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Tracks in snow and population size estimation: the wolf *Canis lupus* in Finland

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The estimation of large carnivore populations presents major logistical challenges. We examined trends in the wolf *Canis lupus* population in Finland using two independent methods. We compared track indices from an annual wildlife winter census based on a constant, nationwide network of transect lines (wildlife triangles) with the number of reproductions confirmed to occur in the same year during 1996 to 2009. Nationwide, and in the eastern management zone, which is the core area of Finnish wolves, the frequency of wolf tracks in wildlife triangles (% of all triangles counted in a given year having wolf tracks) predicted quite well the log transformed number of reproductions taken place in these areas (adjusted R^2-values for linear regression models 0.59 and 0.68, respectively), while not for the western management zone ($R^2 = 0.38$). However, although mean wolf densities were low (< 1 wolf/1000 km^2 nationwide and < 3 wolves/1000 km^2 in the eastern zone), track indices could detect the major trends in Finland's wolf population. A clear reason for this was the substantial changes in population size during the study period.

Being rare and elusive, populations of large carnivorous mammals are difficult to observe due to major methodological challenges in population estimation (Linnell et al. 1998, Thompson 2004, Kindberg et al. 2009). Population size is a main factor determining the well-being and extinction risk of a population (Reed et al. 2003). Various indices can be used to describe population trends. Because Finland is independently responsible for wolf population estimates and management, the number of individuals in the country is the most useful measure, although the population is shared with Russia (Pulliainen 1980, Wabakken et al. 2001, Aspi et al. 2009). Methods used in large carnivore population monitoring vary from opportunistic observations (Linnell et al. 1998), camera traps (Karanth 1995, Rios-Uzeda et al. 2007), a variety of non-invasive genetic methods (Solhberg et al. 2006, Swenson et al. 2011), and extensive radiotracking (Smith et al. 2003, Wydeven et al. 2009).

Historically, wolves *Canis lupus* and other large carnivores were exterminated in many European countries, but during recent decades they have been gradually returning due to their improved legal status and changes in public attitudes (Breitenmoser 1998, Boitani 2003). Recovery of wolf populations has also occurred in northern Europe, but populations in Scandinavia and Finland have remained fragmented (Wabakken et al. 2001), probably due to extensive poaching (Liberg et al. 2011).

To assess population viability and extinction risks, sound monitoring is essential. However, only a few reliable methods exist for estimating population size of large carnivores (Kunkel et al. 2005). Observational data, if corrected for effort, may yield accurate estimates when large numbers of volunteers are available (Kindberg et al. 2009). Monitoring methods for wolves include howling responses (Harrington and Mech 1982, Ausband et al. 2011), counts of packs (Mech 1966, Peterson 1977, Wabakken et al. 2001), surveying predicted rendezvous sites of packs (Ausband et al. 2010), determination of home range density (Ballard et al. 1987, Fuller 1989), and tracking by radio and in snow (Wabakken et al. 2001). Kunkel et al. (2005) reviewed 396 papers related to wolf monitoring; the most commonly used method was territory mapping using radio telemetry. Pack size and family relationships have also been estimated by means of non-invasive genetic sampling at rendezvous sites (Stenglein et al. 2011). However, in very few cases have methods been formally tested (Becker et al. 1998, Wilson and Delahay 2001, Kunkel et al. 2005).

Although wolves exist at low densities, a high volume of winter transect lines might result in track indices that are consistent with major trends in the population size (Högmander and Penttinen 1996, Danilov 2003, Aspi et al. 2009). In Finland, wolf tracks are recorded as part of an annual wildlife winter census based on a constant, nationwide network of transect lines known as wildlife triangles (Lindén et al. 1996). Current population estimates, however, are based primarily on the number of reproductive packs (Kojola 2005), which are fully independent of the recording of wolf tracks

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in winter transects. In Finland, where the mean litter size in early winter is four pups and the proportion of pups in a population is about 40%, a rough estimate of population size can be achieved by multiplying the number of litters by ten (Kojola 2005). To the best of our knowledge, the wolf population trend has not previously been examined by using two independent methods. In this study, we examined how wolf track indices correlate with the estimated number of annual litter reproduction, a fundamental measure in estimating the conservation status of animal populations.

