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REVIEW

Fox *Vulpes vulpes* population trends in Western Europe during and after the eradication of rabies

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ABSTRACT

1. Over several decades, Western Europe experienced an outbreak of sylvatic rabies, eliminated through an EU programme involving large-scale red fox vaccination campaigns. While much work has been done on the dynamics of the virus and on the efficiency of vaccination campaigns, very little attention has been paid to the impact on the large-scale dynamics of the fox population.
2. As Western Europe has now been free of rabies for about 15–20 years, the aims of this review are to characterise the impact of rabies during the outbreak itself and to increase understanding of how fox populations evolved thereafter. The rabies-free populations in the UK are also integrated as a comparative control.
3. Trends in fox populations are based on a review of available data, mainly hunting statistics and a few other methods. The benefits and biases of these methods are also discussed.
4. During the rabies epizootic, fox populations experienced a significant decline and stabilised at lower densities than observed in the past. A demographic explosion followed the vaccination campaigns, and fox populations became larger than had been observed before the epizootic. Rabies vaccination was not the direct cause of this demographic explosion, as rabies-free areas experienced it also. The causes are more to be sought in environmental modifications induced by humans.
5. This demographic explosion was followed by the emergence of urban fox populations throughout Europe. Moreover, the new higher densities favoured the outbreak of other diseases, though their impact was more limited. Around the 2000s, rural fox populations appeared to reach densities close to carrying capacity and populations stabilised. However, subsequently, with some

exceptions, Western European fox populations seem to be experiencing a decline. The ecological consequences of these changes in fox population density may reach the many prey species and competitors of the red fox.

INTRODUCTION

During the second half of the 20th Century, red fox *Vulpes vulpes* populations experienced a rabies epizootic throughout continental Europe. The rabies virus emerged in foxes in the south of the Kaliningrad region of the Russian Federation, following a presumed spill over from domestic dogs (Wandeler 2004). After World War II, the epizootic spread from Poland to Central and Western Europe. The front of the epizootic moved about 20–60 km annually (Pastoret & Brochier 1998, Vitasek 2004). The first cases were reported in Germany in 1947, in Belgium and Luxembourg in 1966, in Switzerland in 1967, in France in 1968 and in the Netherlands in 1974 (Fig. 1; Rabies Bulletin Europe 1977–2013). In the 1970s, the front reached a line, which can be drawn between the Netherlands and Italy, with the westernmost point reached in France in 1982, approximately 1400 km from the original location in Kaliningrad (Vitasek 2004). In all these countries, the various measures that were taken (shooting, trapping, poisoning, and gassing of foxes) failed to stop the progression of the rabies epizootic (Aubert et al. 2004). The British Isles and the Iberian and Scandinavian peninsulas were not affected (Vitasek 2004). In order to mitigate the public health risks for humans and domestic animals, oral rabies vaccines were developed for foxes, followed, from the mid-1980s, by the implementation of large-scale fox vaccination campaigns in the affected countries. These campaigns drastically changed the situation, successfully eliminating fox rabies in these regions (Freuling et al. 2013, Stahl et al. 2014). The last fox rabies cases were recorded in the Netherlands in 1988, Switzerland in 1996, Luxembourg in 1997, Belgium in 1998, France in 1999, and Germany in 2001 (Aubert et al. 2004). In 2018, fox rabies was eliminated from the large majority of the EU territory; the front is now located at the eastern limit of the EU, from Estonia to Romania (Robardet et al. 2019).

The large majority of studies addressing the problem have been focused on the incidence of rabies and on the implementation, efficiency and safety of the vaccination campaigns; the population dynamics of foxes was poorly investigated (Vos 1995, Chautan et al. 2000, Goszczyński et al. 2008). Very little long-term fox abundance monitoring has been carried out during and after the epizootic (Chautan et al. 2000).

The red fox is the most widespread generalist mesopredatory mammal in Western Europe, preying on small mammals and numerous birds, particularly species nesting on the ground (Roos et al. 2018, Kämmerle & Storch 2019), and is a major cause of roe deer *Capreolus capreolus* fawn mortality (Aanes & Andersen 1996, Jarnemo et al. 2004). In addition, foxes can consume larger mammals as carrion, including animals killed by car traffic (Saunders et al. 2010, Schwartz et al. 2018). Foxes are suspected to induce strong predation pressure on their prey species, therefore making them a major target of predator control, particularly in areas where conservation and game hunting programs are applied to a prey species. However, little is known about current dynamics of red fox populations: it is poorly understood if fox populations are still in a phase of demographic explosion, stable, or in decline, or if this trend varies from region to region. This is a major knowledge gap, as fox density has an impact on the risk of resurgence of some diseases affecting the species, domestic animals, and even humans (e.g. sarcoptic mange – Pisano et al. 2019, canine distemper virus – Nouvellet et al. 2013, echinococcosis – Gottstein et al. 2015, borreliosis and anaplasmosis – Dumitrache et al. 2015, canine leishmaniasis – Piantedosi et al. 2016, and tick-borne encephalitis – Haemig et al. 2008, Hofmeester et al. 2017).

With the present analysis, we aim to review demographic trends of the red fox in a selection of West European regions, in order to understand the impact of fox rabies and its elimination by vaccination, as well as the post-vaccination effects on red fox demography.

METHODS

We conducted literature searches using Scopus and Google Scholar. We also used Google to find grey literature (i.e. materials and research produced by organizations outside of the traditional commercial or academic publishing and distribution channels). Our searches used numerous combinations of keywords in the different languages from the study area. We utilised combinations of species name [Latin: *Vulpes Vulpes*; English: (red) fox(es); German: (rot) fuschs (rot)füchse(s); French: renard (roux); Dutch: vos], with key words in connection with rabies [English: fox rabies, fox vaccination; German: Fuchstollwut, Tollwutimpfstoff, Tollwutepidemie, French: rage vulpine, vaccin(ation), Dutch: rabiës vaccin], with key words in connection with the hunting data (English: Hunting, shooting, culling; German: Fuchsstrecke, Fuchsjagd, Jagdstrecken, Jagdstatistik, Jahresstrecke; French: statistique de chasse;

