

Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions

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Monitoring of lynx *Lynx lynx* populations in Scandinavia is largely based around unreplicated minimum counts of family groups, i.e. adult females with dependent kittens. When observations cannot be separated from each other on the basis of back-tracking in the snow it is desirable to use a distance rule to separate observations of groups that are so far apart that they are unlikely to be derived from the same group. We have analysed radio-telemetry derived movement data from five study areas, corresponding to three ecologically different regions, in Scandinavia, and included data from Poland for comparison. We derive examples of two different distance rules; one is a static rule based on home-range size and length which is suitable for observations accumulated during a whole winter, and the other is a dynamic rule suitable for observations collected within 1-7 days of each other. Because of inter-study area variation in home-range size and movement there is a need to use different rules in different regions. Within Scandinavia, average maximum home-range lengths varied from 28 to 54 km, and average maximum daily distances travelled varied from eight to 16 km in the three regions. This implies that locally collected movement data are a prerequisite for application of this type of methodology.

Key words: census, Eurasian lynx, home range, large carnivore, *Lynx lynx*, monitoring, movement

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Following the introduction of more favourable management regulations, Eurasian lynx *Lynx lynx* numbers have increased dramatically throughout Scandinavia since the 1980s. Today lynx are present throughout very large parts of the Scandinavian peninsula. Due to their very large home-range sizes, lynx conservation must take place in multi-use landscapes rather than in protected areas which are too small and are often centred on the alpine-tundra habitats avoided by lynx (Linnell et al. 2000, 2001). Conserving lynx, or any other large carnivore species, in multi-use landscapes requires a very different management strategy than in protected areas. This is mainly a result of the conflicts that inevitably occur with human land-use such as conflicts with hunting interests, domestic sheep *Ovis aries* and semi-domestic reindeer *Rangifer tarandus* (Pedersen et al. 1999, Odden et al. 2002), and a desire to harvest lynx by sports hunters. A result of these issues is that Scandinavian lynx populations are harvested, with the populations in all of Norway, and the reindeer herding areas of Sweden in particular being exposed to heavy harvest (Linnell et al. 1999, Andersen et al. 2003). This intensive management requires good scientific data about the species' biology and effective methods to estimate population size and monitor population trends across the entire area of Scandinavia on an annual basis.

However, because of their low densities and cryptic habits, lynx, like all large carnivores, are difficult to census. While relatively robust indices of presence/absence and population trend can often be obtained for large carnivores (Stahl & Vandel 1998, Stander 1998, Wilson & Delahay 2001), there is also often a need for estimates of actual numbers

to set annual quotas or determine compensation levels (Andrén et al. 2002, Swenson & Andrén 2005). Producing statistical estimates of population size for large carnivores often requires massive sampling effort (Becker 1991, Becker et al. 1998), even when being applied to small study areas. As for many other rare animals, the resultant confidence intervals may be so large as to make the effort impractical for management applications (Taylor & Gerrodette 1993). As a result of practical constraints, many large carnivore census programmes end up adopting a strategy of minimum counts instead of statistical estimates. In order to minimise double counting and to reduce costs, effort tends to focus on reproductive units, such as females with dependent young or natal dens. The actual methodology of distinguishing between discrete observations varies depending on species biology and ecological conditions. In many cases, some form of distance rule is used, often derived from telemetry data (Knight et al. 1995, Landa et al. 1998, Wiegand et al. 1998, Smirnov & Miquelle 1999).

