Back-calculation of large carnivore populations in Finland in 1865–1915

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We estimated population abundances of the bear, lynx, wolf and wolverine in Finland in 1865–1915 by combining official bounty statistics with verified knowledge on annual intrinsic growth and mortality rates of these species. We used an annual backwards iteration method for all of these species, starting from a systematically-adjusted population size in 1915. According to our results, there had been approximately 1000 bears and an equal number of wolves in Finland until their decline started around 1875. As for lynx, it appears that its population increased markedly in the first quarter of our study period, but seemed not to have exceeded 3500 in the 19th century. Concurrently with the assumed strong growth of the lynx population, a marked increase took place in sheep and goats killed by large carnivores. The number of wolverines prior to 1885 appears to have been varying between 300 and 600.

Introduction

In spite of their recent increase in the beginning of the 21st century, the four large terrestrial carnivore species of Finland — brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolf (*Canis lupus*) and wolverine (*Gulo gulo*) — are currently classified as nationally threatened (Rassi *et al*. 2010). It is, therefore, particularly meaningful to try to find out more about the actual abundances of their apparently-viable populations before the decline that supposedly started almost 150 years ago. The hunting bag of carnivores dwindled from the 1870s or 1880s towards the early years of the 20th century. There is no reason to assume that hunting effort on these species, or their susceptibility to hunting, would have decreased

in that period, rather the contrary. Therefore, there appears to be a common understanding that large carnivore bounty records can be considered a density-dependent time series portraying changes in population abundance — particularly the decrease in this case (*see* e.g. Palmén 1910, Palmgren 1915, Pulliainen 1974).

Although the character of large carnivore population trends can be construed from changes in bag records, reliable estimates of actual population sizes in the past are scarce. Kojola (2005) calculated that since annual wolf harvesting in Finland was approximately 400 for two decades in the 1850s and 1860s, the abundance at that time may have been ca. 1000 considering that the wolf population can withstand 29%–34% sustained hunting mortality (Fuller 1989, Śmie-

tana & Wajda 1997, Mech 2001). Based on a genetic analysis of the history of effective wolf population size, Aspi *et al.* (2006) stated that the Finnish wolf population may have even exceeded 1400 individuals prior to the period of population decline in the latter half of the 19th century. A later study by the same group (Jansson *et al.* 2014) suggests that during the last 150 years, mean size of the wolf population was ~300–900 individuals. According to the brown bear bounty records and the estimate that the bear population in Finland can sustain 10% annual harvests (Kojola & Heikkinen 2006), Kojola (2007) calculated that in the mid-1800s the bear population was approximately 1400–1500. We are not aware of similar approximations of past population sizes of the lynx and wolverine in Finland.

In this study, we answer the following questions: (1) How large were the large carnivore populations in Finland in the 1860s and 1870s? (2) At what pace did they start to decline? (3) Do our data provide any evidence of intraguild interactions among these four species? To answer these questions, we used population trajectories for 1865–1915, which we constructed with the help of historical bounty records. As described in more detail in the Material and methods below, we assumed these records to be both accurate and profoundly density-dependent. This information on human-caused mortality was combined with verified knowledge on intrinsic growth rates as well as on natural mortality rates of these species. We use annual backwards iteration, i.e. back-calculation starting from a certain point of time with known or assumed population abundance. In our case it was the year 1915 for all four species.

Back-calculations that make use of bounty data or other harvest records were used for estimating the past population levels of many aquatic mammals (e.g. Smith & Polachek 1979, Reijnders 1994, Gjertz & Wiig 1998, Harding & Härkönen 1999, Kokko *et al.* 1999, Martien *et al.* 1999, Slooten & Dawson 2009) as well as one terrestrial mammal, the Mongolian gazelle *Procapra gutturosa* (Milner-Gulland & Lhagvasuren 1998), but when it comes to large terrestrial carnivores this kind of calculations appear to be uncommon. We are not aware of other examples than those mentioned above (Kojola 2005, 2007).

Material and methods

We used a back-calculation method for estimating past population abundances of the bear, lynx, wolf and wolverine. Even at its simplest, predicting the trajectory of population abundance from N_t to N_{t+n} as well as the back-calculation from N_t to N_{t-n} requires information on total mortality and intrinsic growth rate of the population during the examined period. A starting point for the back-calculation is a simple equation that can be used for temporal abundance changes of populations that are harvested between breeding seasons:

$$N_{t+1} = N_t r_t - k_t - N_t r_t m_t, \qquad (1)$$

where r is the coefficient of annual intrinsic growth rate of an unharvested population (acknowledging natural rates of births, deaths, immigration and emigration), k is the number of individuals killed by man, and m is the coefficient of additional mortality.

Statistics on bag records *k* and livestock damages

The first hunting bounties in Finland were introduced for the brown bear and wolf in the mid-1600s (Royal Decree of Hunting 1647). The lynx, wolverine, red fox, pine marten and approximately 60 species of raptors and other avian pests were included into bounty schemes in three separate legislative reforms during the next couple of centuries. The list of bounty species varied a lot through time, and the bounty scheme finally came to an end in 1975. Pohja-Mykrä *et al.* (2005) gave a thorough review on the history and development of hunting bounties in Finland.

In this study, the annual number of killed large carnivores is based on an official bounty statistics of 1866–1915 (Statistical Yearbooks of Finland 1860–1926). It provided us with the data on human-caused mortality of large carnivores

in Finland during those years (Table 1). Bounty records are available also after 1915, but since tumultuous times and disorder in society tend to affect pest control intensity (Pohja-Mykrä & Mykrä 2006), we decided to end the study period before the troubled times of 1917–1918 (gaining independence and the Civil War) in Finland.

In hunting bounty regimes there is an inbuilt certainty that the accumulated records are accurate. Presumably very few bagged individuals remained unrecorded, and fraudulent double-recording, on the other hand, was made difficult by requesting physical proof of the kill in the form of cut-off body parts or permanently marked pelt (Imperial Declaration on Hunting 1898, Hintze 1906). Mistakes in species identification can, of course, reduce the scientific value of past bag records; there is a miserable example of that relating to birds of prey in Finland (Suomalainen 1916), but when it comes to large mammals misidentification must have been very rare for obvious reasons (Erkamo 1939). In this study, it is thus safe to assume that official bounty statistics give a reliable estimate of human-caused deaths of all four large carnivores in Finland.