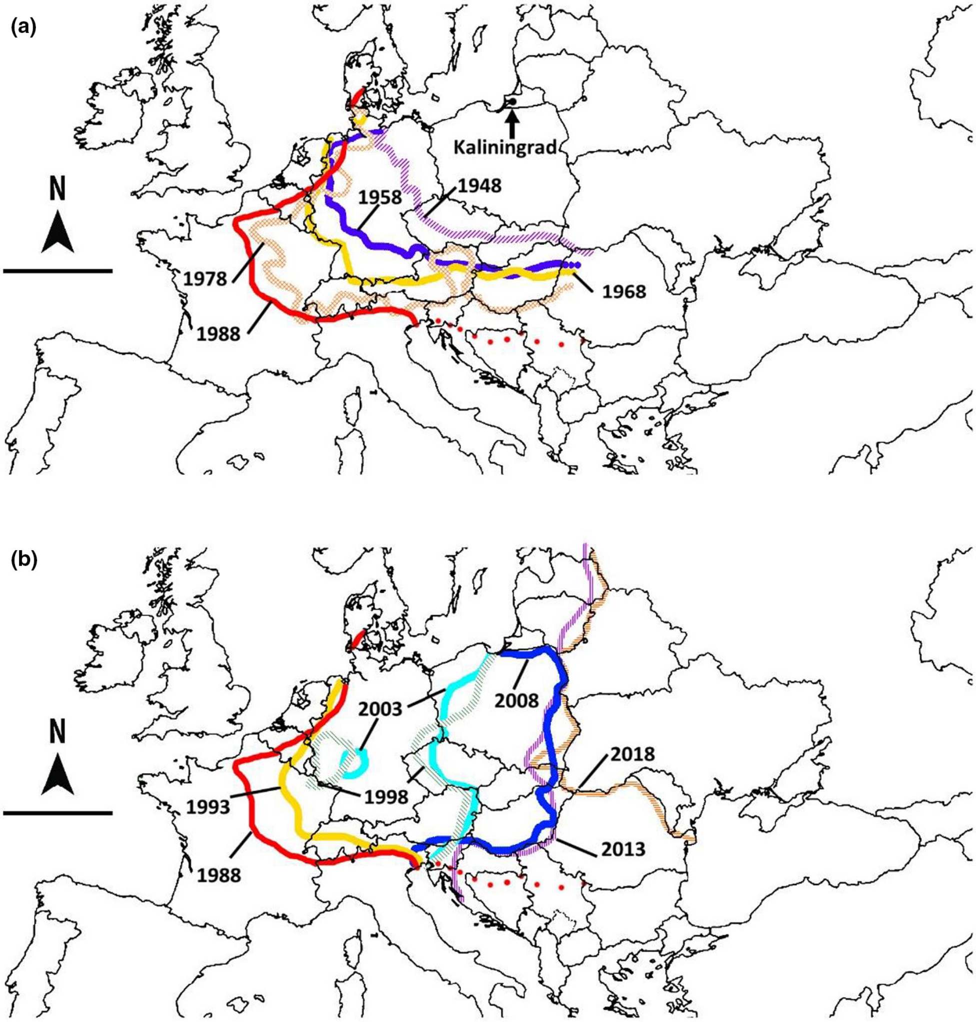

Fig. 1. Successive limits of the red fox *Vulpes vulpes* rabies front in Western Europe from 1948 to 2018: (a) expansion period of the epizootic from East to West; (b) regression period from West to East as a consequence of vaccination campaigns (Rabies Journal Europe, L.E.R.P.A.S., Robardet et al. 2019, www.who-rabies-bulletin.org). Bare scale = 500 km.

Dutch: afschot), and with key words in connection with fox population [population, count(ing), density estimation, monitoring, urban]. We made additional searches to complete specific points developed in this review. We have read more than 175 papers, and consulted the integral of the Rabies Bulletin Europe (37 volumes).

RESULTS

Evaluating fox population trends

The state of a population can be evaluated by using various state variables (e.g. occupancy, population size, and abundance). Occupancy gives us a distribution; information that is relatively poor for determining the health state of a population and its trends. Abundance – in terms of population size, absolute and relative density, or any other relative abundance index – can be more helpful to answer these questions, but usually requires more sampling effort and is typically quantified in more restricted areas.

Long-term methods for monitoring fox abundance are relatively scarce. These methods have been reviewed by Artois (1981), Beltran et al. (1991), Saunders et al. (1995), and Sadlier et al. (2004). No method is perfect and considered to be universally accepted, and all methods suffer from bias.

Hunting statistics (e.g. the number of foxes killed annually by shooting, hunting with dogs, or other methods) are the most easily available data, and therefore, they are frequently used to monitor changes in fox abundance, with the advantage of being applicable over large areas. However, hunting statistics have limits. First, they are logically not available if fox hunting is forbidden. It could be temporarily or structurally limited, for example, in urban areas. Furthermore, the results are directly affected by the hunting effort (e.g. number of hunting licences, hunters' motivation, existence, or absence of incentives; e.g. Chautan et al. 2000, Sadlier et al. 2004). Lastly, the hunting statistics approach entails that killed individuals are removed from the current population. The risk is that if hunting induces too much mortality, the fox population trend will simply be the consequence of the hunting effort against foxes. To be informative about other causes driving the population dynamics, this removal must have little to no impact on the population dynamics.

Other methods can be used to monitor fox abundance, such as camera traps (Dorning & Harris 2019, Jiménez et al. 2019), spotlight counts (Brochier et al. 1999, Ruette et al. 2003, 2015), and counts of road traffic casualties (Baker et al. 2004, Geiger et al. 2018). Indirect signs of presence can be also used, such as track counts, notably snow-tracking (Silva et al. 2009), bait recovery, scat counts (Webbon et al. 2004, Cortázar-Chinarro et al. 2019), and counts of breeding dens (Weber, 1982). Citizen science – a relatively new approach where direct and indirect fox observations can be reported – is particularly useful in areas with a high density of observers, such as urban habitats where the majority of territories are private and inaccessible (Scott et al. 2014, 2018, Walter et al. 2018). Generally, these methods allow us to obtain relative densities. Absolute densities can be also obtained by some analytical methods, such as distance-sampling in transect methods (Ruette et al. 2003) and capture-mark-recapture/resight methods with identification of individuals (Dorning & Harris 2019) or even without identification (Chandler & Royle 2013, Ramsey et al. 2015, Jiménez et al. 2019). Monitoring methods are generally applied over limited spatial scales, rarely at the level of a region or a country. Spotlight and road traffic casualty counts can be used for small-scale estimates, as well as in regional or national monitoring schemes. Indirect monitoring, such as track counts, bait recovery, and scat counts, in transects or quadrats, can be also used at different scales to study fox density trends.

