

ARTICLE

Disease Ecology

An infectious disease outbreak and increased mortality in wild alpine reindeer

Atle Mysterud^{1,2}  | Hildegunn Viljugrein³  | Roy Andersen² |
Geir Rune Rauset²  | Malin Rokseth Reiten³ | Christer M. Rolandsen²  |
Olav Strand² 

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

²Norwegian Institute for Nature Research (NINA), Trondheim, Norway

³Norwegian Veterinary Institute, Ås, Norway

Correspondence

Atle Mysterud

Email: atle.mysterud@ibv.uio.no

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Abstract

Climate changes may lead to tipping points where the epidemiological characteristics of infectious wildlife diseases suddenly change, leading to outbreaks. However, empirically documented cases of the extent to which emerging infectious diseases (EIDs) affect populations of large vertebrates are few, partly because of the limited surveillance of remote wildlife populations. EIDs may potentially lead to higher mortality than mean mortality levels. Here, we quantified the likely impact of digital necrobacillosis on the survival and population dynamics of wild alpine reindeer (*Rangifer tarandus*) in Hardangervidda National Park (NP), Norway. The outbreak of digital necrobacillosis in 2019 contributed to a decrease in the summer survival rate of juveniles to 51% compared to an average of 88% in 2005–2018 and 77% in 2020. However, since the outbreak mainly reduced juvenile survival, the impact on short-term population dynamics was moderate, lowering the population growth rate (λ) before harvest from an average value of 1.18 (2005–2018) to 1.08 (2019) before harvest. In 2019, anomalous climate conditions with a high daily mean temperature combined with the highest recorded daily precipitation in late summer were observed. Further studies are required to document the pathological development of digital necrobacillosis across demographic groups and proximate and ultimate causes of mortality.

KEYWORDS

demography, digital necrobacillosis, disease ecology, National Park, population dynamics, reindeer, survival

INTRODUCTION

Climate change is predicted to increase the likelihood of emerging infectious diseases (EIDs) in wildlife (Jones et al., 2008). In Europe, overall warming temperatures are

predicted (Schär et al., 2004), but the northern regions may also experience periods of increased precipitation that would cause humid environmental conditions. The characteristics of the pathogen transmission routes will determine whether these climate changes are likely to cause EIDs.

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Wildlife diseases can be transmitted either directly via contact between an infected and a susceptible host, indirectly via an arthropod vector, or through environmental contamination. The effect of warming on tick vectors is the main cause of the emergence of Lyme disease and other tick-borne diseases at northern latitudes and higher elevations in both Europe (Medlock et al., 2013; Mysterud et al., 2017) and North America (Clow et al., 2017; Ogden et al., 2020). In contrast, conditions that are more humid may increase the survival of certain pathogens in the environment, which may facilitate outbreaks (McIntyre et al., 2017). For several animal species (e.g., bats), fungal pathogens have caused severe die-offs (Fisher et al., 2012), and widespread amphibian decline is an example of an EID driven by global warming (Pounds et al., 2006). Reduced host conditions may also play a role, and pathogenic outbreaks of normally commensal bacteria may be triggered by specific climate conditions (Robinson et al., 2019).

There are few empirically documented cases of the extent to which EIDs affect populations of large vertebrates. The effect of EIDs on vertebrate population is not necessarily linear. Disease outbreaks may result from gradual changes in environmental conditions reaching tipping points where epidemiological characteristics change suddenly. There is some evidence that mass mortality events, defined as “rapidly occurring catastrophic demographic events that punctuate background mortality levels,” are increasing in animal populations (Fey et al., 2015). This is of particular concern for species of conservation interest. One recent example is the large die-off of Saiga antelopes (*Saiga tatarica*) in 2015 in Kazakhstan (Kock et al., 2018). The outbreak was caused by hemorrhagic septicemia attributable to the bacterium *Pasteurella multocida* serotype B, which is normally a commensal bacterium (Orynbayev et al., 2019). It was assumed that up to 200,000 animals died, based on body counts in some areas (Fereidouni et al., 2019; Robinson et al., 2019), but this comes without any estimated uncertainties or information about how this was calculated. The scarcity of both health and population surveillance often limits our ability to estimate the consequences of severe EID outbreaks.

