



Precision beats interval: appropriate monitoring efforts for management of a harvested Eurasian lynx *Lynx lynx* population

Authors: Danell, Anna C., and Andrén, Henrik

Source: *Wildlife Biology*, 16(4) : 409-418

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/09-118>

BioOne Complete ([complete.BioOne.org](https://complete.bioone.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Precision beats interval: appropriate monitoring efforts for management of a harvested Eurasian lynx *Lynx lynx* population

Anna C. Danell & Henrik Andrén

Adaptive management of wild populations requires good knowledge of the population status. The main way to evaluate management performance is through recurring surveys, which often also serve as a decision basis for harvest quotas. We evaluated the effect of different survey reliabilities and frequencies during 1-4 years on management performance using a stochastic age and stage-specific population model for an Eurasian lynx *Lynx lynx* population. As a proxy for management performance, we looked at the proportion of time that the population remained within a preferred interval, the proportion of time with no harvest, the average harvest number and the total number of surveys during the 50-year period in the simulation. In general, management performance increased with increased monitoring accuracy. More interestingly, a more reliable survey performed less frequently performed better than a less reliable survey performed every year. The management performance was not perfect even with complete knowledge of the population size at the survey, as annual variation in reproduction and survival between the survey (decision based on year t) and harvest (performed in year $t + 1$) sometimes cause the population to be outside the preferred interval. If financial resources are limited, we recommend managers to minimise the error in the survey rather than to increase the frequency of surveys.

Key words: adaptive management, harvest decision, lynx, *Lynx lynx*, management performance, monitoring, survey frequency, survey reliability

Anna C. Danell & Henrik Andrén, Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden - e-mail addresses: anna.danell@ekol.slu.se (Anna C. Danell); henrik.andren@ekol.slu.se (Henrik Andrén)

Corresponding author: Anna C. Danell

Received 21 December 2009, accepted 16 September 2010

Associate Editor: Simon Chamaille-Jammes

Successful adaptive management of wildlife populations requires appropriate monitoring of population size to evaluate the consequences of previous decisions and management actions, and is also a prerequisite basis for making new management decisions (Walters & Hilborn 1978, Shea et al. 2002, McCarthy & Possingham 2007, Hauser & Possingham 2008). Monitoring programmes need to have clear objectives in order to be successful, and the performance of a monitoring programme should be evaluated in relation to its management goals (Goldsmith 1991, Possingham et al. 2001). Two aspects of monitoring are linked to its purpose: the reliability of monitoring needed for immediate decisions, and the frequency of monitoring needed

to detect changes in the population size which can influence the management strategy.

When designing a monitoring programme, in addition to the performance, one also has to consider the costs. While the most accurate monitoring method is often desirable, it may not be economically possible to achieve. Hence, managers often have to compromise between reliability and costs. This has led to the optimisation of cost and monitoring reliability, which has applications in a wide range of wildlife management problems such as invasive species (Bogich & Shea 2008), conservation (Gerber et al. 2005, McCarthy & Possingham 2007) and harvest under uncertainty (Hauser et al. 2006, Månsson et al. submitted manuscript). The

goal must be to have a monitoring programme at the lowest cost possible, which still fulfils the ability to make reliable management decisions (Pople 2008).

The purpose of a management programme may often be to maintain a population at a certain level. However, managing for a fixed number of individuals is impossible. This is partly due to environmental and demographical stochasticity (Lande et al. 2003), but it is also an effect of survey errors. Because managers cannot maintain a population at a precisely set level, the management should be considered successful if the population is maintained within a desired interval.

In the case of large carnivore population management, the trade-off between monitoring cost and reliability becomes very apparent. Monitoring of large carnivores is often difficult and very expensive because the carnivores usually occur at low population densities, have large home ranges and secretive behaviour (Linnell et al. 1998). At the same time, large carnivores cause conflicts with human interests, e.g. livestock depredation. Therefore, in large carnivore management, there are usually two conflicting management goals; to maintain viable carnivore populations and to have small enough populations to minimise conflicts and costs for conflict mitigation (Nowell & Jackson 1996, Breitenmoser et al. 1998, Linnell et al. 2001, Swenson & Andrén 2005). In these cases, with multiple objectives, decision theory provides a thorough basis for making management decisions (Possingham et al. 2001), and to evaluate the management options in relation to the management goal.

The aim of our study was to evaluate the effect of different monitoring strategies (reliability and frequency) on management performance. To be able to use relevant life history parameters, we chose Eurasian lynx *Lynx lynx* management within the Swedish reindeer *Rangifer tarandus* husbandry area as a reference case. Our analysis considered population size and monitoring and harvest of the lynx population. We evaluated management performance for each monitoring strategy by estimating how often the lynx population was of an undesirable size as well as the variation in lynx harvest.

Methods

All problems in decision theory require a set of components. Firstly, clear statements of objectives; in our case a range of desirable population sizes.

Secondly, several management options; in our case different monitoring strategies. Thirdly, the relationship between the management options and the decisions based on available information; in our case a population model and harvest decisions based on survey results. Finally, one should evaluate the different management options in relation to the management objectives; in our case monitoring strategies in relation to desirable population sizes. Each of these components will be covered in the following.