Throughout the 1990s in Scandinavia, efforts were made to develop a minimum count methodology for lynx family groups, i.e. adult females with dependent kittens. Observations of individuals based on tracks in snow were separated either by intensive snow-tracking or the application of an *ad hoc* distance rule (Kvam 1996, Östergren & Segerström 1998). The objective of this paper is to make a step towards formalising the distance rules through the analysis of radio-tracking data from Scandinavian study sites. As home-range sizes vary dramatically within Scandinavia (Linnell et al. 2001), we aimed to produce separate rules for different ecological regions. For comparison, we in-

clude data from Poland where lynx home ranges are an order of magnitude smaller than in Scandinavia. Our intention is not to produce a formal rule for Polish conditions, but to critically examine the extent to which our method can be applied to other circumstances. We present data on the home-range size, home-range lengths, overlaps between neighbours and daily distances moved in order to develop two different distance rules: 1) a dynamic distance rule that can be used to separate between observations made temporally close to each other, and 2) a static distance rule that can be used on accumulated data from a whole season.

Study areas

The fieldwork was conducted in two different areas in Sweden (Sarek and Bergslagen), three areas in Norway (the counties of Nord-Trøndelag, Hedmark and Østfold/Akershus) and one in Poland (Białowieża). The study areas have been described in detail elsewhere (Jędrzejewska & Jędrzejewski 1998, Linnell et al. 2001, Andrén et al. 2002) and key details are summarised in Table 1. For the purposes of analysis we have grouped them into four categories reflecting landscape, prey density and prey species composition. Within Scandinavia, the harvest density of roe deer *Capreolus capreolus* within municipalities provided a rough measure to categorise regions. Data from Sarek and Nord-Trøndelag were pooled as 'Reindeer' areas because of the free access to semi-domestic reindeer as prey. Lynx from the eastern part of Hedmark were treat-

ed as 'Low roe' because of the very low density and patchy distribution of roe deer as the main prey. One lynx from western Hedmark and the lynx from Østfold/Akershus and Bergslagen were grouped as 'Medium roe'. Finally, the Polish study area was placed in a class of its own, 'High roe'.

Methods

Lynx were captured and radio-collared using a combination of four methods: snares placed on kills, walk-through box traps, darting from helicopters, and treeing with trained dogs. Radio-tracking schedules varied between seasons and study areas, but basically consisted of independent locations taken at infrequent intervals, or in sequences with one or more locations taken each day. For purposes of analysis, we have only included data from adult females (N = 44) collected during winter (1 November - 30 April). Home-range data were analysed in Ranges VI (Kenward & Hodder 1996). Statistical tests were performed in SPSS for Windows. In order to avoid artificial inflation of sample sizes we averaged all annual values of home-range size, length and overlaps for each individual or unique dyad. The different radio-tracking schedules led to wide variation in the number of locations that were available, however, we set a minimum of 20 locations so as to include data from the large sample of lynx (but with low tracking frequency) from Sarek. This is not likely to be enough to produce a true estimate of home-range size, but it should approximate one. Like-

Table 1. Environmental characteristics of lynx study areas in Scandinavia and Poland. Densities of large ungulates are approximate and do not include domestic sheep. The habitat codes are BF = Boreal forest, LA = Low alpine tundra, HA = High alpine tundra, and DF = deciduous forest.

Study area	Norway			Sweden		Poland
	Hedmark	Nord-Trøndelag	Østfold/Akershus	Bergslagen	Sarek	Białowieża
Latitude	61°30'N	64°30'N	60°N	59°30'N	67°N	52°30'N
Habitat	BF	BF/LA	BF	BF	BF/LA/HA	DF
Study period	1995-2001	1994-1995	2000-2002	1996-2001	1994-1998	1991-1994
Main prey	Roe deer ^a	Roe deer ^a	Roe deer ^a	Roe deer ^a	Hares	Roe deer ^a
	Red deer	Hares	Hares	Hares	Tetraonids	Red deer
	Wild reindeer	Tetraonids	Tetraonids	Tetraonids		Hares
	Tetraonids					
	Hares					
Domestic prey	Sheep	Reindeer ^a Sheep			Reindeer ^a	
Density of large ungulates (per km ²)	3	1-2	1-10	2-10	0.5-1	10
Ecoregion	Low roe	Reindeer	Medium roe	Medium roe	Reindeer	High roe

^a Main prey.

wise, when calculating distances moved, we have only included females with > 10 movements. Because, we have drawn on data from more than one year, the analysis is based on all adult females, irrespective of their reproductive status in a given year (not all females have kittens each year). This assumes that the presence of kittens in winter does not radically change the behaviour of females during winter, an assumption which our data indicate to be reasonable (Bunnefeld et al. 2006). Therefore, the individual lynx is the unit of data. Because the number of individuals in the Polish data was always ≤ 5 , they are presented as an extreme comparison to give our data perspective.