Reindeer and caribou (*Rangifer tarandus*) are iconic parts of ecosystems and human cultures of the northern Arctic and alpine regions. However, most populations are declining globally (Vors & Boyce, 2009), and the species is listed on the IUCN Red List as vulnerable (Gunn, 2016). Here, we quantified the dynamic consequences of an outbreak of digital necrobacillosis or foot rot disease in 2019 in the largest alpine wild reindeer population in Europe. Digital necrobacillosis is caused by a bacterial infection in which the anaerobic bacterium *Fusobacterium necrophorum* is believed to play a major role (Handeland et al., 2010). This bacterium is a commensal gut bacterium of ruminants

and is known to cause a wide range of diseases in several species (Nagaraja et al., 2005). Due to an ongoing national population monitoring program for cervids, we first quantified the population consequences of the outbreak of digital necrobacillosis in 2019 and substantiated that this caused a mass mortality event, mainly among the young of the year. Secondly, we provided evidence suggesting a causal link between mass mortality and the outbreak of digital necrobacillosis based on the culling of infected reindeer, laboratory confirmation and diagnosis, including bacteriological and pathological examination, of digital necrobacillosis as a cause of lameness in the herd, and video surveillance of herds documenting extensive lameness. Lastly, we looked into climate records to suggest whether anomalous climate conditions may have played a role in triggering the outbreak in 2019, with the prediction that digital necrobacillosis is linked to warm and wet conditions in late summer (Skjenneberg & Slagsvold, 1968).

MATERIALS AND METHODS

Study area

Wild reindeer in Norway live in alpine ecosystems. Populations are managed in 24 geographic units with limited connectivity owing to either natural or man-made barriers. Hardangervidda is a high mountain plateau with an area of 8000 km². The core area has been designated as a national park, which was established with the main aim of conserving wild alpine reindeer. The main elevation range of this area is 1100–1200 m above sea level, with several peaks at 1600–2000 m. The western region experiences coastal climate, that is, relatively mild temperatures with heavy precipitation, whereas the eastern inland region is characterized by continental climate with comparatively colder and drier climate conditions. The wild reindeer population at Hardangervidda is by far the largest in Norway, comprising historically 5000–15,000 individuals, which is roughly one-third of the total wild reindeer population in Norway. The reindeer population is regulated by harvest using sex- and age-specific quotas (Strand et al., 2012). The hunting season operates from 20 August to 30 September. In September 2020, chronic wasting disease was detected in the population, but at an extremely low prevalence (~0.1%) and unlikely to have any population impact at the current stage (Ytrehus et al., 2021).

Population surveillance

We retrieved population monitoring data to enable estimation of demographic parameters in the year 2019 with

outbreak of digital necrobacillosis compared to the other years. Population monitoring of cervids in Norway was initiated in 1991 by the Norwegian Institute for Nature Research and funded by the Norwegian Environment Agency. The reindeer data consisted of four types of annual surveillance data.

1. *Minimum counts*: During winter, the minimum counts were obtained from aerial surveys. This was dependent on whether snow conditions and weather were favorable; hence, this count data were lacking for some years. These counts did not divide groups by sex and age and were organized by the local management board.
2. *Summer counts*: During summer, aerial surveillance is mainly aimed at larger female herds to estimate recruitment, and most adult males are segregated from females during this period. The surveys distinguished calves from yearlings and adult females. The surveys were intended to estimate early recruitment and not fertility, as they were conducted some weeks after calving. Yearlings of both sexes and adult females were counted together; hence, an unknown proportion of male yearlings was mixed in the female herds during summer surveys (Reimers, 2006). Summer counts were used to estimate annual recruitment and calf summer survival for all years. Summer counts are usually not as reliable as minimum counts of preharvest population size due to the low coverage of adult males. Summer counts for 2019 and 2021 were considered an exception to those performing the surveys due to excellent conditions and extra efforts covering a large part of the male population segment; therefore, we also included these summer counts as minimum counts (details given below).
3. *Harvest data*: The fall hunting season (20 August–30 September) provides data on harvest numbers according to sex and age class: juveniles, yearlings, and adults (≥ 2 years of age). These are considered highly reliable in Norway and are assumed to be unbiased in the model.
4. *Demographic composition counts*: During the rutting season, both males and females occur in mixed herds. Surveys of herd composition from the ground were conducted according to sex and age classes, but adult females and female yearlings were counted together. We assumed that the counts were representative of herds not included in the observations. Note that in some years, population coverage was low, typically due to poor weather conditions in this extreme environment, and the proportion of the population observed was estimated in our model (see below).