Management objectives

The chosen primary management goal in our analysis was set to maintain a lynx population at 100 family groups. As managers cannot maintain the population at precisely this level, we consider the population size to be acceptable at 80-120 family groups ($100 \pm 20\%$). We also evaluated the risk of exceeding 140 family groups, as this level means a significant increase in the conflict level for reindeer management.

Monitoring strategies

We chose four different survey accuracies (0.7 ± 0.2 , 0.8 ± 0.1 , 0.9 ± 0.05 and 1 ± 0.0) and four different survey intervals (one, two, three and four years). We assumed that a survey that reports a large proportion of the family groups (high accuracy) also has a high precision. We also tested a state-dependent survey model; we performed a survey every year if a previous survey was < 90 family groups, and up to every fourth year when the estimated population was > 90 family groups. For comparisons we used a strategy which was based on perfect knowledge, i.e. the exact number of family groups known in February. In reality, survey accuracy will be an effect of the management budget, and thereby effort, as well as of conditions in the field.

Lynx population model and harvest strategy

We used a stochastic stage structured population model with four age classes (kittens, 1-year old, 2-years old and ≥ 3 years old) and sex specific survival and harvest rates. Survival (Andrén et al. 2006) and reproduction data (Andrén et al. 2002, complemented with new unpublished data) for different sex and age classes (see Table 2) were obtained from the Scandinavian lynx project in the reindeer husbandry area. The model was based on the events during a 'lynx year'. The kittens were born in June, the survey

was done in February and the harvest was performed immediately after the survey. All these events were treated as pulses, with no extension in time.

We calculated reproduction as the litter size for 2- and ≥ 3 -years old females, respectively. For each year, the mean litter size for the two age classes was randomly sampled from a normal distribution. The litter size for 2-year old females was truncated at zero to avoid negative litter sizes. We estimated the proportion of females without kittens in February based on a Poisson distribution and the given mean litter size (see also Andrén et al. 2002). We assumed that the sex ratio of kittens was 50:50. We chose a correlation of 0.8 between the reproduction of 2-years and ≥ 3 -years old females.

We calculated survival from reproduction to survey and harvest (1 June-31 January) as $S_i^{(8/12)}$, where S_i is annual survival in age category i . Likewise, we calculated survival from harvest to reproduction (1 February-31 May) as $S_i^{(4/12)}$. For each year and age class, the survival value was randomly drawn from a normal distribution and was truncated at 1.0 to avoid survival > 1 . We chose to have the survival rates correlated with one another. The correlation varied between 0.7 and 0.8, with stronger correlation set between males and females within adult age classes than between adult age classes and kittens. We considered the reproduction and survival rates uncorrelated.

We did all modelling using Microsoft Excel® software with PopTools add-in (Hood 2004). We set the initial population size in June year one to 100 family groups, of which 58% were females and 42% were males, and with the initial age-distribution given in Table 1. Our analyses were based on year 6-55. The deterministic population growth (λ), given the mean reproduction and survival shown in Table 2, and without harvest, was 1.06.

We modelled the effect of survey error as a single event. The estimated number of family groups in February was $N_e = N_t \times c_{\text{actual}}/c_{\text{assumed}}$; where N_t was the actual number of family groups in the population at the time when the survey was done, based on the population model described above. The actual proportion of family groups found during the survey (c_{actual}) varied randomly between years according to a normal distribution with a mean of c_{assumed} and the corresponding standard deviations. The assumed proportion of family groups found during the survey (c_{assumed}) was con-

Table 1. Parameter values for survival (based on Andrén et al. 2006) and reproduction (based on Andrén et al. 2002, complemented with new unpublished data) and their variation for different age classes and sexes used in the population model.

Yearly survival	Mean (\pm SD)
Females, 0-1 year	0.407 (\pm 0.067)
1-2 years	0.900 (\pm 0.090)
2-3 years	0.830 (\pm 0.073)
> 3 years	0.830 (\pm 0.073)
Males, 0-1 year	0.463 (\pm 0.076)
1-2 years	0.817 (\pm 0.143)
2-3 years	0.791 (\pm 0.090)
> 3 years	0.791 (\pm 0.090)
Litter sizes	
Females 2 years	0.455 (\pm 0.312)
Females ≥ 3 years	1.543 (\pm 0.122)

stant throughout a simulation and set to 0.7, 0.8 or 0.9 depending on the selected survey effort.

The actual proportion of family groups found (c_{actual}) is most likely < 1 due to e.g. weather and snow related difficulties, survey efforts and budget limits, but may be > 1 , as one family group can be counted as two, thereby causing overestimation of the population. Since the survey counts the number of family groups and not single individuals, the estimated number of family groups in February, N_e , depended not only on the value and standard deviation of c_{actual} , but also on the variation in reproduction and survival of kittens from birth to survey. Thus, the variation in estimated number of family groups in February included both the variation in reproduction and survival as well as the survey error.

