Estimating total lynx *Lynx lynx* population size from censuses of family groups

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Counts of reproductive units, i.e. family groups, constitute the main monitoring index for lynx *Lynx lynx* populations in Scandinavia. However, for some purposes it is necessary to extrapolate from the number of family groups to obtain an estimate of total population size. Using data on survival and reproduction from radio-marked lynx from three Scandinavian study areas, we simulated the lynx population structure in February. The average proportions of family groups out of all independent individuals, i.e. adults and yearlings, in these simulations were 21% ± 2.1 (SD), 22% ± 3.6 and 27% ± 3.1 for the data sets from northern Sweden (Sarek), southeastern Norway (Hedmark) and south-central Sweden (Bergslagen), respectively, and the overall mean for all three study areas was 23% ± 3.8. This translated into extrapolation factors of 6.14 ± 0.44 , 6.24 ± 0.73 and 5.48 ± 0.40 for the three study areas, respectively, leading to an overall mean for all three study areas of 5.95 ± 0.64. We conclude, that it is possible to extrapolate from the number of family groups to obtain an estimate of total lynx population size with a statistical measure of uncertainty.

Key words: census, lynx, monitoring, population simulations, reproduction

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Due to a combination of unregulated hunting and high bounty payments, lynx *Lynx lynx* populations in Scandinavia had been reduced to very low levels by the early to the mid-20th century (Liberg 1997; T. Kvam, unpubl. data). Changes in management regime, including the removal of bounties and periods with various levels of protection, have lead to a dramatic recovery of lynx populations throughout both Norway and Sweden. Presently, reproductive lynx populations are found throughout most parts of the peninsula, with the exception of southwestern Norway and the southernmost parts of Sweden. This recovery has lead to a number of conflicts involving livestock, e.g. domestic sheep *Ovis aries* and semi-domestic reindeer *Rangifer tarandus*, and roe deer *Capreolus capreolus* hunters such that lynx populations require intensive management.

Central to many conservation or management systems is a requirement for effective census and monitoring methods (Goldsmith 1991), and this is also the case for lynx management in Scandinavia for two main reasons. First, compensation payments for semi-domestic reindeer depredation in northern Sweden are linked to the numbers of large carnivores (including lynx) present in the grazing areas, rather than to actual losses. Secondly, lynx hunting is widely practised throughout Scandinavia, both as 'normal' quota hunting and as a means of controlling population growth in areas where conflicts occur. Lynx hunting requires careful regulation because lynx hunters are very efficient given good snow conditions, and because there are no wilderness refuges with potentially unhunted populations of lynx (Linnell, Andersen, Kvam, Andrén, Liberg, Odden & Moa 2001). Therefore, it is important that annual quotas are based on good census data.

Monitoring large carnivore populations is never an easy task under any circumstances (Linnell, Swenson, Landa & Kvam 1998). Because of the logistics of working over very large areas it is often very difficult to obtain statistical estimates of population size, resulting in frequent use of minimum counts (Knight, Blanchard & Eberhardt 1995, Landa, Tufto, Franzén, Bø, Lindén & Swenson 1998, Smirnov & Miquelle 1998).

Currently two different census methods are in widespread use in Scandinavia. In northern Sweden and most of Norway, censuses are based on unreplicated counts of reproductive units (*sensu* Knight et al. 1995), here termed family groups. As kittens usually stay with their mother until they are 10 months old, tracks in the snow from two or more lynx travelling together during early to mid-winter are almost always indicative of a family group (mating does not occur until late March). Observations were made during December-February and separated from each other using a set of rules based on observed home-range sizes and movement rates (Bergström, Bø, Franzén, Henriksson, Nieminen, Overrein & Stensli 1994, Bergström, Attergaard, From & Mellquist 1996, Östergren & Segerström 1998, Östergren, Bergström, Attergaard, From & Mellquist 1998; T. Kvam, unpubl. data). As adult female lynx are territorial (Breitenmoser, Kazensky, Dötterer, Breitenmoser-Würsten, Capt, Bernhart & Liberek 1993, Schmidt, Jedrzejewski & Okarma 1997), this method works well at all but the highest densities.