Study area and methods

The wildlife triangle scheme has been the main technique for monitoring populations of forest game species in Finland since its introduction in 1989. The basic unit in the scheme is an equilateral triangle with four-kilometer compass-straight sides, thus having a total length of 12 km. The total network consists of approximately 1700 triangles with a good nationwide coverage (Fig. 1). About half of the triangles are studied annually in the winter, in most cases by skiing. The transect lines are permanently marked in the field and randomly sample forested environments (Lindén et al. 1996).

In winter counts, snow tracks of about 25 active mammal species are recorded. Track density, the number of crossings per 24 h per 10 km, is used as an index of relative abundance for mammals. There are two ways to standardize the time for tracks to accumulate. First, in the pre-checking of a line, all existing tracks are covered by snow or clearly marked, and in the formal count day or two later, any new crossings are recorded. Alternatively, the count can be performed without pre-checking if a snowfall that has completely covered all of the old tracks one or two days before the count. The winter count period is between 15 January and 28 February, and in northern Finland the inventory period may continue up to 15 March. Further details are provided in Lindén et al. (1996).

During 1989–2010, 17 256 winter counts were completed in Finland, corresponding to a transect length of about 200 000 km. Wolf tracks were found in 306 counts and the total number of tracks was 832. When wolf tracks were observed, the number of tracks per triangle (12 km) varied from 1 to 23.

Reproduction by wolves has been systematically recorded in Finland since 1996 (Fig. 2). The Finnish Game and Fisheries Research Institute (FGFRI) has a volunteer network of about 1700 large carnivore personnels who have annually reported from 1045 (1996) to 5439 (2006) wolf observations using a form and 1:200 000 map. The main function of these data is to map reproductive packs and territory marking pairs, and in most cases the litter observed all before the first snowfall. In early winter (October–January), some new family packs are found. During 1998–2011, FGFRI collared 125 wolves with VHF (very high frequency) (VHF) and GPS (global positioning system) transmitters. Of 96 packs that reproduced at least once during 1998–2011, one or more wolves were collared during this period from 31 packs (32.3%). The capture methods have been described in detail elsewhere (Kojola et al. 2006). Data on the territory boundaries of radio-collared wolves combined with snow tracking by field assistants to avoid double-counting. A great majority



Figure 1. Wildlife triangle transect line network in Finland, each having 12 km transect line.

of wolves (> 90%) in Finland leave their natal pack before they reach the age of 16 months (Kojola et al. 2006), but with the smallest packs (3–4 wolves) it is sometimes impossible to conclude whether reproduction has occurred. Unclear cases constituted 6.0% of all potential reproductions (n = 199) and were excluded. The number of annual reproductions is based on the assumption that only one litter is born in a wolf pack during a given year, given that no two-litter packs were found during the study.

We calculated the proportion of all triangles surveyed that had wolf tracks in a given winter, both for the whole of Finland and separately for the western and eastern management areas (Fig 3). To correct the distribution of the dependent variable, we log transformed the number of litters and regressed the resultant values against the

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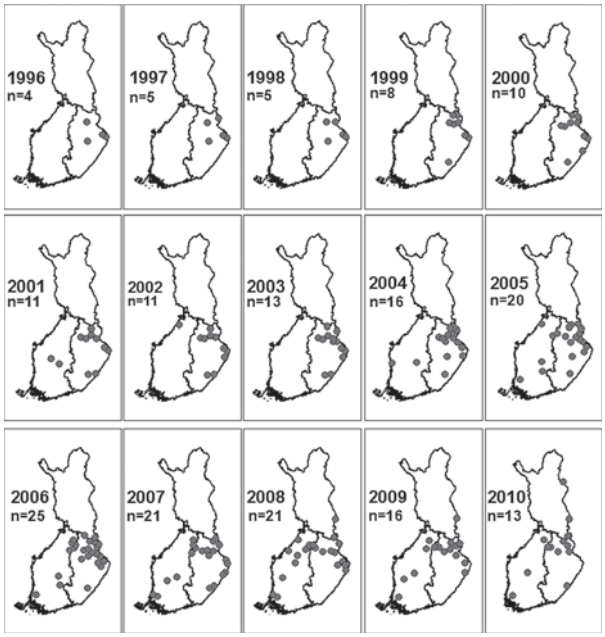


Figure 2. Litters in Finland during 1996–2010.

