Research

Declining survival rates of red foxes *Vulpes vulpes* during the first outbreak of sarcoptic mange in Sweden

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EDITOR'S CHOICE

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Rapid declines in red fox *Vulpes vulpes* populations have followed outbreaks of epizootic mange caused by the mite *Sarcoptes scabiei*. In Sweden, the first outbreak of sarcoptic mange started in 1977/1978 and affected the whole country by 1984. Here we used data on the number of harvested red foxes (51 480) from Gävleborg county (18 199 km²) in Sweden between 1970 and 1994. We used data on the prevalence of sarcoptic mange in a sample of harvested red foxes (2694) from 1974 to 1982. A rapid decline in harvested foxes occurred two to three years after the prevalence of sarcoptic mange first became evident. In the same period, mark–recovery data were used to estimate changes in survival rates, and the best model included an effect of age (young or adult) and period (annual) on the survival and recapture probabilities. The analysis was based on data from 701 young foxes of which 523 were recovered, and 133 adults of which 131 were recovered. Average annual survival was 0.55 (range = 0.53–0.58) for adults and 0.36 (range = 0.32–0.39) for young foxes in the three years preceding the outbreak. During the outbreak and the remaining six years of the study, the average survival was reduced to 0.41 (range = 0.30–0.48) for adults and to 0.25 (range = 0.17–0.30) for young foxes. A population model, based on results on our survival analysis and literature data on fecundity, was developed to project the decline of the fox population. The rate and magnitude of the reduction in projected population and harvested foxes were similar, with both reduced by almost ninety percent. Harvest statistics indicate the fox population recovered to pre-mange densities in less than 10 years after the first detection of mange indicating a rapid development of resistance in the host. This study shows the importance of long-term population monitoring in combination with large-scale field-experiments to devise alternative management options.

Keywords: disease, population crash, red fox, sarcoptic mange, survival, *Vulpes vulpes*

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Introduction

Conservation and management of animal populations require a solid understanding of how different drivers affect population dynamics (Begon et al. 1986, Fryxell et al. 2014). Population models based on survival and reproduction are important management tools (Krebs 1999). They are greatly improved by information on how demographic variables are affected by external conditions, and how these variables vary in space and time (Lande et al. 2003, Mills 2012, Fryxell et al. 2014). Population dynamics are highly sensitive to changes in survival rate, especially when fecundity is low compared to survival (Gaillard et al. 1998, Mills et al. 1999). However, estimates of survival rates and their variance are often difficult to obtain compared to corresponding values for fecundity (Krebs 1999). Age at first reproduction and number of offspring per female can often be directly observed in the field or obtained from reproductive traits of dead animals (Fryxell et al. 2014). Estimates of survival rates, on the other hand, require data collected over a long time-period; commonly estimated by mark–recapture and recovery of marked individuals (White 1982), or by tracking the fate of radio-collared animals (White and Garrott 2012). Moreover, survival rates are often associated with large uncertainty, which limits predictions from population models because of the sensitivity to variation in survival (Gould and Nichols 1998).

Natural catastrophes, such as novel epizootic outbreaks of parasites, increase mortality and can drastically reduce population levels (Mills 2012). For example, the rinderpest virus *Rinderpest morbillivirus* was accidentally introduced to Africa in the late 1880s and resulted in 90% mortality of ungulate populations (van Onselen 1972). The *Myxoma* virus reached the UK in the early 1950s and is estimated to have caused a 99% decline in the European rabbit *Oryctolagus cuniculus* population (Sumption and Flowerdew 1985). An outbreak of Pasteurellosis reduced a regional population of Saiga antelope *Saiga tatarica* in Kazakhstan by 88% in 2015, probably initiated by environmental changes that increased its pathogenicity (Robinson et al. 2019). Rapid declines in red fox (*Vulpes vulpes*, hereafter fox) populations following outbreaks of epizootic mange, caused by the mite *Sarcoptes scabiei*, have been reported from several parts of the world (Baker 2000, Bornstein et al. 2001, Soulsbury et al. 2007). In populations not previously exposed to sarcoptic mange, mortality generally occurs within 3–4 months after infection by the mite (Niedringhaus et al. 2019) until resistance can develop in the population (Bornstein et al. 2001, Niedringhaus et al. 2019). In Britain, the overall population density of foxes declined by > 95% in two years as a consequence of mange (Baker et al. 2000). A detailed study in Japan estimated a 91% decline in harvested foxes and a 52% decline in the population density (Uraguchi et al. 2014). The emergence of sarcoptic mange in Denmark is believed to have contributed to the extinction of foxes on Bornholm island (588 km²) in Denmark (Bornstein et al. 2001).