Harvest quotas have been decided each November/December by the Swedish Environmental Protection Agency (EPA) and are based on the number of family groups found in the survey in February (i.e. 10 months earlier). Thus, there is a lag of almost

Table 2. The stable age distribution in June (i.e. with new-born kittens) given the survival and reproduction values of the initial population.

Age, class and gender	Percent of population
Female, kitten	17.1
1-year old	6.8
2-years old	5.7
≥ 3 -years old	21.6
Male, kittens	17.1
1-year old	7.6
2-years old	5.9

a year between the survey and the harvest decision. The annual harvest rate has varied between 2.3 and 11.3% of the estimated total lynx population within the reindeer husbandry area. The harvest quota (number of lynx) within the reindeer husbandry area from 1998 to 2006 decided by the Swedish EPA has been linearly related to the estimated number of family groups the preceding year ($r^2=0.843$, $df=7$, $P < 0.001$; Fig. 1); $H_t = 1.14 \times N_e - 85$. We used this relationship in the simulations. Thus, the harvest strategy in the simulation was a proportional threshold harvest described as: If $N_e < 90$ then $H_t = 0$; If $N_e \geq 90$ then $H_t = 1.14 \times N_e - 85$ where N_e is the estimated number of family groups in the most recent survey. In years without survey, the harvest quotas remained the same as in the preceding year. Of the harvest, 40% were females and 60% were males with equal distribution across age classes. The harvest took place the following winter, and we assumed that all lynx in the quota were harvested.

Given the relationship between harvest and number of family groups ($H_t = (1.14 \times N_e) - 85$), the conversion factor of 6.14 of family groups to total population size (Andrén et al. 2002) and the deterministic growth rate without harvest ($\lambda = 1.06$, estimated from survival and reproduction given in Table 2), the modelled lynx population is deterministically balancing at 110 family groups or 675 individuals.

Evaluation of monitoring strategies in relation to the management objectives

The simulation procedure for the population dynamics and monitoring is shown in Figure 2. We

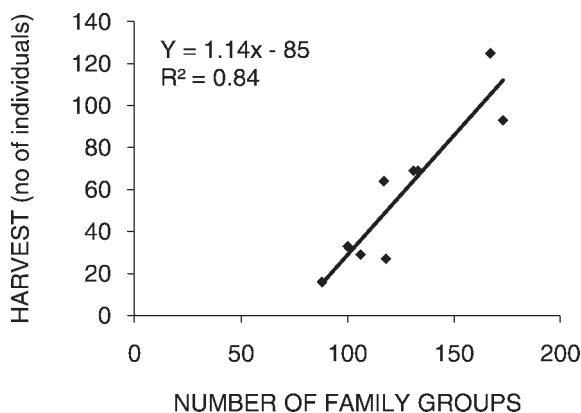


Figure 1. Relationship between the number of family groups in February and the harvest quota decided by Swedish EPA in November the same year (i.e. 10 months later).

evaluated three different survey accuracies and four different survey intervals and a state dependent (adaptive) survey strategy. For each scenario, 1,000 replicates were run and the results were collected as frequencies of different outcomes over 50 years. The outcomes that we calculated were: 1) proportion of cases during simulation in which the simulated population included < 80 family groups, 2) proportion of cases during simulation where the simulated population increased to > 120 and > 140 family groups, respectively, and 3) number of years with no harvest during the 50 years. In the adaptive survey model, we also counted the total number of surveys performed during the 50-year period at different accuracies.

Description of reference case

As a reference case of our study, we chose management of the lynx population in the reindeer husbandry area in Sweden.

The reindeer husbandry area covers 52% (~213,000 km²) of the Swedish land area (SOU 2006:14) and includes the three northernmost counties of Sweden (Norrbotten, Västerbotten and

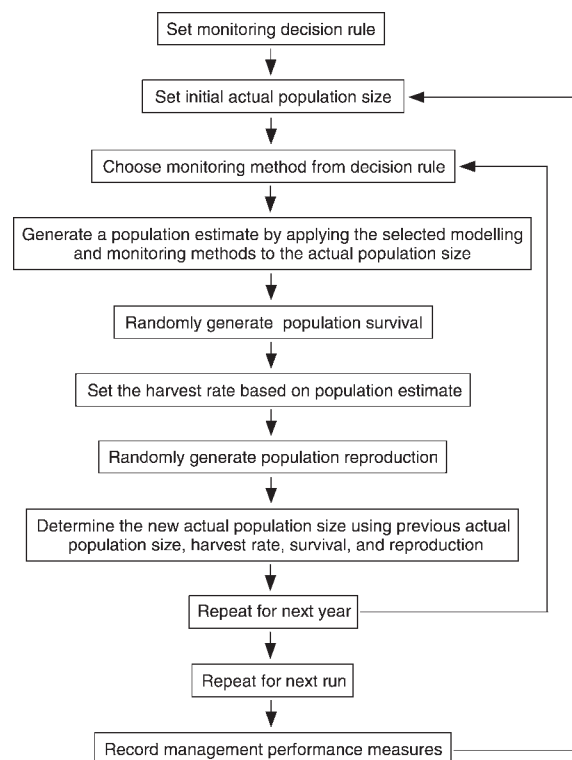


Figure 2. Flow chart describing the sequence of steps in the simulation of lynx monitoring and management.