Static distance rule

The static distance rule is developed to separate accumulated observations that are more than a home-range length (longest axis) apart, i.e. if observations are made further than a home-range length apart, they are likely to come from different individuals. The rule is based around the maximal home-range length or the diameter of a circle of equivalent size, dependent on the shape of the home range. An index of home-range shape was obtained by dividing maximum home-range length by the maximum width perpendicular to the maximum length axis. We averaged annual values for females followed over > 1 winter. An assumption of this approach is that females display territoriality and have limited home-range overlap. This assumption was tested by calculating percentage home-range overlap (100% minimum convex polygon method; MCP) between neighbours (not possible for Østfold/Akershus area at time of analysis due to small sample size).

Dynamic distance rule

This alternative to the static distance rule is developed to separate observations made within one week of each other. We calculated distances moved in a single night from all the linear distances moved by lynx per night (from day bed to day bed). Distances travelled in periods longer than a single night are expressed as the linear distance between the starting point (day 1) and the day time location on each of the following days (i.e. day 1 to day 2, day 1 to day 3, day 1 to day 4). All possible values were extracted from the data sequences, such that, for example, two locations taken four days apart were included in the day 1 to day 4 distance even if the intervening distances (day 1 to day 2 or day 1

to day 3) were not available. For each individual lynx we took the maximum value recorded in each time interval, and then averaged these individual maximum values to get a study area mean. We only included individuals with ≥ 10 movements.

Results and discussion

Static distance rules

Although there was a high degree of overlap between a few pairs of adult female lynx (> 50% in a single case from Sarek), the overall picture was one with clear intra-sexual territoriality, as average percentage overlap between neighbours was < 10% for all study areas (Table 2). This result conforms to that found for other studies of lynx in Europe (Breitenmoser et al. 1993, Schmidt et al. 1997), and indicates that in the majority of cases the assumption of non-overlap between neighbours which is required for the use of a static distance rule will be fulfilled. This includes our Hedmark study area where lynx have the largest home ranges ever recorded for the species (Linnell et al. 2001).

Because of the very large home ranges of the Scandinavian lynx (Table 3) which are much larger than those reported from other European study areas (Breitenmoser et al. 1993, Schmidt et al. 1997, Stahl et al. 2001), the resulting distance rules are very large (see Table 3). For example, in the low roe deer area, the longest female's home range was 83 km. These maximal lengths were largely due to the fact that many home ranges were long and thin, as indicated by the high length/width ratios (see Table 3). This was due to the fact that many of the home ranges were aligned parallel with steep-sided valley systems in the study areas with greatest topographic relief. We therefore suggest that in areas with deep valley systems, the actual maximal length may be more appropriate, whereas in generally flat areas, the diameter of a circle of equivalent size to the home range may be appropriate.

Table 2. Average overlap between neighbouring winter home ranges of adult female lynx in different study areas calculated using 100% minimum convex polygon.

Area	Mean overlap (%), N	Minimum - Maximum (%)
Reindeer	8.1 (14)	0 - 54.3
Low roe	3.7 (12)	0 - 19.4
Medium roe	2.5 (4)	0 - 8.0
High roe (Poland)	3.3 (3)	0 - 8.8

Table 3. Average sizes, maximal and circular lengths and length/width ratios of winter (1 November - 30 April) home ranges for adult female lynx in different study areas, calculated using 100% minimum convex polygons. Data from Poland are excluded from statistical tests due to small sample sizes. Numbers in parentheses represent the number of radio-collared lynx for which data were available.

