# Sustainably Harvesting a Large Carnivore? Development of Eurasian Lynx Populations in Norway During 160 Years of Shifting Policy

John D. C. Linnell · Henrik Broseth · John Odden · Erlend Birkeland Nilsen

Received: 4 November 2008/Accepted: 5 February 2010 © Springer Science+Business Media, LLC 2010

**Abstract** The management of large carnivores in multiuse landscapes is always controversial, and managers need to balance a wide range of competing interests. Hunter harvest is often used to limit population size and distribution but is proving to be both controversialand technically challenging. Eurasian lynx (Lynx lynx) are currently managed as a game species in Norway. We describe an adaptive management approach where quota setting is based on an annual census and chart the population development through the period 1996–2008, as management has become significantly more sophisticated and better informed by the increased availability of scientific data. During this period the population has been through a period of high quotas and population decline caused by fragmented management authority and overoptimistic estimates of lynx reproduction, followed by a period of recovery due to quota reductions. The modern management regime is placed in the context of shifting policy during the last 160 years, during which management goals have moved from extermination stimulated by bounties, through a short phase of protection, and now to quota-regulated harvest. Much management authority has also been delegated from central to local levels. We conclude that adaptive management has the potential to keep the population within some bounded limits, although there will inevitably be fluctuation.

**Keywords** Adaptive management · Eurasian lynx · Harvest · Large carnivore · Historical policy

Europe is home to more than 500 million people and consists of landscapes that have been extensively transformed by human land use for several thousand years. Despite this extreme anthropogenic impact, much of the continent's postpleistocene megafauna remains extant (Linnell and others 2001a), including five species of large carnivore (Eurasian lynx, Lynx lynx; Iberian lynx, L. pardina; brown bear, Ursus arctos; wolf, Canis lupus; wolverine, Gulo gulo). Although these species have survived, their distributions and densities have been constantly and dramatically impacted by humans, both directly through persecution and indirectly through human exploitation of forests and wild ungulates. In general, the last decades of the 19th century and first decades of the 20th century represented the nadir of Europe's large mammals and their forest habitats (Boitani 1995; Breitenmoser 1998; Linnell and others 2009). Since then, and especially in the last 30 years, there has been a dramatic reversal of fortune for many populations, as forest area has increased dramatically (Farrell and others 2000), wild ungulate populations have been restored to record levels in many areas (Milner and others 2006; Andersen and others 2004), and many large carnivore populations have expanded, through either natural expansion (Wabakken and others 2001; Valière and others 2003), reintroduction (Breitenmoser and others 2001), or both (Linnell and others 2009).

However, their return in many areas has been associated with conflicts, both material (Kaczensky 1999) and social

J. D. C. Linnell (☒) · H. Broseth · J. Odden Terrestrial Ecology, Norwegian Institute for Nature Research, Tungasletta 2, 7485 Trondheim, Norway e-mail: john.linnell@nina.no

E. B. Nilsen Faculty of Forestry and Wildlife Management, Hedmark College, 2480 Koppang, Norway

Published online: 06 March 2010



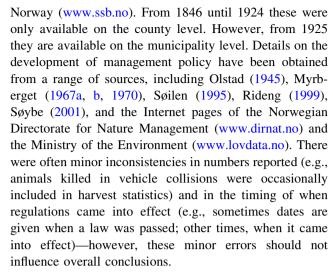
(Skogen and Haaland 2001). These conflicts create difficult management situations that can result in controversy. For example, the use of hunting or lethal control is often applied as a conflict decreasing measure in many situations to keep carnivore populations within desired limits, to empower local people, or to maintain traditional livestock herding activities. However, this killing of carnivores is often controversial, as conservationists feel that too many are being killed, animal rights advocates feel it is often wrong to kill carnivores at all, and many rural interest groups (such as hunters and sheep farmers) feel that too few are being killed (Treves and Naughton-Treves 2005). The result of pressures exerted by these conflicting lobby groups can often be a high degree of political involvement in the technical field of wildlife management (Nie 2003; Sandström and others 2009). This can lead to a highly dynamic and fluid management situation where the actual consequences for the carnivore populations are uncertain. Globally there is very little experience with sustainably managing the harvest of large carnivores, as historical goals have almost always been to exterminate predators, either through direct policy, including the payment of incentives, or through passive neglect (Linnell and others 2001a). Therefore, all case studies of how populations have fared under different management regimes are valuable (e.g., Ross and others 1996; Yamazaki 1996; Creel and Creel 1997; Whitman and others 2004).

However, in order to gain perspective on present-day debates it is vital to view existing management situations within the context of their history (Mykrä and others 2005; Pohja-Mykrä and others 2005). It is also vital to initiate robust monitoring programs such that the effect of policy can be analyzed and to allow management to respond to undesired changes through adaptive management processes (Williams and others 1996).

In this paper we trace the historical development of official policy and population responses for Eurasian lynx in Norway. From 1845 until 1995 our only data to monitor population changes are derived from bounty payments and hunting statistics (Swenson and others 1995; Jedrzejewska and others 1996; Litvaitis and others 2006). From 1996 until the present we have access to annual census data that have been collected within the structured framework of a national monitoring program. Therefore our goal is to give a detailed description of the present-day status of lynx in Norway that is firmly embedded in the historical route it took to this situation.

### Methods

Historical data on bounty payments and hunting statistics have been obtained from diverse databases within Statistics



Since 1996 lynx have been monitored using a common methodology based on unreplicated counts of family groups (sensu Knight and others 1995; Linnell and others 2007a, b). From 1996 to 2002 this monitoring was done more or less on an ad hoc basis by the individual counties. Results from the years 1996 and 1997 have been previously presented in unpublished reports (Kvam 1997). From 2002 and onward the work has been coordinated by the National Large Predator Monitoring Program based at the Norwegian Institute for Nature Research, with the State Nature Inspectorate responsible for verifying field observations. In early 2003 this monitoring program produced its first report of the national population status in 2002. However, the raw data from the pre-2002 period were reanalyzed along with the post 2002 data, such that data for all years are comparable. This reanalysis has led to some changes in the numbers presented by Kvam (1997) for 1996 and 1997, mainly in the direction of slightly lowering his estimates.