Culling of limping reindeer and confirmation of digital necrobacillosis

We retrieved data from the Norwegian Nature Inspectorate (a unit of the Norwegian Environment Agency) to determine if 2019 had more suspected cases of digital necrobacillosis compared to the other years and to verify if a sample of suspected cases could be attributed with certainty to digital necrobacillosis. Management was aimed at limiting population growth through recreational hunting and stabilizing the population at a predefined target population size. Sex- and age-group-specific quotas determined the legal harvest and were provided in the form of physical license cards (Strand et al., 2012). The Norwegian Nature Inspectorate was responsible for inspecting the license cards of the hunters. Hunters were advised to cull animals showing signs of heavy infection, such as impaired body condition or emaciation. In such cases, hunters may choose not to use their license cards. Digital necrobacillosis was assumed if animals displayed lameness in one or more legs accompanied by swelling in the distal parts of the affected leg(s) (Handeland et al., 2010). In addition, if the Norwegian Nature Inspectorate observes lameness in animals, it may decide to cull them. These numbers were then registered separately from the regular harvest numbers and were used as an indication of the level of digital necrobacillosis.

There are several causes of lameness in animals. The Norwegian Wildlife Health Surveillance Program, run by the Norwegian Veterinary Institute, contributed to the laboratory diagnosis and confirmation of digital necrobacillosis. An examination of the affected legs included pathological examination and bacteriology. We examined 29 legs from incoming cases. Digital necrobacillosis was confirmed in at least 22 cases, and even some of the others also had scars, but digital necrobacillosis could not be confirmed with certainty in the remaining cases (M. R. Reiten, unpublished data). In addition, we provided video confirmation of herds with limping reindeer, particularly among the young of the year (Video S1).

Climate data

We retrieved climate data to determine if 2019 had exceptional conditions compared to the other years. From a collection of 1×1 km gridded datasets over Norway based on observational data and interpolation methods (Lussana et al., 2019; Saloranta, 2016), we collected daily records of temperature and precipitation from Hardangervidda during 2005–2021. We calculated mean values per day for the Hardangervidda wild reindeer area

(Mysterud et al., 2021), followed by descriptive statistics per month (minimum, mean, median, 75% quantile, and maximum), and assessed the extent to which 2019 had unusual climatic conditions in terms of high temperature and above-normal precipitation. We focused on the late summer season, which is assumed to be the critical period for the outbreak of digital necrobacillosis (Skjenneberg & Slagsvold, 1968).

Statistical analysis

Estimation of emergence

An EID is defined as a disease with an incidence that increases over time or spatially (Funk et al., 2013). We used a negative binomial model to fit the number of reported digital necrobacillosis cases over the years and assessed whether 2019 fit the overall trend. We used library “MASS” in R version 4.0.3.

Estimation of population size and demographic rates

As a starting point for our analysis of population dynamics, we used an established population estimation model (Nilsen & Strand, 2018), available on GitHub (https://github.com/ErlendNilsen/CiR_usage). This model is well calibrated and is used as a basis for both disease surveillance (Viljugrein et al., 2019) and hunting management (Mysterud et al., 2020) of this population, and updated code and data used here are available in Zenodo (Viljugrein, 2023). It is a hierarchical change-in-ratio model with parameters estimated using Bayesian inference. The model uses all four surveillance time series data as input variables: minimum counts, summer counts, harvest data, and demographic composition counts. The original model (Nilsen & Strand, 2018) estimated the annual summer survival of juveniles (ϕ_1), overall winter survival (ϕ_3), and annual fertility rate (f_1). Winter survival was assumed to be common for all years and in all age categories. The original model was slightly modified to incorporate demographic composition counts in 2020, when all yearlings, both males and females, were summed together with adult females and counts were categorized in the usual manner only for a small subset. The counts of yearling and adult males were summed in the original model.