Area	Area (km ² , mean ± SD)	Maximum length (km, mean ± SD)	Circular diameter (km, mean ± SD)	Length/width ratio (range)
Reindeer	468 ± 240 (8)	38 ± 14 (8)	24 ± 6 (8)	2.8 (1.2-8.0)
Low roe	644 ± 129 (7)	54 ± 15 (7)	29 ± 3 (7)	2.9 (1.1-6.0)
Medium roe	266 ± 155 (12)	28 ± 11 (12)	12 ± 6 (12)	1.7 (1.3-2.3)
High roe (Poland)	74 ± 26 (5)	12 ± 3 (5)	10 ± 2 (5)	1.5 (1.1-1.8)

Home-range sizes varied dramatically between the different eco-regions of Scandinavia (see Table 3), being larger in areas with apparently low prey density (postulated in Linnell et al. 2001 and tested in Herfindal et al. 2005). Therefore, there is a clear need to adjust distance rules to local conditions. The comparison between the Scandinavian and Polish data shows the extreme sensitivity of this distance rule approach to local variation in home-range size. Some of the Scandinavian home ranges were almost an order of magnitude larger than the Polish, while the resulting static distance rules were five times larger.

Although the use of the mean (of all the individual lynx) home-range lengths may be less conservative than the absolute maximal value (of the individual with longest home range), the lengths averaged here are the maximal lengths of the MCP home ranges, which reflect the extreme borders of home ranges and are rarely used in practice. We therefore believe that, if anything, these rules are very conservative. Although our telemetry data are mainly day-bed data, and lynx may use areas by night that lie beyond the range estimated from day data, this is likely to only add a few kilometres to the estimates at most. Being conservative is an acceptable bias in harvest management where conservation is the only objective. However, in the Swedish reindeer herding areas, compensation for depredation is linked to the documented numbers of family groups in the area. In this context, conservative estimates will have economic consequences for reindeer herders and will lead to continued controversy over lynx population size. In such circumstances, it is recommended that static distance rules be supported by the dynamic distance rules.

Dynamic distance rules

Lynx have very irregular movement patterns, tending to be relatively sedentary during the days when

they consume a kill, and then moving further while searching for prey (Pedersen et al. 1999, Jędrzejewski et al. 2002). This leads to much variation in daily movement distances, ranging within 0-55 km. Therefore, we have focused on the mean of the maximum individual straight line movement distances for each temporal interval (numbers of days between observations). This value will make quite conservative family group counts as it is based on maximum movement distances of the individuals. As lynx tend to make a kill every 5-10 days (Breitenmoser & Haller 1993, Okarma et al. 1997, Jobin et al. 2000) cumulative maximum distances moved from a starting point tend to rapidly reach an asymptote. In fact, after only two nights, lynx had moved distances of about 60% of the total distance reached after seven nights (Table 4). As for the static distance rules, the dynamic distance rules varied greatly between regions, with furthest movements in the areas with lowest prey density. Distances moved in the Polish study area were up to one fifth of those from the other areas for the intervals where comparative data existed.

In order to illustrate how the application of the dynamic distance rule works in practice, we calculated the distance between neighbouring females when they were radio-located on the same day in each of the three Scandinavian regions (Table 5). The results clearly show that 1) the average distance between neighbours is greater than the region specific dynamic distance rule, and 2) in > 80% of cases, the neighbours were further apart than the distance rule. This indicates that the application of the dynamic distance rule is likely to achieve accurate separation in the majority of cases. In this test we included all neighbouring females, irrespective of whether they had kittens or not. In real life applications not all neighbours will have kittens, and therefore the risk of error will be smaller (i.e. there is a lower density of family groups than of adult female lynx).

Table 4. Mean and range of the maximum distances moved by individual adult female lynx from a start point to seven consecutive day beds. Only females with > 10 movement events per period class are included.