In this 50-year data series, there were two imperfections that we dealt with in the following way. First, in the ten-year period of 1866–1875, bounty statistics were published only in five-year intervals without any information on annual numbers of killed individuals. Therefore, for the periods 1866–1870 and 1871–1875 we generated mean annual bag records by dividing the pooled five-year data evenly across each period. As a result, a year-to-year variation in bag records during those two periods is absent. Secondly, in 1876, bounty data from the three southernmost counties are missing from the official statistics. To reduce the effect of this shortage, we extrapolated the missing 1876 values for these three counties from their own data of the following four years 1877–1880. As a result of the extrapolation we added 2 bears, 130 lynxes, 250 wolves and 0 wolverines to the total 1876 bag of the whole country (Table 1).

Even if all large carnivores were highly valued and sought after game because of the bounty and their valuable fur, it is possible that a certain small proportion of the bag did not end up in the statistics. It is also possible that occasionally a wounded animal escaped its hunter but died soon after. Such animals are both absent from the statistics and the breeding population. Generally speaking it is obvious that this kind of a statistic is always a minimum estimate of killed animals. References on wounding and loss rates in hunting big game are limited. However, e.g. results by Robinette and Olsen (1944), as cited in Pederson and Harper (1978), and those of Unsworth *et al.* (1993) suggest that wounding and loss rates in deer and elk hunting in the USA are often somewhere between 15% and 20%. When it comes to hunting of large mammalian carnivores in Finland, most of the hunting has been, and still is, carried out when the ground is covered with snow. In such circumstances, the probability of recovering a wounded mammal is high — particularly so if the hunter is well-motivated, as the bounty hunters at that time must obviously have been. Therefore, we estimated the maximum wounding and loss rate to have been 10%. For this reason we added a constant 10% to all annual numbers of killed carnivores, and used these adjusted values for the back-calculations (Table 1). The effect of this +10% adjustment of bag records on the modelled mean size of populations was less than 10% in each of these species: +7.5% for bear, +7.5% for lynx, +8.4% for wolf and +7.2% for wolverine.

As for searching further evidence for the authenticity of the modelled population trends, we gathered data on the annual livestock damages caused by large carnivores. We then examined possible correlation between the damage trends and changes in the modelled population abundance. Data on livestock damages are available from the same official statistics as the bounty data (Statistical Yearbooks of Finland 1860–1926). During the study period, detailed records on livestock damage are available until 1900. Cattle, horses, sheep, goats, pigs, reindeer and fowl are separated in the statistics. We were only interested in the first four classes as they were the ones that occurred throughout the country and were also the primary species in free-ranging forest pasturing. First, we combined the classes of cattle and horses to represent large-sized livestock, and then we put together the data on sheep and goats to represent smaller-sized

Table 1. Data on human-caused mortality of brown bear, lynx, wolf and wolverine in Finland in 1866–1915. The data are based on bounty statistics. In 1866–1876 the statistics were published in five-year intervals. For this reason, the 1866–1870 and 1871–1876 annual data (in italics) are a result of dividing the pooled five-year data evenly across each period. The 1876 bounty data from three counties are missing from the official statistics. Therefore, by extrapolating from the 1877–1880 data for these three counties we added 2 bears, 130 lynxes, 250 wolves and 0 wolverines to the 1876 'killed' values. A constant 10% for all annual numbers of killed carnivores were added to the records and these adjusted values were used for the back-calculations. *See* text for details.

	Bear		Lynx		Wolf		Wolverine	
	killed	+10%	killed	+10%	killed	+10%	killed	+10%
1866	*85*	*93*	*46*	*51*	*311*	*342*	*23*	*25*
1867	*85*	*93*	*46*	*51*	*311*	*342*	*23*	*25*
1868	*85*	*93*	*46*	*51*	*311*	*342*	*23*	*25*
1869	*85*	*93*	*46*	*51*	*311*	*342*	*23*	*25*
1870	*85*	*93*	*46*	*51*	*311*	*342*	*23*	*25*
1871	*84*	*93*	*77*	*85*	*282*	*310*	*39*	*43*
1872	*84*	*93*	*77*	*85*	*282*	*310*	*39*	*43*
1873	*84*	*93*	*77*	*85*	*282*	*310*	*39*	*43*
1874	*84*	*93*	*77*	*85*	*282*	*310*	*39*	*43*
1875	*84*	*93*	*77*	*85*	*282*	*310*	*39*	*43*
1876	108	119	182	200	370	407	83	91
1877	145	160	210	231	342	376	80	88
1878	71	78	146	161	297	327	76	84
1879	133	146	174	191	388	427	96	106
1880	115	127	301	331	321	353	120	132
1881	136	150	478	526	192	211	119	131
1882	85	94	407	448	128	141	76	84
1883	73	80	451	496	91	100	48	53
1884	105	116	417	459	78	86	62	68
1885	80	88	528	581	83	91	46	51
1886	74	81	485	534	55	61	26	29
1887	78	86	325	358	145	160	34	37
1888	93	102	246	271	48	53	50	55
1889	87	96	246	271	30	33	29	32
1890	62	68	138	152	26	29	42	46
1891	106	117	131	144	12	13	59	65
1892	94	103	135	149	14	15	35	39
1893	58	64	115	127	12	13	44	48
1894	63	69	79	87	4	4	30	33
1895	49	54	84	92	11	12	44	48
1896	91	100	86	95	15	17	65	72
1897	62	68	61	67	20	22	61	67
1898	68	75	68	75	17	19	58	64
1899	82	90	67	74	15	17	63	69
1900	54	59	86	95	4	4	54	59
1901	43	47	70	77	21	23	47	52
1902	54	59	67	74	12	13	63	69
1903	53	58	39	43	8	9	80	88
1904	19	21	23	25	5	6	43	47
1905	19	21	36	40	10	11	61	67
1906	22	24	34	37	20	22	34	37
1907	21	23	47	52	45	50	55	61
1908	19	21	47	52	35	39	34	37
1909	40	44	52	57	45	50	95	105
1910	27	30	46	51	10	11	34	37
1911	26	29	14	15	16	18	46	51
1912	22	24	18	20	12	13	44	48
1913	31	34	13	14	21	23	125	138
1914	31	34	13	14	29	32	73	80
1915	13	14	9	10	6	7	16	18

domestic animals vulnerable to large carnivore predation. Bears and wolves are assumed to be the principal adversaries of the former combined class, whereas the latter are preyed upon by all four carnivores (Kaczensky 1999).