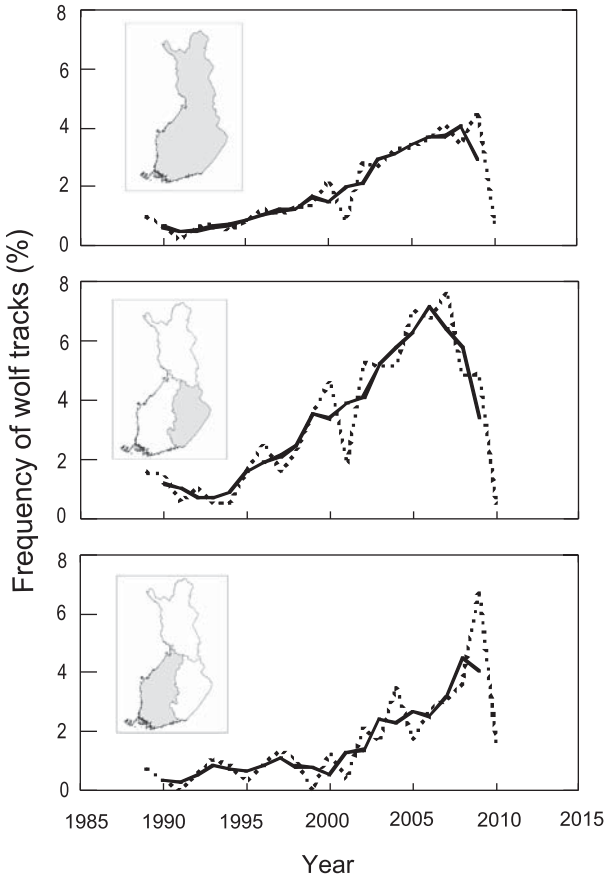


Figure 3. The proportion of wildlife triangles with wolf tracks as original (1989–2010) and smoothed (1990–2009) values for the whole of Finland and the eastern and western management zones.

proportion of triangles with wolf tracks in the previous winter. Linear regression models fitted best with data. We examined residuals and did not find significant autocorrelations.

