends in populations. In general, observations from the public cannot be used alone for any rigorous form of monitoring. They should instead be regarded as providing supporting data for other, more rigorous,

Table 2 Recommendations for a national large carnivore monitoring program for Norway. ROVBASSEN refers to the dead livestock database. All methods could be applied nationwide, except for the den counts, reference area counts, and mark-recapture estimates. The large "X" signifies that greater importance should be attached to the method than those marked with a small "x". A "o" indicates methods that could be applied to a given species, but where it is not regarded as necessary or practical.

		Bear	Lynx	Wolf	Wolverine
ROVBASEN	D	X	X	X	X
Hunter obs	D/I	x	x	x	X
Public reports	D	x	x	X	X
Family groups obs	D/MC	X	X	X	X
Den counts	D/MC	x			X
Track counts	D/I		X	x	X
Reference areas	D/MC/PE	o	X	X	X
Mark recapture	D/PE	X	o	o	O
Harvest data	D/PD/HC	o	X	o	X

D = Distribution, I = Index, MC = Minimum Count, PE = Population Estimate, PD = Population Dynamics, HC = Health & Condition

monitoring methods. Despite these severe limitations, if confirmed reports are collected as part of other field activity, they should be recorded systematically. The main applications for such a system are at a local level (county) so that managers can develop a "feel" for the local situation, and at a national level to get a rough idea of distribution. Funding should be available to allow reports to be verified by experienced personnel. As well as providing some possibly useful observations, such a system would greatly help to involve the public.

Dead livestock. A sheep or semi-domestic reindeer killed by a large carnivore provides physical evidence for the presence of a carnivore at that time. As an acceptable system is already in place to collect these observations and they are stored in a common database (ROVBASEN) we recommend that this database be utilised to its utmost. Changes in distribution of the various species should be easily detected (Aanes et al. 1996). Also examination of the data could potentially provide much information concerning the ecology of sheep depredation (timing, location etc.). Although much uncertainty exists concerning the relationship between carnivore depredation, carnivore density, and sheep density (Linnell et al. 1996, Gudvangen et al. 1998, Lee Allen pers. comm.), further study should clarify the situation. Certainly it seems safe to assume that dramatic changes in sheep losses probably reflect some change in the carnivore population.

Hunter observations. Presently all moose and reindeer hunters must return information to managers about their hunt. Reindeer hunters simply return a card stating whether or not they have managed to shoot their allocated animal. Moose hunting teams fill out a more complex moose-obs ("sett-elt") sheet which records the numbers of animals seen each day of the hunt and the number of hunters that were hunting. This provides an index of moose abundance. Boxes could be added to these sheets asking for observations of large carnivores (brown bear, wolf, wolverine, lynx) and also maybe golden eagles. While it could be expected that the large number of zero values will make the resulting index very insensitive to small changes in carnivore density it should be useful to pick out broad patterns and differences between areas. This is especially interesting as moose hunters in Sweden will begin to fill out a similar sheet from 1998, making international comparison possible. One major problem is that reports cannot be verified, however, a major advantage is that it is one of few methods that can be applied to the snow-free season.

7.4.2 Lynx

We recommend a four-pronged system for monitoring lynx populations, monitoring of family groups, track count indices, harvest monitoring and reference area estimates. The first three methods should be applied nation-wide, while the fourth method will by definition be applied to a

sample of reference areas - for example one or two in every county where lynx are present..

Family groups. We recommend that the counting of family groups continue, making use of accumulated observations throughout the early winter, and first half of the lynx hunt. All reports of family groups should be verified by qualified personnel. However, in order to increase the probability of detecting family groups, we recommend that greater effort should be made to encourage potential hunters to search for the presence of family groups prior to the hunt. In addition, the decision rules used to separate between observations need to be reviewed along with an evaluation of the possibility that other false positives (such as an adult male, or yearling, travelling with an adult female) appear in the data. Variation in movement rates, home range sizes and social system under different ecological conditions need to be considered and preferably verified by research. Family group counts will provide a minimum count of the number and distribution of reproductive events each year.

Track count index. The usefulness of minimum counts of family groups to detect trends in the population would be greatly reinforced if an independent index could be collected each year. Distributing short (1-5 km) transects throughout lynx habitat (at least a few transects per potential lynx home range), which can be skied several times each winter should provide a suitable index. These should adequately detect trends within a population - although comparison of density between populations requires validation. In addition, the transects would help in detecting family groups.

Reference area estimates. A series of 1000-5000 km² areas should be covered using TIP or GTS methods to produce either an estimate or a minimum count for each area. These areas should be distributed throughout the varied habitats of Norway to produce; (1) a series of reference density estimates, (2) validation for comparing track count indices, (3) data on the contribution that family groups make to the total population. If these areas were resurveyed every year, they could also be used to detect trends.

Harvest monitoring. All carcasses of lynx killed in the hunt should continue to be collected and sent in for rapid examination. Knowledge of the age and sex structure of the harvest each year should form a central component of any management strategy, although our methods for optimising the use of this data need to be greatly improved. In addition carcasses should be examined for condition, parasites and diseases.

7.4.3 Wolf

Because of the very low wolf numbers expected to be tolerated within Norway, it will be almost impossible to produce population estimates based on any form of probabilistic sampling survey. The approach that can

best work at present is to investigate all reports that come in from the public. When wolf presence is confirmed in an area, qualified personnel will need to spend time snow-tracking to determine the number of wolves, and their reproductive status from marking behaviour. If a question exists concerning the number of packs in a given area, only intensive GTS surveys will be able to determine if two independent packs exist or not. Telemetry would obviously help this work. Howling surveys during summer may be suitable for verifying presence in an area where there is reason to believe that wolves exist - although data is required to determine if Scandinavian wolves will reply to synthesised howls.

7.4.4 Wolverine

The mainstay of wolverine monitoring should be centred around surveys for natal dens. Because of the difficulties of surveying for dens over large areas, we recommend monitoring annually a series of 1000-5000 km² reference areas where wolverines are known to exist, and the whole of the southern Norwegian core area. Search effort within these limited areas should be so intensive and consistent each year so that the minimum count can be regarded as a total count. Changes in the minimum counts within these reference areas should constitute the main form of monitoring, although efforts should be made to find as many other dens as possible each year. Intensive searches throughout a large region (e.g. Finnmark/Troms, Nordland/Nord-Trøndelag, Sør-Trøndelag/Oppland/Hedmark, SW-Norway) could be made at 4 year intervals, such that at least one region was surveyed each year. The problem of variation in search effort when covering these large areas will mean that the results can only be regarded as minimum counts. The between year variability in reproduction (Landa et al. 1997), and the high proportion of wolverines that do not breed each year (Landa et al. 1998) need to be taken into account when interpreting results. However, it may also be desirable to introduce track count indices for wolverines each year across larger areas to provide a better independent estimate of trend. This would also assist in extrapolating from reference areas to total areas (Swenson et al. 1995). Because wolverines live in remote mountain areas it may be more appropriate to use scooters to cover long transects, rather than the short ones recommended for lynx. Observations of females with cubs from the spring/summer period should also be recorded in the reference areas. As these use quite restricted home ranges (Landa et al. 1998) it should be possible to count family groups in the same way as for bears or lynx, although their detectability is likely to be rather low. Carcasses from harvested animals should be sent in for health examination and determination of age and sex.

7.4.5 Bears

Bears are clearly the most difficult of the large carnivores to monitor. We feel that it is impossible to produce

accurate numbers without the use of telemetry. As bears are meant to be confined to a series of core areas along the border with Sweden there is also less need for precise estimates each year. If these core areas can provide secure habitat, free from poaching, accurate censuses are not so important as for the other species. Therefore we propose a three-pronged system, using spring snow, observations from the public and hunters, and mark-resighting.

Dens. Each spring all reported bear tracks should be investigated and back-tracked to dens if possible. Such activity will produce at best a minimum number, although many bear dens will probably not be found. It will at least confirm bear denning presence and provide data on den habitat selection. Reports of tracks of female bears with cubs should always be investigated, although it is likely that most bears of this category will not be mobile until after snow-melt.

Unduplicated counts. Observations of females with cubs from the public should be investigated. If they are frequent enough, then a Yellowstone-style, unduplicated count of females with COY could be attempted. Analysis of existing data on home range and movement patterns of adult females with COY would be needed to establish suitable rules for separating observations.