In Sweden, in 1972 and 1975, two separate instances of sarcoptic mange in red foxes were reported for the first time, assumed to have originated from an outbreak in the mid 1960s in Finland (Bornstein et al. 2001). Mange then spread rapidly until more or less all of Sweden was affected by 1984 (Danell and Hörnfeldt 1987, Mörner 1992). This decline in the fox population was followed by a large increase in the population levels of many of its prey species (Lindström et al. 1994, Smedshaug 1999, Jarnemo and Liberg 2005), and other generalist predators such as pine marten *Martes martes* and the American mink *Mustela vision* (Small et al. 1993, Carlsson et al. 2010). Swedish bag records imply that the fox population begun to recover in the late 1980s and early 1990s, and in neighbouring Norway, the prevalence of both mange cases and seropositive foxes was significantly lower in 2002–2005 compared to 1994–1995 (Davidson et al. 2008). Sarcoptic mange has since remained in the fox population but has generally been limited to more localized outbreaks (Carricondo-Sanchez et al. 2017).

Despite their historical importance in the fur trade (Martin 1986, Ringaby 2014), foxes are today often considered as vermin because they prey on domestic animals, carry zoonotic diseases and can potentially threaten endangered species (Anderson et al. 1981, Marcström et al. 1989, Seymour et al. 2003, Roos et al. 2018, Laidlaw et al. 2019). Foxes are also opportunistic predators that generally benefit from human settlements (Gallant et al. 2020), especially in northern areas with extensive periods of snow cover (Bartoń and Zalewski 2007). High abundances and long-range dispersal make the fox a likely candidate as a vector for several zoonoses, for example the rabies virus (Steck and Wandeler 1980). We have recently shown that foxes can move long distances in a short time (Walton et al. 2018), and few individuals dispersing hundreds of kilometres have the potential to initiate new outbreaks/disease clusters in places where foxes are common. The potentially hazardous *Echinococcus multilocularis* has recently been discovered in foxes in Sweden (Lind et al. 2011), but has not expanded geographically as rapidly as could be expected. One possible explanation is a lack of suitability and density of rodent species as secondary hosts (Miller et al. 2017). However, despite its importance as predator and vector for disease, few details on fox demography are available from much of its range (Devenish-Nelson et al. 2013). The impact of large outbreaks of mange and other parasites on specific vital rates of host populations in the wild are poorly known despite their importance to population models and management (Hudson et al. 1992, Bloomer et al. 1995, Newey et al. 2007). Based on the prevalence of mange in harvested foxes and reduction in bag sizes, mortality from the mange outbreak in Sweden was assumed to be extensive although survival estimates before and during the outbreak are lacking.

Here, we use data on prevalence of sarcoptic mange in harvested foxes and mark–recovery data in a long-term study of fox dispersal to estimate survival during the outbreak of sarcoptic mange. We used our survival estimates in combination with published data of fecundity to model the population development during the outbreak of sarcoptic mange. We also discuss factors that likely contributed to the rapid emergence, spread and subsequent recovery of red foxes in Sweden.

Study area

Between 1974 and 1983, foxes were captured in central Sweden with 88% of the captures made in the county of Gävleborg (18 199 km^2), the remaining captures occurred in neighbouring counties. This area in Sweden is characterized as the transitional border zone between boreonemoral forests in the south and boreal forests in the north. There is a climatic and topographical gradient from the south to the north with milder and flatter areas in the south to colder and more rolling hills in the north. The mean altitude range from 50 m a.s.l. in the south to 250 m a.s.l. in the north. The mean temperatures average +15°C in summer and −5°C in winter. The ground is generally snow covered from late December up to the end of March and early April (for further details see Willebrand 1988, Small et al. 1993, Sjörs 1999).