Similarly as with the bounty records, the livestock damage statistics in the ten-year period of 1866–1875 are available only in five-year intervals without any information on annual numbers of killed livestock. We generated mean annual damage records for the periods 1866–1870 and 1871–1875 by dividing the pooled five-year data evenly across each period.

The annual data on livestock damages as well as most of the population abundance data were not normally distributed. Therefore, only calculating of Sperman's rank-order correlation between damages and modelled carnivore abundances was possible.

Additional mortality *m* and intrinsic growth rate *r* in earlier studies

We carried out a literature survey of each species' intrinsic population growth and mortality rates that we would need for the calculation. Particularly we searched references on the mean rates of annual total mortality that these species are known to be able to sustain for extended periods of time without any substantial decline. After finding valid references, we defined a range for each species' annual intrinsic population growth: 10%–16% for the bear, 10%–17% for

the lynx, 30%–45% for the wolf and 10%–25% for the wolverine (*see* Table 2 for references). This apparently means that each species is able to compensate similar percentages of annual harvest mortality by next year's breeding. Yet for cautionary reasons we employed a coefficient of additional mortality *m* into the equation; 1%–3% for the bear, and 1%–5% for the lynx, wolf and wolverine (Table 2). This provides a necessary margin to avoid perhaps too low sizes of the past populations and, thus, a too optimistic impression about the ability of these species to withstand hunting offtake in the late 1800s.

Intrinsic growth rate *r* calculated from recent census data

In addition to the earlier research (*see* Table 2), we were also able to approximate intrinsic growth rate of Finnish brown bear, lynx and wolverine populations by utilizing recent census data, and in the case of the former two species also the hunting bag data of Finland. These statistics were provided by the Natural Resources Institute Finland and the Finnish Wildlife Agency, and they were compiled in Liukkonen *et al.* (2006), Mykrä *et al.* (2006), Pohja-Mykrä and Kurki (2008), and Pohja-Mykrä and Kurki (2014).

The 1978–2012 abundance trajectories of the bear and lynx are fairly similar in shape. Both species increased in the early 1990s. The year 1996 precedes a stable/modestly increasing ten-year phase, which is followed by a rapid

Table 2. Species' annual growth rate (*r*) and additional mortality rate (*m*) used in the back-calculations. We searched references for the rates of annual mortality that each of these species can sustain, and by applying them we defined a range for the species' annual population growth coefficient. In the case of bear, lynx and wolverine we also utilized recent population census data of Finland. For cautionary reasons we further included a certain proportion of unknown 'additional' mortality into the back-calculations. The values of *r* and *m* varied stochastically in each iteration round within and including the given range limits.

Species	Annual growth rate (*r*)	Additional mortality (*m*)	References
Bear	0.10–0.16	0.01–0.03	Saether *et al.* 1998, Kojola & Heikkinen 2006, Kojola 2007, this paper: *see* Table 2
Lynx	0.10–0.17	0.01–0.05	RKTL 2012, this paper: *see* Table 2
Wolf	0.30–0.45	0.01–0.05	Mech 2001, Fuller *et al.* 2003, Creel & Rotella 2010, Wiles *et al.* 2011
Wolverine	0.10–0.25	0.01–0.05	Persson 2003, Krebs *et al.* 2004, this paper: *see* text

Table 3. Evened-out growth rates for brown bear and lynx populations in Finland in 1996–2011; 14.4% for bear and 15.3% for lynx. All annual growth rates in this table were calculated to cover the respective annual hunting bag. According to the official population estimates, both species were increasing in the early 1990s. The year 1996 preceded a relatively stable ten-year phase followed by a rapid increase in 2007–2011. During the rapid increase (2008–2011), the observed annual population growth rates of both species were unnaturally high (underlined) suggesting that compared with the actual situation, the annual estimates had been lagging behind. In 2011–2012 the estimated increase of both species stabilized once again. Therefore, the calculation of the evened-out annual growth rates assumes that by being more accurate than the years between them, the population estimates of 1996 and 2011 (in boldface) are also proportionally accurate to each other. Hunting bag statistics are provided by the Finnish Wildlife Agency, and population estimates are provided by the Natural Resources Institute Finland.

Species		1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Bear	hunting bag (N)		96	79	80	91	101	91	68	72	69	77	83	84	130	179	198
	estimated population (N)	**770**	785	805	845	850	840	830	810	820	820	810	890	1050	1170	1515	**1660**
	observed annual growth rate (%)		14.4	12.6	14.9	11.7	10.7	9.6	5.8	10.1	8.4	8.2	20.5	27.4	23.8	44.8	22.6
	evened-out growth rate (%)		14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4
	interpolated population (N)	**770**	785	819	857	886	912	953	1022	1097	1186	1279	1377	1492	1576	1624	**1660**
Lynx	hunting bag (N)		64	63	55	45	58	37	44	65	87	74	103	179	298	371	401
	estimated population (N)	**780**	791	798	828	855	860	870	920	1050	1100	1200	1350	1485	1905	2300	**2430**
	observed annual growth rate (%)		9.6	8.9	10.7	8.7	7.4	5.6	10.9	21.3	13.0	16.1	21.7	23.3	48.6	40.5	23.1
	evened-out growth rate (%)		15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3	15.3
	interpolated population (N)	**780**	835	900	982	1087	1195	1340	1499	1662	1829	2031	2231	2392	2456	2456	**2430**