Mark-resight. When these methods indicate that the bear population in a core area is starting to approach its objective level, we recommend that a mark-resighting survey be conducted. This will require at least one to two years pre-marking, and a total marking of 5-20 bears within each area. Resighting frequency could be optimised by checking the identity of bears associated with marked males during the mating season (Swenson et al. 1994, 1995). The use of camera traps as an additional resight method may be realistic depending on how often bears approach bait.

7.4.6 Structure

At first a series of controlled pilot projects will be needed to adapt the methodology to local conditions. Methods should also be designed so that they are as similar as possible to those being used in Sweden and Finland (e.g. Bergström et al. 1994). At least during these early years it will be vital for a central co-ordination of the different methods and the different species. We would propose a central co-ordinator responsible for planning, analysis and reporting, and then the use of the managers in place in each county to co-ordinate the actual data collection using hunters and the carnivore contacts in each region. After fixed protocols are established it may be possible to delegate a degree of authority to the regional (inter-county) or county level, although it will still be vital for all data to be collected in a central monitoring database.

7.5 Incentives for public involvement

Any type of nation-wide monitoring program for large carnivores is going to require enormous amounts of manpower and time to succeed. Reports of lynx family groups or wolf tracks, the effort required to search for wolverine dens, or back-track on spring snow to a bear den, and to conduct track surveys all require time and many people to be out in the field. In order to keep the price within affordable limits assistance from the public, and hunters and livestock herders in particular, will be required. A system whereby hunting large carnivores, the control of livestock killers, or the issuing of compensation payments is linked to search effort and the documentation that reproducing large carnivores actually exist in an area is vital to motivate public participation. However, before public involvement can be optimised, there is a need for much greater education and training of local contacts to verify observations of animals or tracks. Handbooks and training courses like those developed for North American forest carnivores, cougars and snow leopards (Shaw 1987, Jackson & Hunter 1995, Zielinski & Kucera 1995) could assist in this task. Target groups should include hunters, forest workers, mountain wardens and members of other environmental organisations.

7.6 Co-operation with existing or future monitoring programs

In order to keep costs as low as possible, it might be desirable to explore ways to establish co-operation with existing monitoring programs. The use of hunter observation indices will make use of the reporting structures already in place for reindeer and moose monitoring (Jordhøy et al. 1996, Solberg et al. 1997). The county management authorities already have protocols in place for verifying the species of carnivore responsible for livestock depredation and for verifying the presence of tracks from lynx family groups. The only totally new protocol in these recommendations is to begin collecting indices based on track counts along transects. This work could easily become the responsibility of local hunters or hunting teams and could be combined with the introduction of the Finnish triangle system for monitoring all game species. This is currently under evaluation, and should definitely be co-ordinated with the large carnivore monitoring program if it should be proposed. Although the triangles may not be the best transect format for optimising the detection of carnivore tracks, they will provide a secondary index that could be useful. In addition it might be possible for hunting teams to adopt a "triangle plus one" system whereby a 4x4x4 triangle is skied, together with a single 4 km (for example) transect placed separately to optimise the probability of detecting carnivore tracks within their hunting area.

8 Research and education needs

Before any of these recommended methods can be used on a regular basis, there is a need for further research and development to adapt them to local conditions and to test their sensitivity and power. The following research projects should be given priority;

- (1) Development and verification of rules for unduplicated counts of lynx family groups and bears with COY.
- (2) Modelling population dynamics of lynx and wolverines to aid in the interpretation of harvest data. Large amounts of data from harvest material exists on both species. When combined with the telemetry data that is presently being collected from Scandinavian projects there should be enough to begin developing models.
- (3) Calibration and comparison of methods for lynx and wolverines.
- (4) Our knowledge of wolf survival, reproduction, and movements under Scandinavian conditions is very limited. Better data are clearly required.

The results of these proposed projects, the presently intensive lynx, bear and wolverine research projects, and all other relevant international research need to be presented in an appropriate format (e.g. Myrberget & Sørensen 1981, Shaw 1987, Kaczensky & Huber 1994, Jackson & Hunter 1995, Zielinski & Kucera 1995, Landa 1998) to aid with implementation of the monitoring methods. Accurate monographs, reports and course material summarising large carnivore ecology need to be available for all levels of public education.

Finally, and most importantly, the results of the monitoring program need to be communicated to the public, and especially those individuals that assist in the collection of data. The spatial element of the data in particular could be visualised using simple GIS (Geographic Information System) techniques. As well as printed reports, a large part of the data should be available on the internet, provided suitable security systems protect personal or sensitive information.

9 References

- Aanes, R., Swenson, J. E. & Linnell, J. D. C. 1996. Rovvilt og sauenæring i Norge. I. Tap av sau til rovvilt: en presentasjon av tapets omfang basert på brukeropplysninger. NINA Oppdragsmelding, 434.
- Adamakopoulos, P. & Adamakopoulos, T. 1993. Wolves in Greece: current status and prospects. In: Wolves in Europe - status and perspectives (eds. C. Promberger & W. Schröder), pp. 56-61. Munich Wildlife Society, Munich.
- Adams, L. G., Dale, B. W. & Mech, L. D. 1995. Wolf predation on caribou calves in Denali National Park. In: Ecology and conservation of wolves in a changing world (eds. L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 245-260. Canadian Circumpolar Institute, Alberta, Canada.
- Ahlborn, G. G. & Jackson, R. 1988. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. In: Proceedings of the Fifth Snow Leopard Symposium (eds. H. Freeman), pp. 25-50. International Snow Leopard Trust, Seattle.
- Ahmad, I., Hunter, D. O. & Jackson, R. 1997. A snow leopard and prey species survey in Khunjerab National Park, Pakistan. In: Proceedings of the 8th International Snow Leopard Symposium (eds. R. Jackson & A. Ahmad), pp. 92-95. International Snow Leopard Trust and World Wide Fund for Nature - Pakistan, Islamabad, Pakistan.
- Allen, L., Engeman, R. & Krupa, H. 1996. Evaluation of three relative abundance indices for assessing dingo populations. *Wildlife Research*, 23, 197-206.
- Andersen, R., Linnell, J. D. C., Odden, J., Gangås, L., Ness, E., Karlsen, J., Wannag, A. & Renå, J. T. 1998. Sosial organisering, spredning, reproduksjon og predasjonsatferd hos gaupe i Hedmark: framdriftsrapport 1995-97. NINA Oppdragsmelding, 519: 1-25.
- Anderson, A. E., Bowden, D. C. & Kattner, D. M. 1992. The puma on Uncompahgre Plateau, Colorado. Colorado Division of Wildlife, Technical Publication, 40: 1-116.
- Anker-Nilssen, T., Erikstad, K. E. & Lorentsen, S. H. 1996. Aims and effort in seabird monitoring: an assessment based on Norwegian data. *Wildlife Biology*, 2: 17-26.
- Aoi, T. 1987. Harvest characteristics of brown bears in northern Hokkaido, Japan. International Conference on Bear Research and Management, 7: 93-96.
- Armstrup, S. C., Stirling, I. & Lentfer, J. W. 1986. Past and present status of polar bears in Alaska. *Wildlife Society Bulletin*, 14: 241-254.
- Aune, K. E. 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana. Mountain lion- human interaction, Symposium and workshop, Colorado Division of Wildlife, 86-94.
- Baillie, S. R. 1991. Monitoring terrestrial breeding bird populations. In: Monitoring for conservation and ecology (eds. F. B. Goldsmith), pp. 112-132. Chapman and Hall, London.
- Ballard, W. B., Ayres, L. A., Krausman, P. R., Reed, D. J. & Fancy, S. G. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs*, 135: 1-47.
- Ballard, W. B., McNay, M. E., Gardner, C. L. & Reed, D. J. 1995. Use of line-intercept track sampling for estimating wolf densities. In: Ecology and conservation of wolves in a changing world (eds. L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 469-480. Canadian Circumpolar Institute, Alberta, Canada.
- Ballard, W. B., Whitman, J. S. & Gardner, C. L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs*, 98: 1-54.
- Banci, V., Demarchi, D. A. & Archibald, W. R. 1994. Evaluation of the population status of grizzly bears in Canada. *International Conference on Bear Research and Management*, 9: 129-142.
- Banci, V. & Harestad, A. S. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. *Holarctic Ecology*, 13: 195-200.
- Barnhurst, D. & Lindzey, F. G. 1989. Detecting female mountain lions with kittens. *Northwest Science*, 63: 35-37.
- Becker, E. F. 1991. A terrestrial furbearer estimator based on probability sampling. *Journal of Wildlife Management*, 55: 730-737.
- Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management*, 59: 228-237.
- Beier, P. & Cunningham, S. C. 1996. Power of track surveys to detect changes in cougar populations. *Wildlife Society Bulletin*, 24: 540-546.
- Berg, R. L., McDonald, L. L. & Strickland, M. D. 1983. Distribution of mountain lions in Wyoming as determined by mail questionnaire. *Wildlife Society Bulletin*, 11: 265-268.
- Bergerud, A. T. & Elliot, J. P. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology*, 64: 1515-1529.
- Bergström, M. R., Attergaard, H., From, J. & Mellqvist, H. 1997. Järv, lodjur och varg i renskötselområdet: resultat från 1997 års inventering. Länsstyrelsen Västerbottens län Meddelande, 8: 1-8.
- Bergström, M. R., Bø, T., Franzén, R., Henriksen, G., Nieminen, M., Overrein, Ø. & Stensli, O. M. 1994. Forslag til smordna bestandsovervåkning av bjørn, gaupe, jerv og ulv på Nordkalotten. Nordkalottkommitéens Rapportserie, 34: 1-60.
- Björvall, A. 1978. Björnen i Sverige. Statens naturvårdsverk, Stockholm.
- Blackburn, T. M. & Gaston, K. J. 1996. Abundance-body size relationships: the area you census tells you more. *Oikos*, 75: 303-309.