Methods

Prevalence of sarcoptic mange and harvest data

A long term-project was started in Sweden in the early 1960s to investigate morphological characteristics of foxes in different regions and their potential changes over time. This also included tagging of foxes to study dispersal and other aspects of fox ecology (see below for details on the tagging of foxes and Englund (1980)). Harvested foxes were collected from hunters across different regions, but in this study, we only used foxes from Gävleborg county (n = 2694) to estimate prevalence of sarcoptic mange. Harvested foxes in Gävleborg county were collected from hunters between 1974 and 1982 when low density, presumably an effect of sarcoptic mange, made it difficult to harvest foxes. All carcasses were macroscopically investigated for signs of sarcoptic mange, especially around their ears, elbows, face and legs. The result was added as a binomial variable to the database of individual measurements. Data on number of total foxes harvested in Gävleborg county between 1970 and 1994 were obtained from the Swedish Hunters Association, who has the national responsibility to collect and compile harvest data of small game in Sweden (<www.viltdata.se/>).

Capture and recoveries

Baited wooden box traps were used to capture foxes in autumn and winter between 1974 and 1983. During summer, cubs were captured by nets at or close to the den. Foxes were tagged with a metal id tag in each ear after being weighed and sexed. Age, as adult or young of the year, was determined by size in combination with the degree of tooth eruption and tooth wear. It was not always possible to obtain a reliable estimate of age in late summer and autumn because not all field-assistants had enough training and experience. In total, 1087 foxes were captured and 692 were later recovered. Age was not known for 253 captures and 38 recovered foxes and thus excluded. We used 654 recoveries in our analyses. Specifically, the mark–recovery analysis included data from 701 young foxes of which 523 were recovered, and 133 adults of which 131 were recovered. To follow the breeding cycle of foxes, the year was defined to begin in March and end in February. The mortality cause of recovery was known for 477 individuals.

Analysis

The statistical software R ver. 4.0.5 (<www.r-project.org>) was used for all data handling, analysis and graphical presentation. Mark–recovery data were analyzed using the software Mark ver. 9.0 (Cooch and White 2018) with RMark ver. 2.2.7 (Laake 2013) as an R interface. We estimated the effects of two covariates, age (adult or young) and time (10 occasions) on survival and recapture probabilities. Individual co-variates were not included. Data were transformed to 65 unique encounter histories as dead-recovery (Seber) to fit the format required by Rmark. The transition from young to adults was adjusted by adding a column that depicted age (age.now) (Supporting information). We modified the R-code provided by Dr. M. J. Conroy available at (<https://sites.google.com/site/cmrsoftware/home>) to format the data for Rmark. See Supporting information for list of models and Supporting information for data and R-script.

We expected both survival (S) and recapture (r) rates to differ between age-classes and change between occasions. The overall global model (S(~age.now × time)r(~age.now × time)) included interaction effects between age and occasion for both survival and recapture rates. We modelled all possible combinations of age, survival, recovery and time (occasions). These combinations resulted in 25 hierarchical models (Supporting information). AICc is the default parameter reported by RMark for model selection (Laake 2013), and it was used to compare the performance of different models. We assumed a value of deltaAICc less than 3 to indicate equal model performance (Burnham and Anderson 2004). We used Akaike-weights as conditional probabilities (Wagenmakers and Farrell 2004) to rank the power of different models (Supporting information). Survival estimates and 95% confidence intervals are presented graphically for the nine annual intervals and summarized for the three-year period before the outbreak and the following six year period during the outbreak.

Population projection

We combined our estimates of survival rates and fecundity values from literature to develop a population projection during 1974–1983 using 1000 random values of survival and fecundity for the transition of one year to the next. We assumed an initial population size of 1 in 1974 consisting of 0.45 adults and 0.55 young as reasonable starting values (Englund 1980). The details of the model are described in Supporting information. We used the annual survival distributions obtained in our mark–recovery analysis and excluded values outside the 95% confidence limits.