increase in 2007–2011. In both species, the calculated annual population growth rates in this rapid increase phase were unnaturally high, suggesting that compared with the actual situation in the wild, the annual population estimates were lagging behind during 1996–2011 (Mykrä 2010). From 2011 to 2012, population estimates for both species decreased concurrently. In other words, the years 1996 and 2011 showed as turning points, when a marked population increase in both of these species started and ended, respectively. We, therefore, assumed that in both species the population estimates of those two years were relatively accurate and also proportional to each other. We then used the difference in population estimates of those two particular years for calculating an average growth rate for these species during 1996–2011. This way the census data combined with the actual hunting bag of those years gave a result of $r = 14\%$ for the brown bear and $r = 15\%$ for the lynx (Table 3). Those are minimum values as here we did not assume any additional mortality, compensation of which would obviously require a further increase in the value of r. Even so, these growth rates are well in accordance with the results from the literature survey (*see* Table 2).

When it comes to the wolverine, we did not have any actual mortality data, and used an observed total mortality from a Swedish population instead ($m = 14\%$; Persson *et al.* 2009). This mortality value combined with the 38-year census data of 1978–2014 in Finland gave a result of $r = 19\%$ for the wolverine. In other words, for the constant mortality rate we found a particular value of r that produces a population trend similar to the observed long-term census in Finland. With regard to the wolf, similar approaches based on the census data were unfeasible due to extensive year-to-year variation in estimated wolf population sizes associated with the fact that a significant number of individuals are known to be illegally killed every year (Pohja-Mykrä 2014).

Back-calculation equation

For estimating population sizes prior to 1915 by back-calculating, we transformed Eq. 1 into

the following form suitable for calculating N_{t-1} when N_t is known:

$$N_{t-1} = (N_t + k_t)/[(1 - m_t)r_t] \qquad (2)$$

(k, r and m are explained above). In this study, we always considered the result of this equation to be the population size at the end of the year after intrinsic growth as well as harvest of that year. The equation was annually iterated backwards in a way that for the first round for calculating the population size of 1914, we systematically adjusted the value of population abundance of 1915 (N_{1915}) for all species. Then in subsequent iterations, N_t used in the equation was always N_{t-1} of the previous iteration round. As the data on k in this study cover 50 years (1866–1915), we performed the iteration 50 times using the k value of each year. The values of r and m varied stochastically in each iteration round within and including the range limits given in Table 2 and in the text above. This 50 round iteration we then replicated 100 times to accomplish the effect of stochastic variation on our results.

We adjusted N_{1915} of each species to a level at which the first round of the back-calculation iteration (giving N_{1914} as a result) did not lead to any population decrease or increase, i.e. mean N_{1914} of 100 replicates equalled the set value of N_{1915}. This way the change in the population size in the first iteration round was zero and the effect of the first iteration round on the subsequent rounds was kept at its minimum. Applying this adjustment, the N_{1915} value for the bear was 129 individuals, and 84, 18 and 110 individuals for the lynx, wolf and wolverine, respectively. Regardless of this subjective procedure, the adjusted values of N_{1915} made sense also in terms of what is said about the level of large carnivore abundance in Finland in the 1910s (Palmén 1910, Palmgren 1915).

Sensitivity of the model to variation in N_{1915}

Since the backwards iteration of each species' population size started with an input of a fixed initial value for N_{1915} in the first round, it is obvious that changes in this value would also affect the results of the subsequent rounds. We

examined the validity of the method by testing (Student's two-tailed t-test, df = 198) the sensitivity of the model by incorporating a nine-fold change in N_{1915} for each species; we divided the originally-adjusted N_{1915} by three and used the result of this division as a minimum initial value for the iteration (again producing 100 replicates) and compared it with that of an otherwise similar sample whose initial value was at its maximum by being three times the original N_{1915}. The comparison was made for five different years (ten-year intervals from 1915 backwards: 1905, 1895, 1885, 1875 and 1865). All 40 samples (four species; two test values; five years) were normally distributed (Lilliefors-van Soest test; the smallest p value was 0.103). The above-mentioned nine-fold difference covers basically all sensible alternatives for population sizes that those species could ever have had in Finland in 1915, or any year in the 1910s for that matter. A non-significant t-test result means that a nine-fold difference between the 1915 minimum and maximum test values did not lead to a statistically significant difference in the modelled mean population size in the respective year. It appears that changes in the initial value did not produce significant differences in any of the species' back-calculation results in 1875 and earlier. The same applied to the lynx, wolf and wolverine still in 1885, and to the wolf as late as in 1895. This means that even if we had made a three-fold error in one direction or another in estimating the N_{1915} population size, the back-calculation results would have been reliable before the selected years. Complete results of the t-test are shown in Table 4.

In addition to incorporating limited stochastic variation in r and m (Table 2) into the back-calculations, we also generated separate minimum and maximum abundance trajectories with constant growth rate and mortality. In the minimum abundance trajectory calculation, we kept the growth rate constantly at the highest possible value (upper limit of r in Table 2) while the additional mortality remained at its lowest year after year (lower limit of m in Table 2). The maximum abundance trajectory was calculated similarly, but using the lowest limit of r and the highest m. Even if we trust that our results of replicated back-calculations are fairly accurate,

we also wanted to illustrate the minimum and maximum abundance trajectories as the extreme limits within which the Finnish large carnivore populations have definitely developed during the study period.

Results

The combined results of 100 replicates of back-calculations on brown bear abundance in 1865–1915 suggest a relatively stable period for the first decade (Fig. 1). The population size at that time seems to have been 800–1000 individuals. In the stable phase, the mean size of the back-calculated bear populations ($n = 100$) varied from 901.3 in 1865 to 956.9 in 1875. After that there was an exceptionally steady decline in bear abundance for the next three decades, during which bear numbers decreased by on average 210 individuals per ten years. In the last decade of the study period the decline continued but at a slower pace.