Records of lynx tracks with two or more individuals (assumed to be a family group outside the mating season) are collected by hunters, game wardens, and the public during the period from October 1st to the end of February. These observations are then verified by state-employed wildlife wardens from the State Nature Inspectorate and entered into a national monitoring database (ROVBASEN 3.0). Although the search effort varies between regions, experience has shown that local hunters put in a good deal of time to search for tracks, often in coordinated surveys. Furthermore, most of the counties with large lynx populations have adopted a system of index lines (>1900 transects, each 3 km long) that are examined for tracks on snow once per year, which provides a minimum search effort (Linnell and others 2007b; Odden and others 2008). This index line system is integrated into the National Large Carnivore Monitoring program, and all records of family groups are verified by state wardens. Studies have shown that almost all radio-collared lynx that are known to exist



within an area are detected (e.g., Odden and others 2001). Additional evidence of reproduction such as young of the year being shot, found dead, or killed in vehicle collisions between October 1st and April 30th are also included. Once all observations are available, a standardized set of distance rules derived from telemetry studies is applied to the observations (Linnell and others 2007a). These rules are based on maximal home range sizes and maximal distances traveled within known time periods (Linnell and others 2007a). Home range sizes and movement rates vary between study areas depending on prey availability (Linnell and others 2001a; Herfindal and others 2005a), requiring that different rules are applied in different parts of Norway. Presently three main "prey density" regions are recognized: (1) areas where semidomestic reindeer form the main prey, (2) areas with a relatively low density of roe deer, and (3) areas with a relatively high density of roe deer. The cutoff between high and low roe deer density is at a harvest density of 0.75 roe deer shot per year per 10 km<sup>2</sup>. Two different sets of rules were developed for each region. For observations separated by more than a week, a fixed distance rule based on home range length is used. The program operates with a strict (long and, therefore, conservative) and a normal (shorter) distance rule. The strict rule is the mean of the lengths of 100% minimum convex polygon home ranges of adult female lynx. The normal rule is identical to that used in Swedish lynx monitoring (Östergren and Segerström 1998) and is the mean of the maximum home range lengths divided by the diameter of a circle of the same area. For observations that are closer in time a dynamic distance rule is used, which is based on the mean of the individual maximum day-to-day straight-line-movement distances. Details of the annual censuses are given by Brøseth and Odden (2008) and Odden and others 2008). For simplicity we only present results based on the normal distance rules.

There is no statistical estimate of the number of animals not detected, so that the result is a minimum count of the number of family groups which could be responsible for the total amount of observations. This minimum count of family groups can then be extrapolated to an approximation of total population size (Andrén and others 2002) based on factors developed from survival and reproductive rates for radio-collared lynx (Andrén and others 2006). Different extrapolation factors have been developed for the different prey type regions that take regional differences in demographic parameters into account. We present the monitoring data for Norway as a whole and for eight geographic regions that correspond to the management units that have been operational from winter 2004–2005 onward.

Norwegian hunting seasons extend from April 1st to March 31st. Most lynx are shot during the second half of the winter (February–March), while monitoring occurs in

the period December–February. We attribute all hunting seasons and monitoring seasons to the year at the end of the winter; e.g., harvest statistics from the winter of 1994–1995 are referred to as 1995, and family groups resulting from birth in summer 1994 are attributed to the 1995 season when they were censused.

#### **Results and Discussion**

Policy Development

The history of lynx management (Table 1) can be divided into three broad periods: the bounty years, transition years, and the quota hunting years.

The Bounty Years (1846–1980)

Although wolves and bears were subjected to an official bounty that was paid by locally raised taxes from 1733 (Elgmork 2000), lynx were first covered by a state bounty from 1846. The "law on the extermination of carnivores and protection of other game" was passed in 1845 and introduced a state bounty for all large carnivores and a range of other avian and mammalian predators (Rideng 1999; Søybe 2001). As the title of the law makes clear, the official policy goal at that time was to exterminate the large carnivores because of their depredation on livestock and predation on wild ungulates. The state bounty stayed in place until 1980, with the exception of the years from 1930 to 1955. During that period many of the counties and municipalities continued paying it (Myrberget 1970) from local funds. Lynx were the last of the four large carnivores to have the state bounty removed. For comparison, bears had their state bounty removed in 1930, and even local bounties were banned in 1972, prior to their full protection in Norway in 1973 (Swenson and others 1995), the same year in which wolves were protected in all Norway and wolverines were protected in southern Norway (Landa and others 2000). In addition to the state bounty, a wide range of local bounties was also paid by the counties, municipalities, and local organizations for various periods. While information on these local bounties is poor, a survey from the mid 1960s indicates that the sum of local bounties was two to four times the state bounty (Myrberget 1967a). During that period lynx hunting was not attached to landowner rights in the manner of game species. Therefore, lynx could be hunted by everybody, anywhere, without the need to pay a hunting license, all year round except for the "Christmas protection" period (December 24-31). The only restrictions were on the use of poison, killing traps, and leg-hold traps imposed at various times during the mid 20th century (Table 1).



Quota hunting extended to 11 counties

1996

Transition years Quota hunting Bounty years Period Lynx hunting open to all, without need for landowners does not apply to large carnivores, which remain open Responsibility for census and quotas given to counties Introduction of compensation for lynx-killed livestock Hunting rights for all game transferred to landowner; Counties delegated authorities to set hunting quotas permission. Shooting, poison, leg-hold traps, live-Possible to issue out-of-season permits to control Use of leg-hold traps banned except on bait/kills (ii) no need to pay hunting license, and (iii) no need to have landowner's permission Total ban on use of leg-hold and killing traps Quota regulated hunting opened in 6 counties Quota hunting extended to total of 8 counties Counties encouraged to set female subquotas Confirms that Iynx hunting is (i) open to all, Ban on use of motorized vehicles in hunting Use of poison limited to special permission capture traps, and killing traps allowed Complete protection in south Norway Landowner given hunting rights Ban on live-capture box traps depredating individuals Total ban on poison for everybody Consequences 1 November to 15 April 1 February to 31 March 22 August to 14 April All year except 24-31 Hunting season December All year State bounty introduced State bounty increased State bounty increased State bounty removed; State bounty reinstated State bounty removed left to counties Bounty 1st parliamentary white paper, "On the Management of Bears, Wolverines, Wolves Bern Convention signed; lynx in Appendix Convention on biological diversity signed and protection of other game" comes "Law on extermination of carnivores Introduction of first hunting law III without reservations Bern Convention ratified Revision of hunting law and Lynx in Norway" Hunting law revised CITES Appendix II Revised regulations New regulations New hunting law New hunting law Regulations 1846 1899 1932 9261 0961 1972 1979 0861 1982 1983 9861 1990 1992 1993 *l*ear 1956 1971 1989 1995 1863 1900 1951 1994



