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BRIEF REPORT

The synzootic potential of common epidemics in chamois populations

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Abstract

Southern chamois (*Rupicapra pyrenaica*) is a medium-sized and gregarious mountain ungulate with populations affected by periodic outbreaks of border disease virus (BD), infectious keratoconjunctivitis (IKC), and sarcoptic mange (SM). Even though the impact of each disease on chamois populations has been described in detail, there is a lack of information about the potential impact of concomitant epidemics and the synzootic potential (co-occurring enzootic or epizootic processes producing worse health outcomes in wildlife) on chamois populations. Furthermore, whether a specific order of apparition of epidemics is more or less harmful for the host population is practically unknown not only for chamois but also for most mammal populations. Using a population viability analysis (PVA), we studied the consequences of multiple disease outbreaks with synzootic potential on growth rates and probabilities of extinction of virtual populations exposed to hard winters, density dependence, and co-occurring BD, IKC, and SM outbreaks. Such infections are not under cross-immunity nor density-dependent processes and thus are supposed to affect population demography independently. Heavy snowfalls are also likely to occur in our simulated populations. Our simulations showed that a second outbreak, even caused by a low virulent pathogen, causes an increase in the probability of extinction of the host population with regard to the first outbreak. IKC-BD- and SM-BD-affected populations had a higher risk of becoming extinct in 50 years confirming the extra risk of multiple outbreaks on the viability of the affected populations.

Keywords Emerging infectious diseases · Epidemics · Population viability analysis · *Rupicapra pyrenaica pyrenaica* · Vortex

For more than four decades now, infectious diseases have been recognized as a major demographic driver of wild populations. Virus (Sillero-Zubiri et al. 1996), bacteria (Foreyt and Jessup 1982), fungi (Berger et al. 1998), or helminth (Goodman and Johnson 2011) outbreaks increase the extinction risk of wildlife (Pedersen et al. 2007), threatening global biodiversity (Daszak et al. 2000). Population collapses caused by canine distemper virus in Serengeti lions (*Panthera leo*) (Roelke-Parker et al. 1996) or Ebola in African apes (Leroy et al. 2004) are good examples of such deleterious impacts. Pathogens have the potential to affect almost every life-history trait of mammals including energy storage (Carvalho et al. 2015), fecundity and fertility rates (Rhyan et al. 2001; Sarasa et al. 2011), to fetus development (Aleuy et al. 2020), juvenile recruitment (Rossi et al. 2011,) or adult survival (Pedersen et al. 2007). Further, the main mechanisms for disease-induced extinctions in wildlife are the pre-epidemic population size and the presence of reservoirs (Castro and Bolker 2005).

Even though outbreaks caused by different pathogens are not rare in the wild (Barnett et al. 2018), our knowledge about the impact of synzootics (i.e., co-occurring wildlife diseases) on mammal population demography is scarce. This synzootic concept derives from the term "syndemic", used in human medicine to assess the consequences of multiple diseases acting in tandem in a given socio-economic and environmental conditions on human populations (Singer et al. 2017). This syndemic point of view has barely been applied to wildlife (Sweeny et al. 2021), although the risk of

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suffering from multiple infections in variable environments is the norm (Bordes and Morand 2011; Munson et al. 2008) and thus the likelihood of potential synzootic interactions is great. Knowledge about the impact of infectious diseases on wildlife demographics is mainly based on outbreaks by single pathogens. Information about the impact of synzootics on wildlife is limited and often restricted to the impact of comorbidities. Only a few cases such as European wild rabbit (*Oryctolagus cuniculus*) populations affected by rabbit hemorrhagic disease (RHD) but previously exposed to myxoma virus (Mutze et al. 2002) are a good example of the potential of co-occurring epidemics on host population dynamics. With regard to synzootics, the unprecedented mortalities of African lion populations affected by canine distemper virus (CDV) and *Babesia* spp. in very dry years are an excellent case (Munson et al. 2008).