Area	Number of nights	N	Mean maximum movement from day 1 (km)	Range
Reindeer	1	9	154	7.7 - 35.0
	2	8	174	8.3 - 34.9
	3	7	190	11.1 - 28.7
	4	7	230	15.5 - 31.3
	5	7	271	16.8 - 31.8
	6	7	276	16.5 - 35.4
	7	8	279	17.9 - 42.2
Low roe	1	7	165	10.1 - 26.5
	2	7	242	17.6 - 30.9
	3	7	282	21.6 - 34.0
	4	7	306	21.2 - 36.6
	5	7	324	21.1 - 37.7
	6	7	353	18.7 - 50.0
	7	7	365	20.7 - 55.3
Medium roe	1	11	83	2.8 - 13.6
	2	7	147	7.9 - 16.5
	3	6	160	11.4 - 19.7
	4	7	177	13.3 - 22.0
	5	7	184	13.5 - 24.9
	6	7	188	9.9 - 23.8
	7	6	187	14.6 - 24.9
High roe (Poland)	1	3	73	6.0 - 9.0
	2	3	89	6.8 - 11.3
	3	3	91	6.8 - 11.6
	4	3	87	6.5 - 11.3
	5	3	91	6.6 - 11.3
	6	3	84	6.3 - 11.1
	7	3	96	7.2 - 11.0

Practical considerations and potential biases

One important aspect with the application of this count method is to ensure that observations are made during the times of the year when least errors can be made. Lynx reproduction is highly seasonal throughout Europe, with kittens generally being born in May and June (Arnemo et al. 1999, Reinhardt & Halle 1999, Schmidt 1998). All kittens follow their mothers during the first autumn, and do not usually separate until after late February at the age of ≥ 9 months (Schmidt 1998; J.D.C. Linnell & J. Odden, unpubl. data). No kittens that we have

studied maintained regular contact with their mother after one year of age. Furthermore, males begin associating with adult females in the build-up to the mating season from late February. Therefore, observations collected from October until late February are least likely to contain false positives (two adult lynx in association being recorded as a family group) or false negatives (juveniles having dispersed or having reduced maternal association).

However, even with these limitations on season, there are occasions when independent lynx (adult males and yearlings of both sexes) can travel with adult females for periods of several days (e.g. Pedersen et al. 1999) even outside the mating season. As the tracks of kittens and adults are almost impossible to distinguish based on size, these events could lead to false positives. It is therefore recommended to show caution towards 'family groups' that are detected from only a single observation. As kittens can follow in the exact footsteps of each other and their mother, it is vital that a set of tracks should be snow-tracked for stretches of at least 1 km to determine if it really is from one or more lynx. Determining the number of kittens can require several kilometres of snow-tracking and should therefore only be used with caution as a criteria to separate between different groups. In Norway, we require that tracks of potential family groups be followed for distances of 2 km in all cases, and 3 km in cases where only two lynx are believed to be present (there is a greater chance of a false positive if only two lynx are together, i.e. it is exceptionally rare for three lynx which are not a mother and kittens to be together outside the mating season). Some geographic features such as large ice-free fjords or lakes and high mountain ranges may be useful in separating observations that are closer than the indicated separation distances (Knight et al. 1995). However, care needs to be taken as lynx are good at crossing rivers, frozen fjords or lakes and infrastructure such as roads and railways.

One limitation of these static rules is that they will fail to detect any increases in population size beyond the point where adult female home ranges

Table 5. Average distances (\pm SD) between radio-locations of neighbouring female lynx located on the same day, and percentage of observations further apart than the regionally specific dynamic distance rule (DDR), in the three Scandinavian regions.