Fable 1 Development of regulations governing lynx management in Norway 1846-2004

| Table 1 | Table 1 contined  |        |                        |  |        |
|---------|---|--------|------------------------|--|--------|
| Year    | Regulations   | Bounty | Hunting season         | Consequences Peri  | Period |
| 1997    | 2nd parliamentary white paper, "On Large<br>Carnivore Management," revised<br>regulations |        |                        | Quota hunting extended to 12 counties<br>Specified that lynx were to be excluded from certain<br>areas   |        |
|         |   |        |                        | Live-capture box traps allowed again<br>Trial with local management committees in 2 counties   |        |
| 2000    | Revised regulations   |        |                        | Permit to issue permits to kill depredating individuals can now be given by counties   |        |
| 2002    | Revised regulations   |        | 1 February to 30 April |  |        |
| 2004    | 3rd parliamentary white paper, "Large<br>Carnivores in Norwegian Nature"                  |        |                        | 8 management zones created, with national population goals. Lynx quotas and depredation permits to be set by politically appointed committees in each zone |        |
| 2005    | Revised regulations   |        | 1 February to 31 March |  |        |
|         |   |        |                        |  |        |

The Transition Years (1980–1994)

These years saw a huge number of changes in lynx management. Soon after the state bounty was removed in 1980 a new hunting law came into effect (1982, with the first revisions already in 1983) which effectively transformed lynx from being unprotected to being a game species. The new law also included the major philosophical shift from all species being huntable unless protected to all species being protected unless specifically opening a hunting season. Lynx hunting was attached to landowner rights such that a landowner's permission was needed to hunt, and state hunting licenses needed to be purchased, although there were no limits on the numbers of lynx that could be killed. The 1983 revision of the law was also the first legal text to formally declare that national objectives were to maintain viable populations of all species, including lynx, although the goal of maintaining lynx populations (rather than exterminating as before) had been informally operational within the wildlife management system since at least the 1960s (Myrberget 1970). During the transition years hunting season length was reduced three times, from 9 down to 2 months, and the use of live-capture box traps was banned. Then in February 1992 a hunter in southeastern Norway shot an entire family group (adult female and two kittens). Although perfectly legal, the action received a great deal of media attention, which in turn led to a public outcry (Rideng 1999). Because there was little information on the status of lynx in Norway at that time, the Ministry of the Environment responded to public opinion by temporarily protecting lynx throughout southern Norway (Rideng 1999).

At the same time, parliament was for the first time debating a white paper on the topic of large carnivore management (Ministry of the Environment 1992). The white paper provided the first political statement outlining the twin management goals of conserving carnivores while limiting damage to livestock interests that are still at the core of present-day policy ("The government will ensure the survival of viable populations of bears, wolverines, wolves and lynx in Norway. At the same time the damage caused by large carnivores will be limited as much as possible"). This was the first time lynx had been included under the same umbrella as wolves, bears, and wolverines [their management was already governed by a management plan from 1987 (Vaag and others 1987)], creating what is known today as the "big four" large carnivores. State-paid compensation for livestock killed by lynx was introduced for the first time in 1994 (Fig. 3a). Responsibility for population censuses and setting quotas where populations could support harvest was delegated down to the 18 Norwegian counties. There was no coordinated or standardized attempt to census the populations or coordinate harvest during this period.



**Table 2** Development of the number of reported tracks, lynx family groups, and extrapolated total lynx population size for the period 1996–2008 in Norway

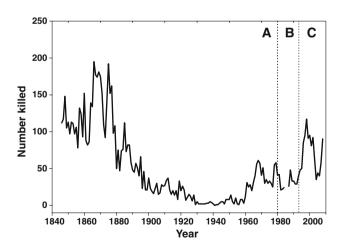
|                                 | 1994                     | 1995 | 1996 | 1997                         | 1998 | 1999 | 2000 | 2001 | 2002 | 2003  | 2004 | 2005 | 2006 | 2007        | 2008 |  |
|---------------------------------|--------------------------|------|------|------------------------------|------|------|------|------|------|-------|------|------|------|-------------|------|--|
| Tracks reported                 |                          |      | 185  | 259                          | 186  | 221  | 161  | 115  | 139  | 103   | 91   | 152  | 191  | 201         | 261  |  |
| Family groups                   |                          |      | 69   | 82                           | 68   | 76   | 61   | 55   | 56   | 46    | 44   | 56   | 65   | 74          | 76   |  |
| Population goal (family groups) | "Sustainable population" |      |      | "Same level as in 1996/1997" |      |      |      |      |      | 65 fa |      |      |      | mily groups |      |  |
| Extrapolated population size    |                          |      | 410  | 486                          | 403  | 448  | 366  | 327  | 332  | 272   | 259  | 329  | 385  | 439         | 452  |  |
| Hunting quota                   | 47                       | 54   | 103  | 146                          | 155  | 139  | 140  | 123  | 116  | 85    | 50   | 51   | 48   | 74          | 96   |  |
| Units with female subquota      |                          |      |      |                              |      |      |      | 8/18 | 7/18 | 7/18  | 7/18 | 7/18 | 5/8  | 5/8         | 7/8  |  |
| Number shot                     | 41                       | 50   | 85   | 95                           | 117  | 91   | 95   | 81   | 92   | 62    | 35   | 44   | 40   | 58          | 90   |  |
| Harvest (% of population)       |                          |      | 21   | 20                           | 29   | 20   | 26   | 25   | 28   | 23    | 14   | 13   | 10   | 13          | 20   |  |

#### The Early Quota Hunting Years (1994–2004)

Following the acceptance of the white paper in 1992, lynx in southern Norway remained fully protected for the 1992– 1993 hunting season. By winter 1994 the counties began to open for quota-regulated lynx hunting. The number of counties with quota-regulated hunting rapidly increased from 6 in 1994 to 12 in 1997. In 1997, parliament debated a second white paper on large carnivore management, which upheld the same principles as the first but included more precise goals for large carnivore populations (Ministry of the Environment 1997). These goals called for lynx populations to be kept at roughly the 1996-1997 levels. However, the white paper also called for the exclusion of lynx from areas where the livestock conflict potential was too high: mainly in western Norway and some coastal areas and islands of northern Norway. These areas were subject to the same harvest regulations as the rest of Norway with the exception that there were no quota limits on the number of lynx that could be killed. In addition, in two of the counties with the largest lynx populations there was to be a trial system where the quota-setting responsibility would be transferred from each county governor's Department of Environmental Affairs to local committees, composed of politicians and interest-group representatives (Guldvik and Arnesen 2001). In the counties with quota limits on lynx harvest there was a trend to introduce regulations and practices designed to prevent potential overharvest. Female subquotas were introduced such that the entire hunt in a county would stop if a certain number of females were killed even before the whole quota was filled (Table 2). In addition, quotas were often assigned to specific subregions within a county in an effort to focus harvest on regions where conflict with livestock was greatest. Finally, a number of counties began to issue the quota in two stages, holding back a part of the quota for some days or weeks. The idea was to reduce the chances of the total quota being exceeded.