Southern chamois (*Rupicapra pyrenaica*) is a medium-sized mountain ungulate classified as a least concern species by the International Union for the Conservation of Nature, with a global population number of around 50,000 (Herrero et al. 2020). Nevertheless, outbreaks of diseases such as sarcoptic mange (SM), infectious keratoconjunctivitis (IKC), and border disease (BD) affect and have caused dramatic declines in local populations of the Pyrenean (*Rupicapra p. pyrenaica*) and Cantabrian (*Rupicapra p. parva*) subspecies (Fernández-Morán et al. 1997; Marco et al. 2007; Fernández-Aguilar et al. 2017).

SM is caused by the burrowing mite *Sarcoptes scabiei* and is a contagious disease of mammals that induces an allergic-type skin reaction resulting in visible hypersensitive lesions and pruritus (Walton et al. 2004). Although sarcoptic mange epizootics usually do not affect long-term population dynamics, the net effect of mange can have serious conservation consequences in remnant or fragmented populations of threatened or endangered species including mountain ungulates (Pence and Ueckermann 2002). Apart from the Cantabrian Mountains, SM has been reported to cause mortality in Alpine chamois (*Rupicapra rupicapra rupicapra*) in the Dolomite Alps in Italy (Rossi et al. 2007). Contrary to the typical assumptions of epidemiological models, SM dynamics in carnivores seem to be frequency- rather than density-dependent. In other words, disease transmission is mainly driven by behaviors mediating contact rates (Devenish-Nelson et al. 2014).

In *Rupicapra* species, social interactions (e.g., contact rates) depend more on social affinities than on any other factors (Crampe et al. 2021). However, in the last work on *Sarcoptes scabiei* transmission (Browne et al. 2022), the authors stated that high population densities and local population sizes would be key factors for *Sarcoptes* transmission in chamois, but they also argued that the rates of contact within each species are poorly understood. So, this density-dependent transmission issue is unclear, and thus, we have decided to not include the density dependence in mange outbreaks in our viability modelling due to a lack of information for density dependence transmission parameters.

SM outbreaks duration is 5 years on average (Serrano et al. 2015). Mortality rates associated with SM are roughly 10.5% for kids, 14% for yearlings, 52.5% for adult females, and 60% for adult males (Fernando-Morán et al. 1997; Rossi et al. 2007).

IKC, on the other hand, is a highly contagious bacterial disease of the eye characterized by inflammation of the conjunctiva and cornea (Nicholas and Giacometti 2012). *Mycoplasma conjunctivae* is considered the major cause of IKC in caprine species (Giacometti et al. 2002). IKC outbreaks are characterized by a short duration (1–2 years), high morbidity, low mortality (around 30%), and spontaneous recovery (Loison et al. 1996). After an IKC epizootic episode, the number of kid and adult females typically decreases between 10 and 19% (Arnal et al. 2013), recovering 1 year after the outbreak. Mortality rates associated with IKC are in 6% of kids, 70% of yearlings, 20% of females, and 9% of males (% of kids, 52% of yearlings) (Loison et al. 1996; Arnal et al. 2013).

On the other hand, BD is caused by a pestivirus (Frölich et al. 2012) and in chamois curses emaciation, depression, weakness and difficulties in locomotion (Marco et al. 2007). Pyrenean chamois population in the Pyrenees decreased by 30% due to disease outbreaks (Frölich et al. 2012), which are considered important drivers for chamois population demography (Serrano et al. 2015). Published reports (Marco et al. 2007; Fernández-Sirera et al. 2012) suggest that mortality rates associated with BD outbreaks are 50.5% for kids, 51.8% for yearlings, 45.7% for females, and 47% for males. The consequences of BD are easily observed 5 years after the first clinical case is detected. The three aforementioned diseases do not induce cross-immunity, and there is no clear evidence for their density-dependent regulation (Fernández-Sirera et al. 2012).

