Biological Conservation 243 (2020) 108456

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Policy analysis

Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling

Olof Liberg[a,*], Johanna Suutarinen[a,1], Mikael Åkesson[a], Henrik Andrén[a], Petter Wabakken[b], Camilla Wikenros[a], Håkan Sand[a]

[a] Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan SE-73091, Sweden
[b] Faculty of Applied Ecology and Agricultural Sciences, Inland Norway University of Applied Sciences, Koppang, Norway

ARTICLE INFO

Keywords:
Canis lupus
Carnivore management
Mortality
Poaching
Wildlife crime
Wolves
Legal culling
Inbreeding

ABSTRACT

Poaching is an important limiting factor for many large carnivore populations worldwide and the effect that legal culling has on poaching rate on wolf (*Canis lupus*) is debated. We used data linked to population monitoring and research to analyze rate and risk of disappearance without known cause for territorial pair-living wolves (n = 444) in Sweden 2000/01–2016/17. Known mortalities included legal kills (n = 103), natural causes (n = 23), traffic (n = 8) and verified poaching (n = 20) but most (n = 189) wolves disappeared without known cause. Careful evaluation of alternative causes supported the assumption that poaching was the most likely reason for the majority of these disappearances. Disappearance rate was0.14 for the entire study period, and increased from 0.09 in 2000/01–2009/10 to 0.21 in 2010/11–2016/17, while a Kaplan-Meier analysis on a sub-sample of radio collared wolves (n = 77) gave an average annual poaching rate of 0.12 for the entire study period and 0.10 and 0.18 for the corresponding two sub-periods. Factors affecting disappearance rate were modeled using logistic regression and Cox proportional hazards regression. Population size had a strong positive effect on disappearance rate in both models, whereas legal culling rate had a negative effect, significant only in the Cox model. The combined effect of legal culling rate and disappearance rate during the latter part of our study period has halted population growth. Our results contribute to an increased understanding of two vital drivers predicted to affect poaching rate: population size and legal culling.

1. Introduction

Illegal killing of wildlife, also termed poaching, is a common and global problem (Challender and MacMillan, 2014; Ripple et al., 2014). Although most acute in species poached for monetary gain, often related to large scale illicit trade (Leader-Williams, 2003; Treves et al., 2014), poaching is also a significant problem for the conservation of large carnivores that threaten and compete with human interests (Ripple et al., 2014; Andrén et al., 2006; Treves and Bruskotter, 2014). Grey wolves (*Canis lupus*) have limited commercial value but are probably the most controversial and conflict-prone carnivore species on Earth (Olson et al., 2015; Mech, 2017). Poaching of wolves appears to be prevalent wherever wolves and humans coexist (Liberg et al., 2012; Von Rushkowski, 2016; Suutarinen and Kojola, 2017; Treves et al., 2017; Murray et al., 2010). The idea that legal harvest or culling might increase tolerance of wolves, and even reduce poaching, has been raised and put in practice (Redpath et al., 2013; Woodroffe and Redpath, 2015; Stien, 2017), but also questioned (Treves, 2009; Epstein, 2017). In an analysis of wolf mortality in Wisconsin and Michigan, Chapron and Treves (2016) concluded that legal culling triggered more, not less, poaching. The authors argued that "liberalizing wolf culling may have sent a negative message about the value of wolves and that poaching prohibitions would not be enforced". The article awoke criticism and a vivid debate on the effect of legal culling on poaching (Stien, 2017; Pepin et al., 2017; Olson et al., 2017; Chapron and Treves, 2017; Chapron and Treves, 2017).

In Europe, and especially in the Nordic countries, illegal killing of large carnivores seems to be largely a rural protest against conservationist restrictions, which are perceived as threats against the residents' traditional rights and the quality of life in the countryside. This view has been extensively supported and discussed in a large and fast growing body of social science literature (Olson et al., 2015; Von Essen et al., 2015; Von Essen et al., 2017; Kaltenborn and Brainerd, 2016; Peterson et al., 2018; Pohja-Mykrä, 2016; Pohja-Mykrä and Kurki,

* Corresponding author at: Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan SE-73091, Sweden.
E-mail address: olof.liberg@slu.se (O. Liberg).
[1] As co-first authors.

https://doi.org/10.1016/j.biocon.2020.108456
Received 30 June 2019; Received in revised form 4 February 2020; Accepted 7 February 2020
Available online 14 March 2020

2014; Pohja-Mykrä, 2017). It has even been suggested that a remedy against poaching of wolves could be to increase legal culling (Kaltenborn and Brainerd, 2016) and turn them into a "valued quarry in traditional hunting" (Pohja-Mykrä, 2017).

One important factor that may obstruct a better understanding of the relationship between legal culling and poaching is the difficulty of quantifying poaching. Poaching is a criminal act and the offenders are therefore expected to conceal the offences. Liberg et al., 2012 coined the term "cryptic poaching" for the hidden proportion of poaching that is not discovered or reported. By combining data from snow-tracking, DNA-analyses and radio telemetry they demonstrated that for Scandinavian wolves, 69% of the total poaching was cryptic. Although radio collaring of individuals is the most common tool to estimate poaching it is also associated with high costs and technical shortcomings, which in turn often result in limited sample size (but see e.g. Murray et al., 2010; Smith et al., 2010). In this study, we used data from several different sources linked to research and the annual monitoring of the wolf population in Sweden to calculate annual rates of known mortality and disappearances without known cause of territorial wolves from one year to the next during 2000/01–2016/17. We then carefully evaluated possible cause behind the increase in disappearance rate of wolves, also considering the possibility of poaching. Our objective was to investigate and quantify factors related to the increased rate of disappearance in the Swedish wolf population. We analyzed the effects of population size, legal culling rate and the level of inbreeding to 1) test whether an increasing population and/or increased legal culling rate was associated with the rate of disappearance in the wolf population, and 2) account for inbreeding as a recent paper reported that inbreeding affects pair-bond duration (Milleret et al., 2016).