Jämtland), as well as parts of the counties of Dalarna and Västernorrland. On average, the total number of reindeer in Sweden has been 255,000 during 2004-2008 (R. Doj, Sami parliament in Sweden, pers. comm.). Semi-domestic reindeer are part of a pastoral production system, where reindeer are herded by indigenous Sámi. The reindeer are moved between seasonal grazing ranges as part of the herding practices. Within the reindeer husbandry area, the reindeer make up the main prey for lynx (Haglund 1966, Pedersen et al. 1999). Large carnivores cause substantial losses for reindeer herders, lynx and wolverine *Gulo gulo* being the most important predators (Swenson & Andrén 2005).

The total Swedish lynx population size has been approximately 290 family groups during 2004-2008 (271-309 family groups monitored in February-March; Andrén & Liberg 2008), which corresponds to approximately 1,500-1,800 individuals (Andrén et al. 2002). The current management goal for the lynx population in Sweden is to maintain at least 300 family groups based on the winter survey (SOU 2007:89), and that the majority of the lynx population should be found outside of the reindeer husbandry area, i.e. in the southern half of Sweden. The lynx population in the reindeer husbandry area was about 115 family groups with an increasing trend from 97 to 141 during 2004-2008 (Andrén & Liberg 2008), corresponding to an average of 700 individuals. The aim of the management of lynx in the Swedish reindeer husbandry area is to balance reindeer losses due to predation with conservation of the lynx.

Within the reindeer husbandry area, the county administration boards have been monitoring lynx annually since 1996. The survey is performed during January and February by snow-tracking and identifying family groups, i.e. adult females with nine month old kittens. Moreover, as kittens usually stay with their mothers until they are 10 months old, and because mating does not occur until late March, tracks in the snow from two or more lynx travelling together during January and February almost always indicate a family group (Linnell et al. 2007a). We separated observations from each other using distance rules based on observed home-range sizes and movements rates (Linnell et al. 2007b). Sampling error could be caused by counting two neighbouring family groups as one or by counting groups with wide movements as two families, causing underestimation or overestimation of the population, respectively. In 2006, the total cost for

the lynx survey within the reindeer husbandry area in Sweden was almost 5 million SEK ~ approximately € 480,000 (Swedish EPA, pers. comm.).

Results

In general, monitoring strategies with higher accuracy improved the management performance, i.e. the lynx population remained within the preferred population interval for a larger proportion of the time. With more effort put into monitoring, i.e. increasing the proportion of family groups found and concurrently decreasing the error of this estimate from 0.7 (± 0.2 SD) to 0.9 (± 0.05 SD), the probability that the population dropped below 80 family groups was halved (from 0.14 to 0.07; Fig. 3). When the interval between surveys was increased, the probability of the lynx population dropping below 80 family groups increased (Fig. 3 and Table 3). However, a more accurate survey usually performed better than a less accurate survey even if performed less frequently (see Fig. 3). The probability that the population dropped below 80 family groups decreased from 0.14 at accuracy 0.7 (± 0.2) performed every year, to 0.10 at accuracy 0.9 (± 0.05) performed every fourth year. With complete knowledge of the population (i.e. accuracy 1.0 ± 0), the probability of the population decreasing below 80 family groups varied between 0.08 if survey was performed every year and to 0.10 if survey was performed every fourth year.

The probability that the population exceeded 120

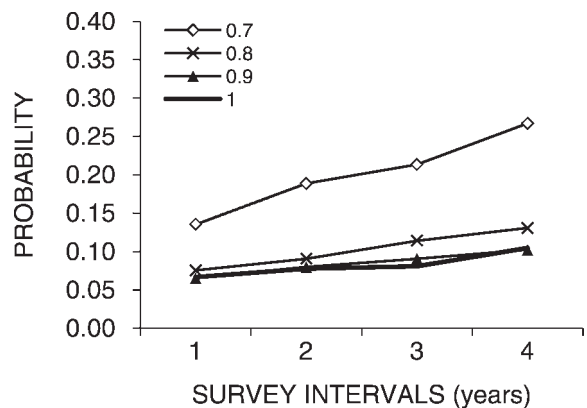


Figure 3. Probabilities (mean of proportion of time) that the number of lynx family groups was below 80 during a 50-year period for the three different survey accuracies, ($c_{\text{assumed}} = 0.7, 0.8$ or 0.9), as well as for perfect knowledge ($c_{\text{assumed}} = 1.0$) and the four different survey intervals (1-4 years).

Table 3. Probabilities (mean \pm SD) that the population will drop below 80 family groups and exceed 120 and 140 family groups, and the proportion of years (mean \pm SD) with no harvest at different survey accuracies and intervals.