In this work, we aimed to simulate the impact of multiple outbreaks on chamois population demography. Our objectives are (I) to explore the consequences of consecutive outbreaks of SM, IKC, and BD on chamois population viability and (II) to determine the specific outbreak pair with the greater demographic impact on the viability of our virtual chamois population. To achieve these objectives, we modelled the consequences of single (SM, IKC and BD) and specific disease outbreak combinations (SM + IKC, SM + BD and IKC + SM) on the viability of a virtual chamois population using a stochastic population viability analysis (PVA, Lacy 1993). Since the impact of chronic BD epidemics is not well understood (Fernandez-Sirera et al. 2012), we have decided not to include a secondary outbreak in BD-affected populations. We expect that multiple outbreaks will have greater negative effects than single outbreaks, but more

particularly, those combinations involving the more virulent pathogens such as BD or SM. From now on, when we discussed about the extinction of the population in the simulation, we refer to the probability that a chamois population can become extinct locally rather than globally after a potential combination of different disease outbreaks.

Population viability analysis was performed in VORTEX 10.1.6.0 (Lacy and Pollak 2015). This computer program simulates the effects of deterministic forces and stochastic events (demographic, environmental, and genetic) to model the growth rate (stoch-r), the final population size (N-all), and the mean probability of extinction (PE). To compare the impact of different simulations, we created a control scenario (pristine population), only affected by winter conditions (Serrano et al. 2015). The effects of heavy winters have also been included in our population viability modelling. This winter effect strongly relies on the local orography, but on average, population reduction due to this natural phenomenon could reach 40% every 10 years (Rughetti et al. 2011). In this scenario, the carrying capacity was fixed at 4000 individuals. We also recreated seven disease scenarios representing single outbreaks (IKC, SM, and BD), and outbreak combinations using the IKC-, SM-, and BD-associated mortalities at specific age classes. In brief, we modelled age and sex-specific mortalities based on the descriptions found in the published reports (Serrano et al. 2015). The likelihood of disease outbreak for each simulation is 0.2 for IKC (the commonest disease in chamois populations) and 0.1 for SM and BD. Two diseases can occur simultaneously or sequentially at the given probabilities. Since there is a likelihood of heavy winters during disease outbreaks, we consider our modelling might reflect the effect of synzootics (comorbidity + adverse environmental conditions, see Sweeny et al. (2021).

Each model scenario was run for 50 years, 1000 iterations, and 20 initial population sizes proportional to the carrying capacity (from 5 to 100%, with an increment of 5% each time). The Vortex software, however, does not provide population-size-specific outputs (see Table 1 and Fig. 1 for a summary). We used non-parametric Mann-Whitney *U* tests to compare the mean growth rate (stoch-r), the average population size of a given scenario at the end of the simulation (averaging both surviving and extinct iterations, N-all), and the probability of extinction (PE) between specific outbreak pairs. We performed all the statistical analyses using the statistical software R 4.2.1 (R Development Core Team 2022).

The probability of extinction in the pristine scenario was equal to zero, and the final population size was stabilized around the carrying capacity as expected in populations with density dependence regulation (Akçakaya and Burgman 1999). The effect of a single outbreak causes a significant decrease in the growth rate of our virtual chamois

Table 1 Mean, minimum (min), and maximum (max) stochastic growth rates of the population, probabilities of extinction, and final population sizes of a hypothetical chamois population of an initial size of 600 individuals and limited by a carrying capacity of 4000 individuals