Throughout central and southern Sweden, and periodically in some smaller areas in Norway, attempts have been made to obtain total counts based on snow-tracking during one-day censuses (Liberg & Glöersen 1995, Odden, Solvang, Maartman, Wabakken, Linnell, Andersen, Haagenrud, Lundqvist & Solberg 2000). In these surveys, hundreds of volunteers (mainly hunters) search an area intensively for lynx tracks 1-2 days after fresh snowfall. An attempt is then made to discriminate between the different individuals or groups by back-tracking each track until it either meets up with another track, or until the day-bed used before the night of the snowfall is located. In practice it is a ground-based form of the widely used aerial reconnaissance survey used for wolves *Canis lupus* in North America (e.g. Gasaway, Stephenson, Davis, Shepherd & Burris 1983). Because of the large amount of manpower required to backtrack all tracks, some of these surveys concentrate on family groups only (Odden et al. 2000). Counting lynx family groups has been selected as the main monitoring method for lynx in national monitoring programmes in both Norway and Sweden (Franzén 1999, Braa, Brainerd, Brøseth, Knutsen & Linnell 2000).

While both of these methods provide reliable minimum counts of the number of family groups present, an indication of total numbers is often required for some management purposes, e.g. determining if a minimum viable population exists. Therefore, it is important that we are able to convert the number of family groups counted into an estimate of total population size (*sensu* Landa et al. 1998). Based on life-table analysis of hunter-shot lynx (Kvam 1990), T. Kvam (unpubl. data) provided a general formula which can be used to convert the number of family groups into total population size. However, life-table analysis has a number of intrinsic weaknesses. Kvam (1990) pooled lynx from all over Norway over a >20-year period. Considering the large ecological gradients that exist in Norway and Sweden, and the dramatic recovering of the lynx populations in Norway and Sweden, there is a clear need to confirm earlier extrapolation factors. During the last decade we have

seen the development of extensive radio-telemetry studies in various study areas in Scandinavia (Andrén, Ahlquist, Andersen, Kvam, Liberg, Lindén, Odden, Overskaug, Linnell & Segerström 1998, Linnell et al. 2001) which provide a far better foundation for studies of lynx population structure and dynamics.

The purpose of this paper is to estimate the extrapolation factor which can be used to convert the number of family groups found in February into total lynx population size. The extrapolation factor was estimated using data on survival and reproduction from radio-marked lynx.

Study areas

The fieldwork was conducted in two different areas in Sweden and one area in Norway (Fig. 1). The northern study area is partly located within the Sarek National Park around Kvikkjokk in the county of Norrbotten (67°00'N, 17°40'E) in northern Sweden and covers about 8,000 km^2. The vegetation ranges from coniferous forest consisting of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* in the eastern parts (about 300 m a.s.l.), over mountain birch *Betula* sp. forest and mountain meadows to high alpine areas with peaks around 2,000 m a.s.l. and glaciers. The tree line is at about 800 m a.s.l.

The central study area is situated in the county of Hedmark in southeastern Norway (61°15'N, 11°30'E) and covers about 8,000 km^2. The topography consists of several parallel river valleys running from north to south at about 200-500 m a.s.l., with hills ranging in elevation within 600-900 m a.s.l. The region is dominated by coniferous forest, covering about 72% of the area. Scots pine and Norway spruce are the dominant tree species, but birch is also well represented, especially in the forest-alpine interface and along rivers. Most of the forest is intensively managed, resulting in a mosaic of even-aged forest stands.

The southern area covers about 6,000 km^2 and is located around the Grimsö Wildlife Research Station (59°30'N, 15°30'E) in the Bergslagen region in south-central Sweden. The area is dominated by coniferous forest, consisting of Norway spruce and Scots pine, which is intensively managed for timber and pulp. The study area ranges in elevation within 30-500 m a.s.l. The proportion of agricultural land is highest in the southern parts (about 20%) and decreases towards the northern parts (<1% of the area). Roe deer are the main prey in the Hedmark and Bergslagen study areas, while semi-domestic reindeer are the main prey in the Sarek area.