- Blanchard, M. M. & Knight, R. R. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation*, 58: 41-67.
- Blanco, J. C., Reig, S. & Cuesta, L. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation*, 60: 73-80.
- Bobek, B., Kosobucka, M., Perzanowski, K. & Plodzien, K. 1993. Distribution and wolf numbers in Poland. In: *Wolves in Europe - status and perspectives* (eds. C. Promberger & W. Schröder), pp. 26-29. Munich Wildlife Society, Munich.
- Boertje, R. D., Valkenburg, P. & McNay, M. E. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management*, 60: 474-489.
- Boitani, L. 1995. Ecological and cultural diversities in the evolution of wolf human relationships. In: *Ecology and conservation of wolves in a changing world* (eds. L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 3-12. Canadian Circumpolar Institute, Alberta, Canada.
- Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation*, 83: 279-289.
- Breitenmoser, U., Kazensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. 1993. Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. *Journal of Zoology*, 231: 449-464.
- Brown, D. E. 1983. The grizzly in the southwest. University of Oklahoma, Norman.
- Brown, D. E. 1992. The wolf in the southwest: the making of an endangered species. University of Arizona Press, London.
- Bull, E. L., Holthausen, R. S. & Bright, L. R. 1992. Comparison of 3 techniques to monitor martens. *Wildlife Society Bulletin*, 20: 406-410.
- Camarra, J. J. 1992. Monitoring techniques of small bear populations: application in the Pyrenees mountains. *International Conference on Bear Research and Management*, 9, 571-581.
- Camarra, J. J. & Dubarry, E. 1997. The brown bear in the French pyrenees: distribution, size, and dynamics of the population from 1988 to 1992. *International Conference on Bear Research and Management*, 9, 31-35.
- Carbyn, L. N., Oosenbrug, S. M. & Anions, D. W. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. *Circumpolar Research Series Number 4*, University of Alberta.
- Caro, T. M. 1994. *Cheetahs of the Serengeti Plains*. Chicago University Press, Chicago.
- Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J. M., Duncan, P., Ballon, P. & Boisaubert, B. 1998. Managing roe deer and their impact on the environment: maximising benefits and minimising costs. *European roe deer: the biology of success* (eds. R. Andersen, P. Duncan & J. D. C. Linnell), Scandinavian University Press, Clark, J. D., Dunn, J. E. & Smith, K. G. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management*, 57, 519-526.
- Clarkson, P. L. & Liepins, I. S. 1994. Grizzly bear population estimate and characteristics in the Anderson and Horton Rivers area, Northwest Territories, 1987-1989. *International Conference on Bear Research and Management*, 9, 213-221.
- Clevenger, A. P., Purroy, F. J. & Campos, M. A. 1997. Habitat assesment of a relict brown bear *Ursus arctos* population in northern Spain. *Biological Conservation*, 80, 17-22.
- Clevenger, A. P. & Purroy, F. J. 1996. Sign surveys for estimating trend of a remnant brown bear *Ursus arctos* population in northern Spain. *Wildlife Biology*, 2, 275-281.
- Conner, M. C. & Labisky, R. F. 1985. Evaluation of radioisotope tagging for estimating abundance of raccoon populations. *Journal of Wildlife Management*, 49, 326-332.
- Conner, M. C., Labisky, R. F. & Progulsk, D. R. 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes, and opossums. *Wildlife Society Bulletin*, 11, 146-152.
- Coy, P. L. & Garshelis, D. L. 1992. Reconstructing reproductive histories of black bears from the incremental layering in dental cementum. *Canadian Journal of Zoology*, 70, 2150-2160.
- Crabtree, R. L., Burton, F. G., Garland, T. R., Cataldo, D. A. & Rickard, W. H. 1989. Slow release radioisotope implants as individual markers for carnivores. *Journal of Wildlife Management*, 53, 949-954.
- Crête, M. & Messier, F. 1985. Evaluation of indices of gray wolf, *Canis lupus*, density in hardwood.conifer forests of southwestern Quebec. *Canadian Field Naturalist*, 101, 147-152.
- Crête, M., Vandal, D., Rivest, L. P. & Potvin, F. 1991. Double counts in aerial surveys to estimate polar bear numbers during the ice-free period. *Arctic*, 44, 275-278.
- Cunningham, S. C., Haynes, L. A., Gustavson, C. & Haywood, D. D. 1995. Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. *Arizona Game and Fish Department Technical Report*, 17, 1-64.
- Dale, B. W., Adams, L. G. & Bowyer, R. T. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology*, 63, 644-652.
- Danilov, P., Helle, P., Annenkov, V., Belkin, V., Bljudnik, L., Helle, E., Kanshiev, V., Lindén, H. & Markovskiy, V. 1996. Status of game animal populations in Karelia and Finland according to