The main difficulty of these methods lies in the variability due to different environments in space and in time. The spotlight method, given a kilometric index, is directly affected by habitat typology and can be applied essentially in open landscapes. Moreover, changes in the habitat year after year can directly impact both detection probability and the actual occupation by foxes along a constant sample itinerary. The road traffic casualty method is directly dependent on the intensity of traffic and the density of the road network. The indirect methods are very sensitive to detection rate in different habitats as well as the persistence of the fox traces, which are dependent on weather and substrates (Baker et al. 2002, Sadlier et al. 2004).

Data allowing the comparison between methods are very rare. Fig. 2 shows data on red fox populations in Switzerland: fox population density markers based on annual number of hunted foxes and annual fox road traffic casualties. Although the data covered different periods, hunted foxes and traffic casualties are significantly correlated ($r^2 = 0.82$; $P < 0.0001$). After a decrease in the 1970s during the rabies epidemic, since the mid-1980s, the fox population clearly increased to reach a plateau in the mid-1990s. However, from the mid-2000s, a decrease is observed in both hunting data and road traffic casualties.

Red fox population trends during the rabies epizootic

RABIES PREVALENCE AND VACCINATION

Switzerland was the first country to use a fox rabies vaccine in the wild, in 1978 (Zanoni et al. 2000), followed by Germany in 1983, Italy in 1984, and Austria, Belgium, Luxembourg, and France in 1986 (Cliquet & Picard-Meyer 2004). The initial years were generally test years, used to evaluate the efficiency of different types of vaccine. Thereafter, more intense large-scale campaigns were undertaken. Other European countries rapidly adopted this strategy of large vaccination campaigns. In every case, the number of fox rabies cases drastically decreased with the ongoing vaccination effort. Fig. 3 shows regional examples of the effect of vaccination on fox rabies prevalence. Numerous analyses have already underlined the direct relationship between the oral vaccination campaigns and the elimination of fox rabies (e.g. Brochier et al. 2001, Aubert et al. 2004, Freuling et al. 2013, Maki et al. 2017).

RED FOX POPULATION TRENDS IN CENTRAL AND WESTERN EUROPEAN COUNTRIES AFFECTED BY RABIES

Fig. 3 utilises the annual number of red foxes hunted as a population density marker. The German examples seem to show a decrease or a stabilisation of the number of foxes hunted during the epizootic. In Luxembourg and Switzerland, this number greatly diminished during the epizootic. For these two countries, Fig. 3 shows the values before the rabies epizootic, whereas for Germany, we do not have enough data from this pre-rabies reference period to conclude that there was a drastic decrease in fox populations. Everywhere, the number of foxes hunted increased remarkably during the vaccination period and thereafter, probably as a consequence of the

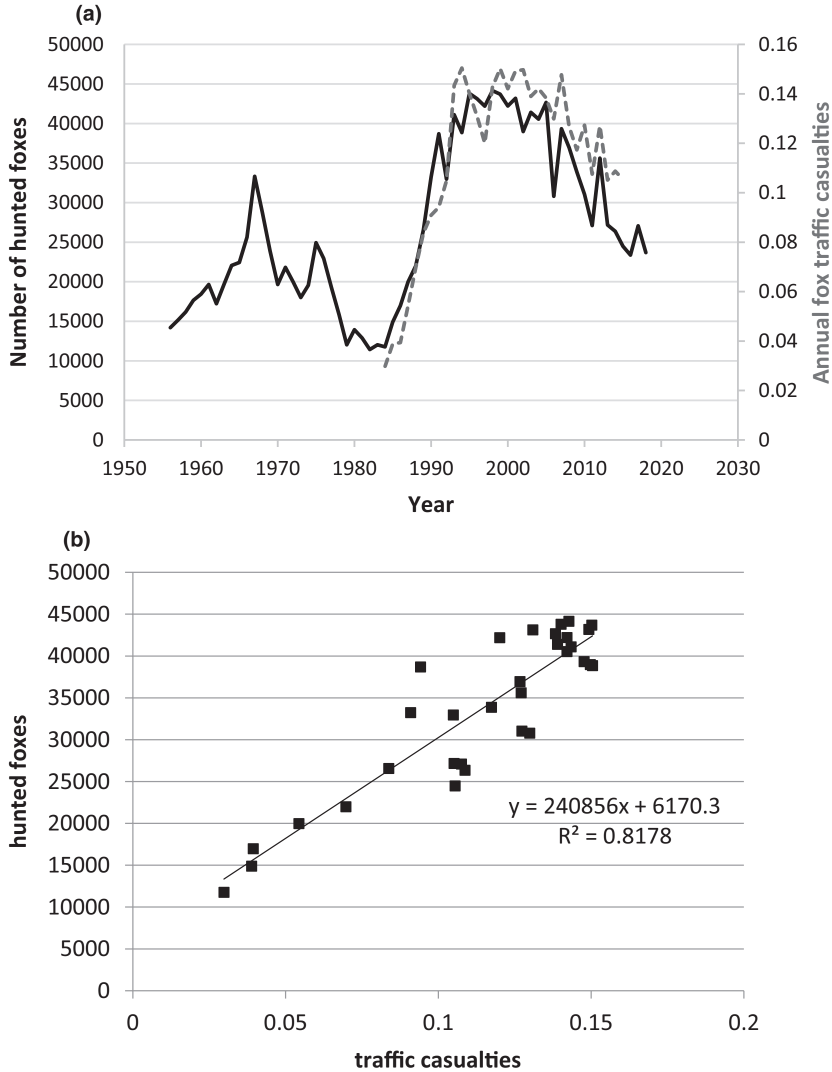

Fig. 2. Red fox *Vulpes vulpes* population trends in Switzerland. (a) Continuous line, y axis on left: annual number of foxes hunted (source: Bundesamt für Statistik, Federal Office for Environment, Switzerland). Dashed line, y axis on right: index of annual fox road traffic casualties from 1986 to 2015, with the y-scale (right) corrected for the sum of kilometres travelled per year in Switzerland (traffic casualties/million vehicles*km, source: Geiger et al. 2018). (b) The relationship between the road traffic casualty index and number of foxes hunted in Switzerland.

increasing fox population size. In Switzerland, Germany, and Belgium, this increase was more progressive and can be explained by the delay between the first tests of vaccination and the massive oral vaccination campaigns. In Lower Saxony and Luxembourg, the campaigns quickly made large-scale use of a proven oral vaccine, and the positive effect on the fox population is therefore observed more rapidly.