For lynx the back-calculated trajectories suggest a marked population increase in the first 10–15 years of the study period (Fig. 1). An increase of the lynx population from 1200–1700 in 1865 to 2700–3300 in 1879 turned to a decade-long steady and immensely steep descent; during the decline there were on average 217 fewer lynxes in the Finnish population every year. This means an average annual decrease rate of 12.5%. In 1890 the mean size of all back-calculated lynx populations ($n = 100$) was 793.2 individuals. After that, the decline continued at a slower pace towards the end of the study period.

Similarly to that of the bear, wolf abundance remained stable between 1865 and 1875 according to 100 replicated back-calculations; at that time the population size appeared to have been around 900–1100 (Fig. 1). During those years the mean number of wolves in back-calculated populations varied from 941.6 in 1870 to 1006.6 in 1865 (n of samples per year = 100). From 1875 onwards a sharp decline ensued and in 15 years wolf abundance decreased by more than 900 individuals. During the first five years of this precipitous decline, the wolf population diminished by on average 119 individuals per year from 1000 to fewer than 400. The recorded number of killed wolves in those five years in the bounty statistics is 1348 (Table 1). In 1887, the population decreased to below 100 and remained at this level for the rest of the time.

Table 4. Sensitivity of the back-calculation results for changes in the 1915 input value. Because all iterations start from a systematically adjusted artificial population size (*see* text for details), we inspect the method validity by testing the sensitivity of the back-calculation for changes in the initial value. Maximum test values are three times the used N_{1915} and minimum test value were one third of the used N_{1915}, i.e. the difference between max and min test values for the initial population size was nine-fold. We compared population sizes (100 replicates) with the maximum and the minimum test values for each of the four species in ten-year intervals from 1915 backwards (1905, 1895, 1885, 1875 and 1865). All 40 samples (two test values × four species × five years) were normally distributed (Lilliefors-van Soest test; the smallest $p = 0.103$). In the table, each non-significant test result (Student's two-tailed t-test: df = 198) means that a nine-fold difference between the 1915 test values did not lead to statistically significant difference in the modelled mean population size in the respective year. The back-calculated mean population sizes of the four carnivore species seem not to be particularly sensitive to ecologically justifiable changes in N_{1915} in the 1860s, 1870s and 1880s.

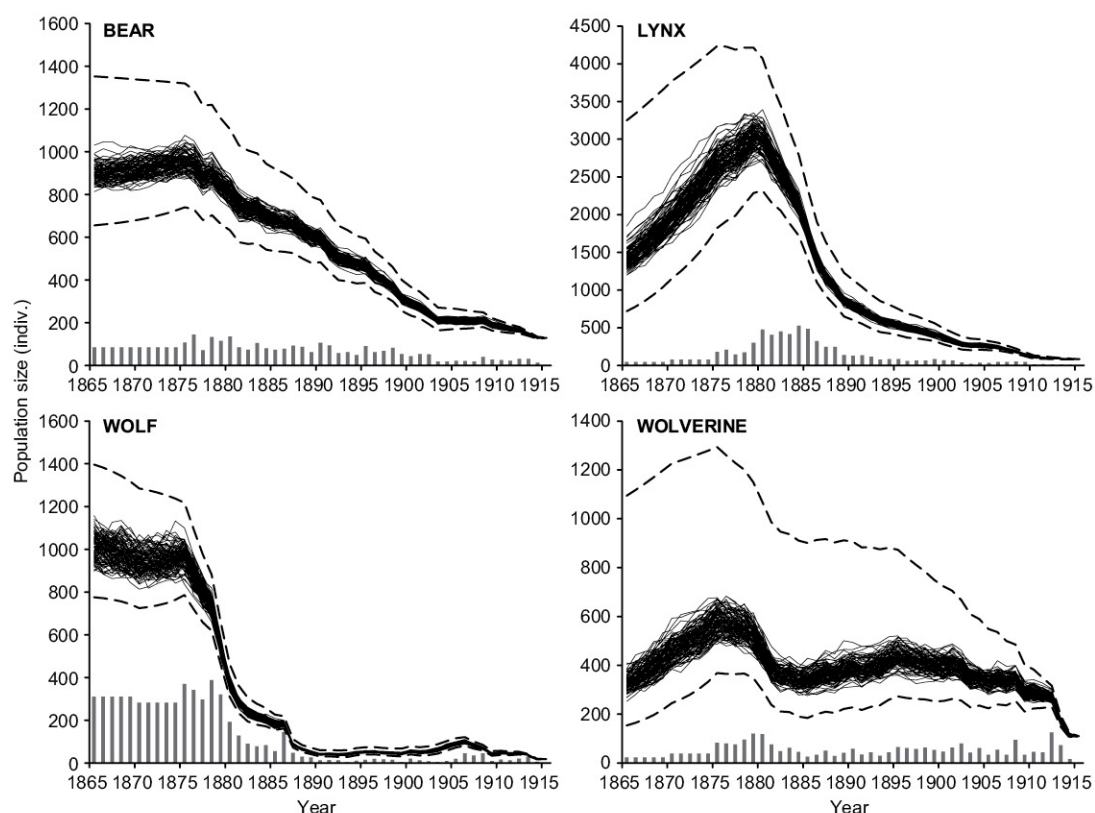| Species	Test values for 1915 population size	Year				
		1905	1895	1885	1875	1865
Bear ($N_{1915} = 129$)	max: 387 (= $N_{1915} \times 3$) min: 43 (= $N_{1915}/3$)	$t_{198} = 87.270$ $p < 0.001$	$t_{198} = 21.141$ $p < 0.001$	$t_{198} = 3.390$ $p < 0.001$	n.s.	n.s.
Lynx ($N_{1915} = 84$)	max: 252 min: 28	$t_{198} = 48.648$ $p < 0.001$	$T_{198} = 8.407$ $p < 0.001$	n.s.	n.s.	n.s.
Wolf ($N_{1915} = 18$)	max: 54 min: 6	$t_{198} = 1.912$ $p = 0.057$	n.s.	n.s.	n.s.	n.s.
Wolverine ($N_{1915} = 110$)	max: 330 min: 37	$t_{198} = 19.702$ $p < 0.001$	$t_{198} = 3.043$ $p = 0.003$	n.s.	n.s.	n.s.