After 2018, there were no winter counts for Hardangervidda. For 2019 and 2021, a large proportion of the adult males were covered by the summer counts; therefore, we used the total summer counts as a count of the preharvest population. The model assumes that

minimum counts are an overall count of population size and that demographic composition counts reflect the demographic composition in the total population (assuming no bias in misclassifications among age categories and that flocks that were not observed, had the same composition as those counted).

Priors were specified as uninformative, if not otherwise stated, by using uniform distributions (0–1) for probabilities and very wide normal distributions for the initial population sizes. The model was run from 2005 to 2021 in R through “rjags” using the R-package “jagsUI” (Kellner, 2019), and the Markov chain Monte Carlo (MCMC) output was summarized using the R-package “MCMCvis” (Youngflesh, 2018). We used three chains of 300,000 iterations and a burn-in period of 50,000, and the chains were thinned by 3. Convergence was assessed by visual inspection of MCMC chains and the Gelman–Rubin statistics.

The available surveys had different formats (details are given above) and coverages of the population from year to year. The minimum counts from winter lacked demographic composition, and in some years, survey (after 2018 for the winter survey) was not conducted or had low population coverage owing to difficult weather conditions in these extreme alpine areas. We assessed the sensitivity of the parameter estimates by exploring alternative model formulations. We ran the model both with and without the inclusion of summer counts for 2019 and 2021.

The baseline model only allowed the summer survival of calves to vary across years. We also fitted a model including year-specific annual survival from preharvest calves to preharvest yearlings but assumed that there was no variation in this annual survival for the first five years (June 2005–October 2009). The simplification (no variation in annual survival for the first years) was done because of low coverage (in 2007) and a lack of fall demographic composition counts in 2008 (Appendix S1: Figure S2F). In this model (termed as the “annual model” in the *Results*), we added a term to separate yearlings and adult males in the demographic composition counts.

RESULTS

Few reindeer with digital necrobacillosis were reported before 2019, when the numbers suddenly peaked and declined again to lower levels in 2020–2021 (Figure 1A). Hence, we could classify this peak in 2019 as an outbreak. The model of disease cases for 2008–2021 gave a significant time trend even after excluding 2019 ($Z = 2.144$, $p = 0.032$).

The population model estimated that the summer survival of calves was 51% (95% credible interval: 48%–54%)