FOX POPULATION TRENDS IN THE UK

Having not experienced a rabies epizootic, fox populations in the UK constitute an ideal control group for comparison to the continental populations exposed to rabies. The British Game and Wildlife Conservation Trust's National Gamebag Census (NGC) gives information about fox population trends (Aebischer et al. 2011, Aebischer 2019). Since 1961, the NGC has provided a long-term index of individuals killed per unit area as part of game management, calculated by a generalised linear model coupled with a generalised additive model. NGC records suggest a population increase in the UK from the 1960s, followed by stabilisation after the 1990s (Fig. 3e). The use of spotlights for night shooting and the banning of poison have probably increased the number of foxes hunted (Aebischer et al. 2011). Foxes' food supply has probably also improved with the increasing release of captive-bred gamebirds (Aebischer et al. 2011).

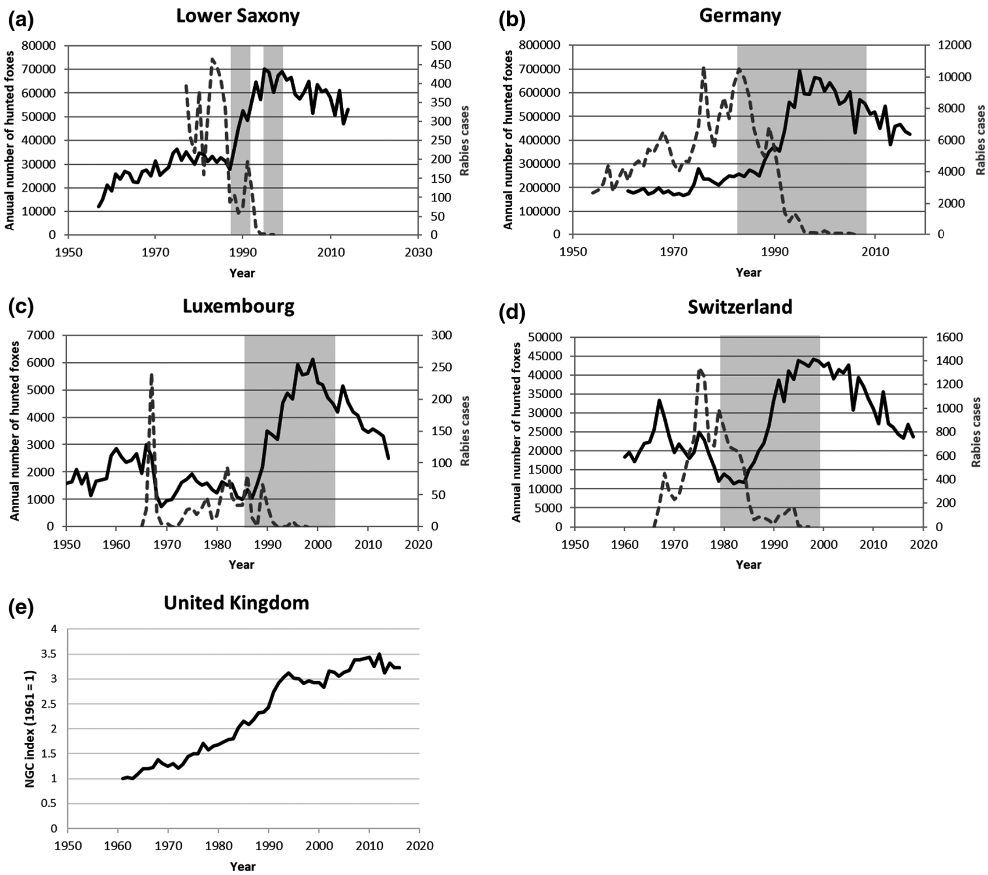

Fig. 3. Relationships between number of red fox *Vulpes vulpes* rabies cases (dashed lines, y axes on right), period of rabies vaccination (shaded time periods) and annual numbers of foxes hunted used as a trend marker for fox population density (continuous lines, y axes on left): (a) in Lower Saxony, Germany; (b) in Germany as a whole; (c) in Luxembourg; (d) in Switzerland; (e) fox population trend in the UK (NGC index) from hunting statistics. Sources for rabies and vaccination data: Germany: Müller et al. 2004, Müller et al. 2012; Luxembourg: Aubert et al. 2004, Maki et al. 2017; Switzerland: Zanoni et al. 2000; Rabies Journal Europe (1977–2013). Sources for numbers of foxes hunted: Lower Saxony: Mehls et al. 2005, Deutscher Jagdverband in DJV Handbuch jagd; Germany: Bellebaum 2003, Deutscher Jagdverband in DJV Handbuch jagd; Luxembourg: Technischer Bericht der Naturverwaltung betreffend Wildtiermanagement und Jagd, Schley et al. 2016; Switzerland: Bundesamt für Statistik, Federal Office for Environment, Switzerland; UK: Aebischer (2019).

Fox population trends after the rabies epizootic

POST-RABIES RED FOX POPULATION TRENDS IN CONTINENTAL WESTERN EUROPEAN COUNTRIES

In the 1990s, hunting data suggest a large increase in abundance for red fox populations that had recently experienced a rabies epizootic followed by an efficient program of vaccination. However, a population cannot grow infinitely; its growth is restricted by limited resources in the environment. We can expect a logistic growth curve, where the growth rate diminishes as population size approaches the environment's carrying capacity (e.g. Edwards & Edwards 2011). Figs 3 and 4 seem to show this tendency very well: after an important increase after the end of the rabies epizootic period (during the 1980s and 1990s for the countries studied here), a progressive stabilisation in the annual number of hunted foxes is observed at the end of the 1990s and in the early 2000s, suggesting that the demographic explosion of red fox populations stopped in the 2000s.