Scenario		Population growth rate		Probability of extinction		Final population size	
		Mean	Interval (min–max)	Mean	Interval (min–max)	Mean	Interval (min-max)
Pristine population		0.0635	0.0620–0.0650	0	-	3723.57	3282.24–3795.69
Single disease outbreaks							
	IKC outbreak	0.0463	0.0440/0.0540	0.25	0.241–0.263	2782.79	2180.39–2857.37
	SM outbreak	−0.0065	−0.0090/0.0080	0.229	0.217–0.780	1441.52	597.53–1594.47
	BD outbreak	−0.0326	−0.0370/−0.003	0.534	0.524–0.571	767.86	345.47–865.86
Combined disease outbreaks							
	IKC + SM outbreaks	−0.0349	−0.0410/−0.0090	0.47	0.370–0.549	619.67	245.59–711.92
	IKC + BD outbreaks	−0.0533	−0.0610/−0.0160	0.634	0.594–0.700	343.22	126.57–430.72
	SM + IKC outbreaks	0.0323	0.0290/0.0410	0.253	0.241–0.264	1288.04	1590.07–1398.56
	SM + BD outbreaks	−0.0400	−0.0460/−0.0100	0.559	0.537–0.617	585.72	213.31–667.66

Simulations were estimated for 50 years and 1000 iterations. The pristine population (control) was only affected by the carrying capacity, the IKC, SM, and BD single outbreaks of infectious keratoconjunctivitis (IKC), sarcoptic mange (SM), and border disease (BD), and the IKC + SM, IKC + BD, SM + IKC, and SM + BD combined disease outbreaks