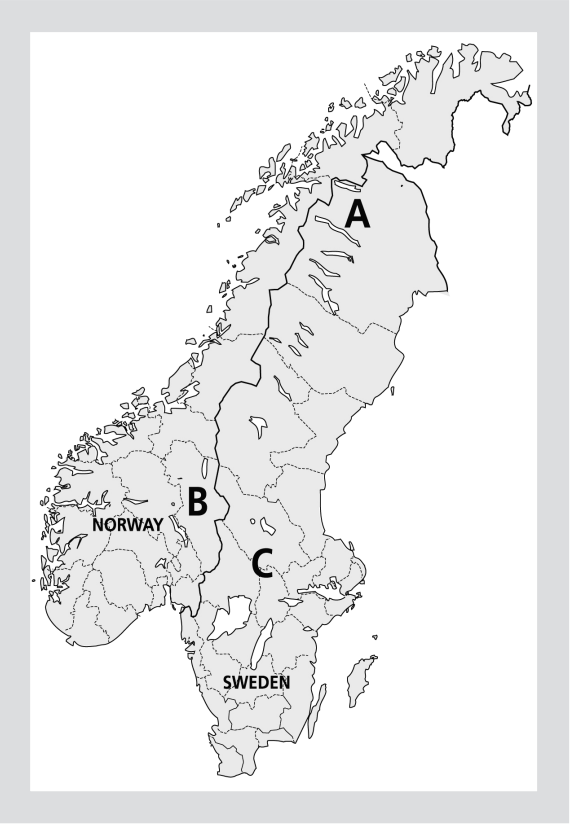

Figure 1. Map of Scandinavia showing the three study sites where data were collected: A) northern area, centered around Sarek National Park; B) central area, based within Hedmark county; C) southern area in the Bergslagen region.

Further details on the study areas are provided in Pedersen, Linnell, Andersen, Andrén, Lindén & Segerström (1999) and Linnell et al. (2001).

Methods

Lynx were live-captured using a variety of methods, including darting from a helicopter, unbaited walk-through box-traps, foot-snares placed at fresh kills, and chasing into trees by dogs (Nybakk, Kjørstad, Overskaug, Kvam, Linnell, Andersen & Berntsen 1996). The lynx were immobilised with a mixture of Ketalar and Rompun and equipped with either radio-collars or implanted transmitters. In the Hedmark and Bergslagen areas we also radio-marked neonatal kittens at the age of 5-6 weeks using implanted radio-transmitters (Arnemo, Linnell, Wedul, Ranheim, Odden & Andersen 1999).

The lynx were radio-tracked at least 2-4 times per months. Most radio-collars had mortality functions, which enhanced our chances of determining the fate of

the lynx. Animals were approached on foot if a collar signalled in mortality mode, or if the animal had not moved for some days. Sometimes resident lynx suddenly disappeared from their known home range. If we had no indication of radio failure, e.g. irregular signal, we classified these lynx as having been illegally shot. As we were able to follow dispersing juveniles for several hundred kilometres, it is unlikely that we failed to detect adult dispersal. In June each year the reproductive status of all females was checked. Females with kittens are very sedentary and adopt a central place foraging strategy markedly different from normal lynx movement pattern (Schmidt 1998). Therefore, it was possible to locate the natal lair and count kittens by closely tracking the female (Arnemo et al. 1999).

We estimated survival rates of radio-collared lynx and their standard errors using the staggered entry design, which is a modified Kaplan-Meier estimate (Pollock, Winterstein, Bunck & Curtis 1989). As lynx are long-lived animals several individuals are used in more than one year to estimate the number of individuals at risk. However, to avoid pseudo-replication we only used the number of unique individuals to estimate the standard error. For kittens that were not marked in natal lairs we estimated the survival rate from birth to radio-marking in February using the Mayfield estimate (Krebs 1999). We divided the survival estimate into males and females, three age classes (kittens <12 months, yearlings 12-24 months and adults >24 months old) and the three study areas.

To estimate the structure of the lynx population in February, we used the survival and reproduction estimates and their standard errors in a simulation (Tables 1 and 2). We used 1 June as the start of a lynx-year (most births occur in the last week of May; Arnemo et al. 1999), and we assumed that survival was the same for all months. Thus, survival from June to February was estimated from annual survival to the power of 9/12. In the simulations (N = 1,000 per study area) all the survival and reproduction estimates were selected at random within the ranges given by the standard error. Thus, we assumed that the different survival and reproduction variables were independent of each other. Furthermore, the survival rates of kittens from the same litter were assumed to be independent of each other. The adult sex ratio was obtained by assuming an equal sex ratio of kittens and then a sex specific survival in the three age classes (0-1 year, 1-2 year and ≥2 year olds). From the simulations we obtained the population structure in February, i.e. the number of females and males of the three age classes. Using these data it is possible to calculate the mean number of kit-

Table 2. Mean number of kittens per female in June, standard error (SE) and total number of individuals in the three study areas, as used in the simulations.