However, in the 2000s and 2010s, the trends of the number of foxes hunted vary among the regions and countries (Fig. 4). In Austria, the population has stabilised. In Switzerland, Luxembourg, and Germany, the number of foxes hunted has recently decreased but is far from reaching the lowest levels observed in the 1980s, and even of reaching the pre-rabies levels (see Fig. 3c,d). In Switzerland, road traffic casualty data suggest the same decreasing trend (Fig. 2). In Wallonia, southern Belgium, the data may even suggest an increase in fox numbers in the last 20 years (Fig. 4b, slope test $P < 0.001$), although not as significant as that

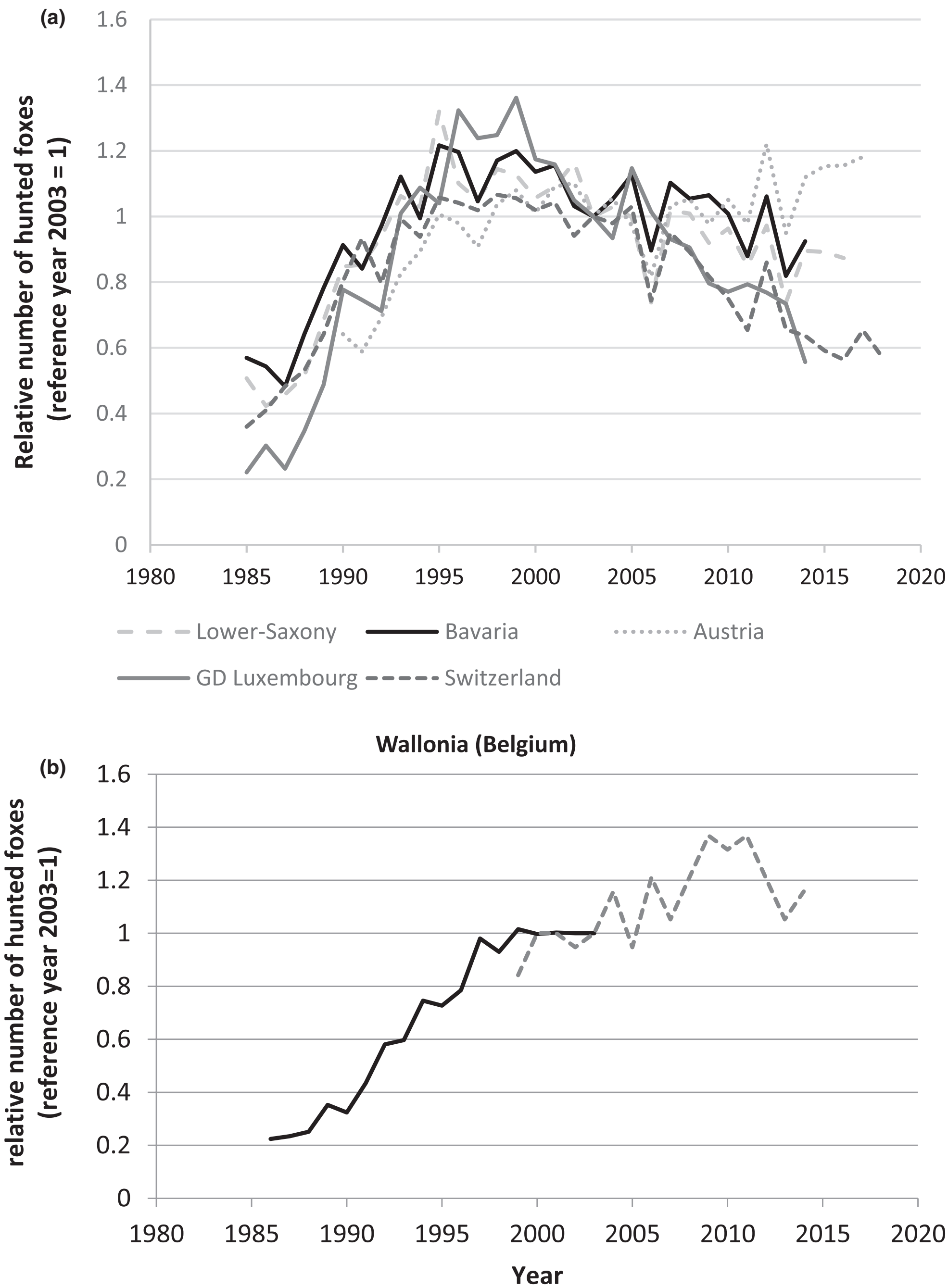

Fig. 4. (a) Trends in the numbers of red foxes *Vulpes vulpes* killed, used as a population density marker in several regions and countries that have experienced a fox rabies epidemic and that are free (or nearly free) of rabies since 2000. Sources: Germany: DJV Handbuch jagd; Austria: Maurer 2018, Bundesanstalt Statistik Österreich; Luxembourg: Schley et al. 2016; Switzerland: Federal Statistical Office. (b) Red fox trends in relative numbers of individuals killed in Wallonia (southern Belgium) based on the total number hunted in Wallonia (1986–2003, continuous line); and total number of foxes killed (1999–2014, dashed line) based on the data from five hunting districts that have complete data (sources: statistics Walloon Hunting Councils). For both graphs, 2003 is the reference year to calculate the relative number (2003 = 1).

seen in the 1990s, during the vaccination period. However here, potential bias cannot be excluded, as the sampling area is small (five hunting districts). Recently, new data from 23 hunting districts (2007–2015) showed even slightly higher values of this population index (statistics provided by the hunting councils in Wallonia).

Fig. 4a shows that in the 2000s–2010s, several peaks and dips in fox numbers in various places are remarkably synchronised (in particular, the dips of 2006 and the peaks of 2012, with the exception of Luxembourg), which, considering that the hunting efforts in different regions are probably independent, could be a consequence of environmental conditions varying over time. Appendix S1 shows that, from 2000, the relative numbers of foxes hunted in all regions included in the analysis are significantly correlated, with Austria standing out as an exception.