- winter track count data. Finnish Game Research, 49, 18-25.
- Dean, F. C. 1987. Brown bear density, Denali National Park, Alaska, and sighting efficiency adjustment. International Conference on Bear Research and Management, 7, 37-44.
- Difenbach, D. R., Conroy, M. J., Warren, R. J., James, W. E., Baker, L. A. & Hon, T. 1994. A test of the scent station survey technique for bobcats. Journal of Wildlife Management, 58, 10-17.
- Eberhardt, L. L., Blanchard, B. M. & Knight, R. R. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology, 72, 360-363.
- Eberhardt, L. L. & Knight, R. R. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management, 60, 416-421.
- Eberhardt, L. L., Knight, R. R. & Blanchard, B. M. 1986. Monitoring grizzly bear population trends. Journal of Wildlife Management, 50, 613-618.
- Elgmork, K. 1988. Reappraisal of the brown bear status in Norway. Biological Conservation, 46, 163-168.
- Elgmork, K. 1991. Vurdering av bjørnebestander ved hjelp av elgjegere I: Det sentrale Sør-Norge 1966-68 og 1976-78. Fauna, 44, 269-274.
- Elgmork, K. 1992. Bjørn i Vassfaret og i Hedmark. Fauna, 45, 216-223.
- Elgmork, K. 1996. The brown bear *Ursus arctos* L. in Norway: assessment of status around 1990. Biological Conservation, 78, 233-237.
- Elgmork, K. 1997. Brown bear density based on observations by moose hunters. International Conference on Bear Research and Management, 9, 119-123.
- Elgmork, K., Brekke, O. & Selboe, R. 1976. Pålitelighet av meldinger om spor og sportegn av bjørn fra Vassfartraktene. Fauna, 29, 45-50.
- Fitzhugh, E. L. & Gorenzel, W. P. 1985. Design and analysis of mountain lion track surveys. In: Cal-Nevada Wildlife 1985 (eds. W. F. Laudenslayer), pp. 78-87. Western Section, The Wildlife Society,
- Fitzhugh, E. L. & Smallwood, K. S. 1997. Techniques for monitoring mountain lion population levels. In: Proceedings of the third mountain lion workshop (eds. R. H. Smith), pp. 69-71. Arizona Chapter, The Wildlife Society, Prescott, Arizona.
- Fjelline, D. P. & Mansfield, T. M. 1997. Method to standardize the procedure for measuring mountain lion tracks. In: Proceedings of the third mountain lion workshop (eds. R. H. Smith), pp. 49-51. Arizona Chapter, The Wildlife Society, Prescott, Arizona.
- Forbes, G. J. & Theberge, J. B. 1996. Response by wolves to prey variation in central Ontario. Canadian Journal of Zoology, 74, 1511-1520.
- Fox, J. L. & Chundawat, R. S. 1997. Evaluation of snow leopard sign abundance in the upper Indus valley. In: Proceedings of the 8th International Snow Leopard Symposium (eds. R. Jackson & A. Ahmad), pp. 66-74. International Snow Leopard Trust and World Wide Fund for Nature - Pakistan, Islamabad, Pakistan.
- Fox, J. L., Sinha, S. P., Chundawat, R. S. & Das, P. K. 1991. Status of the snow leopard *Panthera unica* in Northwest India. Biological Conservation, 55, 283-298.
- Fox, J. L., Ytterstad, E. & Overrein, Ø. 1990. A wolverine population index in Troms fylke (bestandsregistrering avjerv i Troms fylke. Fylkesmannen i Troms Miljøvernavdelingen Rapport, 23, 1-19.
- Fraser, D. 1984. A simple relationship between removal rate and age-sex composition of removals for certain animal populations. J. Appl. Ecol., 21, 97-101.
- Fraser, D., Gardner, J. F., Kolenosky, G. B. & Strthearn, S. 1982. Estimation of harvest rate of black bears from age and sex data. Wildlife Society Bulletin, 10, 53-57.
- Fritts, S. H. & Mech, L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs, 80, 1-79.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs, 105, 1-41.
- Fuller, T. K., Berg, W. E., Radde, G. L., Lenarz, M. S. & Joselyn, G. B. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin, 20, 42-55.
- Fuller, T. K. & Keith, L. B. 1980. Wolf predation dynamics and prey relationships in northeastern Alberta. Journal of Wildlife Management, 44, 583-602.
- Fuller, T. K. & Sampson, B. A. 1988. Evaluation of a simulated howling survey for wolves. Journal of Wildlife Management, 52, 60-63.
- Galentine, S. & Fitzhugh, E. L. 1997. Standardizing photographs of puma tracks for digital processing. In: Proceedings of the fifth mountain lion workshop (eds. W. D. Padley), pp. 37-39. Southern California Chapter, The Wildlife Society, San Diego California.
- Garshelis, D. L. 1992. Mark-recapture density estimation for animals with large home ranges. In: Wildlife 2001: populations (eds. D. R. McCullough & R. H. Barrett), pp. 1098-1111. Elsevier Applied Science, London.
- Garshelis, D. L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Eastern Workshop on Black Bear Reserach and Management, 10, 120-144.
- Garshelis, D. L. 1993. Monitoring black bear populations: pitfalls and recommendations. In: Proceedings of the 4th Western Black Bear Workshop (eds. J. A. Keay), pp. 123-144. Technical Report NPS/NRWR/NRTR-93/12, National Park Service. Natural Resource Publications Office, Denver.

- Garshelis, D. L. & Visser, L. G. 1997. Enumerating metapopulations of wild bears with an ingested biomarker. *Journal of Wildlife Management*, 61, 466-480.
- Gasaway, W. C., Boertje, R. D., Grangaard, D. V., Kelleyhouse, D. G., Stephenson, R. O. & Larsen, D. G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs*, 120, 1-59.
- Gasaway, W. C., Stephenson, R. O., Davis, J. L., Shepherd, P. E. K. & Burris, O. E. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildlife Monographs*, 84, 1-50.
- Gjershaug, J. O., Thingstad, P. G., Eldoy, S. & Byrkjeland, S. 1994. Norsk fugleatlas: hekkefuglenes utbredelse og bestandsstatus i Norge. Norsk Ornitologisk Forening, Klaebu.
- Godfrey C. L., Vaughan, M. R., Martin, D. D. & Steffen, D. E. 1998. Reconstruction of Virginia's exploited black bear population. *International Conference on Bear Research and Management - Abstract*, 11, 17.
- Golden, H. N. 1993. Furbearer track count index: testing and development. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Report, Project W-24-1, 1-48.
- Golden, H. N., Route, W. T. & Becker, E. F. 1993. Wolverine demography and ecology in southcentral Alaska: Project outline and phase I progress report. Alaska Department of Fish and Game, Division of Wildlife Conservation and National Park Service, Wrangell-St. Elias National Park and Preserve, 1-27.
- Goldsmith, F. B. 1991. *Monitoring for conservation and ecology*. Chapman and Hall, London.
- Griffiths, M. & Van Schaik, C. P. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, 7, 623-626.
- Gros, P. M., Kelly, M. J. & Caro, T. M. 1996. Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. *Oikos*, 77, 197-206.
- Gudvangen, K., Landa, A., Swenson, J. E. & Røskoft, E. 1998. Jerv og sau i Snøhettaområdet. (eds. T. Kvam), NINA Fagrapport, In press
- Gula, R. & Frackowiak, W. 1996. Size and age structure of the brown bear (*Ursus arctos*) population in the Bieszczady mountains. *Journal of Wildlife Research*, 1, 65-69.
- Gunson, J. & Markham, R. 1993. Management plan for black bears in Alberta. Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division, Wildlife Management Planning Series, 10, 1-115.
- Hanby, J. P., Bygott, J. D. & Packer, C. 1995. Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro crater and the Serengeti plains. In: *Serengeti II: dynamics, management and conservation of an ecosystem* (eds. A. R. E. Sinclair & P. Arcese), pp. 315-331. University of Chicago Press, London.
- Harding, P. T. 1991. National species distribution surveys. In: *Monitoring for conservation and ecology* (eds. F. B. Goldsmith), pp. 133-154. Chapman and Hall, London.
- Harrington, F. H. & Mech, L. D. 1982. An analysis of howling response parameters useful for wolf pack censusing. *Journal of Wildlife Management*, 46, 686-693.
- Harris, R. B. 1986. Grizzly bear population monitoring: current options and considerations. Miscellaneous Publication No. 45, Montana Forest and Conservation Experiment Station,
- Harris, R. B. & Metzgar, L. H. 1987. Estimating harvest rates of bears from sex ratio changes. *Journal of Wildlife Management*, 51, 802-811.
- Harrison, R. L. 1997. Chemical attractants for central American felids. *Wildlife Society Bulletin*, 25, 93-97.
- Heggberget, T. M. & Myrberget, S. 1979. Den norske bestand av oter 1971-1977. *Fauna*, 32, 89-95.
- Hellawell, J. M. 1991. Development of a rationale for monitoring. In: *Monitoring for conservation and ecology* (eds. F. B. Goldsmith), pp. 1-14. Chapman and Hall, London.
- Helle, E., Hele, P., Lindén, H. & Wikman, M. 1996. Wildlife populations in Finland during 1990-1995, based on wildlife triangle data. *Finnish Game Research*, 49, 12-17.
- Helle, P. & Nikula, A. 1996. Usage of geographic information systems (GIS) in analyses of wildlife triangle data. *Finnish Game Research*, 49, 26-36.
- Hopkins, R. A. 1990. Ecology of the puma in the Diablo Range, California. PhD Thesis, University of California, Berkeley,
- Hornocker, M. G. 1969. Winter territoriality in mountain lions. *Journal of Wildlife Management*, 33, 457-464.
- Hornocker, M. G. & Hash, H. S. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology*, 59, 1286-1301.
- Hovey, F. W. & McLellan, B. N. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology*, 74, 1409-1416.
- Högmander, H. & Penttinen, A. 1996. Some statistical aspects of Finnish wildlife triangles. *Finnish Game Research*, 49, 37-43.
- Huber, D., Kusak, J. & Radisic, B. 1996. Analysis of efficiency in live-capture of European brown bears. *Journal of Wildlife Research*, 1, 158-162.
- Hundertmark, K. J., Becker, E. & Schwartz, C. C. 1989. Development of population assessment techniques for lynx. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Report, Project W-23-2, 1-8.
- Ionescu, O. 1993. Current status and prospects for the wolf in Romania. In: *Wolves in Europe: status and*