Survey conditions		Results			
Proportion found (\pm SD)	Survey Interval (years)	Probability < 80 family groups	Probability > 120 family groups	Probability > 140 family groups	Proportion of years with no harvest
0.7 (\pm 0.2)	1	0.135 (\pm 0.12)	0.283 (\pm 0.18)	0.110 (\pm 0.12)	0.375 (\pm 0.11)
	2	0.189 (\pm 0.15)	0.272 (\pm 0.19)	0.118 (\pm 0.13)	0.396 (\pm 0.12)
	3	0.214 (\pm 0.15)	0.302 (\pm 0.19)	0.154 (\pm 0.15)	0.436 (\pm 0.12)
	4	0.267 (\pm 0.18)	0.289 (\pm 0.19)	0.153 (\pm 0.15)	0.429 (\pm 0.14)
0.8 (\pm 0.1)	1	0.075 (\pm 0.08)	0.353 (\pm 0.18)	0.134 (\pm 0.12)	0.224 (\pm 0.11)
	2	0.091 (\pm 0.09)	0.344 (\pm 0.17)	0.134 (\pm 0.12)	0.226 (\pm 0.12)
	3	0.114 (\pm 0.10)	0.353 (\pm 0.18)	0.152 (\pm 0.13)	0.293 (\pm 0.13)
	4	0.131 (\pm 0.11)	0.348 (\pm 0.18)	0.165 (\pm 0.14)	0.272 (\pm 0.14)
0.9 (\pm 0.05)	1	0.065 (\pm 0.06)	0.347 (\pm 0.18)	0.121 (\pm 0.12)	0.175 (\pm 0.10)
	2	0.080 (\pm 0.07)	0.344 (\pm 0.17)	0.131 (\pm 0.12)	0.183 (\pm 0.12)
	3	0.091 (\pm 0.08)	0.364 (\pm 0.17)	0.151 (\pm 0.13)	0.241 (\pm 0.12)
	4	0.102 (\pm 0.09)	0.366 (\pm 0.17)	0.162 (\pm 0.13)	0.209 (\pm 0.13)
1.0 (\pm 0.0)	1	0.067 (\pm 0.06)	0.340 (\pm 0.18)	0.121 (\pm 0.12)	0.165 (\pm 0.11)
	2	0.078 (\pm 0.07)	0.347 (\pm 0.17)	0.125 (\pm 0.12)	0.166 (\pm 0.12)
	3	0.081 (\pm 0.07)	0.363 (\pm 0.16)	0.147 (\pm 0.12)	0.218 (\pm 0.12)
	4	0.105 (\pm 0.09)	0.355 (\pm 0.17)	0.150 (\pm 0.12)	0.206 (\pm 0.13)

family groups increased with higher accuracy in the survey and varied between 0.27 and 0.37 (Fig. 4). The probability that the population exceeded 140 family groups increased with survey frequency, but not with survey accuracy. For all monitoring strategies, the probability that the population would exceed 120 family groups was higher than the probability that the population would drop below 80 family groups (see Table 3).

The number of years with no harvest was higher

for the less reliable surveys (Fig. 5), ranging between 21.4 years out of 50 years (42.9%) for accuracy 0.7 (\pm 0.2) performed every fourth year and 8.7 years (17.4%) for accuracy 0.9 (\pm 0.05) performed every year. With complete knowledge (accuracy 1.0 \pm 0) and survey performed every year, the number of years with no harvest was 8.2 years out of 50 years (16.5%).

When using the state-dependent monitoring scheme, with a survey every year if the population

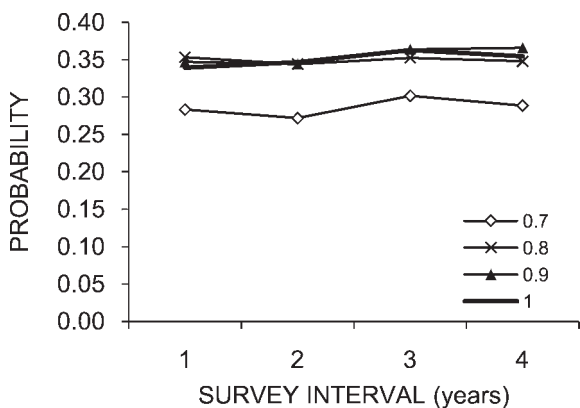


Figure 4. Probabilities (mean of proportion of time) that the number of lynx family groups was > 120 family groups during a 50-year period for the three different knowledge accuracies ($c_{\text{assumed}} = 0.7, 0.8$ and 0.9), as well as for perfect knowledge ($c_{\text{assumed}} = 1.0$), and the different survey intervals (1-4 years).