FOX POPULATION TRENDS IN THE UK, 2000S AND 2010S

In the UK, the NGC index suggested a stabilisation of the red fox population in the 1990s–2000s (Fig. 3e), and even perhaps a slight increase in the 2000s–2010s (Fig. 5; Aebischer 2019). The British Trust for Ornithology's Breeding Birds Survey (BBS) is another index of population trend of birds and mammals published since 1995 based on sightings and spatial models of relative abundance (Massimino et al. 2018). BBS data corroborate the stabilisation in the 1990s–2000s (Battersby 2005, Aebischer et al. 2011), but recent data show a decline in fox observations throughout the UK, particularly in the 2010s (Sainsbury et al. 2019; Fig. 5). This decline is not well understood, but could be linked to the significant decrease in rabbits *Oryctolagus cuniculus* (important fox prey) observed in the UK (Aebischer 2019). Mattews et al. (2018) underlined that the NGC index does not consider survey effort, and it is not known whether the observed differences reflect changes in population size. With these two contradicting trends, Mathews et al. (2018) consider the British red fox population to be unknown.

RURAL AND URBAN FOX POPULATIONS

Urbanisation, notably urban sprawl, has increased strongly during the last century. The development of urban areas induces major modifications in environmental conditions and resources. These changes cause a serious threat to many species, whereas others such as the red fox take advantage of this anthropogenic environment (Gaston 2010, Ineichen et al. 2012, Johnson & Munshi-South, 2017). In recent decades, the red fox has become abundant in urban areas throughout Europe (Geiger et al. 2018).

The phenomenon of urban foxes was first documented in UK cities in the 1980s (Harris & Smith 1987, Scott et al. 2014). Some consider that urban foxes represent a small proportion of the total UK fox population (Harris et al. 1995, Sainsbury et al. 2019), and others consider that rural and urban populations are not significantly different in size (Mathews et al. 2018). In continental Europe, red fox populations also colonised urban and peri-urban areas at the end of the rabies epizootic or thereafter (Brochier 1989, de Blander et al. 2007, and Geiger et al. 2018). However, this colonisation began well before in rabies-free areas such as Paris (Brosset 1975), Brussels (Brochier 1989), and Oslo (Christensen 1985). The success of the red fox's adaptation to urban environments is not surprising for a species that has a diverse feeding ecology and is able to live in a wide variety of habitats (Voigt & Macdonald 1984, Harris 1986). Foxes readily find advantages to living in urban environments with abundant anthropic food resources and shelters, and the absence of hunting (Brochier 1989, Contesse et al. 2004, Oro et al. 2013, Kimmig et al. 2020). The densities observed in urban fox populations are typically higher than those found in

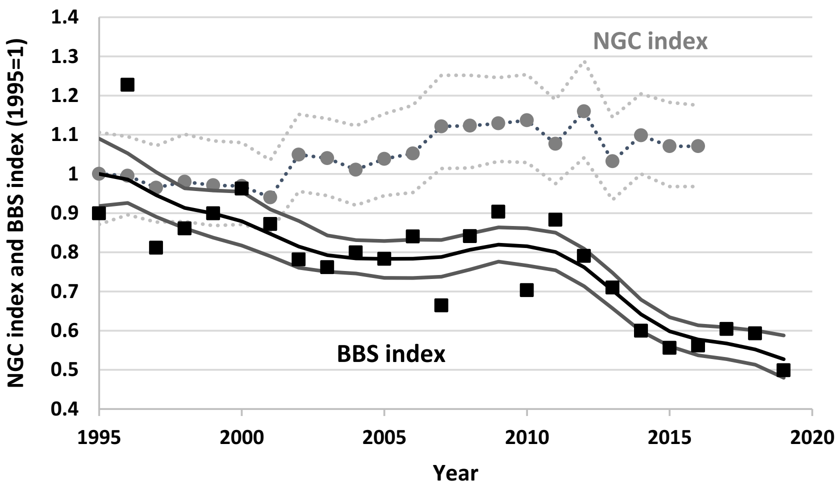

Fig. 5. Rural red fox *Vulpes vulpes* population trends in the UK since 1995: National Gamebag Census index (NGC; 1995–2016) and Breeding Bird Survey index (BBS; 1995–2019), 1995 = 1. NGC values and 95% confidence intervals (CIs) are from Aebischer (2019), based on the 1961–2016 model, but the values are corrected here to consider 1995 as the reference year. For the BBS index, the unsmoothed data [■] and smoothed curve with 95% CIs are illustrated; data from www.bto.org/our-science/projects/bbs/latest-results/mammal-monitoring.

rural areas and in other natural milieus (Mathews et al. 2018, Scott et al. 2018).

It is suggested that physical and behavioural (i.e. via avoidance behaviours) urban barriers lead to animal population subdivisions, with the possibility to reduce gene flow across these different subpopulations (Johnson & Munshi-South 2017, Santangelo et al. 2018). Although urban and rural foxes are not strictly separated populations, the gradient of conditions on the rural-urban continuum leads foxes to adapt their behaviours to local conditions (Gloor et al. 2001, Soulsbury & White 2015). Some studies provide evidence for population differentiation between rural and urban foxes (Wandeler et al. 2003, DeCandia et al. 2019), while others seemingly indicate ongoing urban-rural gene flow (Kimmig et al. 2020).

DISCUSSION

Hunting data as indicators of fox population trends

Using hunting statistics as indicators of fox density and population trends can be questionable, as killing individuals can directly impact the population size. However, in order for this to have a major effect, the hunting effort must be very high so that a large proportion of the population is removed. Culling is frequently underlined as a poor method of managing fox abundance for two reasons: firstly, removing such a large proportion of the population is very hard and even perhaps impossible to achieve, and secondly, the immigration rate is barely affected (Brochier et al. 1999, Baker et al. 2002, Rushton et al. 2006, Lieury et al. 2015, Comte et al. 2017). Hunting therefore cannot be considered alone as the major factor driving red fox population trends.