In December 2003 the government presented to parliament the third white paper on large carnivore management in 11 years (Ministry of the Environment 2003). After much debate a modified version was accepted by a large parliamentary majority in May 2004, with the changes in management coming into effect in early 2005. From the point of view of lynx there were two significant changes. First, management was moved from the 18 counties to 8 regional units (Fig. 1), where a committee composed of elected representatives from the county assemblies assumed responsibility for setting quotas (Sandström and others 2009). These units correspond either to some large counties or to an aggregation of two or more smaller counties. This was an attempt to decentralize management to a biologically meaningful scale and increase public acceptance for



**Fig. 1** Numbers of lynx shot in Norway from 1846 to 2008. Period A, the time when state bounties were operational; Period B, the timeafter state bounty was removed but before limits were placed on harvest; Period C, the time during which a quota has limited annual harvests



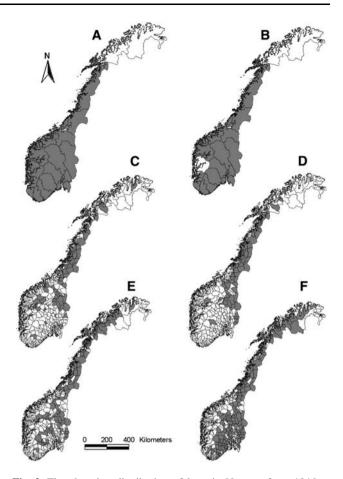
management decisions through the empowerment of elected representatives as outlined in the white paper of 2003. Second, national population goals for each region were set by central government, such that the regional committees have clear frames within which they can operate. Each committee will be able to call on technical expertise from one of the county management authorities within their region, and will only have power to set quotas once their region has reached its population goals. The regional committees also have been required to develop large carnivore management plans for their region.

### Patterns of Conflict

Lynx are associated with three major conflicts in Norway. First, domestic sheep are grazed in forests and mountains throughout Norway during summer. Most flocks are freegrazed, without fencing, supervision, or guarding. The result is widespread depredation on livestock (Odden and others 2002; Zimmermann and others 2010). Losses of sheep are basically related to the size of the lynx population (Herfindal and others 2005b) and the number of sheep compensated annually has fluctuated between 6000 and almost 10,000 since 1994 (Fig. 3a). These very high depredation rates are supported by ecological studies of lynx (Odden and others 2002) and telemetry studies of sheep mortality rates. Second, semidomestic reindeer are grazed by the Sami ethnic group in central and northern Norway. Reindeer are also highly vulnerable to depredation by lynx, although the exact numbers and factors influencing losses are still debated (Sunde and others 2000). Annual compensation figures lie between 2300 and 3300 reindeer. Third, roe deer hunters perceive lynx as being a major competitor for their shared quarry (Nilsen and others 2009). It is reasonable to suspect that both of the latter conflicts are also related to the size of the lynx population. Therefore, lynx management is regarded by politicians, managers, and the public as a process of balancing the need to maintain viable lynx populations with the need to minimize conflicts with sheep herders, reindeer herders, and hunters.

# Changes in Numbers Shot

Using harvest statistics to detect changes in population size requires some caution. In the early years there was undoubtedly some forgery, for example, with arctic fox skins being handed in as lynx (Søybe 2001). However, the high monetary value of the bounty led to improved control on the side of the state and strong motivation on the part of the hunter to report the kill, implying that records are likely to be reasonably complete and accurate. At least up until 1992 there was also little motivation for poaching, as



**Fig. 2** The changing distribution of lynx in Norway from 1846 to 2008 as indexed by administrative units where at least one lynx was shot in the given periods. **a, b** Data are available only on the level of the county. **c-f** Data are on the municipality level. The years included in are **a** 1846–1885 (early years of bounty harvest), **b** 1886–1925 (period of rapid decline), **c** 1926–1965 (the low-population phase), **d** 1966–1980 (period of slight recovery; bounty still in place), **e** 1981–1993 (postbounty period), and **f** 1994–present (quota regulated harvest)

hunting was effectively not limited by quotas. Therefore, we believe that for the period from 1846 to 1992 the public records provide an accurate record of the numbers of lynx being killed each year, and that the harvest statistics and bounty payments provide a general picture of the distribution and relative size of the lynx population (Swenson and others 1995; Jedrzejewska and others 1996; Litvaitis and others 2006). An exception may be the period from 1930 to 1955, when the state bounty was removed. It was assumed by central management agencies that the counties and municipalities would take over the bounty payments, although it is not known to what extent they did this. This may have reduced both the motivation to hunt and the accuracy with which the kills were reported. Also, during the years of the Second World War when Norway was occupied (1941-1945), hunting weapons were confiscated, and even after the war ammunition was in short supply and

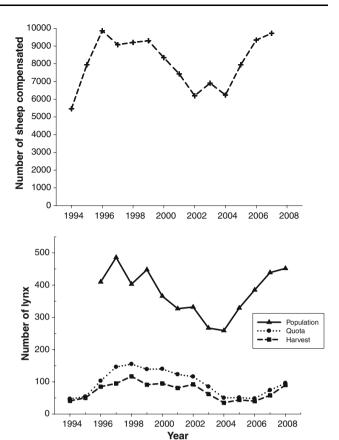


rationed. From 1992 onward the harvest data are less useful as a direct index of population size, as the harvest was usually limited by the size of the quota. Furthermore, the increasing conflict with farmers and hunters, and the limits on permissible harvest, presumably led to an increase in poaching. Poaching is presently a common cause of death among radio-collared lynx (Andrén and others 2006).

Bearing these limitations in mind, the hunting statistics indicate that for the first 30 years after the bounty was introduced, there was no detectable change in population distribution or size (Figs. 1, 2), although the annual bag varied substantially. However, following 1880 the population went into a steep decline, reaching its nadir in the 1930s and 1940s. For the reasons discussed above, the hunting statistics during this period may not be directly comparable with the previous and subsequent periods, creating an impression that the reduction was greater than it appears. However, contemporary accounts confirm the fact that lynx were very rare during this period—being found mainly in the central Norwegian county of Nord-Trøndelag, with a few individuals surviving in southern Norway (Olstad 1945; Myrberget 1970).