Microtines are an important food source for foxes, and fox fecundity is correlated with the vole cycle in the northern boreal forests (Englund 1970). We used fecundity values (female cub/female adult) for adult and young foxes respectively during low (0.55 and 0.25), high (2.75 and 1.25) and medium (1.25 and 1.25) abundance of microtines estimated from a long-term study in the boreal forest (Englund 1970). That study reported a peak or crash to occur once every four-to-five-year period resulting in an average annual probability of 0.22 for either peak or crash and 0.55 for a medium year. Combining variation in fecundity with the probability of microtine abundance resulted in an overall mean (standard deviation) for fecundity to 1.43 (0.76) for adults, and 1.03 (0.42) for young. It is likely that females suffering from infestation with sarcoptic mange would show reduced fecundity. The proportion of young in the harvested foxes was higher than 0.75 in all years during the period of 1974–1979, and substantially lower than 0.70 in the period of 1980–1983. The pooled data for these two periods resulted in an average ratio of young foxes in the first period of 0.77, compared to 0.63 in the second period ($\chi^2 = 26.26$, df = 1, p < 0.0001). However, we chose a conservative approach and did not reduce the fecundity estimates for the population projection from 1980 because of potential bias of the age composition of harvested foxes. Our main objective was to estimate the effect of the reduced survival from our previous analysis. The population projection was correlated with the change in number of harvested foxes with time lags of 0–4 years.

Results

The prevalence of sarcoptic mange among harvested foxes showed a rapid increase from 2% infected animals in 1978, when first detected, to 40% infected animals four years later. This was reflected by a similar rapid decrease in number of harvested foxes from 1980 to 1985 (Fig. 1). In 1985, the number of harvested foxes had declined to only 10% of the previous peak levels of the early-1970s. From 1986, bag size again increased and almost reached previous peak levels in 1994 when 2300 harvested foxes were reported. Note that we lack data on the prevalence of sarcoptic mange from 1983.

Of the 477 recovered foxes with known mortality cause, hunting was the most common cause of recovery for both adult and young foxes (89% [95% C.I. = 0.83–0.92] and 88% [95% C.I. = 0.84–0.93]). A somewhat larger proportion of adults were found dead or weak than were young foxes, 6% [95% C.I. = 0.03–0.10] versus 3% [95% C.I. = 0.01–0.06], while foxes killed by traffic was more common for young foxes compared to adult foxes, 9% [95% C.I. = 0.06–0.13] versus 5% [95% C.I. = 0.03–0.09]. There was no relationship between age and cause of recovery ($\chi^2 = 3.882$, df = 2, p-value = 0.144).

Average annual survival was 0.55 (range = 0.53–0.58) for adults and 0.36 (range = 0.32–0.39) for young foxes in the three years preceding the outbreak. During the outbreak and the remaining six years of the study, the average survival
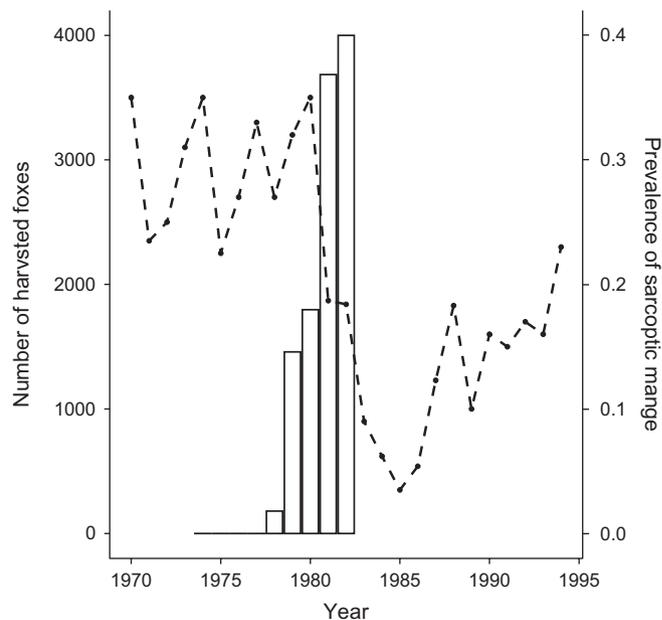

Figure 1. Number of harvested foxes (dashed lines) and prevalence of sarcoptic mange (bars) in foxes collected from hunters in Gävleborg county. Data on the prevalence of sarcoptic mange are not available after 1982.

was reduced to 0.41 (range = 0.30–0.48) for adults and 0.25 (range = 0.17–0.30) for young foxes, a reduction of 0.14 (25%) for adults and 0.11 (31%) for young foxes.