Another potential bias from killing data stems from the hunting effort. Though the number and density of hunters varies a lot between countries, the number of hunters (and hunting permits) seems relatively stable in recent decades for Belgium and Switzerland, while it declined in Luxembourg and France, and increased in Germany and Austria (Massei et al. 2015, Bundesamt für Umwelt – Switzerland). Since early 1990s, the number of hunters in 16 countries in Europe has decreased by about 18% (Massei et al. 2015). This decrease is mainly observed in Mediterranean countries (except in the Balkans; Massei et al. 2015). In the area studied in the present review, the observed values of hunter numbers in 2012 are about 10-30% of the 1982 values. All these tendencies were very progressive, following linear trends as a function of years. These very weak variation modifications of the number of hunters are absolutely not connected with the growth rate variations observed in fox populations. We thus consider that using hunting statistics as a proxy of fox population density in the present review is relevant.

During the rabies period, hunting pressure on the red fox was high, notably because many regions and countries temporarily promoted incentives to kill foxes for public and animal health reasons. However, many of the foxes that were killed were left in the field and not reported, particularly when incentives were absent. In the late 1980s and 1990s, the World Health Organization and the World Organization for Animal Health recommended (without incentive) monitoring of the effectiveness and safety of vaccination by testing killed foxes (for detection of the tetracycline marker in bones, titration of antibodies in serum, and diagnosis of rabies). This new sampling effort could also partially explain the increase in the hunting figures. Once vaccination was deemed to be effective and efficient, the incentives gradually disappeared. Small wild game hunters continue to kill foxes because they are perceived as potential rivals. Large wild game hunters gradually lost interest in hunting foxes.

The comparison of hunting data with other methods of evaluating fox population trends is rare. In Switzerland, the strength of the correlation between hunting data and road traffic casualties is impressive and can help justify using hunting data to study trends in fox population densities (Fig. 2). However, although the correlation appears to be strong in Switzerland, this might not be the case in other countries or regions. For instance, in UK fox populations in the 2010s, we have seen a possible counter-example where NGC and BBS indexes indicate different trends over the years: respectively, a stabilisation of hunted red fox numbers, and a decrease in red fox detection rate (Fig. 5).

Summary of red fox population trends

In the present work, we aimed to assess red fox population trends during and after the fox rabies epizootic. If hunting data can be considered indicators of fox population density, the general population trends in Western Europe can be summarised as follows. Data for the pre-rabies period are very rare, but suggest that population density was significantly lower than in the 2010s. When pre-rabies data are available, a sharp population decline was observed in the beginning of the epizootic. During the rabies outbreak, which lasted about four decades, fox populations within the infected areas experienced a lack of growth or even a decline (though local growth cycles were observed). Populations then experienced a demographic explosion in the 1990s, after the gradual elimination of rabies by an international programme of oral vaccination. Rabies was eliminated from many European countries and the disease front is now being pushed back to the EU's eastern border. After the beginning of the vaccination campaigns, these populations were experiencing logistic growth curves with strong growth at the beginning and then stabilising at the end of the 1990s – early 2000s, suggesting that these populations had reached the carrying capacity of their environment, at levels far higher than those observed in the past. In addition, foxes have colonised urban environments more and more. It is even possible that rural populations have stabilised while urban populations are still increasing. Furthermore, the change in fox populations in non-urban environments seems to be variable according the region: decreasing (Germany, Luxembourg, Switzerland), stable (Austria, France; Ruette et al. 2015), and still increasing (Belgium).

Causes of excess mortality during and after the rabies period

Rabies is lethal for an infected fox, and in a newly infected fox population, 60–80% of the resident foxes perish (Voigt et al. 1985). After a local demographic crash, the occurrence of rabies typically stays low during 2–3 years, until the population density recovers to a threshold value; after 3–5 years, a second peak may occur (Ginsberg & Macdonald 1990, Holmala & Kauhala 2006). The oral vaccination campaigns stopped the cyclic occurrences previously observed. However, it is too simple to conclude that rabies was the only cause of the decline of fox populations during the rabies period. Other indirect causes of mortality were induced by humans to counter the epizootic, mainly by shooting, trapping, poisoning, and gassing. Thus, the excessive mortality during the rabies period is the cumulative result of these direct and indirect mortalities.

Other diseases can also induce a high mortality rate in foxes, in particular, sarcoptic mange and the canine distemper virus (CDV). However, when diseases share the same host, the alteration in fox population structure caused by the presence of one disease affects the dynamics of the other diseases (Nouvellet et al. 2013, Pisano et al. 2019). In the case of the tapeworm *Echinococcus multilocularis,* foxes are a normal end-host of the parasitic cycle and canids suffer little to no mortality from it. There is no large-scale impact of this disease on fox population dynamics; therefore, we do not discuss it further.

Sarcoptic mange in red foxes, induced by a skin-dwelling mite *Sarcoptes scabei* var. *vulpes*, can have either an enzootic or an epizootic nature; in the latter case, the epizootic gradually shifts into enzootic (Pisano et al. 2019). Mange epizootics have induced high mortality rates (up to 90% of population mortality): in Fennoscandia and Denmark in the 1960s-1990s, as well as locally in the UK in the 1990s (Holt & Berg, 1990, Lindström 1991, Soulsbury et al. 2007). In Switzerland, this disease was less frequent in areas affected by rabies, but after the elimination of rabies, sarcoptic mange re-emerged, where it had apparently disappeared and spread epidemically, until it occurred almost all over the country (Pisano et al. 2019). It seems that, except in some rabies-free regions, rabies negatively impacted the occurrence of mange, thus limiting its impact during the 1960s-1990s. Sarcoptic mange now affects foxes in numerous European countries, causing generally low and cyclic mortality spikes with short-term local population decreases (Pence & Ückermann 2002, Pisano et al. 2019).

In experimental conditions, 40% of foxes infected with CDV died within 21 days post-injection (Zhao et al. 2015); however, some individuals can survive and become sero-positive (Nouvellet et al. 2013). Serological investigations for CDV in some fox populations in Europe have identified antibody prevalence rates of 4–26% (e.g. Frölich et al. 2000, Damien et al. 2002, Sobrino et al. 2008), suggesting that CDV circulates in foxes in Europe. A recent rabies epizootic in Italy revealed a negative interaction between CDV and rabies (Nouvellet et al. 2013). As with mange, after the elimination of rabies, CDV spread more significantly throughout the European fox population. However, the trade-off between CDV-induced mortality rate and the fox population's reproduction rate – and thus, the real impact of CDV on the fox population density – is currently unclear.