Fig. 1. Back-calculated abundance trajectories of the brown bear, lynx, wolf and wolverine in Finland in 1865–1915. Each graph shows 100 replicated year-to-year backwards iterations (solid lines) starting from a systematically-adjusted initial population size value in 1915. The used equation incorporates actual human-caused mortality (annual bounty statistics of 1866–1915), and limited stochastic variation in additional mortality and annual population growth rate. Dashed lines show back-calculated minimum and maximum abundance trajectories with constant predetermined annual growth rate and mortality. *See* text for details of the back-calculations. Bars show annual bag records from the bounty statistics. Note different scale of *y*-axes.

In the first decade of the study period, the wolverine population seemed to have ascended from 300–400 to 500–650, and then dropped again close to the initial numbers in less than ten years (Fig. 1). The mean size of back-calculated populations (*n* = 100) increased from 328.1 (1865) to 577.8 (1875), and then decreased to 359.1 (1882). In 1882 a long and relatively stable period began, when wolverine abundance remained between 300–400 and 400–500 for almost 30 years. In 1909 the mean size of back-calculated wolverine populations decreased to below 300 individuals.

At the beginning of the study period, the minimum and maximum population sizes calculated using predetermined constant population demographic parameters were 655 and 1352 individuals for the bear, 720 and 3249 for the lynx, 775 and 1396 for the wolf, and 154 and 1094 for the wolverine (Fig. 1). As time moves on, both the minimum and maximum trajectories gradually approach the cluster of replicated back-calculations.

According to our results, it is probable that the late 19th century population decreases of large carnivores in Finland began a few years before the actual fall in bag records. In other words, there appears to be a time lag between population decline and bag record decline. This is most evident at the beginning of the steep declines in the population trajectories of the lynx, wolf and wolverine in the late 1870s and early 1880s (Fig. 1).

When the trajectories of all four species are visualised in proportion to each other, it is evi-
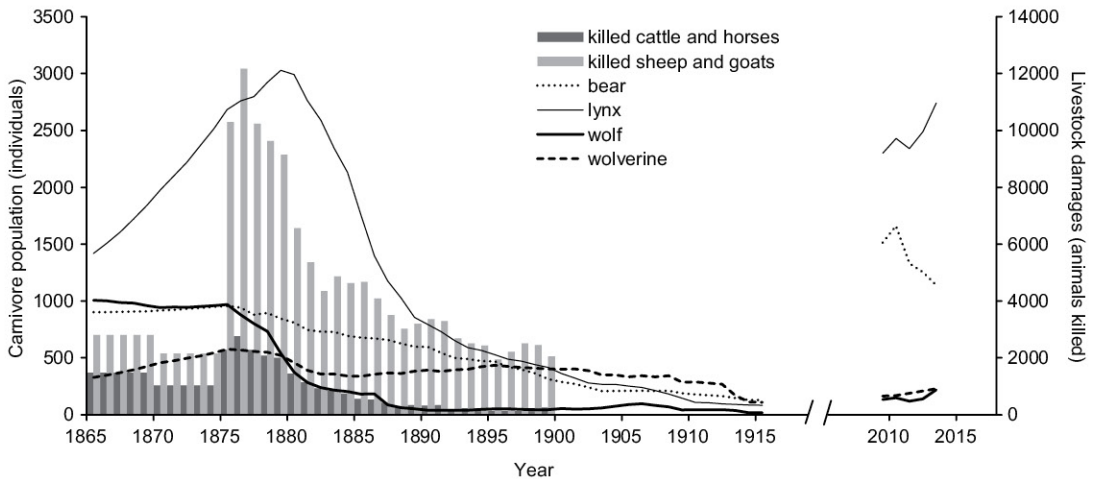
Fig. 2. Late 19th and early 20th century back-calculated abundances (left-hand-side *y*-axis) of the brown bear, lynx, wolf and wolverine populations in Finland. The abundances of all four species are in proportion to each other. We calculated the trajectories on the basis of official bounty statistics and population demographic variables verified by research. Each trajectory shows a mean of 100 replicated back-calculations (*see* text for details of the method). Grey bars (right-hand-side *y*-axis) show the annual numbers of livestock killed by large carnivores. For comparison, short lines on the right-hand side of the graph show 2010–2014 abundances of the four species. Present-day population estimates are from the Natural Resources Institute, Finland.

dent that the performance of the lynx population diverges greatly from all others (Fig. 2). The abundances of the other three species varied much more consistently during the study period. Only the relatively rapid decline of the wolf in 1875–1885 deviates from that of the remaining bear and wolverine. The annual number of cattle and horses killed seems to reflect changes in populations of bear and especially wolf, whereas the combined number of sheep and goats killed show a distinct peak during the last years of the lynx increase. Because of the pooled five-year data for the periods 1866–1870 and 1871–1875, we are not able to tell anything about the year-to-year variation in the numbers of livestock damages at the beginning of the study period. Therefore, the actual trajectory of the sheep and goat damage increase in 1866–1875 is not known.

During the period of annual livestock damage records (1876–1900) there was a concurrent continuous decreasing trend in all examined livestock damages as well as in all carnivore abundance numbers except for the wolverine. As the wolverine is very much attached to reindeer, in this study it was not particularly "interesting" as an object to us when it comes to livestock damages. Due to the concurrent decreasing trends,

the correlations between large-sized/small-sized livestock damages and bear/lynx/wolf abundance were in all cases very strong (Spearman's correlation: $r_s > 0.800$, $n = 25$ in all cases).