- perspectives (eds. C. Promberger & W. Schröder), pp. 51-55. Munich Wildlife Society, Munich.
- Jackson, R., Hunter, D. O. & Emmerich, C. 1997. SLIMS: an information management system for promoting the conservation of snow leopards and biodiversity in the mountains of central Asia. In: Proceedings of the 8th International Snow Leopard Symposium (eds. R. Jackson & A. Ahmad), pp. 75-91. International Snow Leopard Trust and World Wide Fund for Nature - Pakistan, Islamabad, Pakistan.
- Jackson, R. & Hunter, D. O. 1995. Snow leopard survey and conservation handbook. International Snow Leopard Trust, Seattle.
- Jaeger, M. M., Pandit, R. K. & Haque, E. 1996. Seasonal differences in territorial behavior by golden jackals in Bangladesh: howling versus confrontation. *Journal of Mammalogy*, 77, 768-775.
- Jakubiec, Z. 1990. Distribution of the brown bear in Poland and problems concerning its protection. *Aquilo*, 27, 51-57.
- Jedrzejewska, B., Jedrzejewski, W., Bunevich, A. N., Milkowski, L. & Okarma, H. 1996. Population dynamics of wolves *Canis lupus* in Bialowieza Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. *Mammal Review*, 26, 103-126.
- Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A. N. & Milkowski, L. 1996. Population dynamics (1869-1994), demography, and home ranges of the lynx in the Bialowieza Primeval Forest (Poland and Belarus). *Ecography*, 19, 122-139.
- Jolicoeur, H., Kennedy, G. & Lemieux, R. 1993. Radioisotope tagging for the determination of black bear population densities in Quebec. Proceedings 11th Eastern Black Bear Workshop (eds. E. P. Orff), pp. 208-220. New Hampshire Fish and Game Department,
- Jordhøy, P., Strand, O., Skogland, T., Gaare, E. & Holmstrøm, F. 1997. Oppsummeringsrapport, overvåkingsprogram for hjortevilt - villreindelen 1991-95. Norwegian Institute for Nature Research Fagrapport, 022, 1-57.
- Kaczensky, P. 1996. Livestock-carnivore conflicts in Europe. Munich Wildlife Society,
- Kaczensky, P. & Huber, T. 1994. Wer was es ? Zentralstelle Österr, Landesjagdverbände,
- Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333-338.
- Karanth, K. U. 1989. Tigers in India: a critical review of field censuses. In: Tigers of the world: biology, biopolitics, management, and conservation of an endangered species (eds. R. L. Tilson & U. S. Seal), pp. 118-132. Noyes Publishers, New Jersey.
- Kendall, K. C., Metzgar, L. H., Patterson, D. A. & Steele, B. M. 1992. Power of sign surveys to monitor population trends. *Ecological Applications*, 2, 422-430.
- Kennedy, G., Jolicoeur, H., Gauvin, J. P. & Lemieux, R. 1993. Assessment of the health and environmental hazards of tagging black bears with radioisotopes. Proceedings 11th Eastern Black Bear Workshop (eds. E. P. Orff), pp. 198-207. New Hampshire Fish and Game Department,
- Kenney, J. S., Smith, J. L. D., Starfield, A. M. & McDougal, C. W. 1995. The long term effects of tiger poaching on population viability. *Conservation Biology*, 9, 1127-1133.
- Klein, D. R. 1959. Track differentiation for censusing bear populations. *Journal of Wildlife Management*, 23, 361-363.
- Knight, R. R., Blanchard, B. M. & Eberhardt, L. L. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin*, 23, 245-248.
- Knight, R. R., Blanchard, B. M. & Eberhardt, L. L. 1988. Mortality patterns and population sinks for Yellowstone Grizzly bears, 1973-1985. *Wildlife Society Bulletin*, 16, 121-125.
- Kolenosky, G. B. 1986. The effects of hunting on an Ontario black bear population. International Conference on Bear Research and Management, 6, 45-56.
- Kolstad, M., Kvam, T., Mysterud, I., Sørensen, O. J. & Wikan, S. 1984. Bjørnen (*Ursus arctos* L.) i Norge: utbredelse og bestand 1978-1982. Direktoratet for vilt og ferskvannsfisk Viltrappport, 31, 1-68.
- Kolstad, M., Mysterud, I., Kvam, T., Sørensen, O. J. & Wikan, S. 1986. Status of the brown bear in Norway; Distribution and population 1978-1982. *Biological Conservation*, 38, 79-99.
- Kruuk, H. 1995. Wild otters: predation and populations. Oxford University Press, Oxford.
- Kruuk, H., Gorman, M. & Parrish, T. 1980. The use of ⁶⁵Zn for estimating populations of carnivores. *Oikos*, 34, 206-208.
- Kutilek, M. J., Hopkins, R. A., Clinite, E. W. & Smith, T. E. 1983. Monitoring population trends of large carnivores - using track transects. In: Renewable resource inventories for monitoring changes and trends (eds. Bell, J. F. & T. Atterbury), pp. 104-106. College of Forestry, Oregon State University, Corvallis, Oregon.
- Kvam, T. 1984. Age determination in European lynx by incremental lines in tooth cementum. *Acta Zoologica Fennica*, 171, 221-223.
- Kvam, T. 1997. Bestandsestimat for gaupe 1995-96 og 1996-97. NINA Rapport,
- Kvam, T. 1990. Population biology of the European lynx (*Lynx lynx*) in Norway. Dr.scient thesis, University of Trondheim,
- Kvam, T., Strand, O. & Sørensen, O. J. 1987. Jereinventering i Snøhetta-området våren 1986. Direktoratet for naturforvaltning rovtiltrappport, 1, 1-13.