2. Material and methods

Wolves in Sweden belong to the Scandinavian population shared with Norway, where approximately 85% of the population is residing on the Swedish side [(Wabakken et al., 2001; Wabakken et al., 2018), Fig. A1 in Appendix A]. After being functionally extinct on the Scandinavian peninsula by the end of the 1960s, wolves recolonized permanently the area during the 1980s from the Finnish-Russian population (Wabakken et al., 2001). The Swedish population increased to more than 400 wolves in 2015, after which it decreased [(Wabakken et al., 2018), Fig. A1 in Appendix A]. The population is concentrated to the south-central part of Sweden, dominated by boreal forest, with moose (*Alces alces*) and roe deer (*Capreolus capreolus*) as main prey [for details of habitat see (Mattisson et al., 2013). The study started in the winter of 2000/01, because this was the start of regular collection of DNA-samples from the wolf population. Although we have population monitoring data up to the winter 2018/19, we set the end of the study to 2016/17, to account for the risk that a territorial individual could simply be missed during one or two monitoring seasons.

Wolf policy and management, including culling policy, differs distinctively between Sweden and Norway (Liberg et al., 2010). As one important point with the study was to analyze the relation between disappearance rate and legal culling rate, and the latter was not synchronized between the countries, the study was limited to territories in Sweden including border territories. A separate analysis for Norway was not possible due to small sample size. Sweden is a member of the European Union (and Norway is not) where large carnivore management and conservation is regulated by the European Union's Habitats Directive (Council Directive 92/43/EEC) that lists the wolf among species with strict protection. Before 2010, permits to kill wolves in Sweden were issued only for livestock depredating wolves and boldly behaving individuals. In 2008, the Swedish government opened for quota hunting of wolves, and the first hunt was conducted in January–February 2010. These quota hunts have been repeatedly contested and in some years stopped by court decisions, and since 2011, there is an ongoing discussion between the Swedish government and the European Commission regarding the legality of this type of wolf culling (Darpö, 2011; von Essen and Allen, 2017).

Wolf monitoring is conducted annually during the winter months from October to March. The monitoring work in Sweden and Norway is completely integrated, and the annual reports cover both countries and are prepared in full co-operation between the countries (Liberg et al., 2012Liberg et al. 2012b; Naturvårdsverket, 2007 Naturvårdsverket 2007; Naturvårdsverket, 2014 Naturvårdsverket 2014) The probability for any certain wolf to be detected and recorded is the same in both countries. The central authority in Sweden with responsibility for the monitoring is the Swedish Environment Protection Agency SEPA. . SEPA has delegated the responsibility for analysis of data and preparing of annual monitoring reports to the Swedish Wildlife Damage Center, while the regional counties are responsible for the field work. More than 100 qualified field technicians are working during the monitoring season to register wolf tracks and signs of territoriality (scent-marks), and to collect samples (feces, urine, blood and hair) for DNA-analyses. Monitoring effort has increased with wolf population size. Number of kilometers of wolf tracks followed on snow increased from 3305 km in 2000/01 to 4938 in 2010/11 in all Scandinavia. Tracking distance was not reported after 2011, but number of analyzed DNA-samples collected increased from 735 in 2010/11 to 3579 in 2016/17. The monitoring personnel also get help from the public, local hunters and NGO's, who report fresh wolf tracks. The social status of each identified wolf was categorized as either territorial or non-territorial. Territorial wolves were identified from their scent-marking behavior. Finding and individually identifying (through DNA-analyses of collected samples) both adults in each territorial pair had highest priority (Naturvårdsverket 2014) . A near complete pedigree has been reconstructed for the whole Scandinavian wolf population. Up to 2016/17 it contained 266 different breeding pairs, of which full kin relationships could be reconstructed for 260 (Liberg et al., 2005; Åkesson et al., 2016; Åkesson and Svensson, 2019). The pedigree reconstruction is described in (Åkesson et al., 2016) and was based on approximately 12,500 successfully analyzed DNA-samples. In total, 1929 individuals have been identified with only 6 that could not be assigned to parents included in the pedigree (Åkesson and Svensson, 2019).

For each monitoring year (from May to April the next year, hereafter called "year") in the period 2000/01–2016/17, we recorded the presence of wolves that were established in scent-marking territorial pairs where both partners were identified individually, regardless whether having offspring or not (n = 444 wolves: 213 females, 231 males). Proportion of territorial pairs where this criterion was not met decreased from 12 to 6% during the study period due to an increased monitoring effort (Fig. B1, Appendix B). The reason for limiting our study to this segment of the wolf population was that identifying these wolves had the highest priority in the monitoring work and their scent-marking behavior and territory fidelity made them possible to re-locate in consecutive years with high reliability (see Appendix B), which is difficult or impossible for other wolves.

A wolf's annual presence was determined through individual identification by DNA-analysis of samples from the individual itself or from its offspring of the year. The annual status of each study wolf was classified into one of the following categories: *i*) alive and still established in a pair, *ii*) legal culling including both damage control and quota hunting, *iii*) other causes (traffic-killed and natural non-human caused deaths like disease, accidents and old age), *iv)* disappeared for unknown reasons (recorded neither in Sweden nor in Norway that monitoring year or in later years), or *v*) censored. Verified poaching cases, determined with criteria given in (Liberg et al., 2012), were included in category *iv*. Seven wolves that disappeared at an age older than 10 years were assumed dead of old age and included in category *iii*. The term "lost" was used to cover all cases within categories *ii* to *iv*, i.e. dead or disappeared. Rates were calculated as number of wolves in respective category in relation to population at risk the same year. Population at risk was equal to the number of territorial pairs where

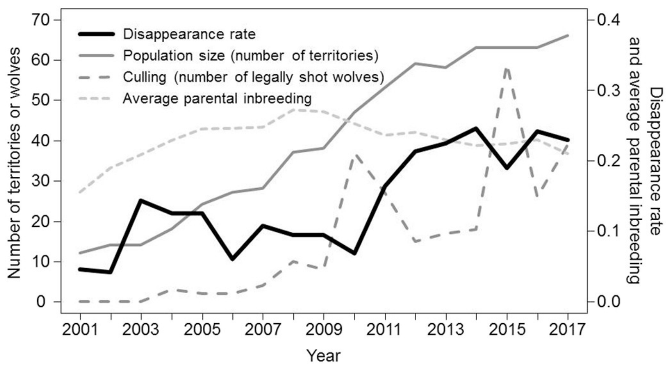

Fig. 1. Disappearance rate of paired territorial wolves, number of territories used as proxy for population size, number of legally killed wolves and average parental inbreeding for wolves in Sweden, 2000/01–2016/17. On the X-axis, 2001 stands for 2000/2001, etc.

both partners were identified individually that year, multiplied with two.