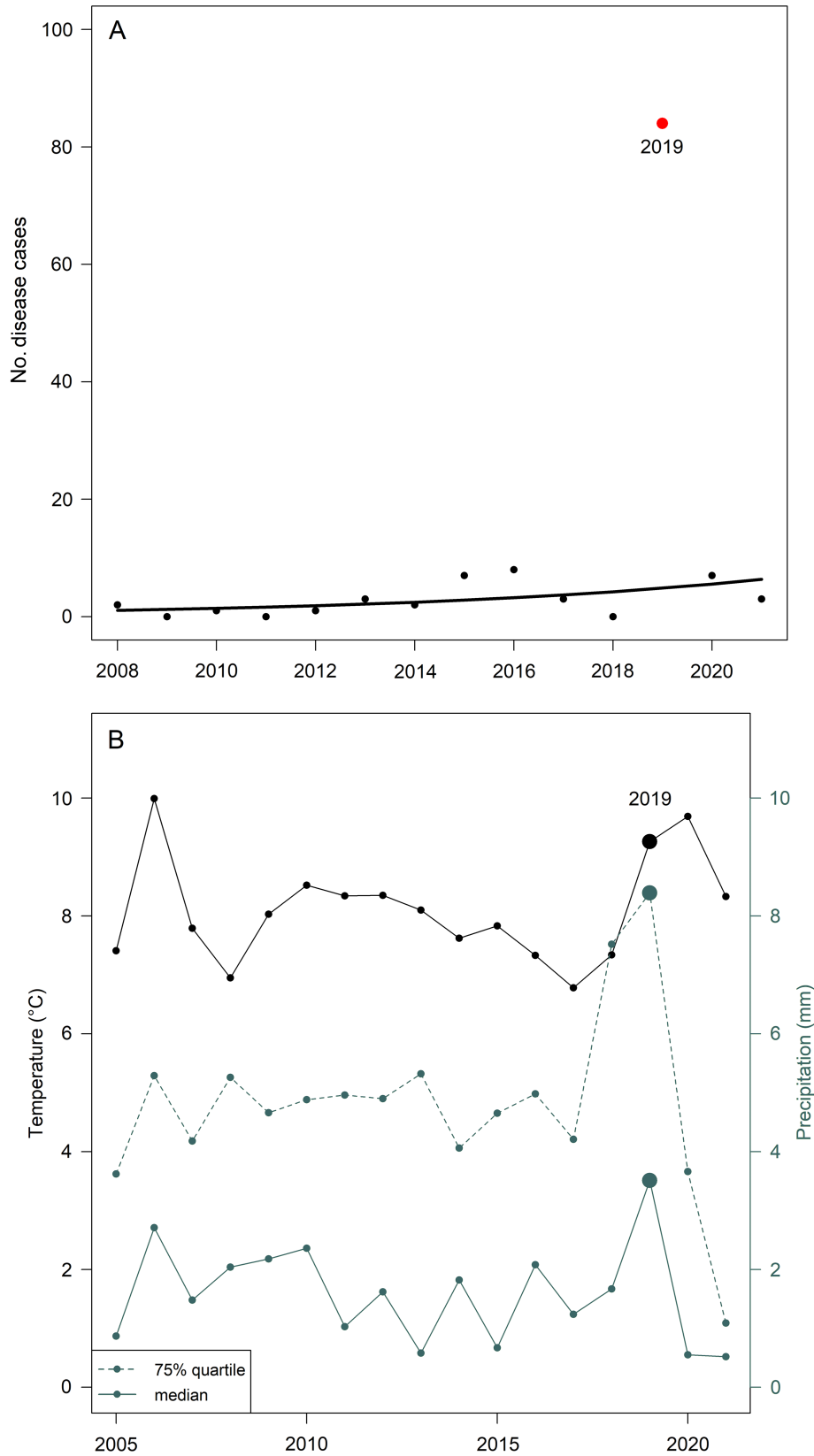


FIGURE 1 (A) Number of reported cases of reindeer with digital necrobacillosis (foot rot) in Hardangervidda National Park, Norway. The fitted trend is a negative binomial model estimated for 2008–2021; notably, 2019 was a clear outlier to this weak positive trend. Data were derived from the Norwegian Nature Inspectorate (SNO), a unit of the Norwegian Environment Agency. (B) Time series of climate variables indicated that during 2005–2021, August 2019 recorded the highest mean daily temperature and the highest median (and 75% percentile) daily precipitation.

in 2019, when the outbreak of digital necrobacillosis occurred, compared to an average summer survival of 88% (range: 58%–99%, median = 91%) during 2005–2018 and 77% (95% CrI: 75%–79%) in 2020 (Figure 2A). Note that in addition to an estimated 1038 (SD = 66) reindeer calves dying in 2019, 54 reindeer calves and some yearlings and adults were shot by hunters owing to visible signs of lameness (Figure 1A). The overall winter survival rate was estimated to be 94% (95% CrI: 93%–94%). Female fecundity averaged 65% (logit-scale mean, 95% CrI: 61%–69%) but was variable among years (median = 67%, range: 48%–75%, Appendix S1: Figure S1B). The outbreak of digital necrobacillosis in 2019 was estimated to reduce annual population growth (λ) before harvest from an average of 1.18 (2005–2018) to 1.08 (95% CrI: 1.07%–1.09%) (Figure 2B).

Estimation of survival rates for some years was likely influenced by the low coverage of the population in surveys (Appendix S1: Figure S1E,F) and by the assumptions made regarding to what extent annual, seasonal, and demographic details were included in the parameterization (Appendix S1: Note 1). The low summer survival rates estimated for 2019 appeared to be robust according to the details in the model specification (Appendix S1: Figures S1A and S2A). The “annual model” estimated a low survival rate for calves surviving from harvest 2018 to yearling preharvest 2019 (Appendix S1: Figure S2B).

Although the season of this mortality was uncertain, it may indicate that the yearlings also had a low summer survival rate in 2019.