Age class	Mean	SE	No of individuals
Sarek:			
1 year old	0.0	-	12
2 years old	0.625	0.420	8
3 years old and older	1.605	0.158	38
Hedmark:			
1 year old	0.0	-	9
2 years old	0.375	0.376	8
3 years old and older	1.364	0.251	22
Bergslagen:			
1 year old	0.0	-	7
2 years old and older	2.048	0.288	21

Table 1. Mean yearly survival estimates and their standard errors (SE; Pollock et al. 1989) for lynx males and females according to the three age classes (0-1, 1-2, >2) for the Sarek, Hedmark and Bergslagen study areas, as used in the simulations.

Sex	Age-class (years)	Mean	SE	Number of individuals	Number of 'radio-months'
Sarek:					
♂	0-1	0.395	0.074	39	251
♂	1-2	0.724	0.155	15	140
♂	>2	0.900	0.050	17	341
♀	0-1	0.455	0.093	27	186
♀	1-2	0.833	0.134	13	138
♀	>2	0.923	0.041	17	442
Hedmark:					
♂	0-1	0.624	0.244	12	78
♂	1-2	0.825	0.179	10	82
♂	>2	0.860	0.112	8	241
♀	0-1	0.832	0.121	12	78
♀	1-2	0.600	0.213	11	64
♀	>2	0.832	0.086	13	366
Bergslagen					
♂	0-1	0.265	0.102	20	78
♂	1-2	0.560	0.166	7	35
♂	>2	0.886	0.057	12	296
♀	0-1	0.525	0.121	19	97
♀	1-2	0.833	0.139	7	75
♀	>2	0.857	0.087	9	165

tens per adult female in February (i.e. number of females and males in the youngest age class divided by the number of females in the oldest age class). A Poisson distribution was then used to get the proportion of adult females without kittens. Given a mean value a Poisson distribution gives the proportions of different integers (zero, one, two and so on). Thus, assuming a Poisson distribution it is possible to get the proportion of adult females without kittens from the calculated mean number of kittens per adult female. Subtracting the number of adult females without kittens from the total number of adult females gives the number of family groups. Finally, the factor used to convert the number of family groups found in February into total lynx population size was the ratio of total lynx population (adding together all females and males in the three age classes) to the number of family groups obtained from the Poisson distribution (see above).

Results and discussion

The proportions of adult females without kittens (zero-value) pooled over all years in the Sarek area were 28% (N = 46) in June and 41% (N = 39) in February. These two proportions of zero-values were not significantly different from an expected Poisson distribution given the observed mean litter sizes of 1.43 kittens in June and 0.92 kittens in February per adult female ($\chi^2 = 0.50$, df = 1, P = 0.48 in June, and $\chi^2 = 0.03$, df = 1, P = 0.87 in February).

In Hedmark, the proportions of adult females without kittens pooled over all years were 37% (N = 35) in June and 46% (N = 28) in February), and the mean litter sizes were 1.1 in June and 0.80 in February. These proportions of zero-values were not significantly different from an expected Poisson distribution given the observed mean litter sizes ($\chi^2 = 0.23$, df = 1, P = 0.63 in June, and $\chi^2 = 0.03$, df = 1, P = 0.87 in February).

In Bergslagen, the proportions of adult females without kittens pooled over all years were 24% (N = 21) in June and 50% (N = 10) in February, and the mean litter sizes were 2.05 in June and 0.70 in February. These proportions of zero-values were not significantly different from an expected Poisson distribution given the observed mean litter sizes ($\chi^2 = 2.22$, df = 1, P = 0.14 in June and $\chi^2 = 0.01$, df = 1, P = 0.98 in February). Thus, the assumption in the simulation that the proportion of females without kittens could be estimated from a Poisson distribution seems likely.

The proportion of family groups to all independent individuals (i.e. adults and yearlings) in the simulations varied between 13 and 28% for the Sarek area (mean: 21% ± 2.1 (SD)), between 11 and 37% for Hedmark (mean: 22% ± 3.6) and between 17 and 36% for Bergslagen (mean: 27% ± 3.1; Fig. 2). The overall mean for all three areas combined was 23% ± 3.8.