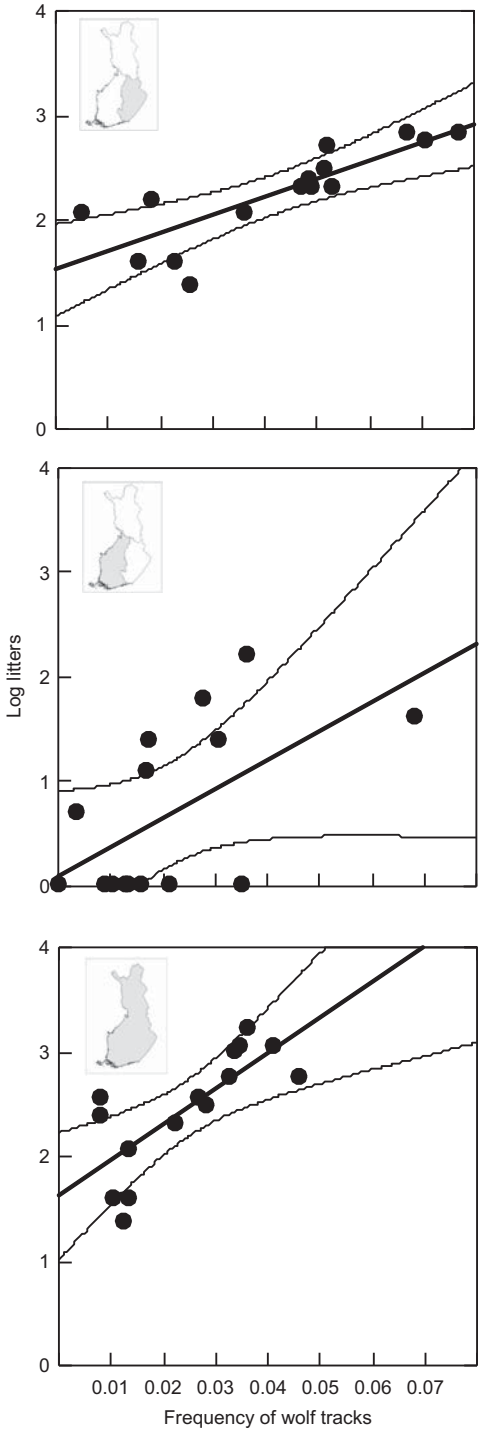


Figure 4. The relationship between the frequency of wolf tracks and the number of yearly litters (log transformed) during 1996–2009 in Finland, showing the adjusted R^2-values and 95% confidence limits revealed by linear regression models.

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Table 1. Output of linear models to study whether the number of reproductions of wolfs (i.e. dependent variable) is associated with the proportion of wolf occupancies in the wildlife triangles (i.e. independent variable) separately in the western, eastern management zones of Finland and in the entire Finland (data pooled from western, eastern and northern management zones) during 1996–2010 (n = 15 years in all models, see methods). The values of slopes (β) and their standard errors (SE) are reported. The significance of the predictor variable was assessed with the *F* statistics between the null model (intercept only) and the full model (a model with predictor variable). 95% confidence intervals of slopes (β) and R^2 of the models are reported. Dependent variables were log-transformed before testing.

Region	β	SE	$F_{1,13}$	p	95% confidence intervals
Western[a]	31.1550	10.9940	8.0300	0.0141	7.4040, 54.9060
Eastern[b]	15.6200	2.9600	27.9000	0.0002	9.2300, 22.0000
Entire Finland[c]	30.9650	7.1780	18.6000	0.0008	15.4600, 46.4700

[a]$R^2 = 0.382$, [b]$R^2 = 0.682$, [c]$R^2 = 0.589$

Results

During 1996–2000, wolves only reproduced within the eastern wolf management zone (Fig. 2). Since then, the distribution of the reproductive population has expanded to the western management zone. The smoothed frequency of wolf tracks in Finland increased by 11% per year during 1996–2006 and then decreased by 6% per year during 2007–2009. The number of annual litters behaved similarly, increasing by 18% during 1996–2006 and decreasing by 11% during 2007–2009. The track frequency also grew in the eastern management zone during 1996–2006, while it declined from 2007 to 2009 (Fig. 3). In the western zone, growth continued until 2008.

In the eastern management zone and on a countrywide scale, the number of litters per year correlated well with the frequency of wolf tracks in wildlife triangles (Fig. 4, Table 1). This frequency accounted for 59% and 68% of the variation in the log transformed number of annual litters in the eastern management zone and the entire country, respectively. In the western management zone, however, the corresponding figure was only 38% (Table 1). The difference between the eastern and western zones might be due to lower number of litters in the west which would increase randomness in the process.

Discussion

The magnitude of changes in wolf population size in Finland was considerable. The reproductive population increased five-fold within 10 years and then decreased by 40% within four years. Such a rate of increase (18% per year) is consistent with a legal harvest that varied between 10–20% of the population estimate during 1996–2005 (Kojola 2005, see also Fuller et al. 2003). Fluctuating dynamics are rare in present-day populations of wolves in Europe, where they are described as being stable or increasing (Boitani 2003, Salvatori and Linnell 2005, Liberg et al. 2011). The decrease of 15% per year during 2006–2009 when the legal harvest was < 10% per year (Kojola unpubl.), indicates that wolf numbers were primarily controlled by poaching. Increased dispersal from Finland could not account for the observed population decline, because only a few wolves have annually been observed to move to the west (Scandinavia; Seddon et al. 2006).