- Kvam, T. & Sørensen, O. J. 1983. Utviklingen i jervestammen i snøhettaområdet i perioden 1979-1982. Arbeidsrapport fra rovviltprosjektet, 4, 1-14.
- Lancia, R. A., Nichols, J. D. & Pollock, K. H. 1996. Estimating the number of animals in wildlife populations. In: Research and management techniques for wildlife and habitats (eds. T. A. Bookout), pp. 215-253. The Wildlife Society, Bethesda, Md.
- Landa, A. 1998. Spor og tegn. Direktoratet for Naturforvaltning, Trondheim.
- Landa, A. & Skogland, T. 1995. The relationship between population density and body size of wolverines *Gulo gulo* in Scandinavia. *Wildlife Biology*, 1, 165-175.
- Landa, A., Strand, O., Linnell, J. D. C. & Skogland, T. 1998. Home range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology*, in press.
- Landa, A., Strand, O., Swenson, J. E. & Skogland, T. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*, 75, 1292-1299.
- Landa, A., Tufto, J., Franzén, R., Bç, T., Lindén, M. & Swenson, J. E. 1998. Active wolverine dens as a minimum population estimator in Scandinavia. *Wildlife Biology*, 4, in press.
- Laundré, J. W. 1981. Temporal variation in coyote vocalization rates. *Journal of Wildlife Management*, 45, 767-769.
- Lebreton, J. D. & North, P. M. 1993. The use of marked individuals in the study of bird population dynamics. Birkhauser Verlag, Basel.
- Lee, J. & Taylor, M. 1994. Aspects of the polar bear harvest in the Northwest Territories, Canada. *International Conference on Bear Research and Management*, 9, 237-243.
- Liberg, O. & Glörsen, G. 1995. Lodjurs - och varginventeringar 1993-1995. Viltforskningsrapporter fra Svenska Jägareförbundets, 1-30.
- Lindén, H., Helle, E., Helle, P. & Wikman, M. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research*, 49, 4-11.
- Linzey, F. G., Barber, K. R., Peters, R. D. & Meslow, E. C. 1986. Responses of a black bear population to a changing environment. *International Conference on Bear Research and Management*, 6, 57-64.
- Linzey, F. G., Thompson, S. K. & Hodges, J. I. 1977. Scent station index of black bear abundance. *Journal of Wildlife Management*, 41, 151-153.
- Linzey, F. G., Van Sickle, W. D., Ackerman, B. B., Barnhurst, D., Hemker, T. P. & Laing, S. P. 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management*, 58,
- Linnell, J. D. C., Smith, M. E., Odden, J., Kaczensky, P. & Swenson, J. E. 1996. Strategies for the reduction of carnivore - livestock conflicts: a review. NINA Oppdragsmelding, 443,
- Logan, K. A., Irwin, L. L. & Skinner, R. 1986. Characteristics of a hunted mountain lion population in Wyoming. *Journal of Wildlife Management*, 50, 648-654.
- Logan, K. A., Sweanor, L. L., Ruth, T. K. & Hornocker, M. G. 1996. Cougars of the San Andres mountains, New Mexico. New Mexico Department of Game and Fish, Federal Aid in Wildlife Restoration, Project W-128-R, 1-290.
- Lorentsen, S. H. 1997. Det nasjonale overvåkings-programmet for sjøfugl: resultater fra hekkesesongen 1997. Norwegian Institute for Nature Research Oppdragsmelding, 516, 1-83.
- Løvdal, I., Olsen, K. M. & van der Kooij, J. 1998. Statusrapport fra Prosjekt Pattedyratlas - februar 1998. *Fauna*, 51, 2-8.
- Mace, R. D., Manley, T. L. & Aune, K. E. 1994. Factors affecting the photographic detection rate of grizzly bears in the Swan Mountains, Montana. *International Conference on Bear Research and Management*, 9, 245-252.
- Mace, R., Manley, T. & Aune, K. 1990. Use of systematically deployed remote cameras to monitor grizzly bears. *Montana Department of Fish, Wildlife and Parks*, 1-29.
- Mace, R. D., Minta, S. C., Manley, T. L. & Aune, K. E. 1994. Estimating grizzly bear population size using camera sightings. *Wildlife Society Bulletin*, 22, 74-83.
- Mace, R. D. & Waller, J. S. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *Journal of Wildlife Management*, 61, 39-52.
- Maddock, A. H. & Mills, M. G. L. 1994. Population characteristics of African wild dogs *Lycan pictus* in the eastern Transvaal lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67, 57-62.
- Maehr, D. S., Land, E. D. & Roof, J. C. 1991. Florida panthers. *National Geographic Research and Exploration*, 7, 414-431.
- Mano, T. 1987. Population characteristics of brown bears on Oshima Peninsula, Hokkaido. *International Conference on Bear Research and Management*, 7, 69-74.
- Mano, T. 1995. Sex and age characteristics of harvested brown bear in the Oshima peninsula, Japan. *Journal of Wildlife Management*, 59, 199-204.
- Mattson, D. J. 1997. Sustainable grizzly bear mortality calculated from counts of females with cubs-of-the-year: an evaluation. *Biological Conservation*, 81, 103-111.
- McCarthy, T. M. & Munkhtsog, B. 1997. Preliminary assessment of snow leopard sign surveys in Mongolia. In: Proceedings of the 8th International Snow Leopard Symposium (eds. R. Jackson & A. Ahmad), pp. 57-65. *International Snow Leopard*

- Trust and World Wide Fund for Nature - Pakistan, Islamabad, Pakistan.
- McCullough, D. R. 1986. The Craigheads' data on Yellowstone grizzly bear populations: relevance to current research and management. International Conference on Bear Research and Management, 6, 21-32.
- McCullough, D. R. 1996. Spatially structured populations and harvest theory. *Journal of Wildlife Management*, 60, 1-9.
- McLean, P. K. & Pelton, M. R. 1994. Estimates of population density and growth of black bears in the Smoky Mountains. International Conference on Bear Research and Management, 9, 253-262.
- McLellan, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age - sex composition. *Canadian Journal of Zoology*, 67, 1856-1860.
- Mech, L. D. 1986. Wolf population in the central Superior National Forest, 1967-1985. USDA Forest Service North Central Forest Experiment Station Research Paper, NC-270, 1-6.
- Mertzanis, G. 1990. The brown bear in Greece. *Aquilo*, 27, 67-70.
- Mertzanis, G. 1994. Brown bear in Greece: distribution, present status, ecology of a northern Pindus subpopulation. International Conference on Bear Research and Management, 9, 187-198.
- Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. In: Ecology and conservation of wolves in a changing world (eds. L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 187-198. Canadian Circumpolar Institute, Edmonton.
- Messier, F. & Crête, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia*, 65, 503-512.
- Miljøverndepartementet (1996-97. Om rovviltforvaltning. Stortings Melding 35,
- Miller, S. D. 1990. Impact of increased bear hunting on survivorship of young bears. *Wildlife Society Bulletin*, 18, 462-467.
- Miller, S. D. 1990. Population management of bears in North America. International Conference on Bear Research and Management, 8, 357-373.
- Miller, S. D. & Miller, S. M. 1990. Interpretation of bear harvest data. Alaska Department of Fish and Game, Final Report, W-22-6 through W-23-3, 1-90.
- Miller, S. D., White, G. C., Sellers, R. A., Reynolds, H. V., Schoen, J. W., Titus, K., Barnes, V. G., Smith, R. B., Nelson, R. R., Ballard, W. B. & Schwartz, C. C. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. *Wildlife Monographs*, 133, 1-55.
- Mills, M. G. L. 1996. Methodological advances in capture, census, and food habits studies of large African carnivores. In: Carnivore behavior, ecology, and evolution (eds. J. L. Gittleman), pp. 223-242. Cornell University Press, London.
- Mills, M. G. L. & Gorman, M. L. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, 11, 1397-1406.
- Mladenoff, D. J. & Sickley, T. A. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. *Journal of Wildlife Management*, 62, 1-10.
- Mladenoff, D. J., Sickley, T. A., Haight, R. G. & Wydeven, A. P. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology*, 9, 279-294.
- Mortensen, A. J. 1996. Sportakseringer på gaupe i Gudbrandsdalen og Ottadalen 1993-1996. Fylkesmannen i Oppland Miljøvernavdelingen Rapport, 13/96, 1-13.
- Myrberget, S. 1988. Hunting statistics as indicators of game population size and composition. *Statistical Journal of the United Nations*, ECE 5, 289-301.
- Myrberget, S. & Sørensen, O. J. 1981. Spor og sportegn etter store rovdyr. *Viltrapport*, 15, 1-118.
- Mysterud, I. 1991. Vurdering av bjørnbestander ved hjelp av elgjegere II: Hedmark 1976-78. *Fauna*, 44, 275-284.
- Mysterud, I. & Mysterud I. 1995. Perspektiver på rovdyr, ressurser og utmarksnæringer i dagens- og framtidens Norge: en konsekvensutredning av rovviltforvaltningens betydning for småfenøring, reindrift og viltinteresser. Sluttrapport, KUR-prosjektet, Norsk sau og geitalslag., 336pp.
- Nagy, J. A. & Gunson, J. R. 1990. Management plan for grizzly bears in Alberta. Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division, Wildlife Management Planning Series, 2, 1-164.
- Noss, R. F. & Cooperrider, A. Y. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington D.C.
- Nowell, K. & Jackson, P. 1996. Wild cats: status survey and action plan. IUCN, Gland, Switzerland.
- Noyce, K. V., Garshelis, D. L. & Coy, P. L. 1998. Vulnerability of black bears to trap and camera sampling and implications for mark-recapture studies. International Conference on Bear Research and Management - Abstract, 11, 32.
- Östergren, A. & Segerström, P. 1998. Familjegrupper av lodjur - metod för antalsbedömningar. Länsstyrelsen Västerbottens län Meddelande, 2, 1-5.
- Paloheimo, J. E. & Fraser, D. 1981. Estimation of harvest rate and vulnerability from age and sex data. *Journal of Wildlife Management*, 45, 948-958.
- Pelton, M. R. 1972. Use of foot trail travellers in the Great Smoky Mountains National Park to estimate black bear (*Ursus americanus*) activity. International Conference on Bear Research and Management, 2, 36-42.