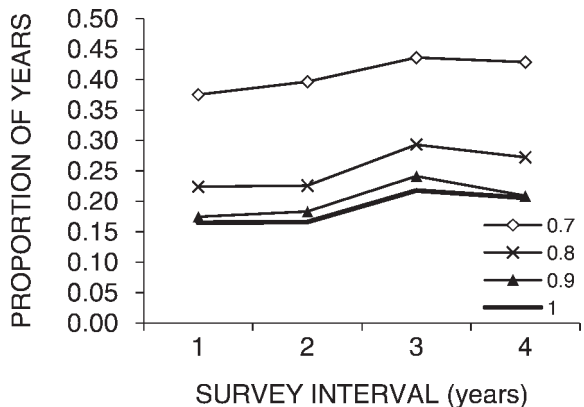


Figure 5. Mean proportion of years with no harvest during a 50-year period for three different survey accuracies ($c_{\text{assumed}} = 0.7, 0.8$ and 0.9), as well as for perfect knowledge ($c_{\text{assumed}} = 1.0$) at different survey intervals (1-4 years).

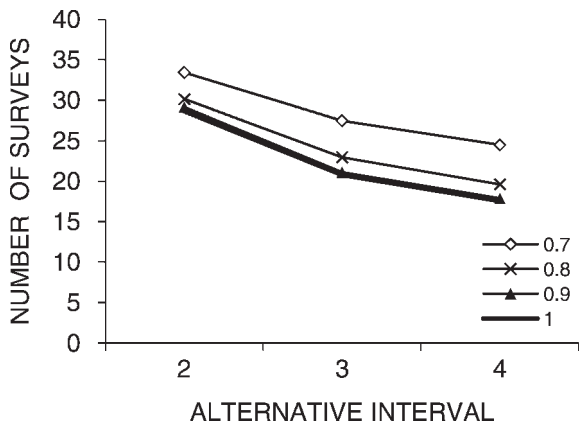


Figure 6. Total number of surveys performed during a 50-year period at different survey accuracies ($c_{\text{assumed}} = 0.7, 0.8$ or 0.9), as well as for perfect knowledge ($c_{\text{assumed}} = 1.0$), with adaptive survey policy. Surveys were performed every year when population according to the most recent survey was < 90 family groups, and with the alternative interval when the population was > 90 family groups.

was < 90 family groups, and alternatively 2-4 year intervals, the number of surveys during the 50-year period varied between $18 (\pm 4.1)$ and $29 (\pm 2.8)$ at a survey accuracy of $0.9 (\pm 0.05)$. The number of surveys performed at a less reliable survey $0.7 (\pm 0.2)$ varied between $26 (\pm 2.9)$ surveys when maximum survey interval was four years, and $33 (\pm 5.3)$ when maximum survey interval was two years (Fig. 6). The proportion of years with no harvest was highest (0.43) at the least reliable survey (0.7 ± 0.2) with an alternative survey interval of two years. With state-dependent monitoring, complete knowledge and alternative survey interval of four years, the proportion of years with no harvest decreased to 0.175 .

Discussion

Based on our study, managers should design the survey in a manner which secures that the accuracy is at least 0.8 , and when financial resources are limited, managers are better off increasing survey accuracy rather than decreasing survey interval. This level relates well to the current monitoring accuracy in Scandinavia. During four monitoring events in Sweden during 1996-2004, five of seven (71%) radio-marked family groups, and 15 of 17 (88%) radio-marked individuals were found (Liberberg & Andrén 2006). The distinct difference in the probability of the population dropping below 80

family groups between accuracy $0.7 (\pm 0.2)$ and accuracy $0.8 (\pm 0.1)$, implies that it is beneficial to increase the accuracy, and thereby decreasing the error of the survey. In Norway, such an improvement of the survey was achieved by tracking along deliberate lines instead of randomly tracking lynx during the survey (Linnell et al. 2007a). Besides increasing the survey intensity, the accuracy can also be improved by allowing more days to pass between snowfall and the monitoring event. Based on two large field surveys in Norway in 1999 and 2001, Linnell et al. (2007a) found that 80% of the lynx individuals were detected at surveys performed three nights after snowfall, and that 91% were detected at surveys performed five nights after snowfall.

The quantitative performance levels in our study are related to the assumptions and simplifications that are used in all simulations, and thus not to a real Eurasian lynx population located within the reindeer husbandry area of northern Sweden. However, we believe that the performance rankings of the monitoring strategies investigated are reliable, as we used survey accuracies reported from field tests and relevant estimates of survival and reproduction.

The frequency of monitoring had less effect on management performance than it did on the reliability of the survey. Our results concord with Pople (2008) who similarly found that the increasing survey precision decreased the probability of the population of kangaroo *Macropus* sp. dropping to an unacceptably low level (i.e. quasi-extinction) even with decreased survey frequency. However, we also need to take into account the time it takes for managers to respond to changes in population size. Solberg & Sæther (1999) showed that it took on average two years for moose managers to respond to changes in the population. Decreasing the survey frequency would further increase the harvest response time to changes in population size, and thus reduce the management performance. In our simulation, the harvest quotas remain constant over the years with no surveys. This exaggerates the effect of over- or underharvesting at lower monitoring frequency.

The large between-year variations in reproduction add to the difficulties of accurately predicting the population development. If a relatively small proportion of females reproduce one year, the population size will be underestimated in a survey. As a consequence, all decisions based on this survey may reinforce the pattern and cause an under-

harvest of the population. Likewise, if a relatively high proportion of females have reproduced, the population may be overestimated and subsequently lead to an overharvest. The effect of such over- or underestimates will be stronger if the survey interval is longer.