Year of disappearance was defined to be the last year with presence recorded. If contact was lost with both partners the same year without known reason, they were both categorized as disappeared. Since this study was solely based on the pair living segment of the population, wolves that lost their partner and remained single the following year (12 females, 25 males) were censored until they got a new partner (2 females, 6 males) or to the end of the study (10 females, 19 males). All individuals alive at the end of the study period were censored at that time (36 females, 36 males).

We analyzed disappearance rate at the population level and disappearance risk at the individual level in relation to three covariates (Fig. 1): *i*) population size, measured as the number of territorial pairs, including also pairs that were excluded from the population at risk because only one or none of the partners had been identified individually *ii*) legal culling rate calculated by dividing the number of all legally killed wolves (both damage control and quota) during the whole monitoring year by the number of territorial pairs the same monitoring year, and *iii*) pedigree-based inbreeding coefficient (F). At the individual level we used F from each individual whereas at the population level we used the mean annual inbreeding coefficient for all breeding wolves (Liberg et al., 2005; Åkesson et al., 2016). Four wolves were immigrants and their inbreeding coefficient was set to zero. We standardized the continuous variables to a mean of zero and a standard deviation of one (Schielzeth, 2010) (Fig. 2).

We used logistic regression (generalized linear model, glm) to model disappearance rate at the population level. The response variable was binary (disappeared or not disappeared for each individual wolf) and the data were pooled into years as number of disappeared/not disappeared wolves. Wolves entered the population at risk in the monitoring season they were first recorded as a territorial pair and exited at the time of mortality/disappearance event or when being censored. We created a candidate set of disappearance rate models including all possible combinations of the three covariates and an intercept only model resulting in a total of eight candidate disappearance rate models.

We used Cox proportional hazards regression to model disappearance risk at the individual level. We estimated the overall cause-specific risks, i.e. cumulative incidences, using the 'survfit' function of the Survival package. We examined the individual level risk factors related to disappearance with the Andersen-Gill extension of the Cox regression in a competing risks framework (Andersen and Gill, 1982; Lunn and McNeil, 1995; Heisey and Patterson, 2006). We constructed the survival data in a long format with each row representing one time-step (from one monitoring season to the next). We stratified the data based on the possible events: *i*) legally killed, *ii*) killed in traffic or died from natural causes, or *iii*) disappeared (including verified cases of poaching). Finally, we pooled the data among years resulting in enter = 1 and exit = 2 for all wolves and created all possible combinations of the three covariates resulting in a total of seven candidate risk models.

All analyses were conducted with program R, version 3.5 (R Core Team, 2018). Cox regression was performed using package 'Survival' (Therneau, 2015). We based the model selection on corrected Akaike information criterion (AICc) using package 'MuMIn' (Barton, 2018) for both logistic regression and Cox models, and for multi-model inference we calculated the model averaged coefficients and the relative variable importance (RVI) values.

During the study period we also equipped 77 territorial wolves (39 females, 38 males) with either GPS-collars (63 collars, Simplex, Televilt International, Lindesberg, Sweden or GPS-Plus Vectronic Aerospace, Berlin, Germany) or VHF radio collars (14 collars, Telonics Mod. 500, Mesa, Arizona, U.S.A.) Success rate of scheduled GPS-positions were on average close to 90% or higher. VHF collars were monitored both from the ground and from the air at least once but most often 2–4 times a week. Mortality was detected either through a mortality indicator on VHF-collars or through automatic SMS messages from the GPS-collars. Necropsy of dead animals were generally made within one week after the recovery of the animal at the Swedish National Veterinary Institute

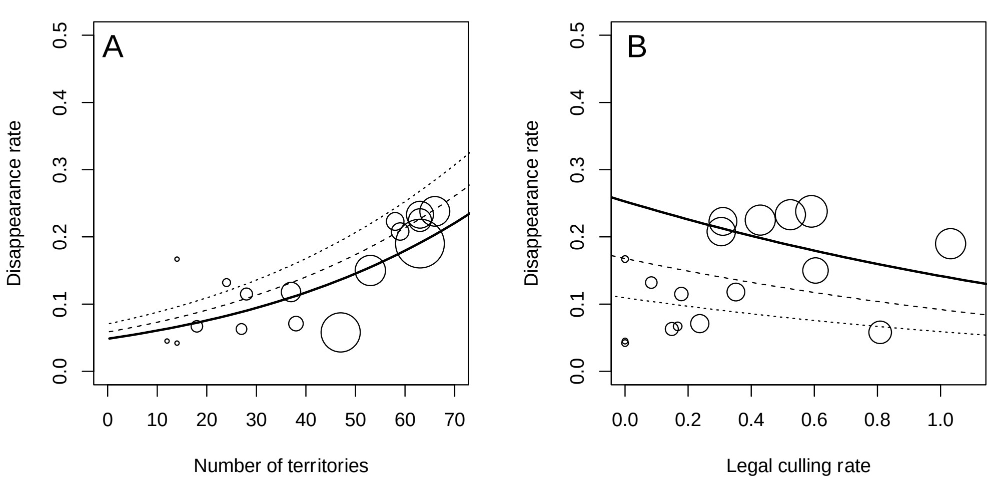

Fig. 2. A) Disappearance rate in relation to number of wolf territories in Sweden, 2000/01–2016/17. The lines show the predicted disappearance rate according to Cox model (Table 2). The dotted line is the prediction at no culling, the dashed line at a culling rate 0.30 and the black line at culling rate of 0.60. Legal culling rate is number of legally hunted wolves divided by the number of wolf territories. The size of circle markers is related to harvest rate and the biggest markers should mainly be below the dashed line. B) Disappearance rate in relation to legal culling rate. The lines show the predicted disappearance according to Cox model (Table 2). The dotted line in is the prediction at 20 wolf territories, the dashed line at 40 wolf territories and the black line at 60 wolf territories. The size of circle markers is related to number of wolf territories and the biggest markers should mainly be above the dashed line.

Table 1
Model selection table for factors affecting the disappearance rate of territorial wolves in Sweden 2000/01–2016/17 on population level, using logistic regression models with standardized independent variables (population size, culling rate and average parental inbreeding), degrees of freedom (df), corrected AIC (AICc), AICc differences (ΔAICc), AICc weight (ωi) and evidence ratios in relation to the top ranked model (ω1/ωi). Below are relative variable importance (RVI) and model-averaged coefficients (± SE and 95% CI) for variables included in the models.