- Pelton, M. R. & Marcum, L. C. 1977. The potential use of radioisotopes for determining densities of black bears and other carnivores. In: Proceedings of the 1975 Predator Symposium (eds. R. L. Phillips & C. Jonkel), pp. 221-236. Montana Forest and Conservation Experiment Station, University of Montana, Missoula.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Parks Service Scientific Monograph Series, 11, 1-210.
- Peterson, R. O. 1995. The wolves of Isle Royale: a broken balance. Willow Creek Press, Minocqua, Wisconsin.
- Pletscher, D. H., Ream, R. R., Boyd, D. K., Fairchild, M. W. & Kunkel, K. E. 1997. Population dynamics of a recolonizing wolf population. *Journal of Wildlife Management*, 61, 459-465.
- Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107,
- Potvin, F. 1987. Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec. *Canadian Journal of Zoology*, 66, 1266-1273.
- Powell, R. A., Zimmerman, J. W., Seaman, D. E. & Gilliam, J. F. 1996. Demographic analyses of a hunted black bear population with access to a refuge. *Conservation Biology*, 10, 224-234.
- Rabinowitz, A. 1993. Estimating the Indochinese tiger *Panthera tigris corbetti* population in Thailand. *Biological Conservation*, 65, 213-217.
- Reynolds, H. V. & Garner, G. W. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. *International Conference on Bear Research and Management*, 7, 59-68.
- Rice, C. G., Rohlman, J., Beecham, J. & Pozzanghera, S. 1998. Are bait stations useful for monitoring black bear populations ? some approaches to power analysis. *International Conference on Bear Research and Management - Abstract*, 11, 38.
- Rose, M. D. & Polis, G. A. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology*, 79, 998-1007.
- Ross, P. I. & Jalkotzy, M. G. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management*, 56, 417-426.
- Ross, P. I., Jalkotzy, M. G. & Gunson, J. R. 1996. The quota system of cougar harvest management in Alberta. *Wildlife Society Bulletin*, 24, 490-494.
- Rossell, C. R. & Litvaitis, J. A. 1994. Application of harvest data to examine responses of black bears to land-use changes. *International Conference on Bear Research and Management*, 9, 275-281.
- Rudis, V. A. & Tansey, J. B. 1995. Regional assessment of remote forests and black bear habitat from forest resource surveys. *Journal of Wildlife Management*, 59, 170-180.
- Schaller, G. B., Junrang, R. & Mingjiang, Q. 1988. Status of the snow leopard *Panthera unica* in Qinghai and Gansu Provinces, China. *Biological Conservation*, 45, 179-194.
- Schmidt, K., Jedrzejewski, W. & Okarma, H. 1997. Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, 42, 289-312.
- Schonewald-Cox, C., Azari, R. & Blume, S. 1991. Scale, variable density, and conservation planning for mammalian carnivores. *Conservation Biology*, 5, 491-495.
- Schwartz, C. C. & Becker, E. F. 1988. Development of population assessment techniques for lynx. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Report, Project W-22-6, 1-28.
- Schwartz, C. C., Becker, E. F. & Hundertmark, K. J. 1988. Development of population assessment techniques for lynx. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Report, Project W-23-1, 1-8.
- Schweinsburg, R. E., Lee, L. J. & Latour, P. B. 1982. Distribution, movement and abundance of polar bears in Lancaster Sound, Northwest Territories. *Arctic*, 35, 159-169.
- Seber, G. A. F. 1986. A review of estimating animal abundance. *Biometrics*, 42, 267-292.
- Seidensticker, J. C., Hornocker, M. G., Wiles, W. V. & Messick, J. P. 1973. Mountain lion social organization in the Idaho primitive area. *Wildlife Monographs*, 35, 1-60.
- Seydack, A. H. W. 1984. Application of a photo-recording device in the census of larger rain-forest mammals. *South African Journal of Wildlife Research*, 14, 10-14.
- Shaw, H. G. 1977. Impact of mountain lion on mule deer and cattle in northwestern Arizona. In: Proceedings of the 1975 Predator Symposium (eds. R. L. Phillips & C. Jonkel), pp. 17-32. Montana Forest and Conservation Experiment Station, University of Montana, Missoula,
- Shaw, H. G. 1987. Mountain lion field guide. Arizona Game and Fish Department, Special report number 9, 1-47.
- Shaw, H. G., Woolsey, N. G., Wegge, J. R. & Day, R. L. 1988. Factors affecting mountain lion densities and cattle depredation in Arizona. Arizona Fish and Game Department Final Report, Federal Aid in Wildlife Restoration Project W-78-R, 1-16.
- Smallwood, K. S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. *Environmental Conservation*, 24, 283-289.
- Smallwood, K. S. 1994. Trends in California mountain lion populations. *Southwestern Naturalist*, 39, 67-72.
- Smallwood, K. S. & Fitzhugh, E. L. 1997. Differentiating mountain lion and dog tracks. In: Proceedings of the third mountain lion workshop (eds. R. H. Smith), pp. 58-63. Arizona Chapter, The Wildlife Society, Prescott, Arizona.

- Smallwood, K. S. & Fitzhugh, E. L. 1993. A rigorous technique for identifying individual mountain lions *Felis concolor* by their tracks. *Biological Conservation*, 65, 51-59.
- Smallwood, K. S. & Fitzhugh, E. L. 1991. The use of track counts for mountain lion population census. Mountain lion- human interaction, Symposium and workshop, Colorado Division of Wildlife, 59-67.
- Smallwood, K. S. & Schonewald, C. 1996. Scaling population density and spatial pattern for terrestrial mammalian carnivores. *Oecologia*, 105, 329-335.
- Smietana, W. & Wajda, J. 1997. Wolf number changes in Bieszczady National Park, Poland. *Acta Theriologica*, 42, 241-252.
- Smirnov, E. N. & Miquelle, D. G. 1998. Long term monitoring to assess trends and population dynamics of the Amur tiger in Sikhote-Alin Zapovednik, Primorski Krai, Russia. In: *Riding the tiger: meeting the needs of wildlife and people in Asia* (eds. J. Seidensticker, P. Jackson & X. Christie), pp. xxx-xxx. Cambridge University Press, Cambridge.
- Smith, R. V., Belk, M. C. & Black, H. L. 1998. A shape analysis of American black bear tracks. *International Conference on Bear Research and Management - Abstract*, 11, 116.
- Solberg, E. J., Heim, M., Sæther, B. E. & Holmstrøm, F. 1997. Oppsummeringsrapport overvåkingsprogram for hjortevilt Elg 1991-95. NINA Fagrapport, 030, 1-68.
- Solberg, E. J. & Sæther, B. E. submitted. How well do moose-observations predict population size ? a comparison of two independent population size indices. *Wildlife Biology*,
- Solvang, H. 1998. Resultat av gaupe/ulv registrering 25/1 1998. Norges Jeger og fiskerforbund - Hedmark, 13p.
- Spiridonov, G. & Spassov, N. 1990. Status of the brown bear in Bulgaria. *Aquilo*, 27, 71-75.
- Spreadbury, B. R., Musil, K., Musil, J., Kaisner, C. & Kovak, J. 1996. Cougar population characteristics in southeastern British Columbia. *Journal of Wildlife Management*, 60, 962-969.
- Stephenson, R. O. & Karczmarczyk, P. 1989. Development of techniques for evaluating lynx population status in Alaska. *Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Report, Project W-23-1*, 1-95.
- Støen, O. G. 1994. The status and food habits of the tiger (*Panthera tigris*) population in the Karnali floodplain of Royal Bardia National Park, Nepal. MSc Thesis, Agricultural University of Norway, Ås.
- Swenson, J. E. 1991. Evaluation of a density index for territorial male hazel grouse *Bonasa bonasia* in spring and autumn. *Ornis Fennica*, 68, 57-65.
- Swenson, J. E., Sandegren, F., Wabakken, P., Bjärvall, A., Söderberg, A. & Franzén, R. 1994. Bjørnens historiske og nåværende status og forvaltning i Skandinavia. Norsk Institutt for Naturforskning Forskningsrapport, 53, 1-23.
- Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation*, 70, 9-17.
- Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, 1, 11-25.
- Swenson, J. E. & Wikan, S. 1996. A brown bear population estimate for Finnmark County, North Norway. *Fauna Norveigica Series A*, 17, 11-15.
- Swenson, J. E. & Sandegren, F. 1996. Sustainable brown bear harvest in Sweden estimated from hunter-provided information. *Journal of Wildlife Research*, 1, 229-232.
- Swenson, J. E., Sandegren, F. & Söderberg, A. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology*, 67, in press.
- Sørensen, O. J., Overskaug, K. & Kvam, T. 1990. Status of the brown bear in Norway 1983-86. *International Conference on Bear Research and Management Monograph Series*, 8, 17-23.
- Sæther, B. E., Engen, S., Swenson, J. E., Bakke, Ø. & Sandegren, F. 1997. Levedyktighetsanalyser av shandinaavisk brunbjørn. NINA Fagrapport, 025, 1-41.
- Sæther, B. E., Engen, S., Swenson, J. E., Bakke, Ø. & Sandegren, F. 1998. Viability of Scandinavian brown bear *Ursus arctos* populations: the effects of uncertain parameter estimates. *Oikos*, 82, in press.
- Taberlet, P. & Bouvet, J. 1992. Bear conservation genetics. *Nature*, 358, 197.
- Taberlet, P., Mattock, H., Dubois-Paganon, C. & Bouvet, J. 1993. Sexing free-ranging brown bears *Ursus arctos* using hairs found in the field. *Molecular Ecology*, 2, 399-403.
- Taberlet, P. & Waits, L. P. 1998. Non-invasive genetic sampling. *Trends in Ecology and Evolution*, 13, 26-27.
- Taylor, B. L. & Gerrodette, T. 1993. The use of statistical power in conservation biology: the vaquita and northern spotted owl. *Conservation Biology*, 7, 489-500.
- Taylor, M. & Lee, J. 1994. Tetracycline as a biomarker for polar bears. *Wildlife Society Bulletin*, 22, 83-89.
- Testa, J. W., Holleman, D. F., Bowyer, R. T. & Faro, J. B. 1994. Estimating populations of marine river otters in Prince William Sound, Alaska, using radiotracer implants. *Journal of Mammalogy*, 75, 1021-1032.
- Theberge, J. B. 1991. Ecological classification, status, and management of the gray wolf, *Canis lupus*, in Canada. *Canadian Field-Naturalist*, 105, 459-463.