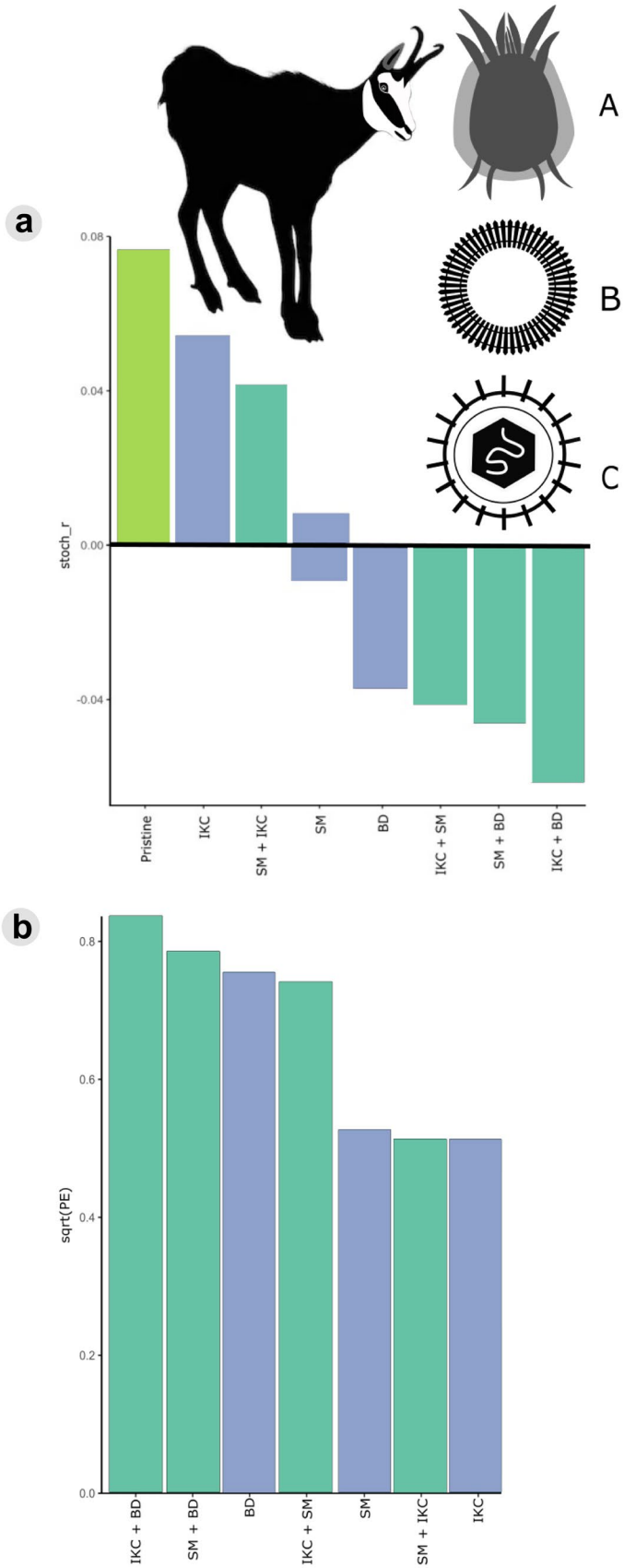

Fig. 1 **a** Mean stochastic growth rates (stoch-r) and **b** mean probabilities of extinction (PE), of a hypothetical chamois population of an initial size of 600 individuals and limited by a carrying capacity of 4000 individuals. Our modelling scenarios were the following: pristine population (population only limited by the carrying capacity in light green), the single outbreak scenarios (in blue color), and combined disease outbreaks (dark green). Infectious keratoconjunctivitis (IKC), sarcoptic mange (SM), and border disease (BD). In **b**, sqrtPE of our pristine chamois population was equal to zero. A, B and C respresnt *Sarcoptes scabiei Mycoplasma* spp and a pestiviurs respectively

population. Compared to pristine populations, the mean probability of extinction after a single disease outbreak increased from 0.22 for SM to 0.53 for BD epidemics that means that 22% and 53% of the simulated populations get extinct, respectively. IKC outbreaks resulted in an intermediate probability of extinction value (0.25, see Table 1).

Our population viability modelling clearly shows the negative impacts of a second disease outbreak. PE increased after a second disease outbreak but in particular after BD epidemics. Along the same lines, the growth rate and population size decreased after the second outbreak. For example, SM or BD outbreaks in chamois populations initially affected by IKC resulted in lower growth rate ($W_{IKC\ vs\ IKC\text{-}SM} = 400$, p value = 5.8 e-10, $W_{IKC\ vs\ IKC\text{-}BD} = 400$, p value = 6.02 e-10) and final population size ($W_{IKC\ vs\ IKC\text{-}SM} = 400$, p value = 1.45 e-11, $W_{IKC\ vs\ IKC\text{-}BD} = 400$, p value = 1.5 e-10), but higher PE ($W_{IKC\ vs\ IKC\text{-}SM} = 400$, p value = 6.73 e-08, $W_{IKC\ vs\ IKC\text{-}BD} = 400$, p value = 6.76 e-08) than those only affected by IKC. The same happened in SM-affected populations suffering BD outbreaks, where the growth rate ($W_{SM\ vs\ SM\text{-}BD} = 400$, p value = 5.1 e-08) and final population sizes ($W_{SM\ vs\ SM\text{-}BD} = 336$, p value = 9.2 e-07) are lower than in populations only affected by SM. Final population sizes in mixed epizootics decreased in 59% ($W_{SM\ vs\ SM\text{-}BD} = 400$, p value = 6.7 e-08). For example, the mean probability of extinction for IKC + SM outbreaks is 0.47, whereas = 0.25 or 0.22 for single IKC or SM epizootics.

Despite the limitations of our work (e.g., some disease combination outbreaks have not yet been described in natural conditions, and we have only considered demographic consequences, but not transmission or recovery), it seems therefore clear that concomitant outbreaks have potential synzootic effects posing an additional threat to the viability of chamois populations previously affected by one of these three diseases. Interactions among co-infecting pathogens not only alter host pathology and disease spread at different levels of biological organization (Jonhson et al. 2015), but also the long-term demography of the affected populations.

Managers in charge of chamois populations chronically affected by infectious diseases should take into account the demographic impacts of synzootics increasing efforts in disease surveillance to avoid new disease epidemics even caused by low virulent pathogens. Our results underline the importance of health surveys to forecast the potential consequences of synzootics on the local extinction risk of wild mammal populations.

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Author contribution CGA, RV, AJ, and ES conceived and designed the modelling; CGA performed the analytic calculations and performed numerical simulations; CGA and ES wrote the manuscript with the support from JRLO, RV, and AJ. All authors discussed the results and contributed to the final manuscript.

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Data Availability The data that support the findings of this study are available from the corresponding author, (CGA, ES), upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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