The year 2019 had an unusual combination of having the third highest mean daily temperature and the highest median daily precipitation recorded in the time series (Figure 1B). Overall, there was no correlation between the mean daily temperature and precipitation in August ($r = 0.228$ with median rainfall; $r = 0.088$ with 75% quartile rainfall).

DISCUSSION

We provided a rare case of quantifying the population dynamic consequences of an outbreak of an EID in a species of conservation concern, wild alpine reindeer, in the Hardangervidda National Park, Norway. Based on the analysis of the population surveillance data, we classified this as a mass mortality event in the juvenile segment of the population. We provided several lines of evidence for a causal relationship between the disease outbreak and increased mortality: (1) A high number of reindeer with assumed digital necrobacillosis were shot in 2019 by the Norwegian Nature Inspectorate (Figure 1A). (2) Laboratory confirmation of digital necrobacillosis was made in a large majority of the incoming cases. (3) The high mortality rate

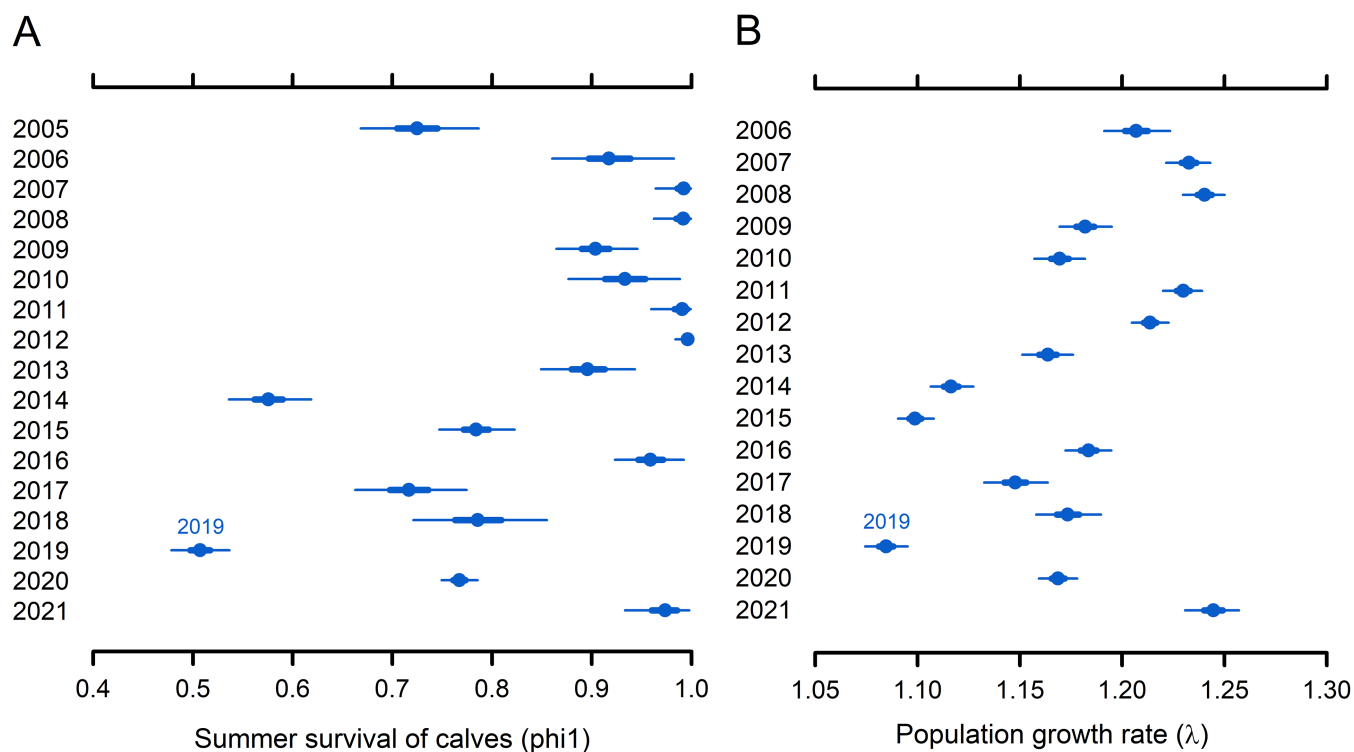


FIGURE 2 Estimated (A) summer survival (ϕ_1) of reindeer calves and (B) population growth rate (λ) for 2005–2021 in Hardangervidda, Norway.

of juveniles occurred in late summer and early fall (between the summer survey and the demographic composition count in fall), well before starvation mortality in winter (our results). (4) Video surveillance of herds documented extensive lameness (Video S1).