Even with perfect knowledge of the number of family groups of lynx in February, the population was below the desired level 8-10% of the time (see Fig. 3). These failures occur because of the variations in both reproduction and survival, and because the survey is performed in February and the harvest quota is decided 10 months later. The management performance measures would improve if the harvest quota for the harvest in March was based on the monitoring results obtained in January-February, just before. In this way, harvest quotas would be based on the latest population estimate, with less time for variation in survival and reproduction.

In our study, the goal was to maintain a population at approximately 100 family groups, and the management was considered successful at population levels between 80 and 120 family groups. In the simulations we used a harvest strategy based on the harvest decisions made by the Swedish EPA. As this harvest strategy deterministically balances the lynx population at 110 family groups or 675 individuals, it is not surprising that it was more likely to get a population > 120 family groups than < 80 family groups.

The differences between survey accuracies and frequencies were not as apparent when looking at the proportion of time the population increased above 120 or 140 family groups. This likely depends on the used harvest strategy being conservative, as management authorities today are committed to a precautionary approach (Harwood & Stokes 2003). Hauser & Possingham (2008) also showed that an action (harvest strategy) with known moderate benefits is preferred over a strategy with uncertain but marginally larger expected benefits. To further improve the management performance, the optimal harvest strategy should be evaluated along with the optimal monitoring interval and reliability in order to find a robust strategy (Milner-Gulland et al. 2001). Whether the higher risks of a population increasing above the upper threshold are acceptable, is a function of the cost for maintaining such high populations, and would best be determined after discussions among the managers and stakeholders.

Our study also raises the question of which temporal and spatial scale the management should be performed at. While our study investigated the management of about 100 family groups, management may occur at a much smaller management scale, as regional or local management is voiced as an alternative. Managing at a smaller scale (i.e. fewer lynx family groups) would probably decrease the management performance, as variation in growth rate increase due to a larger effect of demographic stochasticity on smaller populations (Lande et al. 2003). A different temporal scale may also alter the management strategies. For example, if management uses discount functions which weigh future rewards more heavily, it does not necessarily encourage active learning of the populations' reactions to management measures, and consequently will result in more conservative harvest strategies (Moore et al. 2008).

At lower population densities, it may be needed to improve the survey effort further, in order to have similar detectability as in an area with higher density (Linnell 2007a). In our study, the improvement in performance was only marginal between a survey accuracy of $0.8 (\pm 0.1)$ and higher accuracies. Thus, it is important to weigh the benefit from increasing the survey accuracy against the added costs (Wilson & Delahay 2001). Improving the survey accuracy from 0.8 to 0.9, may be an unreasonable cost in relation to the benefits of management of such an improvement. In this case, the combination of several different survey methods may result in a more reliable result, and still be affordable (Månsson et al. submitted manuscript).

Hauser et al. (2006) showed that it is more important to have frequent surveys when the population level is close to population thresholds. The need to monitor depends on the level of the previous population estimate, and also on the precision of the estimate. The use of threshold surveys (i.e. to survey more frequently when a previous survey is below a threshold) showed that at lower survey reliabilities, the number of surveys needed increased. The economical gain from doing a less reliable survey may thus be absorbed by the fact that surveys have to be performed more often.

Acknowledgements - Our work was funded by the Swedish Environmental Protection Agency (partly within the research programme 'Adaptive management of fish and wildlife populations'), the World Wide Fund for Nature (Sweden) and the private foundation 'Olle Engkvist,

byggmästare'. A.C. Danell gratefully acknowledges the Swedish Foundation for International Cooperation in Research and Higher Education (STINT) for scholarship and Dr. Anthony M Starfield, University of Minnesota, for valuable insight in the world of modelling. We thank Olof Liberg, Jens Persson and Guillaume Chapron for valuable comments in preparation of the study and on previous versions of this manuscript.