The decline was especially noticeable from 1977 when the prevalence of sarcoptic mange substantially increased in harvested foxes (Fig. 2). The survival estimates are from the best-fit model that include a change in survival and recapture probability over time, and separate for adult and young foxes [S(~age.now + time)r(~age.now + time)] (Supporting information). This model carried 99% of the Akaike-weight, and the next best model had a deltaAICc of 10.8 compared to the best-fit model.

The population projection based on the distribution of declining survival and stable fecundity show a rapid decline that began in 1977 (Fig. 3). By 1982, the median population size was 11% of its initial size in 1974. The projected decline occurred during a six-year period (1977–1983) due to decreased survival. This is a similar rate as the decline in the number of harvested foxes but with a time lag. Setting a time lag of two-years resulted in a high positive correlation of 0.98 (t = 15.01, df = 8, p < 0.001) between the decline in the population projection and the decline in number of harvested foxes.

Discussion

Our study demonstrates the sensitivity of a red fox population to changes in survival rates caused by an epizootic outbreak of sarcoptic mange. Survival steadily decreased during the outbreak, and led to a rapid decline in red fox abundance by ca 90%. A similar pattern was observed during a mange
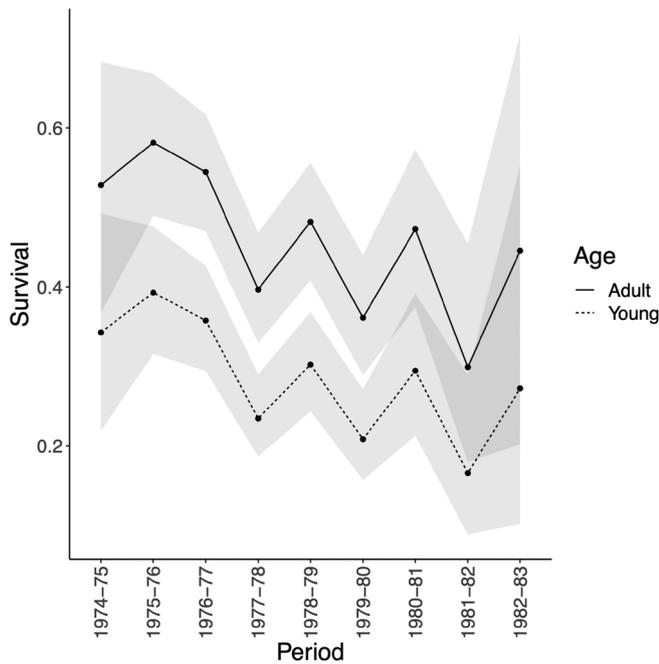
Figure 2. Annual survival estimates of adult and young foxes from mark–recovery analysis during the outbreak of sarcoptic mange. The shaded area represents the 95% confidence interval.

outbreak in Hokaido, Japan (Uraguchi et al. 2014). During the outbreak in Hokaido, the estimated overall survival declined to between one-third and two-thirds compared to survival rate before the outbreak (Uraguchi et al. 2014). In our study, the decline of the projected population and number of harvested foxes was quite similar in magnitude and rate, but with a two-year time lag. A time lag, where a decline
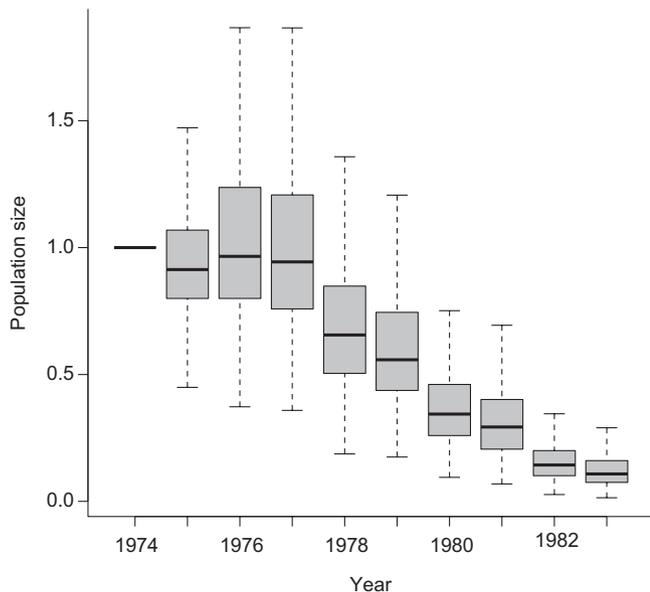

Figure 3. Population projection of the decline during the outbreak of sarcoptic mange in red foxes in Gävleborg county, Sweden. Initial total population size was set to 1.

in population decrease before the number of harvested foxes, would be expected because infected foxes were probably more vulnerable to hunting. Furthermore, hunters likely increased their hunting effort, partly due to the ambition among hunters to reduce the number of infected foxes close to human settlements that could infect dogs *Canis lupus familiaris* (Bornstein et al. 2001).