The main paradigm in the population ecology of ungulates is that juvenile survival is lower and more variable than adult survival, which is high and constant (Gaillard et al., 1998). This pattern of age-specific mortality is seen across a range of different proximate causes of mortality, but exceptions occur, such as the high adult mortality from cougar (*Puma concolor*) predation on adult bighorn sheep (*Ovis canadensis*) (Festa-Bianchet et al., 2006) and chronic wasting disease in deer (Samuel & Storm, 2016). Digital necrobacillosis in reindeer on Hardangervidda lowered the survival of juveniles with a high level of certainty. This was consistent with the reported high susceptibility of juveniles to outbreaks in semi-domestic reindeer (Skjenneberg & Slagsvold, 1968). The annual survival of the calves from the fall of the year before (2018) to yearlings in the fall of the outbreak (2019) was also lower than normal (Appendix S1: Note 1), which may indicate that even summer survival of yearlings was affected. Digital necrobacillosis has also been observed in adults but to a lesser extent. Due to the limitations set by the surveys, our approach cannot directly estimate excess mortality of the adults in 2019, but the limited effect on the population growth rate suggests that adult female survival was high. Variations in recruitment rates have a more limited impact on population growth rates than factors affecting adult female survival (Gaillard et al., 1998). Hence, although this was by definition a mass mortality event (Fey et al., 2015), the reindeer population is likely to recover quickly when mortality does not notably affect adult females. This is similar to the effect of rain-on-snow events, which lock winter pastures to reindeer. Such extreme events typically remove young and extremely old animals, leaving the prime-aged female segment of the population largely intact (Hansen et al., 2019). A lower density may also increase vital rates. After an outbreak of keratoconjunctivitis in a chamois (*Rupicapra rupicapra*) population, the population bounded back in 5 years due to higher fecundity after the population reduction (Loison et al., 1996). Outbreaks must therefore be frequent to limit the population over the long term.

Digital necrobacillosis is a well-known disease in semi-domestic reindeer and is known as “slubbo” among Sami reindeer herders (Skjenneberg & Slagsvold, 1968). The first reported outbreak of digital necrobacillosis among wild alpine reindeer in Norway was reported in 2007 (Handeland et al., 2010). However, it is plausible that the disease has been present in wild reindeer at low prevalence for longer periods. Since digital necrobacillosis is a relatively new phenomenon among wild reindeer of southern

Norway, there are many aspects of the pathology and its consequences that remain uncertain. The pathological verifications of digital necrobacillosis during the 2019 outbreak at Hardangervidda were based on inspection of submitted legs sent to the Norwegian Veterinary Institute. In these samples, the presence of *F. necrophorum* was verified in open wounds in the skin in addition to variable levels of pathological changes in the different structures of the feet, including the hooves (M. R. Reiten, unpublished data).

There are several bacteria that may cause infections in hooves of ungulates. An outbreak of lameness in North American elk (*Cervus canadensis*) has been developing in Washington State, USA, in recent decades (Han & Mansfield, 2014). Pieces of evidence suggest this is mainly caused by a *Treponema* sp. infection, a spirochaete bacteria (Clegg et al., 2015), which is known to cause hoof infection in domestic sheep and cattle. A recent study documented presence of both Fusobacteria and Tenericutes in addition to *Treponema* sp. in cases of hoof disease in elk, suggesting it may be a polybacterial infection (Wild et al., 2022). *Treponema* sp. has so far not been detected in a limited sample derived from reindeer from several areas of Norway (M. R. Reiten, unpublished data), but a wider screening for the possible presence of *Treponema* sp. is currently ongoing. Foot rot in sheep (ovine foot rot) in Norway is caused by another bacteria, *Dichelobacter nodosus* (Gilhuus et al., 2013). This bacteria (*D. nodosus*) was documented to spillover from sheep and caused foot rot in alpine ibex (*Capra ibex*) in Switzerland (Moore-Jones et al., 2021). There is a certain overlap of grazing domestic sheep and reindeer on Hardangervidda, though the densities of sheep are low in the main ranges used by reindeer during summer. However, *D. nodosus* was not found in inspected hooves from reindeer with digital necrobacillosis (Handeland et al., 2010). There is thus no evidence that foot rot in sheep can be connected to the digital necrobacillosis in reindeer (or vice versa) in Norway.