Area	Number of neighbours	Number of locations on the same day	Mean distance	Minimum-maximum distance	% observations > DDR
Reindeer	16	310	29.8 (18.1)	0.0 - 97.9	81
Low roe	13	559	37.6 (20.9)	1.5 - 115.5	85
Medium roe	7	122	17.5 (8.7)	1.1 - 55.9	88

form a continuous mosaic across the entire area sampled. Beyond this point, it is unclear if home ranges will decrease in size in a density dependent manner, or if females will become less territorial and tolerate greater home-range overlap. Because of heavy hunting pressure in Norway and the Swedish reindeer husbandry area which effectively limits population growth at present (Andersen et al. 2003), this situation is only likely to occur in central and southern Sweden, but may also be an issue in other parts of Europe where lynx are not hunted. Combining static and dynamic distance rules should overcome this weakness to some extent. Also, in practice, not all adult female lynx will reproduce each year; in fact in some populations and in some years almost 50% will either not reproduce or not be followed by surviving kittens in the winter (Andrén et al. 2002). This will make it easier to separate between neighbouring family groups, especially in saturated territorial mosaics. Under these situations it is also important to consider what these rules are actually estimating. Rather than effectively mapping out the distinct groups (which our analysis indicates that they are effective at when lynx occur at low to medium density), at very high density the rules will produce a conservative estimate of the minimum number of lynx that are likely to have been responsible for the observed tracks, even if the occasional track is assigned to the wrong family. This type of problem is inherent in the nature of minimum counts.

However, if there is an impression that the territorial mosaic is super-saturated and that animals are overlapping, the only alternative is to conduct intensive censuses where animals are separated based on back-tracking in the snow (Liberg & Glöersen 2000). Even this method can have errors associated with it as there is a risk that some animals are not located at all, or that through poor-tracking or bad snow conditions, field personnel will fail to connect track sequences that are in fact continuous. Another alternative is to combine the rule-based minimum counts with an index (e.g. track counts; Linnell et al. 2007) which should not suffer from these problems at high density, and has the advantage that it reflects the density of all age and sex classes of lynx, not just the reproductive females. Another approach at very high density would be to select a random sample of areas and perform sampling based estimates, using either tracks (Becker et al. 1998), or faecal DNA methods (Flagstad et al. 2004). In effect, there are no perfect techniques,

especially those that are cost-effective, and the limitations of each must be borne in mind when making management decisions based on the results.

When applying these rules, a decision will need to be made as to which rule to use. For example, the most conservative would be to apply the absolute maximum values, although a more realistic approach could be to use the mean of the individual maximums. In Norway, the static rules are applied to produce two estimates, a conservative rule (the mean of the maximum values) and a less conservative rule (the mean of the mean maximum length and the mean circular diameter; Brøseth et al. 2003). In Norway, we begin to separate groups where possible using the static distance rules, resorting to the dynamic rules only when observations are spatially close to each other. The choice depends on the degree to which a conservative result is to be prioritised. What is crucial is that the choice of rules is made using home range and movement data from a population that has a similar ecology and prey density, as the results from Poland effectively illustrate how lynx movements can vary widely between study areas. What we do not yet know enough about is the stability of home-range sizes and movement parameters over time, especially in the face of changing lynx density, changing prey density and social disruption. Ongoing research will hopefully shed light on this important source of potential variation.

This method was developed in Scandinavia where tracks in snow are the most common 'observation'. Tracks can be easily validated by trained personnel, and in Norway all accepted observations are checked by wardens from the State Nature Inspectorate. Other types of observation such as photographs of females with kittens, and kittens shot or killed in traffic collisions can also be used as spatially explicit evidence for reproduction. However, for all observations it is important that data are validated. From our experience many visual observations of 'lynx' are of other species, and we have recorded many incidences of hunters mistaking tracks of red foxes *Vulpes vulpes* or wolverine *Gulo gulo* for those of lynx. The application of this methodology for low density species like lynx requires the input of observations from the public. This implies that checking observations is especially important, and that creating a network of experienced personnel to carry out this task is vital (Stahl & Vandel 1998). One important aspect is that, while the public may be motivated to report observations during the first years of such a programme, their interest often decreases with

time. It is therefore desirable to maintain some form of structure in the search for observations (only really suitable in areas where good tracking snow exists), such as organising hunters to take part in large-scale, one-day censuses (e.g. Liberg & Glöersen 2000, Odden et al. 2001), or ensuring that a minimum search effort is made each year (Linnell et al. 2007) by having a network of transects that are examined at least once a year.