There was also a clear positive correlation between annual damages to large-sized and smaller-sized livestock (Spearman's correlation: $r_s = 0.604$, $n = 35$ for all data, and $r_s = 0.958$, $n = 25$ for the 1876–1900 annual data), but the diminishing total number of damages suggests an overall decrease in livestock predation. It is notable, however, that a five-year mean of the small-sized/large-sized livestock damage ratio increased markedly during the study period. It was 1.9 in 1866–1870, 2.1 in 1871–1875, 4.5 in 1876–1880, 5.2 in 1881–1885, 9.0 in 1886–1890, 11.6 in 1891–1895 and 15.1 in 1896–1900. That is, more sheep and goats were killed and eaten for each head of cattle and horses during the course of the study period.

Discussion

The population declines portrayed by the trajectories modelled in this study are in accordance with a considerable number of historical

references of that time (Mela 1882, Böök 1905, Palmén 1905, Mela & Kivirikko 1909, Palmén 1910, Palmgren 1915). Although in many studies particular emphasis was put on the wolf, declines in populations sizes of all four species were mentioned repeatedly in various sources. Those authors themselves lived to witness the dwindling populations, and in addition some of them referred to a reduction in bounty records accumulated at that time. Furthermore, it is worth mentioning that these species' declines coincided not only with each other but with improvements in the accessibility of hunting grounds and quick development in firearm technology, as well as with the early organisation of hunting associations and advisory services for hunters regarding pest control (Ylänne 1950, Kairikko 1991, Hyytinen 2003).

As per estimates given recently on large carnivore abundances in Finland after the mid-1850s, our results are very similar to findings of studies employing either calculus or genetic evidence. To a certain extent, similar calculations were used, but their methodology seemed to be only cursorily described (Kojola 2005, 2007 and Kojola unpubl. data as cited in Aspi *et al.* 2006). As far as we are aware, no stochastic variation was incorporated into population growth or mortality rates in these studies. The Finnish wolf history based on genetic evidence (Aspi *et al.* 2006, Jansson *et al.* 2014) is also well in concert with our results, which increases credibility of both methods.

Ermala (2003) provided large carnivore bag records even for an earlier period of 1845–1865. In that study, the annual mean wolf catch in those years is said to have been 390–490 individuals. We tested those numbers in a back-calculation reaching up to the year 1845. It is noteworthy that in this test run the mean wolf population size (again 100 replicated iterations) in the mid-1840s was 1400 and decreasing. This is exactly what was concluded by Aspi *et al.* (2006). Ermala's work (2003) is a regularly cited reference for large carnivore bag records and population decline in the 19th century Finland. There are, however, certain shortcomings in this particular paper. References are not given in that study at all, and substantial inconsistencies can be found in the numbers of killed wolves

and lynxes when compared with official bounty statistics. Ylänne (1950) and Lappalainen (2005) provided mean numbers as high as 685–700 for the annual wolf bag in the late 1850s, but Lappalainen specified further that these quantities also include pups taken from dens. In general, it is an obvious deficit in the Finnish bounty data that young age classes are not separated in the statistics even though the paid bounties were in many cases different between adults and juveniles (Pohja-Mykrä *et al.* 2005).

The possibility of time lags between population declines and bag record declines is apparently overlooked in earlier references relying upon bounty data (e.g. Erkamo 1939, Pulliainen 1974, Ermala 2003). In those studies, the reduction in the number of killed individuals in the bag records is assumed to indicate that population decline is setting off at the same moment. Our findings, however, imply that the population decrease can actually have started even if the bag records remained at high levels (Fig. 1). The origin of this observed time-lag may be in hunters' dedication and skills in large carnivore hunting. As long as total mortality remains below the intrinsic growth rate, the population is increasing. When hunting mortality gradually rises, the increasing population trend turns to a stable phase and eventually into a slight decrease. With a further upsurge in killings — stimulated and sustained by the above-mentioned reasons in the late 1800s — the population size turns to a rapid decrease before it is reflected in the bag records. This may then create a time lag between abundance curves and bag records. It is also possible that a declining prey base in the late 1800s (Mela 1882, Mela 1902, Mela & Kivirikko 1909) brought carnivores closer to human settlements and their vulnerability to hunting remained high for some years despite dwindling populations. This, too, would create a similar time lag between population sizes and catch curves. It is worth mentioning that the observed time lag is not connected to the back-calculation method, since a forward iteration employing Eq. 1 and an array of model assumptions similar to the back-calculation method produces an exactly similar result showing the same kind of delay.

The abundance trajectories modelled in this study are basically of two types. Those for

the brown bear and wolf are consistent with the notion of dwindling carnivore populations of that time with a more or less stable phase early in the study period followed by an evident decrease. The trajectories for the lynx and wolverine, in turn, show an increase at the beginning of the study period and then they decrease more or less rapidly towards very low numbers in the early 1900s.

Even though hunting obviously explains the population declines of both bear and wolf, it is worth noting that the motivations behind sportsmen's devotion to hunting of these two species varied. The decrease of the wolf is steep and rapid whereas the number of bears dwindles gradually towards the end of the century. The sole reason for hunting of wolves was to deliberately drive the whole species into extinction but with the bear the population decrease is much more a result of inadvertent overharvesting of a valued game species (Finska Jagtförening 1900, Palmén 1905, Mykrä *et al*. 2015). The wolf is also an exceptional species in a way that the intensity of its persecution was not dependent on the bounty sum. People were inclined to seriously allocate their time and resources into hunting wolves even with lower bounties, while in the case of other large carnivores the persecution seems to have intensified with increasing bounty value (Pohja-Mykrä *et al*. 2015). In addition to persecution, other reasons, such as changes in the prey base could also explain the observed population declines of large carnivores. However, in this case there seems to be no actual need for searching alternative explanations, since the recorded levels of hunting mortality as such seem to have been high enough to decimate all four species to very low numbers by 1915.