- Thompson, I. D., Davidson, I. J., O'Donnell, S. & Brazeau, F. 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology*, 67, 1816-1823.
- Torres, S. G., Mansfield, T. M., Foley, J. E., Lupo, T. & Brinkhaus, A. 1996. Mountain lion and human activity in California: testing speculations. *Wildlife Society Bulletin*, 24, 451-460.
- Van Dyke, F. G. & Brocke, R. H. 1987. Searching technique for mountain lion sign at specific locations. *Wildlife Society Bulletin*, 15, 256-259.
- Van Dyke, F. G. & Brocke, R. H. 1987. Sighting and track reports as indices of mountain lion presence. *Wildlife Society Bulletin*, 15, 251-256.
- Van Dyke, F. G., Brocke, R. H. & Shaw, H. G. 1986. Use of road track counts as indices of mountain lion presence. *Journal of Wildlife Management*, 50, 102-109.
- Van Hensbergen, H. J. & White, G. C. 1995. Review of methods for monitoring vertebrate population parameters. In: *Integrating people and wildlife for a sustainable future* (eds. J. A. Bissonette & P. R. Krausman), pp. 489-508. *Wildlife Society, Maryland*.
- Van Sickle, W. D. & Lindzey, F. G. 1991. Evaluation of a cougar population estimator based on probability sampling. *Journal of Wildlife Management*, 55, 738-743.
- Vila, C., Castroviejo, J. & Urios, V. 1993. The Iberian wolf in Spain. In: *Wolves in Europe - status and perspectives* (eds. C. Promberger & W. Schröder), pp. 104-109. *Munich Wildlife Society, Munich*.
- Vincent, J., Gaillard, J. & Bideau, E. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriologica*, 36, 315-328.
- Vincent, J. P., Hewison, A. J. M., Angibault, J. M. & Cargnelutti, B. 1996. Testing density estimators on a fallow deer population of known density. *Journal of Wildlife Management*, 60, 18-28.
- Wabakken, P. 1993. Wolves in Sweden and Norway. In: *Wolves in Europe - status and perspectives* (eds. C. Promberger & W. Schröder), pp. 8-13. *Munich Wildlife Society, Munich*.
- Wabakken, P., Kvam, T. & Sørensen, O. J. 1984. Wolves *Canis lupus* in southeastern Norway. *Fauna Norvegica Series A*, 50-52.
- Wabakken, P., Linnell, J. D. C. & Andersen, R. 1996. Ulv i Hedmark. En utredning foretatt i forbindelse med Forsvarets planer for Regionfelt Østlandet, del 6. *NINA Oppdragsmelding*, 417, 1-16.
- Wabakken, P. & Maartmann, E. 1994. Sluttrapport for bjørn-sauprosjektet i Hedmark 1990-1993. *NINA forskningsrapport*, 058, 1-49.
- Wabakken, P. & Maartmann, E. 1997. Bestandsstatus for ulv i sørøst-Norge og Skandinavia i 1996. *Fylkesmannen i Hedmark Miljøvernvedlingen Rapport*, 8/97, 1-19.
- Wabakken, P., Sørensen, O. J. & Kvam, T. 1982. Ulv *Canis lupus* L. i sørøst-Norge: registeringsproblemer og minimumsbestand. *Viltrapport*, 20, 1-38.
- Wabakken, P., Sørensen, O. J. & Kvam, T. 1983. Wolves (*Canis lupus*) in southeastern Norway. *Acta Zoologica Fennica*, 174, 277.
- Wards, R. M. & Krebs, C. J. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology*, 63, 2817-2824.
- Wasser, S. K., Houston, C. S., Koehler, G. M., Cadd, G. G. & Fain, S. R. 1997. Techniques for application of faecal DNA methods to field studies of Ursids. *Molecular Ecology*, 6, 1091-1097.
- Weaver, J. L., Paquet, P. C. & Ruggiero, L. F. 1996. Resilience and conservation of large carnivore conservation in North America. *Conservation Biology*, 10, 964-976.
- White, G. C. & Garrott, R. A. 1990. *Analysis of wildlife radio-tracking data*. Academic Press Inc., London.
- Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Corillera Cantabrica; Spain. *Ecological Monographs*, In press.
- Wielgus, R. B. & Bunnell, F. L. 1994. Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. *Biological Conservation*, 67, 161-166.
- Woodroffe, R., Ginsberg, J. & Macdonald, D. W. 1997. *The African wild dog: status survey and conservation action plan*. IUCN Publications, Cambridge.
- Yoccoz, N. G., Steen, H., Ims, R. A. & Stenseth, N. C. 1993. Estimating demographic parameters and the population size: an updated methodological survey. In: *The Biology of Lemmings* (eds. N. C. Stenseth & R. A. Ims), pp. 565-587. *Academic Press, London*.
- Young, B. F. & Ruff, R. L. 1982. Population dynamics and movements of black bears in east central Alberta. *Journal of Wildlife Management*, 46, 845-860.
- Zielinski, W. J. & Kucera, T. E. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. *United States Department of Agriculture, Forest Service, General Technical Report, PSW-GTR-157*, 1-163.
- Zielinski, W. J. & Stauffer, H. B. 1996. Monitoring *Martes* populations in California: survey design and power analysis. *Ecological Applications*, 6, 1254-1267.
- Zielinski, W. J. & Truex, R. L. 1995. Distinguishing tracks of marten and fisher at track-plate stations. *Journal of Wildlife Management*, 59, 571-579.

Appendix

Latin names of species referred to in the text

Felids

Tiger - *Panthera tigris*
Eurasian lynx - *Lynx lynx*
Canada lynx - *Lynx canadensis*
Cougar - *Puma concolor/Felis concolor*
Bobcat - *Lynx rufus*
Snow leopard - *Panthera uncia*

Canids

Wolf - *Canis lupus*
Coyote - *Canis latrans*
Red fox - *Vulpes vulpes*
Dingo - *Canis familiaris*

Mustelids

Badger - *Meles meles*
Eurasian otter - *Lutra lutra*
North American otter - *Lutra canadensis*
Wolverine - *Gulo gulo*
American marten - *Martes americana*
Eurasian pine marten - *Martes martes*
Fisher - *Martes pennanti*

Ursids

Brown bear - *Ursus arctos*
Black bear - *Ursus americanus*
Polar bear - *Ursus maritimus*
Panda - *Ailuropoda melanoleuca*
Raccoon - *Procyon lotor*