Beginning in 1960 the population appeared to increase again, first in density and then in distribution (Figs. 1, 2). The numbers shot each year remained fairly stable up until protection in 1992. There has been much speculation about the reasons for this increase, with various authors attributing it to improved prey availability as roe deer populations increased (Andersen and others 2004), a decline in the interest in lynx hunting, as the older generation of hunters died away, and of immigration from the lynx population in Sweden, which had increased following protection (Myrberget 1961, 1970). Once quota hunting started in 1994 there was a dramatic increase in the numbers being shot and the geographic distribution of these kills. This peaked in 1998, with a harvest of 117 animals. This was the highest number killed in a single year since 1877. After this peak the harvest declined again; by 2004 it had returned to levels typical of the 1960-1990 period. From 2005 and beyond there has been a substantial recovery in the size of the population.

Therefore, based on the indications provided by harvest numbers, Norwegian lynx populations seem to have undergone a fall (from 1890 to 1930), a rise (1960–1997), a new fall (1997–2004), and a new recovery (2005–2008). While many anecdotes and independent data (such as depredation rates on sheep) indicate that there was a real increase in the early to mid 1990s, there was a dramatic increase in hunter interest in lynx hunting following the controversy of protection and the introduction of quota limitations. Once limits were placed on the harvest, many more people wanted to take part than in the previous years when there were no limits. Our own observations indicate that the interest in lynx hunting is enormous. Large hunting



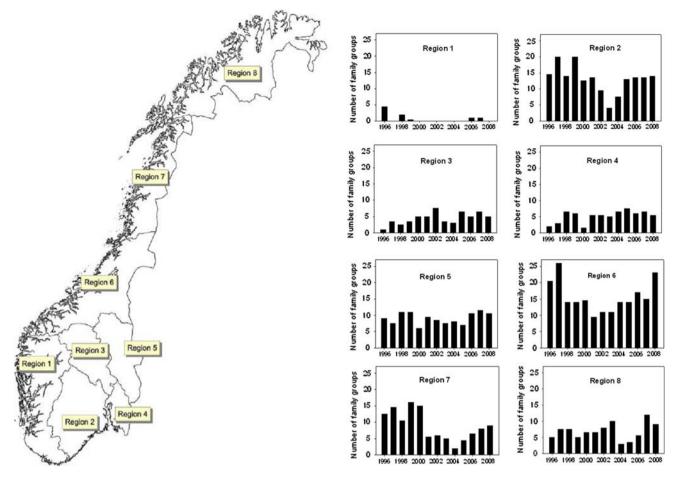
**Fig. 3** Development of numbers of sheep compensated following lynx depredation, lynx harvest, lynx quota, and lynx population size in the period 1994–2008

teams, of up to 100 people, spend weeks prior to the opening of the hunting season searching for, and following, lynx tracks. In many counties quotas are filled in a matter of days if snow conditions are favorable. This occasionally leads to overfilling of quotas, as there are inevitable delays between the reporting of a kill and other hunters updating themselves as to whether the quota was still open. Likewise, the steepness of the decline in numbers shot during the 2003–2004 probably overestimates the real magnitude of decline in population size. Rather it reflects a response by management to correct the sharp decline revealed by monitoring data (see below) and reducing the quota accordingly.

# Monitoring-Based Population Development

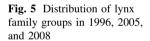
When viewed at the national level the monitoring data show a very clear pattern of a fluctuating population (Fig. 3). From a peak in 1997 the population declined constantly until 2004. The overall decline for this period, estimated from regression lines, was 43% until 2004 (slope = -25.2,  $R^2 = 0.8$ , P = 0.01). However there is a good deal of variation between regions (Fig. 4). Within 4 years of the introduction

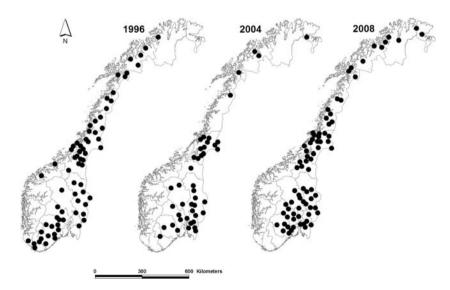




**Fig. 4** The eight large carnivore management regions which have become operational in Norway since 2004, with regional goals for the numbers of annual reproductions (post 2004), and histograms of

regional lynx population development 1996–2008 (expressed as number of family groups)





of quota hunting, lynx had been exterminated from southwestern Norway (Region 1; Figs. 4, 5), and by 2004 severe declines were apparent in southern Norway (Region 2) and the two central Norwegian regions (Regions 6 and 7; Fig. 4), while the populations maintained relatively constant levels in the other four regions (Fig. 4). Despite these reductions in



distribution, lynx remained well distributed in the south-eastern (Regions 4 and 5) and central (Region 3) areas, although the thin distribution in the north (Region 8) gives grounds for concern (Figs. 4, 5). In many ways the 2005 population distribution closely resembles the distribution during the 1960s and 1970s (Fig. 2). The expansion north-ward and southwestward that characterized the 1996 distribution had effectively been reversed, or at least greatly reduced (Fig. 5). The data from 2005 to 2008 indicate that the population has recovered again, exceeding the national goals in many regions. There has been no new colonization of southwestern Norway (Region 1), which is also not intended in the new management plan (Ministry of the Environment 2003).

Given the historical development of policy, it seems somewhat surprising that the population should decline so rapidly in a period (1997–2004) when there was an unprecedented degree of limitation on hunting activity (method restrictions, season length, quota limitation), on the one hand, and an abundance of good monitoring data (see above) and biological and demographic data on lynx (e.g., Andrén and others 2006; Herfindal and others 2005a), on the other hand. Possible explanations lie in three causes: (1) fragmented management authority, (2) lack of specific regional population goals, and (3) time lags in management responses. The survival data collected on radio-collared lynx during this period allow us to exclude the possibility of other processes such as disease; by far the vast majority of lynx die from direct human causes (Andrén and others 2006).