An increasing number of killed lynxes in the 1870s has been interpreted as an ability of the lynx population to increase because of lower numbers of wolves (Palmén 1910, Erkamo 1939, Pulliainen 1974, Salo 2007). A general hypothesis in those studies is that the lynx is the subordinate species expected to be negatively affected by intraguild competition with wolf and also from direct predation by wolves. Wikenros *et al*. (2010) showed, however, that this hypothesis did not hold in Sweden in 2003–2007. In their study area, the main prey of the lynx was roe deer

(*Capreolus capreolus*). Wolves have a broader prey spectrum, although they mostly preyed upon moose (*Alces alces*). These authors suggest that in this case the coexistence of lynxes and wolves might be facilitated by high densities of roe deer. In comparison, prey abundances in Finland during our study period were much lower than in present-day Sweden (Mela 1882, 1902, Böök 1905, Mela & Kivirikko 1909). The relations between lynxes and wolves might have been different in a way that with a poorer prey base the decrease in the wolf population might actually have benefited the lynx.

Alternatively, this assumed lynx increase referred to in earlier studies and observed in our study could also be artificial. Erkamo (1939) suggested a plausible explanation that the increase of the lynx in Finnish bounty statistics in the 1870s could result from the simple fact that hunters started to allocate more effort to hunting the lynx after the decline of the wolf and bear.

All things considered, it is difficult to say whether this assumed rapid increase of the lynx in the 1870s actually took place or is it just an anthropogenic increment in the bounty statistics. It might be assumed that its correspondence with the conspicuous increase in sheep and goat damages provides a noteworthy piece of anecdotal evidence. Forest pasturing of free-ranging livestock was a norm and in general they were extremely vulnerable to large carnivore predation. As an example, the statistics reveal that at least 135 903 heads of cattle, sheep, pigs and horses were killed by large carnivores in Finland in a 20-year period of 1866–1885 (Statistical Yearbooks 1860–1926). That is an over 40-fold more as compared with the livestock damages in 2001–2010. Of all damages to livestock caused by large carnivores, it is sheep and goats that typically fall prey to lynxes (Odden *et al*. 2008). The mean annual number of sheep and goats killed increased from 2812 in 1866–1870 to 10 295 a decade later in 1876–1880. A remarkable co-occurrence of assumed lynx population increase and increasing damages to sheep and goats can be seen in Fig. 2. Damages to large-sized livestock, on the other hand, seem to follow the trend in wolf abundance. After the almost total decimation of wolf after 1890, sheep

and goat damages remained at a certain level decreasing only slightly.

As said earlier, the abundance trends for the bear, lynx and wolf correlated with the livestock damages in 1876–1900. Even though the damage peak of small-sized livestock seems to coincide with the increase in the lynx population, the significance of this coincidence is diminished by the fact that at that time numbers of bears and wolves were also almost at their highest (Fig. 2). A simple calculation of daily food intake by the examined carnivores (bear approx. 10, lynx 3 and wolf 4 kg per day during the livestock pasture season of 200 days) reveals that in theory any of these species alone could have been responsible for the observed damages to sheep and goats. Therefore, as accurate annual records on damages during 1865–1875 are missing, the connection between the lynx and smaller livestock remains an open question.

All these observations together with the ever-increasing smaller livestock/large livestock damage ratio suggest, however, that the timing and magnitude of the most conspicuous population changes in our modelling results can be correct. As stated earlier, the apparent sharp decrease of wolves was eagerly reported in the late 1800s since in those days it was a remarkable state of affairs to realise that wolf observations in a certain region accumulated no more. On the other hand, for the lynx almost no proof except the trend in bounty records is presented for its population growth. Palmén (1910), however, stated that according to hunting chronicles of the 1850s, the lynx was deemed "relatively abundant", whereas in similar accounts from the 1870s and 1880s the species was told to be so plentiful that considerable numbers were bagged in many parishes in central and southern Finland. Therefore, from various pieces of indirect evidence we are inclined to consider that a substantial increase in the lynx population actually took place in 1865–1880, and it was not a mere statistical delusion due to intensified hunting.

The modelled trajectory of wolverine abundance shows a moderate increase from 300–400 to 500–600 in the beginning of the study period in 1865–1875. The assumed increase in the lynx population covered those years too, whereas wolves started to decline sharply in the 1870s.

Koskela *et al.* (2013) concluded that in their study area in eastern Finland during 2005–2009, wolverines favoured wolf presence, which supports the findings that wolverines benefit from wolves through increased scavenging opportunities, although it is also known that wolverines seem to adjust their behaviour in order to avoid wolf predation (van Dijk *et al.* 2008). Khalil *et al.* (2014) investigated potential relationships between the wolverine and both of the larger species, the wolf and lynx, with elegant modelling using bounty statistics from Norway and Sweden for the period 1846–1922. Their findings support a view that there is a negative association between the wolverine and wolf as long as wolf numbers remain above a certain threshold. Below that threshold the net effect of wolves is supportive towards wolverines. A more straightforward result in their paper was that wolverines seem to benefit from the lynx presence irrespective of its density. This supports our observation of possible concurrent increase of the wolverine and lynx in 1865–1875.

To conclude, we suggest that based on our results there were approximately 1000 bears and an equal number of wolves in Finland until their decline started around 1875 (Figs. 1 and 2). The current number of bears is 1.5 times higher, whereas the wolf population of today is still only one fourth of that in the past. It is therefore fair to assume that the lynx population increased markedly in the first quarter of our study period, but that perhaps it did not exceed 3500 in the 19th century. Currently there is roughly the same number of lynxes living in Finland. As for wolverines, their number prior to 1885 appears to have varied between 300 and 600. That is just about twice the population of the 2010s (Fig. 2).

The accuracy of our estimates for N_{1915} for each species is difficult to validate today, 100 years afterwards, but if the actual 1915 population size did remain within the range shown in Table 4, the precision of the calculated trajectories improves also later in the study period.

A key issue in this kind of examination is, in particular, the consistency of the intrinsic population growth rate (*r*) used in the calculations. Circumstances then and now can be very different and perhaps considerable recovery took place for example in the prey base of large car-

nivores, which could nowadays manifest itself as improved breeding success and reduced mortality. On the other hand, in the literature we did not find any indications that the breeding success of large carnivores was particularly low in the past. We believe that the limits we set for the growth value *r* and the "extra" mortality *m* are reasonable, and that our consequent results are reliable and also useful as a historical reference for large carnivore abundances at the turn of the 20th century.

Acknowledgements

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