Model	df	AICc	ΔAICc	ω_i	ω_1/ω_i
Culling rate + population size	3	83.21	0.00	0.41	–
Culling rate + inbreeding + population size	4	84.31	1.10	0.23	1.78
Population size	2	84.73	1.52	0.19	2.16
Inbreeding + population size	3	84.93	1.72	0.17	2.41
Culling rate + inbreeding	3	111.09	27.88	0	–
Inbreeding	2	111.72	28.51	0	–
Culling rate	2	111.85	28.64	0	–
Intercept only	1	111.97	28.76	0	–
Variable	RVI	Model-averaged coefficient ± SE			95% CI
Population size	1.00	0.66 ± 0.15			0.35 to 0.97
Culling rate	0.64	−0.22 ± 0.11			−0.46 to 0.01
Inbreeding	0.30	−0.18 ± 0.12			−0.44 to 0.06
Intercept	–	- 1.94 ± 0.11			−2.18 to −1.70

(SVA). All procedures, including capture, handling and collaring of wolves [see details in (Sand et al., 2006)] fulfilled ethical requirements and have been approved by the Swedish Animal Welfare Agency (Permit C150/15, C407/12, C281/6).

The collared territorial wolves were included in the logistic regression and Cox analyses described above, where they were treated the same way as the un-marked wolves. However, as a complement to those analyses, we applied a Kaplan-Meier cause-specific survival analysis with staggered entry design (Pollock et al., 1989) to the radio-tracking data we received from these 77 territorial collared wolves, representing 118 "wolf-years". To get a rough estimate how representative the mortality rates in territorial wolves were for the whole population, we also applied the Kaplan-Meier analysis to radio-tracking data from 46 non-territorial wolves, followed for the same period and representing 34 wolf-years. The position data were collected into the Wireless Remote Animal Monitoring (Dettki et al., 2013) database system for data validation and management. We identified three mortality causes: *i*) legal culling, *ii*) verified poaching and cryptic poaching, according to criteria in (Liberg et al., 2012) (for discussion of uncertainty to identify cryptic poaching, see reference (Liberg et al., 2012)), and *iii*) other mortality including traffic deaths and natural mortality. Because this sample was too small to split on single years, we compared two periods of time, 2000/01–2009/10 and 2010/11–2016/17, to examine the changes in cause-specific mortality rates over time. A breaking point between 2009/10 and 2010/11 was chosen because this was the time when the process of disagreement between Sweden and the European Union on wolf management using quota hunting started and public protest started influencing quota sizes (Darpö, 2011).

3. Results

Of the 444 territorial wolves included in the study, 343 (77%) were recorded in one of the three classes of lost wolves while the rest (n = 101) were censored. 103 wolves (51 females, 52 males) were legally culled, 31 (14 females, 17 males) died of other causes (23 natural and 8 traffic kills), and 209 (102 females, 107 males) wolves were classified as disappeared, including 20 radio-marked wolves where poaching was confirmed according to criteria given in (Liberg et al., 2012). The average total annual loss rate including both known mortalities and disappearance was 0.23 (95% CI 0.18 to 0.28).

Annual legal culling rates of territorial wolves increased during the period from zero the first few years up to 0.02–0.06 in the period 2003/04–2008/09 (Fig. 1, Table A1 in Appendix A). After quota hunts were introduced in 2010 the culling rate of territorial wolves ranged between 0.05 and 0.15. During the whole study period the rate of mortality from other causes (traffic and natural) fluctuated between zero and 0.06 without any overall temporal trend (logistic regression, p = 0.87, Table A1 in Appendix A). During the first 10 years of the study the average annual disappearance rate was 0.09 (range 0.04–0.17), followed by an increase to 0.21 (range 0.15–0.24) in 2010/11–2016/17, with an average annual disappearance rate of 0.14 for the entire study period.

Among lost territorial wolves, the individual risk of being legally culled was 0.25 (95% CI 0.17–0.34), of dying of other causes 0.13 (95% CI 0.07 to 0.20), whereas the risk of disappearing was 0.61 (95% CI 0.51 to 0.71). The combined annual risk to be lost at all due to legal culling was 0.06 (0.23*0.25; 95% CI 0.04–0.09), dying from other causes 0.03 (95% CI 0.02–0.04) and disappearing 0.14 (95% CI 0.10–0.18).

The Kaplan-Meier analysis of the collared territorial wolves gave similar levels of mortality (Table A1b in Appendix A). Legal culling rate over the years was 0.02; traffic-caused death rate 0.01, natural death rate 0.03, and poaching including both verified and cryptic cases had a rate of 0.12. Both legal culling rate and poaching rate increased from the first (2000/01–2009/10) to the second (2010/11–2016/17) part of the study, whereas traffic and natural death rates remained at low levels throughout the study years (Table A1b in Appendix A). Kaplan-Meier analysis of the collared non-territorial wolves gave higher mortality rates on all death causes, 0.10 for legal culling, 0.11 for traffic, 0.14 for natural deaths and 0.26 for poaching, but the difference between the two categories of wolves was not statistically significant, although for poaching it was close (χ^2 = 3.51, df = 1, p = .061).

Both population size and culling rate were included in the top ranked model explaining disappearance rate at the population level (Table 1, Fig.2). Population size was positively and culling rate negatively related to disappearance rate with population size as the most important variable with the highest relative variable importance (RVI 1.00) followed by culling rate (RVI 0.64). The effect of population size was 3.0 times stronger than the effect of culling rate (Table 1). Average parental inbreeding level had a negative effect on disappearance rate but with lower relative variable importance (RVI 0.30). The model was significant for the effect of population size (the conficence interval did not overlap zero), but not for culling rate and inbreeding.

Population size was the most important variable and positively related to disappearance risk also at individual level (Table 2), and here the negative effect of culling rate (RVI = 0.88) was also significant. The effect of population size was 2.4 times stronger than the effect of culling rate (Table 2), and the effect of inbreeding was low (RVI = 0.37) and non-significant (Table 2).