The 1997 white paper set a goal of maintaining the lynx population close to the levels they were at in 1997. However, there was also a desire to reduce lynx populations in the southwestern counties, because of potential conflicts with sheep farming, and in the central counties, which had relatively dense lynx populations and high conflicts with semidomestic reindeer herding (Ministry of the Environment 1997). As planned, the hunting virtually exterminated lynx from the west and southwest and severely reduced lynx in central Norway. However, the dramatic decrease in Telemark and Nordland counties was not planned. Clearly if the national population was to be kept stable while reducing local populations, there should have been a balancing increase in some areas. However, no other counties allowed any increase in their lynx population such that the overall effect was a national decrease. Therefore, the fragmentation of management authority at the county level led to a lack of holistic planning until the national monitoring program was first able to produce an updated national survey for the entire period 1996–2002, in 2003. This summary led to instructions being issued from the central Directorate for Nature Management to the counties recommending a dramatic reduction in quota and harvest for the 2004 hunting season (Table 2; Fig. 3).

Time lags in management's response to population change are a well-known problem in harvest management of game species [e.g., Solberg and others (1999) for moose, Alces alces, harvest]. Psychology plays an important part in the willingness of managers to react to monitoring data. There is a tendency to believe that "there are hidden animals not counted" when data indicate a reduction in population size, thus causing high harvests to continue even when a population has begun to decline (Swenson and Sandegren 1996). This problem is made worse when operating with minimum count data (like the family group counts), as there is no statistical estimate of uncertainty regarding the number of family groups not found. Furthermore, during the late 1990s there was a constant conflict among researchers, managers, and hunters over population estimation, with hunters, and some managers, dramatically overestimating lynx population size (Skogen 2003). Local political pressure from livestock and hunting interests may have also played a role in hindering the counties from reacting sooner to perceived declines. These factors combined would have tended to make local managers slow to reduce quotas in response to indications of population decline.

Another factor which has to be considered is the delay in being able to compile and analyze data. At present it has not been possible to estimate the size of the lynx population in the same year that the data are needed for quota setting: this is because the monitoring program depends heavily on observations made during the first weeks of hunting. The result is that managers have potentially only had access to the previous year's estimate (from before the hunting season) to set this year's quota.

Finally, there is the issue of the time it takes results from scientific research to enter the management system. The use of standardized distance rules only emerged from 2001 to 2002, and these were based on research conducted during the period from 1992 to the present. Earlier estimates of lynx population growth rates had led to the belief that lynx could tolerate harvest rates well over 20%. More recent analysis of data collected from telemetry indicates that 17% may be a maximum (Andersen and others 2003; Henriksen and others 2005; Andrén and others 2006), although this number relies heavily on the number of adult females in the harvest. The dramatic increase in harvest from 1995 to 1997 clearly exceeded the level of sustainability (Table 2), with harvests regularly exceeding 20% of the estimated population size. It was first in 2004 that the harvest dropped to <17% of the population. This revised estimate also fails to include poaching—which studies have shown to be a major cause of mortality (Andrén and others 2006). In some regions it is actually surprising that the population has survived as well as it has in the face of the heavy mortality from harvest and other causes of mortality. It appears that sharing a border with Sweden, where lynx are more abundant and subject to



far lower harvest rates, has buffered the Norwegian lynx population through immigration. One example is the region of Akershus-Østfold, which has a stable population despite an average 35% hunting rate from 2000 to 2003 (Andrén and others 2006). Also, the starting point was overly optimistic, as the estimates made by Kvam (1997) have since been revised downward, given the increased availability of telemetry data from a wider range of study sites (Linnell and others 2007a) and a more strict interpretation of the veracity of observations.

Overall, it is possible to explain the period of overharvest of Norwegian lynx through a combination of fragmented management without access to centrally produced monitoring data, time lags in both the reaction to monitoring data and the inclusion of scientific results in management, and an overoptimistic starting point with respect to both population status and population growth rates. The main critique that can be raised with the benefit of hind-sight is that the responsible authorities failed to exercise the precautionary principle, i.e., erring on the side of caution (with respect to the potential impact on the lynx population) when faced with uncertainty.

However, there can be few excuses for the future. A national monitoring program is now in place such that all decision-making bodies have access to standardized and upto-date estimates of population status. Furthermore, regulations require that these decision-making bodies use these estimates as their foundation for decision making. Good scientific data on lynx demographics exist so that we now have a more realistic idea of potential population growth rates and therefore of quota sizes that are likely to be sustained. The need to include nonharvest mortality like poaching and vehicle collisions is realized, such that it is now clear that the whole potential rate of increase is not available for hunters. Regional population goals are now in place such that each region's decision-making body has to relate to its own population's status and goals. Furthermore, we have just had a practical demonstration that overharvest can dramatically reduce a population in 7-9 years despite having intensive regulations of hunter effort. Fortunately, there was still a widely distributed population of lynx throughout Norway, and there is a long border with Sweden that lynx can immigrate from, which permitted rapid recovery. The reduction in harvest intensity in the period 2005-2008 has resulted in an increase in the lynx population again to such an extent that in 2008 it exceeded the stated management goals in many regions.

## Conclusions

This summary shows the manner in which human management policy has been the dominant factor in shaping the size of a large carnivore population in human landscapes (Swenson and others 1995; Jedrzejewska and others 1996). It also shows how difficult it can be to sustainably manage the harvest of a large carnivore species, even when harvest controls and monitoring data are available. The decline in lynx during the early monitoring period has been used by some environmentalists to call for a ban on lynx hunting. However, the subsequent increase shows that adaptive management does work, and that management agencies were able to reverse the undesired decline, albeit after a significant delay. Despite the difficulties in achieving sustainability of lynx harvest, we believe that in the current high-conflict context of Norwegian large carnivore management, allowing hunting has at least some conflict reduction benefits within both the livestock depredation conflict (Herfindal and others 2005b) and the wider social conflict (Skogen 2003). Viewed as a whole, the current Scandinavian population is so large [currently 1800-2000 animals (Linnell and Brøseth 2004; Liberg and Andrén 2004)] that the current risk of extinction must be considered to be quite low. This gives management some room for error in the short term, as they gain experience at managing lynx harvests. All in all, this is a unique historical experiment, as extermination policies have given way to a quest for sustainability. Adaptive management provides a potentially functional tool, although there are clear challenges. The delegation of some management authority to the eight regions is another unique part of the experiment which attempts to balance science with political and social acceptance. Given uncertainties in population estimation and variation in reproductive rates between year and regions (Andersen and others 2003), and the political nature of the decision-making process, it is unlikely that it will be possible ever to achieve a perfectly stable population size. Rather, we must learn to expect constant fluctuations, with the subsequent challenge being to keep these within acceptable limits. The long-term future of the management system could be enhanced by addressing some of the depredation conflicts in a proactive manner through mitigation, rather than depending heavily on harvest. There will also be a need to respond to future changes in environmental conditions that could influence lynx demographics (e.g., climate- or harvest-induced changes in prey populations) or our ability to census or harvest lynx (e.g., climate change could reduce snow cover and therefore the possibility of collecting track observations).