The potential role of coinfections for the development of necrobacillosis and the proximate cause of mortality in reindeer remain open questions. Digital necrobacillosis causes open wounds in the skin on the hooves. This can also be a site of entry for other pathogenic bacteria causing infections in other part of the body and/or septicemia, which may also contribute to the animal's death. The calves with digital necrobacillosis will have difficulties following the herd (Video S1), and consequently suffer from reduced nutritional intake and stress. Reduced foraging is likely to cause many of them to die of starvation. The direct infection and reduced condition may also interact with other proximate causes of mortality. There can be considerable predation by golden eagles (*Aquila chrysaetos*) on reindeer calves (Norberg et al., 2006), which is also observed to occur on Hardangervidda

(S.-E. Lund, personal communication). There are no data to determine whether calves with digital necrobacillosis are more likely to be predated, though it appears likely.

A time series of multiple outbreaks is required to determine the environmental conditions that were the ultimate cause of the outbreaks. Historically, digital necrobacillosis in semi-domestic reindeer was prevalent when the animals were kept in small areas for milking and the soil became wet and muddy (Riseth et al., 2020). Under such environmental conditions, bacteria can easily invade skin. Traditional knowledge links larger outbreaks to both keeping reindeer in restricted areas and warm and humid summers, as the pathogen is an anaerobic bacterium thriving under humid conditions (Skjenneberg & Slagsvold, 1968). The main period of mortality was between the summer counts in July and the demographic structure counts in October. Consistent with this, the late summer of 2019 had a high mean temperature combined with unusually high levels of precipitation (Figure 1B). As we had an outbreak in only one year, it is nevertheless premature to conclude with certainty regarding the role of environmental conditions in the outbreak. Currently, during summer, reindeer in Hardangervidda use a small part of the available range, possibly because of the disturbance from hiking and tourism (Gundersen et al., 2020). This crowding increases effective population density and may provide conditions for more effective environmental transmission.

Our study provides a rare case suggesting an outbreak of digital necrobacillosis caused a mass mortality event in reindeer, but many aspects warrant further study: What is the duration of the infection and pathological development? What is the proximate mechanism by which *F. necrophorum* cause mortality? To what extent do coinfections play a role for lameness and mortality? What role does animal condition play for individual susceptibility? What is the infection rate of older reindeer, does it cause any mortality, or do they recover? What combination of climate variables, habitat selection (for wet and muddy soils), and effective population density are required to cause an outbreak? Reindeer populations are threatened on a global scale (Gunn, 2016; Vors & Boyce, 2009), and the Hardangervidda National Park was established to protect the largest population of wild alpine reindeer in Europe. Surveillance of both disease and population parameters within a One Health framework (Blackburn et al., 2016) requires urgent attention to assess the impacts of EIDs and to provide a basis for mitigation.

AUTHOR CONTRIBUTIONS

Atle Mysterud, Christer M. Rolandsen, and Olav Strand initiated this study. Hildegunn Viljugrein performed statistical analyses. Olav Strand and Roy Andersen were

responsible for conducting population surveys. Geir Rune Rauset organized the data. Malin Rokseth Reiten provided data on digital necrobacillosis and wildlife health surveillance. Atle Mysterud drafted the manuscript using the codrafting methods and results given by Hildegunn Viljugrein. All authors have edited and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data and code (Viljugrein, 2023) are available from Zenodo: <http://doi.org/10.5281/zenodo.7624490>.

ORCID

Atle Mysterud  <https://orcid.org/0000-0001-8993-7382>

Hildegunn Viljugrein  <https://orcid.org/0000-0002-3798-5267>

Geir Rune Rauset  <https://orcid.org/0000-0002-6345-3029>

Christer M. Rolandsen  <https://orcid.org/0000-0002-5628-0385>

Olav Strand  <https://orcid.org/0009-0002-6189-6309>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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