4. Discussion

In this study we demonstrate that disappearance rate (including

Table 2
Model selection table for factors affecting the disappearance risk of territorial wolves in Sweden 2000/01–2016/17 on individual level, using Cox models with standardized independent variables (population size, culling rate, inbreeding coefficient), degrees of freedom (df), corrected AIC (AICc), AICc differences (ΔAICc), AICc weights (ω_i) and evidence ratios in relation to the top ranked model (ω_1/ω_i). Below are relative variable importance (RVI), hazard ratio (HR) and model-averaged coefficients (± SE and 95% CI) for variables included in models.

Model	df	AICc	ΔAICc	ω_i	ω_1/ω_i
Culling rate + population size	2	3640.13	0.00	0.57	–
Culling rate + population size + inbreeding	3	3641.60	1.48	0.27	2.11
Population size	1	3643.40	3.27	0.11	5.18
Population size + inbreeding	2	3644.92	4.78	0.05	11.40
Culling rate	1	3669.38	29.25	0.00	–
Inbreeding	1	3670.97	30.84	0.00	–
Culling rate + inbreeding	2	3671.01	30.88	0.00	–
Variable	RVI	HR	Model-averaged coefficient ± SE		95% CI
Population size	1.00	1.60	0.46 ± 0.09		0.27 to 0.65
Culling rate	0.88	0.82	−0.19 ± 0.08		−0.35 to −0.02
Inbreeding	0.37	1.02	0.04 ± 0.06		−0.07 to 0.17

cases of verified poaching) in the Swedish wolf population has increased during the recent years and together with legal culling now has halted population growth. We also demonstrate that population size was positively related to disappearance rate, while legal culling rate was negatively related.

Similar to Chapron and Treves (Chapron and Treves, 2016), we have not been able to demonstrate poaching directly and unequivocally. A critical question in this study is the link between "disappearance" and "poaching". Wolf individuals can disappear for several reasons, where cryptic poaching is one possibility. Other causes can be missed identifications in the monitoring, divorce (i.e. both partners live but one or both did not pair again), other unknown mortality and long-distance emigration (details and data referring to a discussion of alternative explanations for these disappearances are given in Appendix B). Missed identifications during the monitoring are unlikely to explain the increased disappearance rate as the latter does not decrease with increased monitoring effort, but rather the opposite (Fig. B1 in Appendix B). This is corroborated by the fact that the probability for completely failing to identify (observation error) one or both individuals in an earlier identified territorial wolf pair for one monitoring season was only 0.02 and for two consecutive seasons 0.003 (see Appendix B). Divorces where both adult individuals stayed alive after the divorce but did not find a new partner have never been confirmed in the Scandinavian population (Milleret et al., 2016). Density dependent processes could potentially have led to an increased natural mortality in the latter part of our study since high density and saturated wolf populations in areas with low human impact show high natural mortality rates through intraspecific strife and starvation (Mech and Boitani, 2003; Cubaynes et al., 2014). However, the wolf density in Sweden is still relatively low with large territory sizes and abundant food resources (Mattisson et al., 2013) and peaked in 2014/15 with a density of approximately 5/1000 km^2 (Wabakken et al., 2018), which is far below the levels reported to lead to density dependent mortality (Cubaynes et al., 2014). Natural mortality in radio-collared wolves was only 3% and did not increase with time (Table A1 in Appendix A). Further, the proportion of natural deaths among dead wolves handled within the Swedish national program for post-mortem analysis in wild animal shows a non-significant decreasing trend with time (logistic regression, $p = .24$, Fig. B3 in Appendix B), i.e. opposite to the time trend in disappearances. Long-distance emigration has not been observed for territorial adult wolves in Scandinavia (SKANDULV records, unpublished data) and seems to be extremely rare generally (Mech and Boitani, 2003). But the strongest support for the assumption that most disappearances were caused by poaching come from the comparison between the disappearance rates and the poaching rates revealed by data from the collared wolves. The mean values for the whole study period were 0.14 and 0.12 respectively, and for the first half of the study period it was 0.09 and 0.10 while for the second period it was 0.21 and 0.18 respectively (Table A1, Appendix A). Thus, we conclude that although we have not been able to demonstrate that disappearance = poaching in an unambiguous way, we have presented both data and strong arguments (above and in Appendix B) supporting the assumption that the majority of the disappearances of territorial wolf individuals from one season to the next in this study were caused by poaching.

Models including population size ranked highest explaining the observed variation in disappearance of territorial wolves, both on population and individual level. Legal culling rate had a negative, and weaker, explanatory power on both levels. This difference between the two explanatory factors may be due to low human tolerance towards wolves that cannot be solved by a restricted legal culling alone unless this also results in a reduced population size (Von Essen et al., 2017; Pohja-Mykrä, 2016; Gangaas et al., 2013). Restricted culling quotas might even be perceived as more provoking than a total ban on hunting (Suutarinen and Kojola, 2018). Frequent changes in signals from authorities on future management have also been seen to cause more poaching (Olson et al., 2015). This could have contributed to the increase in the disappearance rate of wolves in Sweden after 2009/10, when issued harvest quotas started being questioned, reduced or in some years totally prohibited by court decisions after vivid public protests and interference by the European Union (Darpö, 2011; von Essen and Allen, 2017).

The rate of disappearance found (range 0.04–0.24, mean 0.14) is comparable or higher than most reported poaching rates on wolves. In North America, reported poaching rates commonly range between 0.05 and 0.10 (Adams et al., 2008; Pletscher et al., 1997; Stenglein et al., 2018). In a large study from three adjacent areas in Northern Rocky Mountains in USA, the average annual rate of poaching was 0.06 (Smith et al., 2010). However, these rates could be underestimates because cryptic poaching was not accounted for (Treves et al., 2017). In Europe, where wolves live in closer proximity to humans, poaching rates on wolves seem to be higher (Liberg et al., 2012; Huber et al., 2002; Boitani and Ciucci, 1993; Blanco and Cortés, 2007). In neighboring Finland, estimated poaching rates were even higher than those found in this study (Suutarinen and Kojola, 2017).