**Acknowledgments** Funding for this research was primarily provided by ear-marked financing from the state budget to the Ministry of the Environment through the Norwegian Directorate for Nature Management to the National Large Predator Monitoring Program.



Additional financing was provided by the Norwegian Institute for Nature Research and the Research Council of Norway.

#### References

- Andersen R, Linnell J, Odden J, Andrén H, Sæther BE, Moa PF, Herfindal I, Kvam T, Brøseth H (2003) Gaupe—bestandsdynamikk, bestandsutvikling og høstingsstrategier [Lynx—population dynamics, development, and harvest]. NINA Fagrapport 059
- Andersen R, Herfindal I, Linnell JDC, Odden J, Liberg O, Sæther BE (2004) When range expansion rate is faster in marginal habitats. Oikos 107:210–214
- Andersen R, Odden J, Linnell JDC, Odden M, Herfindal I, Panzacchi M, Høgseth Ø, Gangås L, Brøseth H, Solberg EJ, Hjeljord O (2005) Gaupe og rådyr i sørøst-Norge:oversikt over gjennomførte aktiviteter 1995–2004 [Lynx and roe deer in southeastern Norway: activity 1995–2004]. NINA Rapport 29:1–41
- Andrén H, Linnell JDC, Liberg O, Ahlqvist P, Andersen R, Danell A, Franzén R, Kvam T, Odden J, Segerstrom P (2002) Estimating total lynx (*Lynx lynx*) population size from censuses of family groups. Wildlife Biology 8:299–306
- Andrén H, Linnell JDC, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T, Franzén R, Segerström P (2006) Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23–32
- Boitani L (1995) Ecological and cultural diversities in the evolution of wolf human relationships. In: Carbyn LN, Fritts SH, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Alberta, pp 3–12
- Breitenmoser U (1998) Large predators in the Alps: the fall and rise of man's competitors. Biological Conservation 83:279–289
- Breitenmoser U, Breitenmoser-Würsten C, Carbyn LN, Funk SM (2001) Assessment of carnivore reintroductions. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge, pp 241–281
- Brøseth H, Odden J (2008) Minimum antall familiegrupper, bestandsestimat og bestandsutvikling for gaupe i Norge 2008 [Minimum number of family groups, population estimate and population development for lynx in Norway 2008]. NINA Report 384:1–19
- Creel S, Creel NM (1997) Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. African Journal of Ecology 35:83–93
- Elgmork K (2000) Abundance of brown bears and wolves in central south Norway after 1733 as revealed by bounty records. Fauna Norvegica 20:1–8
- Farrell EP, Führer E, Ruyan D, Andersson F, Hüttl R, Piussi P (2000) European forest ecosystems: building the future on the legacy of the past. Forest Ecology and Management 132:5–20
- Guldvik I, Arnesen T (2001) Med rovdyr og politikk i utmarka: evaluering av rådgivende utvalg for rovviltforvaltning og forsøk med rovviltnemnder [With carnivores and politics in the wild lands: evaluating the advisor committee for carnivore management and the trial with local management committees]. Østlandsforskning rapport no. 02/2001. Lillehammer, Norway
- Henriksen H, Andersen R, Hewison AJM, Gaillard JM, Bronndal M, Jonsson S, Linnell JDC, Odden J (2005) Reproductive biology of captive Eurasian lynx Lynx lynx. European Journal of Wildlife Research 51:151–156
- Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R (2005a) Prey density, environmental productivity, and home range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology, London 265:63–71

- Herfindal I, Linnell JDC, Moa PF, Odden J, Austmo LB, Andersen R (2005b) Does recreational hunting of lynx reduce depredation losses of domestic sheep. Journal of Wildlife Management 69:1034–1042
- Jedrzejewska B, Jedrzejewski W, Bunevich AN, 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
- Kaczensky P (1999) Large carnivore depredation on livestock in Europe. Ursus 11:59–72
- Knight RR, Blanchard BM, Eberhardt LL (1995) Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248
- Kvam T (1997) Bestandsestimat for gaupe 1995–96 og 1996–97 [Population estimate for lynx 1995–96 and 1996–97]
- Landa A, Linnell JDC, Swenson JE, Røskaft E, Moskness I (2000) Conservation of Scandinavian wolverines in ecological and political landscapes. In: Griffiths HI (ed) Mustelids in a modern world: conservation aspects of small carnivore-human interactions. Backhuys, Leiden, Netherlands, pp 1–20
- Liberg O, Andrén H (2004) Sweden. In: von Arx M, Breitenmoser-Würsten C, Zimmermann F, Breitenmoser U (eds) Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA Bericht, pp 191–198
- Linnell JDC, Brøseth H (2004) Norway. In: von Arx M, Breitenmoser-Würsten C, Zimmermann F, Breitenmoser U (eds) Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA Bericht 19e, pp 146–153
- Linnell JDC, Swenson JE, Andersen R (2001a) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4:345–350
- Linnell JDC, Andrén H, Odden J, Liberg O, Andersen R, Moa P, Kvam T (2001b) Home range size and choice of management strategy for lynx in Scandinavia. Environmental Management 27:869–879
- Linnell JDC, Odden J, Andrén H, Liberg O, Andersen R, Moa PF,
  Kvam T, Segerström P, Schmidt K, Jedrzejewski W, Okarma H
  (2007a) Distance rules for minimum counts of Eurasian lynx
  Lynx lynx family groups under different ecological conditions.
  Wildlife Biology 13:447–455
- Linnell JDC, Fiske P, Herfindal I, Odden J, Brøseth H, Andersen R (2007b) An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. Wildlife Biology 13:456–466
- Linnell JDC, Breitenmoser U, Breitenmoser-Würsten C, Odden J, von Arx M (2009) Recovery of Eurasian lynx in Europe: What part has reintroduction played? In: Hayward M, Sommers M (eds) Reintroduction of top-order predators. Wiley-Blackwell, Oxford, UK, pp 72–91
- Litvaitis J, Tash JP, Stevens CL (2006) The rise and fall of bobcat populations in New Hampshire: relevance of historical harvests to understanding current patterns of abundance and distribution. Biological Conservation 128:517–528
- Milner J, Bonenfant C, Mysterud A, Gaillard J-M, Csányi S, Stenseth NC (2006) Temporal and spatial development of red deer harvesting in Europe—biological and cultural factors. Journal of Applied Ecology 43:721–734
- Ministry of the Environment (1992) Om forvaltning av bjørn, jerv, ulv og gaupe (Rovviltmeldingen) [White paper on the management on bears, wolverine, wolf and lynx in Norway]. Stortingsmeldingen 27(1991–1992):54
- Ministry of the Environment (1997) Om rovviltforvalting [On large carnivore management]. Stortingsmelding 35 (1996–1997)
- Ministry of the Environment (2003) Rovvilt i norsk natur [Carnivores in Norwegian nature]. Stortingsmelding 15 (2003–2004)