The sarcoptic mange spread rapidly following the initial outbreak in Scandinavia in 1977, and most of the peninsula was affected in the course of ca 10 years (Lindström et al. 1994). In our study area, Walton et al. (2018) showed that dispersing foxes can travel hundreds of kilometers in a few weeks. Moreover, a GPS telemetry study of red foxes demonstrated regular and long excursions outside their home ranges (own observations). Hence, parasite transmission was probably facilitated by the high dispersal capacity of foxes and regular contact with other individuals outside their home ranges. However, there are indications that the outbreak of sarcoptic mange had less effect on the fox population in the northern tundra dominated landscape (Carricondo-Sanchez et al. 2016), which was probably explained by a low fox density due to harsh winter conditions and low food abundance in northern Sweden (Bartoń and Zalewski 2007, Gomo et al. 2017). Devenish-Nelson et al. (2014) explored a susceptible–exposed–infected model of foxes and sarcoptic mange, and found that the per capita rate of infectious contact was constant despite increases in the number of infected individuals. However, fox densities in this modelled population of Bristol, UK, were about one hundred times higher than that in most of Scandinavia (Wegge et al. 2019). We expect group size to be lower in our study area compared to most of UK due to lower food availability (von Schantz 1984). We expect dispersal and direct contact among inter-group foxes to be more common in our low-density population compared to the Bristol population where inter- and intra-group encounters are low (Devenish-Nelson et al. 2014).

Both hosts and parasites will benefit from a co-evolution and rapid development of resistance in the host. Such a parallel evolution has been found in rabbits and myxomatosis after its introduction in several countries (Alves et al. 2019), and we suspect that fox populations show a similar response to sarcoptic mange. This is supported by the findings of a decrease in visible skin lesions despite stable sub-clinical infections after a decade into the first outbreak of sarcoptic mange in Norway (Davidson et al. 2008). A lower pathogenicity will potentially reduce the effect on fecundity and survival, and make the sarcoptic mange persistent in the fox population.

The rapid recovery of the fox population was probably also, in part, enhanced by increased prey densities (Lindström et al. 1994), and an ample amount of slaughter remains left in the forests from the more than 100 000 harvested moose in Sweden (Gomo et al. 2017). Furthermore, the abundance of apex predators, such as large carnivores and golden eagles *Aquila chrysaetos*, did not appear to have been abundant enough to ecologically trap the fox population at a low density (Walker et al. 1981, Elmhagen and Rushton

2007). Thus, the niche of the fox in the Swedish landscape was still available for exploitation by the recovering fox populations.

The appearance of sarcoptic mange in the Swedish fox population was in effect a large-scale natural experiment that revealed the importance of foxes in the boreal food web (Lindström et al. 1994). We used this natural experiment to show that a rather modest reduction in annual survival was sufficient to drastically reduce the fox population in less than a decade. This large effect would probably not be seen if increased harvest mortality reduced survival with the same magnitude, as compensatory mechanisms such as increased fecundity and net immigration would be expected to compensate for such mortality in a healthy population. Though details on fox demography are lacking across much of its range, population models investigating the influence of external conditions on demographic variables are highly relevant for the management of this important predator and vector for zoonotic diseases. It is obvious that long-term population monitoring in combination with large-scale field-experiments are important (Smith et al. 2017). Experimental manipulation will reveal how intrinsic and extrinsic factors affect demographic rates and population changes. Such knowledge can provide reliable projections of population development and form a basis for management recommendations (Krebs 1999).

Author contributions

Tomas Willebrand: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Gustaf Samelius**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Zea Walton**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Morten Odden**: Conceptualization (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Jan Englund**: Data curation (equal); Methodology (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jdfn2z3cb> (Willebrand et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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