A number of studies have provided estimates on how large human-caused mortality a wolf population can sustain before declining. Based on data from 18 North American wolf populations, Fuller (1989) concluded that the breaking point was 0.29, and at lower levels human-caused mortality was compensatory to other mortality (but see Stenglein et al., 2018 for further discussion on the role of compensatory mortality in wolves). This estimate was supported in a later study (Adams et al., 2008). Creel and Rotella (2010) demonstrated considerably lower levels, i.e. 0.22 for the Northern Rocky Mountain population, and 0.25 for other North American wolf populations, but their results were questioned by Gude et al. (2012) for including years with poor monitoring in their analysis and not considering variation in recruitment rates. Fuller et al. (2003) also pointed to variation in productivity as the main reason for the great variation in levels for sustainable culling between studies.

Importantly, none of these studies considered the extent of poaching. As it is likely that there is a large variation also in this factor, it will have a strong effect on the estimated size of maximum sustainable human offtake. In our study, legal culling rate never exceeded 0.16 (Table A1 in Appendix A), and was only weakly negatively correlated to population growth ($r = 0.19$, $p = .47$) with an estimated break point for zero growth at 0.27. However, if disappearance rate also was included, the correlation improved considerably ($r = 0.40$, $p = .11$), and resulted in an estimated break point at 0.38 (Fig. B4 in Appendix B). Assuming that the majority of observed disappearances in our study were caused by poaching, this illustrates the importance to consider poaching when estimating the relation between human offtake and population growth.

Since our analysis of disappearances is based solely on territorial wolves, it could be questioned how representative this category is for the whole population. However, the Kaplan-Meier survival analysis of collared wolves gave a close to statistically significantly higher poaching rate in non-territorial wolves, which indicates that the disappearance rate we found in territorial wolves rather is a conservative measure of poaching rate for the whole population. Even in the case of a real difference, this might not matter much for the demography of the population since the territorial wolves constitute the reproductive segment of the population, and thus have far more impact on population growth than the non-territorial members of the population.

5. Conclusions

Managing large carnivores in human dominated landscapes is probably one of the most challenging problems facing conservation authorities all over the world (Woodroffe, 2000), where poaching is a key issue (Carter et al., 2016). A prerequisite for appropriate actions is information on the magnitude of the problem. By using detailed knowledge about the identity of territorial wolves in Sweden we have been able to elucidate a disappearance rate that by far surpasses most poaching rates reported for large carnivores. Considering that this type of data rarely is available, we suspect that poaching rates in many areas may be underestimated. Recent awareness of the shortcomings of traditional methods to measure "cryptic" poaching supports this assumption (Treves et al., 2017; Stenglein et al., 2018).

Our results indicate that legal culling may have some dampening effect on large carnivore poaching. We acknowledge that this is a controversial issue and we believe the discussion on this multi-sided topic (Epstein, 2017) is likely to be continued and hope that our study will stimulate further research on the relation between legal culling and poaching. Although we have not been able to measure poaching in a direct and unequivocal way, our results provide managers with important information when considering the impact that legal culling may have on poaching of controversial large carnivores. However, the combined effects of legal culling and disappearance during the latter part of our study period has halted the population growth. Therefore, our results indicate that legal culling is an unlikely option in the near future for Swedish wolf management where instead the population is likely regulated by poaching.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108456.

Funding

This work was supported by Swedish Environmental Protection Agency [NV-08503 and SEPA 2015-2017 NV-01337-15]; Finnish Foundation for Nature Conservation; the Aurora Doctoral Program of the Thule Institute, University of Oulu; Norwegian Environment Agency; Swedish Association for Hunting and Wildlife Management [Org. 2017/18–5855/2017, 5855/2018]; Marie-Claire Cronstedt's foundation and WWF Sweden; FORMAS (2019-01186).

CRediT authorship contribution statement

Olof Liberg: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Data curation. **Johanna Suutarinen:** Methodology, Software, Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **Mikael Åkesson:** Methodology, Investigation, Data curation, Writing - review & editing. **Henrik Andrén:** Validation, Formal analysis, Writing - review & editing. **Petter Wabakken:** Methodology, Investigation, Writing - review & editing, Data curation. **Camilla Wikenros:** Investigation, Writing - review & editing, Project administration, Funding acquisition. **Håkan Sand:** Methodology, Investigation, Writing - review & editing, Data curation, Project administration, Funding acquisition.

Declaration of competing interest

We declare that we have no conflicts of interest regarding our manuscript "Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling."

Acknowledgements

We thank the numerous field technicians and central staff on the County Administrative Boards and the Wildlife Damage Center in Sweden who organized and performed the tracking and collecting of DNA-samples, and the personnel on the DNA-laboratory at Grimsö Wildlife Research Station, especially Anna Danielsson and Eva Hedmark. We especially want to thank Linn Svensson on the Wildlife Damage Center who compiled all data from the monitoring. We also thank Erik Ågren and the Swedish National Veterinary Institute for kindly providing us with post mortem data, and Ilpo Kojola for assistance and advice all along.

References

Adams, L.G., Stephenson, R.O., Dale, B.W., et al., 2008. Population dynamics and harvest characteristics of wolves in the central brooks range, Alaska. Wildl. Monogr. 170, 1–25. https://doi.org/10.2193/2008-012.

Åkesson M, Svensson L. 2019 Sammanställning av släktträdet över den skandinaviska vargpopulationen fram till 2018. Rapport från Viltskadecenter 2019-3, ISSN: 978-91-985247-0-3 (Pedigree on the Swedish wolf population up to 2018; (In Swedish with captions in English)).

Åkesson M, Liberg O, Sand H, et al.. 2016 Genetic rescue in a severely inbred wolf population. Mol. Ecol.. 25, 4745–4756. (doi: https://doi.org/10.1111/mec.13797?) https://doi.org/10.1111/mec.13797?).

Andersen, P.K., Gill, R.D., 1982. Cox's regression model for counting processes: a large sample study. Ann. Stat. 10, 1100–1120.

Andrén, H., Linnell, J.D.C., Liberg, O., et al., 2006. Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. Biol. Conserv. 131, 23–32. https://doi.org/10.1016/j.biocon.2006.01.025.

Barton, K., 2018. MuMIn: multi-model inference. R package version 1.40.4. Available from. https://CRAN.R-project.org/package=MuMIn.

Blanco, J.C., Cortés, Y., 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. J. Zool. 273, 114–124. https://doi.org/10.1111/j.1469-7998.2007.00305.x.

Boitani, L., Ciucci, P., 1993. Wolves in Italy: critical issues for their conservation. In: Promberger, C., Schröder, W. (Eds.), Wolves in Europe: Current Status and Perspectives. Munich Wildlife Society, Ettal, Germany, pp. 75–90.