- Mykrä S, Vuorisalo T, Pohja-Mykrä M (2005) A history of organised persecution and conservation of wildlife: species categorizations in Finnish legislation from medieval times to 1923. Oryx 39:275–283
- Myrberget S (1961) Gaupestammen vår [Our lynx population]. Jakt-Fiske-Friluftsliv 1961:348–350
- Myrberget S (1967a) Skuddpremiesatser på ulv, jerv, gaupe og bjørn [Bounty payments for wolves, wolverines, lynx and bears]. Norsk Natur 1967:42–48
- Myrberget S (1967b) Økonomisk utbytte av jakten på gaupe, jerv, ulv og bjørn [Economic gain from hunting lynx, wolverines, wolves and bears]. Jakt-Fiske-Frilutsliv 1967:546–548
- Myrberget S (1970) Den norske bestand av jerv Gulo gulo (L.) og gaupe Lynx lynx (L.) [The Norwegian populations of wolverine and lynx]. Meddelelser fra Statens Viltundersøkelser 2:1–35
- Nie MA (2003) Beyond wolves: the politics of wolf recovery and management. University of Minnesota Press, London
- Nilsen EB, Linnell JDC, Odden J, Andersen R (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. Journal of Animal Ecology 78:741–751
- Odden J, Solvang H, Maartmann E, Wabakken P, Linnell J, Andersen R, Haagenrud H, Lundqvist O, Solberg HO (2001) Registrering av ulv og gaupe i Hedmark 2001: Rapport fra registrering 13. januar 2001 [Lynx and wolf census in Hedmark 2001]. Fylkesmannen i Hedmark Miljøvernavdelingen Rapport 11/2001, pp 1–26
- Odden J, Linnell JDC, Moa PF, Herfindal I, Kvam T, Andersen R (2002) Lynx depredation on domestic sheep in Norway. Journal of Wildlife Management 66:98–105
- Odden J, Andersen R, Brøseth H, Linnell JDC (2008) Gauperegistering i utvalgte fyler 2008 [Lynx registration in selected counties 2008]. NINA Report 375:1–28
- Olstad O (1945) Jaktzoologi [Game ecology]. J. W. Cappelens Forlag, Oslo
- Östergren A, Segerström P (1998) Familjegrupper av lodjur—metod för antalsbedämningar [Lynx family groups as a means for population census]. Länsstyrelsen Västerbottens län Meddelande 2:1–5
- Pohja-Mykrä M, Vuorisalo T, Mykrä S (2005) Hunting bounties as a key measure of histroical wildlife management and game conservation: Finnish bounty schemes 1647–1975. Oryx 39:284–291
- Rideng M (1999) Jakten på makten: en studie av utformingen av norsk rovdyrpolitikk [The quest for power: the development of Norwegian large carnivore policy]. Master's thesis. Institutt for Admininistrasjon og Organisasjonsvitenskap, University of Bergen, Bergen
- Ross PI, Jalkotzy MG, Gunson JR (1996) The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490–494
- Sandström C, Pellikka J, Ratamäki O, Sande A (2009) Management of large carnivores in Fennoscandia: new patterns of regional participation. Human Dimensions of Wildlife 14:37–50

- Skogen K (2003) Adapting adaptive management to a cultural understanding of land use conflicts. Society and Natural Resources 16:435–450
- Skogen K, Haaland H (2001) En ulvehistorie fra Østfold:samarbeid og konflikter mellom forvaltning, forskning og lokalbefolkning [A wolf tale from Østfold: cooperation and conflict between management, research and local people]. NINA Fagrapport 52:1–51
- Søilen E (1995) Sportsmenn i veideland. Norges Jeger og Fiskerforbund. Oslo
- Solberg EJ, Sæther BE, Strand O, Loison A (1999) Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology 68:186–204
- Søybe E (2001) Tallenes fortellinger [The tale of statistics]. Samfunnsspeilet/Statistisk sentralbyrå, Oslo
- Sunde P, Kvam T, Bolstad JP, Bronndal M (2000) Foraging of lynxes in a managed boreal-alpine environment. Ecography 23:291–298
- Swenson JE, Sandegren F (1996) Sustainable brown bear harvest in Sweden estimated from hunter-provided information. Journal of Wildlife Research 1:229–232
- Swenson JE, 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
- Treves A, Naughton-Treves L (2005) Evaluating lethal control in the management of human-wildlife conflict. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife: Conflict or coexistence?. Cambridge University Press, Cambridge, pp 86– 106
- Vaag AB (1987) Landsplan for forvaltning av bjørn, jerv og ulv [Action plan for managing bears, wolverines and wolves]. Naturforvaltning Rapport 6:1–35
- Valière N, Fumagalli L, Gielly L, Miquel C, Lequette B, Poulle ML, Weber JM, Arlettaz R, Taberlet P (2003) Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling of a period of 10 years. Animal Conservation 6: 83–92
- Wabakken P, Sand H, Liberg O, Bjärvall A (2001) The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Canadian Journal of Zoology 79:710–725
- Whitman K, Starfield AM, Quadling HS, Packer C (2004) Sustainable trophy hunting of African lions. Nature 428:175–178
- Williams BK, Johnson FA, Wilkins K (1996) Uncertainty and the adaptive management of waterfowl harvests. Journal of Wildife Management 60:223–232
- Yamazaki K (1996) Social variation of lions in a male-depopulated area in Zambia. Journal of Wildlife Management 60:490–497
- Zimmermann A, Baker N, Linnell JDC, Inskip C, Marchini S, Odden J, Rasmussen G, Treves A (2010) Contemporary views on human-carnivore conflicts in Wild Rangelands. In: Du Toit J, Kock R, Deutsch J (eds) Can rangelands be wildlands? Wildlife and livestock in semi-arid ecosystems. Wiley-Blackwell, London