In summary, we do not view this as a method with universal application. It requires many observations, a structured reporting system, a species with territorial behaviour and local data on movement patterns. It also has the weakness of not being based on a formal statistical sampling procedure. However, it can potentially work for a wide range of species, and is the only method that we were able to devise to produce acceptable results for an area as large as Scandinavia on an annual basis.

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References

- Andersen, R., Linnell, J., Odden, J., Andrén, H., Sæther, B-E., Moa, P.F., Herfindal, I., Kvam, T. & Brøseth, H. 2003: Gaupe - bestandsdynamikk, bestandsutvikling og høstingsstrategier. - Norsk institutt for naturforskning fagrapport 059, 29 pp. (In Norwegian).
- Andrén, H., Linnell, J.D.C., 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.
- Arnemo, J., Linnell, J.D.C., Wedul, S.J., Ranheim, B., Odden, J. & Andersen, R. 1999: Use of intraperitoneal radio-transmitters in lynx kittens *Lynx lynx*: anaesthesia, surgery and behaviour. - *Wildlife Biology* 5: 245-250.
- Becker, E.F. 1991: A terrestrial furbearer estimator based on probability sampling. - *Journal of Wildlife Management* 55: 730-737.
- Becker, E.F., Spindler, M.A. & Osborne, Y.O. 1998: A population estimator based on network sampling of tracks in the snow. - *Journal of Wildlife Management* 62: 968-977.
- Breitenmoser, U. & Haller, H. 1993: Patterns of predation by reintroduced European lynx in the Swiss Alps. - *Journal of Wildlife Management* 57: 135-144.
- Breitenmoser, U., Kazensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. 1993: Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. - *Journal of Zoology (London)* 231: 449-464.
- Brøseth, H., Odden, J. & Linnell, J. 2003: Minimum antall familiegrupper, bestandsestimat og bestandsutvikling i Norge 1996-2002. - Norwegian Institute for Nature Research Oppdragsmelding 777, pp.1-29. (In Norwegian).
- Bunnefeld, N., Linnell, J.D.C., Odden, J., van Duijn, M.A.J. & Andersen, R. 2006: Risk-taking by Eurasian lynx in a human-dominated landscape: effects of sex and reproductive status. - *Journal of Zoology (London)* 270: 31-39.
- Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerstrom, P. & Ellegren, H. 2004: Colonization history and non-invasive monitoring of a reestablished wolverine population. - *Conservation Biology* 18: 676-688.
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. 2005: Prey density, environmental productivity, and home range size in the Eurasian lynx (*Lynx lynx*). - *Journal of Zoology (London)* 265: 63-71.
- Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. - Springer, Berlin, 450 pp.
- Jędrzejewski, W., Schmidt, K., Okarma, H. & Kowalczyk, R. 2002: Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). - *Annales Zoologica Fennici* 39: 29-41.
- Jobin, A., Molinari, P. & Breitenmoser, U. 2000: Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. - *Acta Theriologica* 45: 243-252.
- Kenward, R.E. & Hodder, B. 1996: RANGES VI: Program Manual. - Institute of Terrestrial Ecology, United Kingdom.
- Knight, R.R., Blanchard, B.M. & Eberhardt, L.L. 1995: Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. - *Wildlife Society Bulletin* 23: 245-248.
- Kvam, T. 1996: Bestandsestimat for gaupe 1995-96. - Unpublished NINA report, pp.1-19. (In Norwegian).
- Landa, A., Tufto, J., Franzén, R., Bø, T., Lindén, M. & Swenson, J.E. 1998: Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. - *Wildlife Biology* 4: 159-168.
- Liberg, O. & Glöersen, G. 2000: Rapport från lo- och varginventeringen 2000. (In Swedish with an English summary: Report from lynx and wolf census 2000). - Svenska Jägarförbundet, 18 pp.