Carter, N.H., López-Bao, J.V., Bruskotter, J.T., et al., 2016. A conceptual framework for understanding illegal killing of large carnivores. Ambio 46, 251–264. https://doi.org/10.1007/s13280-016-0852-z.

Challender, D.V.S., MacMillan, D.C., 2014. Poaching is more than an enforcement problem. Conserv. Lett. 7, 484–494. https://doi.org/10.1111/conl.12082.

Chapron, G., Treves, A., 2016. Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. Proc. R. Soc. B 283. https://doi.org/10.1098/rspb.2015.2939.

Chapron, G., Treves, A., 2017. Reply to comment by Pepin et al. 2017. Proc. R. Soc. B 284, 20162571. https://doi.org/10.1098/rspb.2016.2571.

Chapron, G., Treves, A., 2017. Reply to comments by Olson et al. 2017 and Stien 2017. Proc. R. Soc. B 284, 20171743. https://doi.org/10.1098/rspb.2017.1743.

Creel, S., Rotella, J.J., 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PLoS One 5, e12918 (doi: .1371/journal.pone.0012918).

Cubaynes, C., MacNulty, D.R., Stahler, D.R., et al., 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). J. Anim. Ecol. 83, 1344–1356.

Darpö, J., 2011. Brussels advocates Swedish Grey wolves. On the encounter between species protection according to Union law and the Swedish wolf policy. European Policy Analysis 8, 1–20.

Dettki H, Ericsson G, Giles T, et al. 2013 Wireless Remote Animal Monitoring (WRAM) - a new international database e-infrastructure for telemetry sensor data from fish and wildlife, in The European Society of Telemetry (ed). Proceedings Etc 2012: Convention for Telemetry, Test Instrumentation and Telecontrol. Books on Demand, pp. 247–256, ISBN: 978-3-7322-5646-4.

Epstein, Y., 2017. Killing wolves to save them? Legal responses to 'tolerance hunting' in the European Union and United States. RECIEL 26 (19–2).

von Essen, E., Allen, M.P., 2017. From obstructionism to communication: local, national and transnational dimensions of contestations on the Swedish wolf cull controversy. Environ. Commun. 11, 654–666. https://doi.org/10.1080/17524032.2016.1269821.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105.

Fuller, T.K., Mech, L.D., Cochrane, J.F., 2003. Wolf population dynamics. In: Mech, D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. The University of Chicago Press, Chicago, Illinois, USA, pp. 161–191.

Gangaas, K.E., Kaltenborn, B.P., Andreassen, H.P., 2013. Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. PLoS One 8, 68849. https://doi.org/10.1371/journal.pone.0068849.

Gude, J., Mitchell, M.S., Russell, M.E., et al., 2012. Wolf population dynamics in the U.S. northern rocky mountains are affected by recruitment and human-caused mortality. J. Wildl. Manag. 76, 108–118.

Heisey, D.M., Patterson, B.R., 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. J. Wildlife Manage. 70, 1544–1555. https://doi.org/10.2193/0022-541X(2006)70[1544:AROMTE]2.0.CO;2.

Huber, D., Kusak, J., Frković, A., et al., 2002. Causes of wolf mortality in Croatia in the period 1986-2001. Veterinarski Arhiv 72, 131–139.

Kaltenborn, B.P., Brainerd, S.M., 2016. 2016 Can poaching inadvertently contribute to increased public acceptance of wolves in Scandinavia? Eur. J. Wildl. Res. 62, 179–188. https://doi.org/10.1007/s10344-016-0991-3.

Leader-Williams, N., 2003. Regulation and protection: Successes and failures in rhinoceros conservation. In: Oldfield, S. (Ed.), The Trade in Wildlife: Regulation for Conservation. Earthscan, London.

Liberg, O., Andrén, H., Pedersen, H.C., et al., 2005. Severe inbreeding depression in a wild wolf (Canis lupus) population. Biol. Lett. 1, 17–20. https://doi.org/10.1098/rsbl.2004.0266.

Liberg, O., Aronson, Å., Brainerd, S.M., et al., 2010. The re-colonizing Scandinavian wolf population: Research and management in two countries. In: Musiani, M., Boitani, L., Paquet, P.C. (Eds.), The World of Wolves: New Perspectives on Ecology, Behaviour and Management. University of Calgary Press, Calgary, Alberta, Canada.

Liberg, O., Aronson, Å., Sand, H., et al., 2012. Monitoring of wolves in Scandinavia. Hystrix 23, 29–34. https://doi.org/10.4404/hystrix-23.1-4670.

Liberg, O., Chapron, G., Wabakken, P., et al., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B 279, 910–915. https://doi.org/10.1098/rspb.2011.1275.

Lunn, M., McNeil, D., 1995. Applying cox regression to competing risks. Biometrics 51, 524–532. https://doi.org/10.2307/2532940.

Mattisson, J., Sand, H., Wabakken, P., et al., 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 3, 813–825. https://doi.org/10.1007/s00442-013-2668-x.

Mech, L.D., 2017. Where can wolves live and how can we live with them? Biol. Conserv. 2010, 310–317. https://doi.org/10.1016/j.biocon.2017.04.029.

Mech, L.D., Boitani, L., 2003. Wolf: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Milleret, C., Wabakken, P., Liberg, O., et al., 2016. Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. J. Anim. Ecol. 86, 43–54. https://doi.org/10.1111/1365-2656.12587.

Murray, D.L., Smith, D.W., Bangs, E.E., et al., 2010. Anthropogenic deaths are partially compensatory in recovering wolf population. Biol. Conserv. 143, 2514–2524. https://doi.org/10.1016/j.biocon.2010.06.018.

Olson, E.R., Stenglein, J.L., Shelley, V., et al., 2015. Pendulum swings in wolf management led to conflict, illegal kills, and a legislated wolf hunt. Conserv. Lett. 8, 351–360. https://doi.org/10.1111/conl.12141.

Naturvårdsverket, 2007. Naturvårdsverkets föreskrifter och allmänna råd om inventering av björn, varg, järv, lodjur och kungsörn. NFS 2007:10. Naturvårdsverkets författningssamling.