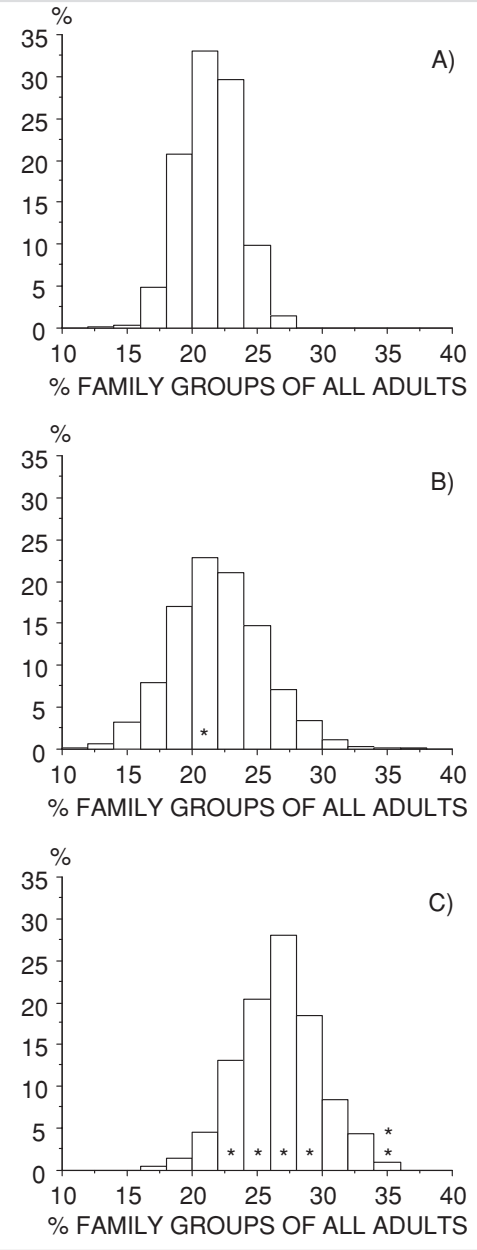

Figure 2. Frequency distribution of the proportion of family groups to all adults in February for the study areas A) Sarek, B) Hedmark and C) Bergslagen. The asterisk in B) indicates an observed value obtained from a lynx census performed in the area, and the asterisks in C) indicate observed values obtained from six different lynx censuses.

In the one-day censuses organised by the Swedish Association for Hunting and Wildlife Management, all lynx are counted, and family groups are defined as two or more individuals found together. These censuses were performed in 1993, 1994, 1995, 1996, 1998 and 2000 covering several counties in central Sweden surrounding the Bergslagen study area (Liberg & Glöersen 1995, Glöersen 1996, Glöersen & Liberg 1998, Liberg & Glöersen 2000). The proportion of family groups to all independent individuals (i.e. adults and yearlings) was 21.6% (N = 162), 24.9% (N = 189), 27.5% (N = 447), 35.2% (N = 196), 27.9% (N = 441) and 34.2% (N = 333) in the respective year (see Fig. 2). In a census performed in January 1999 in Hedmark, the proportion of family groups to all independent individuals (i.e. adults and yearlings) was 22% (N = 18; Odden et al. 2000).

If six numbers are selected at random (i.e. the same sample as the number of censuses in Sweden) from the simulations the observed proportions from the one-day censuses in central Sweden were significantly higher than in the Sarek (Mann-Whitney U-test: $N_1 = N_2 = 6$, U = 1, P = 0.006) and Hedmark data sets (Mann-Whitney U-test: $N_1 = N_2 = 6$, U = 3, P = 0.016), but not significantly different from the Bergslagen data set (Mann-Whitney U-test: $N_1 = N_2 = 6$, U = 15, P = 0.63). The ecological region in which the one-day censuses were performed is the same as the ecological region in which the Bergslagen study area is situated. Similarly the mean (22%) was identical for both the overall value from the simulations and the one-day census in Hedmark. These independent samples support the conclusion that our simulations based on telemetry data reflect the standing populations and that the regional differences are real.

The mean factors used to convert the number of family groups in February into an estimate of total lynx population size were 6.14 ± 0.44, 6.24 ± 0.73 and 5.48 ± 0.40 in the Sarek, Hedmark and Bergslagen areas, respectively (Fig. 3). The overall mean for all three areas was 5.95 ± 0.64. The maximum factors were 8.72, 10.10 and 7.21 in the Sarek, Hedmark and Bergslagen areas, respectively, whereas the minimum factors were 5.17, 4.47 and 4.54, respectively. However, in 90% of simulations the factors were between 5.54 and 6.88 in the Sarek area, between 5.24 and 7.61 in the Hedmark area and between 4.93 and 6.14 in the Bergslagen area (see Fig. 3). Corresponding numbers from the Swedish one-day censuses were: 6.12 in 1993, 5.49 in 1994, 5.08 in 1995, 4.26 in 1996, 5.06 in 1998 and 4.59 in 2000 (Liberg & Glöersen 1995, Glöersen 1996, Glöersen & Liberg 1998, Liberg & Glöersen 2000). In a census from Hedmark the factor was 5.5 (Odden et al. 2000). The