The observed correlation between track frequency and the count for the number of litters does not mean that the number of litters was correctly estimated. Calculations of the effective population size based on the genetic analysis of samples collected from 1996–2005 yielded about 40 breeders, which is at the same level as the estimated number of litters (Aspi et al. 2006). They used the temporal approach and several statistical methods to estimate the variance effective size of the population using data that were received typing mostly wolves that were legally shot.

Without any other monitoring data, winter track counts could reveal the recent changes in Finland's wolf population. The residual variance for the applied linear models might, for example, be due to variation in weather and snow conditions. However, because these vary across different locations (Rasmus et al. 2004) it was not necessary to take such variation into account in the current, large-scale consideration.

Track indices may provide a sound option when continuous pack-based monitoring of the population size is not possible. Checkpoints with intervals of some years and indices for trends between checkpoint years could make a combination that works adequately when a large number of field volunteers are available for observation (Kindberg et al. 2009, 2011). Winter track counts were able to reveal trends in the Finnish wolf population, although the mean population density was extremely low, being less than one wolf per 1000 km^2. Wolves live in packs and therefore have a highly clustered distribution pattern. This increases the randomness in the occurrence of wolf tracks. Systematic track counts seemed to indicate major trends, even with the small and widespread wolf population existing at low densities.

Densities of large carnivores can be estimated using network sampling and helicopter or fixed-wing aircraft survey for tracks in snow (Becker et al. 1998, Patterson et al. 2004, Golden et al. 2007). This method provides an accurate and repeatable way to estimate wolf density but tracking wolves in forested areas can be time-consuming and therefore relatively expensive (Patterson et al. 2004).

Cryptic poaching of wolves may occur in pulses that lead to the removal of an entire pack during late winter after the wildlife triangles have been counted (Kojola et al. unpubl.). This might have an impact on the relationship between track frequency and the number of litters, especially in the western management zone, where wolves have recently occupied

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territories. In such areas, human acceptance is often even poorer than in regions where people are more used to the presence of wolves (Bisi et al. 2007).

There are statistical methods to convert the track density of mammals into absolute population density. The first application was already introduced in the 1930s (Formosov 1932) and the technique has been widely used in Russia. Högmander and Penttinen (1996) presented a thorough description of the reasoning and also introduced methods to estimate the variance in track density. Following the principles of stereology, track density (the number of transect crossings per unit length) can be converted to track intensity (the total length of track of a species per unit area (e.g. square kilometers) (see Weibel 1980 for the basics). After this, the biological parameter needed in the conversion is the estimated (or measured) average movement distance per 24 h for individuals of the focal species. There are some data concerning mid-winter daily movements of wolves in Finland based on radio-telemetry, but the annual data are too scanty to produce population size estimates; the annual number of wolf tracks is low and strongly influenced by chance (which is why we used the smoothing technique in for visualization the trends). Clear changes that occurred in Finland's wolf population can be detected also in track indices.

To test this technique, we pooled data from the years 2002–2009, when the population estimates and also the numbers of snow tracks along wildlife triangles were highest. South of the reindeer husbandry area (with low numbers of wolves), 32 771 km of snow count transects were inspected and 552 wolf tracks were observed. The mean population estimate during these years was 205 individuals. Using these figures in the conversion formula, the balance was achieved with a mean daily distance of movement by wolves of 25.9 km. Interestingly, this is close to figures published in several studies (Poland, 27 km in Jedrzejewski et al. 2001, central Italy, Ciucci et al. 1997), and also consistent with our data (Kojola et al. unpubl.). It therefore appears that the assumptions underlying the conversion logic may be valid. However, because the mean annual track numbers are low (mean 69 during 2002–2009 when the population size was largest) and strongly affected by chance, we have been reluctant to make annual population estimates based on track observations. Track indices may provide a sound option when continuous monitoring for population trends is not possible. Results yielded in winter track counts were correlated with population estimates based on other methods despite the mean population density being extremely low, with less than one wolf per 1000 km^2. When mapping territories of packs and pairs, and snow-tracking for pack size can be performed at annual basis (Wabakken et al. 2001, Wydeven et al. 2009, Liberg et al. 2012), track indices do not provide essential data.

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