Naturvårdsverket, 2014. Varg: Instruktioner för fastställande av familjegrupp, revirmarkerande par och föryngring (Wolf: Instructions for determining family group, territorial pair and reproductions) www.naturvardsverket.se. Naturvårdsverket and Rovdata.

Olson, E.R., Crimmins, S.M., Beyer, D.E., et al., 2017. Flawed analysis and unconvincing interpretation: a comment on Chapron and Treves. Proc. R. Soc. B 284, 20170273. https://doi.org/10.1098/rspb.2017.0273.

Pepin, K.M., Kay, S.L., Davis, A.J., 2017. Comment on: 'blood does not buy goodwill: allowing culling increases poaching of a large carnivore' Proc. R. Soc. B 284, 20161459. https://doi.org/10.1098/rspb.2016.1459.

Peterson, M.N., von Essen, E., Hansen, H.P., Peterson, T.R., 2018. Shoot, shovel and sanction yourself: self-policing as a response to wolf poaching among Swedish hunters. Ambio 2018. https://doi.org/10.1007/s13280-018-1072-5.

Pletscher, D.H., Ream, R.R., Boyd, D.K., et al., 1997. Population dynamics of a recolonizing wolf population. J. Wildlife Manage. 61, 459–465. https://doi.org/10.2307/3801296.

Pohja-Mykrä, M., 2016. Felony or act of justice? Illegal killing of large carnivores as defiance of authorities. J.Rural Stud. 44, 46–54. https://doi.org/10.1016/j.jrurstud.2016.01.003.

Pohja-Mykrä, M., 2017. Community power over conservation regimes: techniques for neutralizing the illegal killing of large carnivores in Finland. Crime Law Soc. Change 67, 439–460. https://doi.org/10.1007/s10611-016-9666-y.

Pohja-Mykrä, M., Kurki, S., 2014. Strong community support for illegal killing challenges wolf management. Eur. J. Wildl. Res. 60, 759–770. https://doi.org/10.1007/s10344-014-0845-9.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildlife Manage. 53, 7–15. https://doi.org/10.2307/3801296.

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org.

Redpath SM, Young J, Evely A, et al. RJ.2013 Understanding and managing conservation conflicts. Trends Ecol. Evol. 28, 100–109. (doi:https://doi.org/10.1016/j.tree.2012.08.021).

Ripple, W.J., Estes, J.A., Beschta, R.L., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. https://doi.org/10.1126/science.1241484.

Sand, H., Wikenros, C., Wabakken, P., Liberg, O., 2006. Effects of hunting group size, snow depth and age in the success of wolves hunting moose. Anim. Behav. 72, 781–789. https://doi.org/10.1016/j.anbehav.2005.11.030.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x.

Smith, D.W., Bangs, E.E., Oakleaf, J.K., et al., 2010. Survival of colonizing wolves in the northern rocky mountains of the United States, 1982–2004. J. Wildlife Manage. 74, 620–634. https://doi.org/10.2193/2008-584.

Stenglein, J.L., Wydeven, A.P., Van Deelen, T.R., 2018. Compensatory mortality in a recovering top carnivore: wolves in Wisconsin, USA (1979–2013). Oecologia 187, 99–111. https://doi.org/10.1007/s00442-018-4132-4.

Stien, A., 2017. Blood may buy goodwill: no evidence for a positive relationship between legal culling and poaching in Wisconsin. Proc. R. Soc. B 284, 20170267. https://doi.org/10.1098/rspb.2017.0267.

Suutarinen J, Kojola I. 2017 Poaching regulates the legally hunted wolf population in Finland. Biol. Conserv. 215, 11–18. (doi.org/https://doi.org/10.1016/j.biocon.2017.08.031).

Suutarinen, J., Kojola, I., 2018. One way or another: predictors of wolf poaching in a legally harvested wolf population. Anim. Conserv. 21, 414–422. https://doi.org/10.1111/acv.12409.

Therneau, T.M., 2015. A Package for Survival Analysis in S. Version 2.38. Available from. http://CRAN.R-project.org/package=survival.

Treves, A., 2009. Hunting for large carnivore conservation. J. Appl. Ecol. 46, 1350–1356. https://doi.org/10.1111/j.1365-2664.2009.01729.x.

Treves, A., Bruskotter, J.T., 2014. Tolerance for predatory wildlife. Science 344, 476–477. https://doi.org/10.1126/science.12526.

Treves, A., Wittemyer, G., Northrup, J.M., et al., 2014. Ivory poaching drives decline in African elephants. PNAS 111, 13117–13121. https://doi.org/10.1073/pnas.1403984111.

Treves, A., Artelle, K.A., Darimont, C.T., Parsons, D.R., 2017. Mismeasured mortality: correcting estimates of wolf poaching in the United States. J. Mammal. 98, 1256–1265. https://doi.org/10.1093/jmammal/gyx052.

Von Essen E, Hansen HP, Nordström-Källström et al.. 2015. The radicalization of rural resistance. How hunter counterpublics in the Nordic countries contribute to illegal hunting. J Rural Studies 39:199–2019.

Von Essen, E., Hansen, H.P., Peterson, M.N., Peterson, T.R., 2017. Discourses on illegal hunting in Sweden: the meaning of silence and resistance. Environ. Sociol. 4, 1–11. https://doi.org/10.1080/23251042.2017.1408446.

Von Rushkowski, E., 2016. Wolves welcome!? Lessons learned from 15 years of wolf recovery in Germany. Int. Wolf 26, 12–13.

Wabakken, P., Sand, H., Liberg, O., Bjärvall, A., 2001. The recovery, distribution and population dynamics of wolves on the Scandinavian Peninsula, 1978-98. Can. J. Zool. 79, 710–725. https://doi.org/10.1139/cjz-79-4-710.

Wabakken, P., Svensson, L., Maartmann, E., et al., 2018. Bestandsovervåking av ulv vinteren 2017-2018. Bestandsstatus for store rovdyr i Skandinavia 1-2018 (In Swedish with Abstract in English). Report to the. Swedish Environmental Protection Agency (ISSN 2387-2950 (dig.) ISBN 978-82-426-2924-1).

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3, 165–173. https://doi.org/10.1111/j.1469-1795.2000.tb00241.x.

Woodroffe, R., Redpath, S.M., 2015. When the hunter becomes the hunted. Science 348, 1312–1314. https://doi.org/10.1126/science.aaa8465.