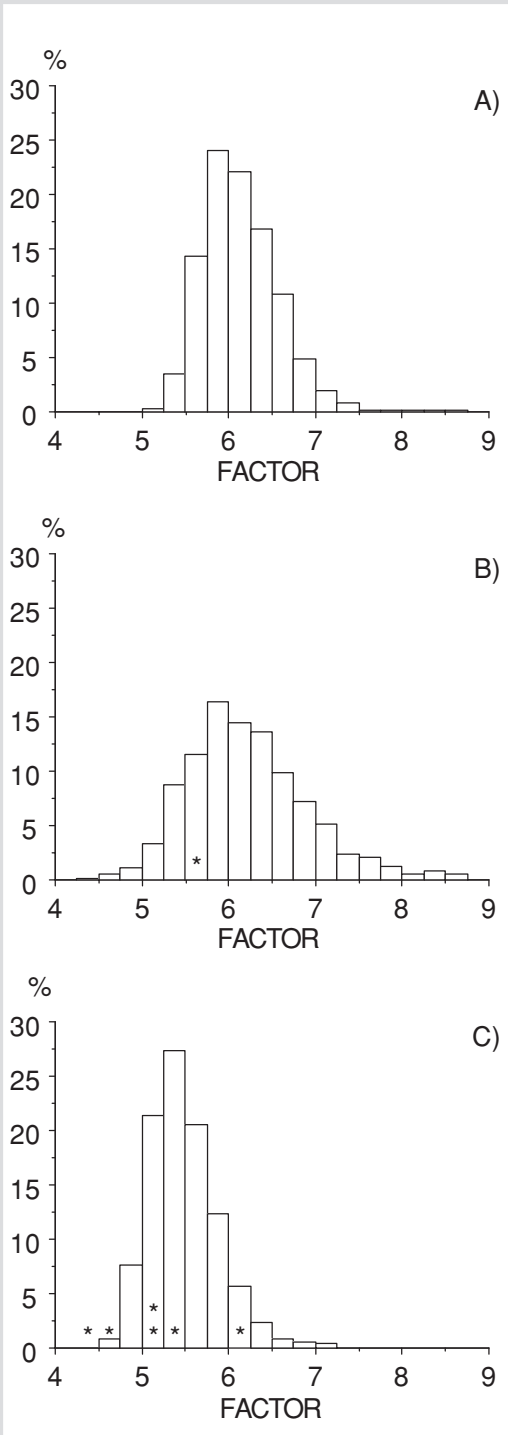

Figure 3. Frequency distribution of the factor used to convert the number of family groups found in February to total lynx population size in the study areas A) Sarek, B) Hedmark and C) Bergslagen. The asterisk in B) indicates an observed value obtained from a lynx census performed in the area, and the asterisks in C) indicate observed values obtained from six different lynx censuses.

numbers from the Swedish lynx census were significantly different from six randomly selected simulated numbers for the Sarek and Hedmark data sets (Mann-Whitney U-test: $N_1 = N_2 = 6$; U = 5, P = 0.037 and U = 3, P = 0.016, respectively), but not significantly different for the Bergslagen data set (Mann-Whitney U-test: $N_1 = N_2 = 6$, U = 10, P = 0.20). These extrapolation factors also lie within the values of 5.5 and 6.0 obtained from life-table analysis of Norwegian lynx (Kvam 1990, 1997).

The two measures, i.e. the proportion of family groups to all independent individuals (adults and yearlings) and the factor used to convert the number of family groups in February into total lynx population size, are measures of more or less the same population response. A low proportion of family groups and a large multiplication factor results from low reproduction and/or low kitten survival. Generally, lynx reproduction was higher in the Bergslagen area than in the Hedmark and Sarek areas (see Table 2).

Thus it is possible to extrapolate from a count of the number of family groups to an estimate of total population size with a statistical measure of uncertainty. However, it is important to emphasise that this standard deviation merely reflects uncertainty in the extrapolation factor, and not in the underlying number of family groups recorded. A census based on this approach is only as good as the effort put into searching for, and discriminating between, family groups. The differences in extrapolation factors between the study areas are relatively large and, clearly, managers must carefully assess which population is most similar to their own. The inter-study site differences in reproductive parameters are also mirrored by differences in home-range size (Linnell et al. 2001). Further elucidation of the between-site differences in lynx ecology is a major theme for future activities of the Scandinavian lynx projects.

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