- Linnell, J.D.C., Andersen, R. & Kvam, T. 1999: Eurasian lynx in Norway: the realities of managing a large carnivore in a multi-use landscape. - *Cat News* 30: 19-20.
- Linnell, J.D.C., Andersen, R., Kvam, T., Andrén, H., Liberg, O., Odden, J. & Moa, P. 2001: Home range size and choice of management strategy for lynx in Scandinavia. - *Environmental Management* 27: 869-879.
- Linnell, J.D.C., Fiske, P., Herfindal, I., Odden, J., Brøseth, H. & Andersen, R. 2007: An evaluation of structures snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. - *Wildlife Biology* 13: 456-466.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. 2000: Conservation of biodiversity in Scandinavian boreal forests: Large carnivores as flagships, umbrellas, indicators, or keystones? - *Biodiversity and Conservation* 9: 857-868.
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. & Andersen, R. 2002: Lynx depredation on domestic sheep in Norway. - *Journal of Wildlife Management* 66: 98-105.
- Odden, J., Solvang, H., Maartmann, E., Wabakken, P., Linnell, J., Andersen, R., Haagenrud, H., Lundqvist, O. & Solberg, H.O. 2001: Registrering av ulv og gaupe i Hedmark 2001: Rapport fra registrering 13. januar 2001. - Fylkesmannen i Hedmark Miljøvernavdelingen Rapport, 11/2001, pp.1-26. (In Norwegian).
- Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R. & Jędrzejewska, B. 1997: Predation of Eurasian lynx on roe deer *Capreolus capreolus* and red deer *Cervus elaphus* in Białowieża Primeval Forest, Poland. - *Acta Theriologica* 42: 203-224.
- Östergren, A. & Segerström, P. 1998: Familjegrupeer av lodjur - metod för antalsbedämningar. - Länsstyrelsen Västerbottens län Meddelande 2: 1-5. (In Swedish).
- Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P. & Lindén, M. 1999: Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. - *Wildlife Biology* 5: 203-212.
- Reinhardt, I. & Halle, S. 1999: Time of activity of a female free-ranging lynx (*Lynx lynx*) with young kittens in Slovenia. - *Zeitschrift für Säugetierkunde* 64: 65-75.
- Schmidt, K. 1998: Maternal behaviour and juvenile dispersal in the Eurasian lynx. - *Acta Theriologica* 43: 391-408.
- Schmidt, K., Jędrzejewski, W. & Okarma, H. 1997: Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval Forest, Poland. - *Acta Theriologica* 42: 289-312.
- Smirnov, E.N. & Miquelle, D.G. 1999: Long term monitoring to assess trends and population dynamics of the Amur tiger in Sikhote-Alin Zapovednik, Primorski Krai, Russia. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge, pp. 61-70.
- Stahl, P. & Vandel, J.M. 1998: Distribution of the lynx in the French Alps. - *Hystrix* 10: 3-16.
- Stahl, P., Vandel, J.M., Herrenschmidt, V. & Migot, P. 2001: The effect of removing lynx in reducing attacks in sheep in the French Jura mountains. - *Biological Conservation* 101: 15-22.
- Stander, P.E. 1998: Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. - *Journal of Applied Ecology* 35: 378-385.
- Swenson, J.E. & Andrén, H. 2005: A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. - In: Woodroffe, P., Thirgood, S. & Rabinowitz, A. (Eds.); *People and wildlife: conflict or coexistence*. Cambridge University Press, Cambridge, pp. 323-339.
- Taylor, B.L. & Gerrodette, T. 1993: The use of statistical power in conservation biology: the vaquita and northern spotted owl. - *Conservation Biology* 7: 489-500.
- Wiegand, T., Naves, J., Stephan, T. & Fernandez, A. 1998: Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Corillera Cantabrica; Spain. - *Ecological Monographs* 68: 539-570.
- 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.