References

- Andrén, H. & Liberg, O. 2008: Den svenska lodjursstammen 2004 - 2008. - Grimsö Forskningsstation, Swedish University of Agricultural Sciences, Rapport, 74 pp. (In Swedish).
- Andrén, H., Linnell, J.D.C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzén, R., Kvam, T., Odden, J. & Segerström, P. 2002: Estimating total lynx *Lynx lynx* population size from censuses of family groups. - *Wildlife Biology* 8(4): 299-306.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., 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(1): 23-32.
- Bogich, T. & Shea, K. 2008: A state dependent model for the optimal management of an invasive metapopulation. - *Ecological Applications* 18(3): 748-761.
- Bowden, D.C., White, G.C. & Bartmann, R.M. 2000: Optimal allocation of sampling effort for monitoring a harvested mule deer population. - *Journal of Wildlife Management* 64(4): 1013-1024.
- Breitenmoser, U., Breitenmoser-Würsten, C. & Capt, S. 1998: Reintroduction and present status of the lynx (*Lynx lynx*) in Switzerland. - *Hystrix* 10: 17-30.
- Gerber, L.R., Beger, M., McCarthy, M.A. & Possingham, H.P. 2005: A theory for optimal monitoring of marine reserves. - *Ecology Letters* 8: 829-837.
- Goldsmith, B. 1991: *Monitoring for conservation and ecology*. - Chapman and Hall, London, UK, 275 pp.
- Haglund, B. 1966: De stora rovdjurens vintervanor (In Swedish with an English summary: Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow.) - *Swedish Wildlife Research* 4: 81-310.
- Harwood, J. & Stokes, K. 2003: Coping with uncertainty in ecological advice: lessons from fisheries. - *TRENDS in Ecology and Evolution* 18(12): 617-621.
- Hauser, C.E., Pople, A.R. & Possingham, H.P. 2006: Should managed populations be monitored every year? - *Ecological Applications* 16: 807-819.
- Hauser, C.E. & Possingham, H.P. 2008: Experimental or precautionary? Adaptive management over a range of time horizons. - *Journal of Applied Ecology* 45: 72-81.
- Hood, G.M. 2004: PopTools version 2.6.4. - Available at: <http://www.cse.csiro.au/poptools> (Last accessed on 30 November 2010).
- Lande, R., Engen, S. & Sæther, B-E. 2003: *Stochastic population dynamics in ecology and conservation*. - Oxford University Press, Oxford, UK, 212 pp.
- Liberg, O. & Andrén, H. 2006: Lodjursstammen i Sverige 1994-2004. En utvärdering av inventeringsresultat och metoder. (In Swedish with an English summary: The lynx population in Sweden 1994-2004. An evaluation of census data and methods.) - Report Wildlife Damage Center/Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, 39 pp.
- Linnell, J.D.C., Fiske, P., Herfindal, I., Odden, J., Brøseth, H. & Andersen, R. 2007a: An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. - *Wildlife Biology* 13(4): 456-466.
- Linnell, J.D.C., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P., Kvam, T., Brøseth, H., Segerström, P., Ahlqvist, P., Schmidt, K., Jędrzejewski, W. & Okarma, H. 2007b: Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. - *Wildlife Biology* 13(4): 447-455.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. 2001: Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. - *Animal Conservation* 4(4): 345-349.
- Linnell, J.D.C., Swenson, J.E., Landa, A. & Kvam, T. 1998: Methods for monitoring European large carnivores - A worldwide review of relevant experience. - Norwegian Institute of Natural Agriculture, Oppdragsmelding 549: 1-38.
- Månsson, J., Hauser, C.E., Andrén, H. & Possingham, H.P. (submitted): Optimal survey method choice for wildlife management. - *Wildlife Biology*.
- McCarthy, M.A. & Possingham, H.P. 2007: Active adaptive management for conservation. - *Conservation Biology* 21(4): 956-963.
- Milner-Gulland, E.J., Shea, K., Possingham, H.P., Coulson, T. & Wilcox, C. 2001: Competing harvest strategies in a simulated population under uncertainty. - *Animal Conservation* 4: 157-167.
- Moore, A.L., Hauser, C.E. & McCarthy, M.A. 2008: How we value the future affects our desire to learn. - *Ecological Applications* 18(4): 1061-1069.
- Nowell, K. & Jackson, P. 1996: Management of big cats near people. - In: Nowell, K. & Jackson, P.(Eds.); *Status survey and conservation action plan: Wild cats*. IUCN, Switzerland, pp. 180-192.
- Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andrén, H., Lindén, M. & Segerström, P. 1999: Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. - *Wildlife Biology* 5(4): 203-211.
- Pople, A.R. 2008: Frequency and precision of aerial surveys for kangaroo management. - *Wildlife Research* 35: 340-348.

- Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. & Pulliam, H.R. 2001: Making smart conservation decisions. - In: Soulé, M.E. & Orians, G.H. (Eds.); Conservation Biology: Research priorities for the next decade. Island Press, Washington, USA, pp. 225-244.
- Shea, K., Possingham, H.P., Murdoch, W. & Roush, R. 2002: Active adaptive management in insect pest and weed control: intervention with a plan for learning. - Ecological Applications 12(1): 927-936.
- Solberg, E.J. & Sæther, B-E. 1999: Hunter observations of moose *Alces alces* as a management tool. - Wildlife Biology 5(2): 107-117.
- SOU 2006: 14 Samernas sedvanemarker. (In Swedish with an English summary: Sami lands based on immemorial rights.) - Swedish Government Report, 550 pp.
- SOU 2007: 89 Rovdjuren och deras förvaltning. (In Swedish with an English summary: The predators and their management.) - Swedish Government Report, 680 pp.
- Swenson, J.E. & Andrén, H. 2005: A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. - In: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds.); People and Wildlife: Conflict or Coexistence? Cambridge University Press, Cambridge, UK, pp. 323-339.
- Walters, C.J. & Hilborn, R. 1978: Ecological optimization and adaptive management. - Annual Review of Ecological Systems 9: 157-188.
- Wilson, G.J. & Delahay, R.J. 2001: A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. - Wildlife Research 28: 151-164.