The post-rabies red fox density

The density of red foxes is clearly higher after recovery from the rabies epizootic than it was before. Even in regions and countries that never experienced fox rabies, such as the UK, a strong increase in fox numbers was observed while other western European countries were being impacted by rabies. It is very likely that, if these countries had not experienced a period of rabies outbreak, fox populations would have increased in 1970–1980, as was observed in the UK. We have already discussed the development of dense urban fox populations exploiting the abundance of shelters and foods and the absence of hunting. Moreover, this boom in the fox demographic was also observed outside cities. Modifications of the landscape can also explain this increase. In rural environments, the increase of available resources and homogenisation of the landscape seems to promote outbreaks, notably in their frequency, of micromammals such as voles (Dalkvist et al. 2011, Truchetet et al. 2014), which are an important part of the fox diet. Additionally, humans have provided supplementary available prey: road kills, poultry, and release of reared small game (e.g. pheasants *Phasianus colchicus*; mallards *Anas platyrhynchos*; and partridges *Alectoris rufa*), many of which (34–81% in the UK) end up being taken by foxes (Baker et al. 2006).

The Eurasian lynx *Lynx lynx* and grey wolf *Canis lupus* may affect the fox through intraguild predation and/or supply of carrion from their prey (Wikenros et al. 2017). Vogt et al. (2018) found that the fox makes up 5.9% of lynx's diet in the Swiss Alps. Some studies suggest the lynx can have a limiting effect on fox populations (e.g. Pasanen-Mortensen et al. 2013) but others show a positive effect (e.g. Wikenros et al. 2017). In their territories, wolves can induce a negative effect on fox abundance by inducing avoidance behaviours in foxes, even though direct predation is rare (<0.2% of wolf diet in Sweden; Wikenros et al. 2017). However, the impact of the fox's numerous competitors is unclear (for instance the European badger *Meles meles*; stone marten *Martes foina*; raccoon *Procyon lotor*; birds of prey; corvids; domestic, feral, and wild cats *Felis silvestris*; and raccoon dogs *Nyctereutes procyonides*). The golden jackal *Canis aureus*, a dominant competitor for the fox (Farkas et al. 2017), is currently rare, but is spreading into some parts of Europe. Finally, the red fox in Western Europe is essentially controlled by the environmental carrying capacity, notably the availability of food.

Causes of recent decline in rural areas

With the exception of Belgium, France, and Austria, the available data show a general decline in the number of foxes killed. The fairly sharp decline in foxes killed in Luxembourg has been an argument for a hunting ban since 2015. However, the fox population numbers currently observed remain much higher than during the rabies crisis. Several hypotheses could explain the decline in numbers of foxes killed by hunters.

The first hypothesis would be that the targeted hunting effort on the fox has recently declined. We have seen that the number of hunters (and hunting permits) does not explain the declining trend. However, within the hunter population, hunting effort directed towards foxes after the end of the rabies period has probably decreased. Nevertheless, it is difficult to conclude that this explains the trend. If this is the case, the current trend estimate values for foxes would be underestimated by the hunting data. Scarce data based on any index other than hunting data, such as road traffic casualties in Swiss foxes or the BBS index in the UK, also indicate a decrease, which would not be directly due to a bias in hunting effort. A second hypothesis would be that the hunting effort is too high and has negatively impacted the fox populations. We have already discussed this point: the killing of foxes does not seem to affect fox populations, which does not support this explanation.

A third hypothesis would be that after reaching the environmental carrying capacity, foxes have exerted pressure on their resources, in particular, causing a decrease of their prey density, which has led in turn to a gradual decline in the fox population. Though this has been proven for ground-breeding birds (e.g. Côté & Sutherland 1997, Roos et al. 2018, Tobajas et al. 2020), it is more difficult to suggest that micromammal populations are actually impacted directly by the fox, as they are much more subject to interannual variations due to changing meteorological conditions and food availability (Baker et al. 2006). Foxes are opportunist predators that are unlikely to be affected by decreases in one type of prey if others are still present in numbers. During years with low micromammal densities, foxes take more ground-breeding birds (e.g. Marcström et al. 1988). In the UK, an explanation for the possible decrease in fox populations would be the decrease of rabbits. However, this decrease in the rabbit population is mainly a consequence of myxomatosis rather than fox overcrowding.

A fourth hypothesis is regression following the impact of a new disease. Indeed, high densities can improve disease transmission. After the elimination of rabies, we have seen that other fatal diseases reappeared in Europe; these may induce negative growth rates. However, according to recent data, though CDV may lead to a decrease in the growth rate, it may not be enough to cause a decline in fox numbers. Sarcoptic mange could potentially induce this effect when it is epizootic, as it may cause a drop in fox numbers in the event of a severe outbreak (Pisano et al. 2019).

Ecological impacts of a modification of fox population density

The most important ecological impact of an increase in red fox density is the inflation in the predation rate. The aim here is not to review the demographic impact on all fox prey species, since the fox is a major mesopredator of many small and medium-sized mammals, as well as birds, especially ground-breeding birds. The impact of changes in fox density on prey is difficult to assess and synthesise, notably due to the wide range of possible prey species, of competitive predators, of habitats, and of prey densities. However, there are circumstances where the presence and abundance of foxes can have a dramatic impact on certain prey. A first example is birds nesting in colonies on or close to the ground, which can be very significantly affected by predation or by regular disturbance (e.g. Kadlec 1971, Southern et al. 1985, Lavers et al. 2009).

A second example is the impact of a sarcoptic mange epizootic in Scandinavia. Before the epizootic, red fox population sizes followed vole *Microtus* ssp. densities; the grouse *Lyrurus tetrix* and hare *Lepus europaeus* and *Lepus timidus* populations generally decreased in years with low vole numbers, but increased after a year with high vole densities (Lindström et al. 1987, 1994). A similar phenomenon of fox predation redirection is noted with the predation of young capercaillie *Tetrao urogallus* in years of low vole densities in the French Jura (Leclercq et al. 1997). Vole populations are not impacted by the decline and recovery of the fox population; they are probably more affected by plant productivity and snow depth. In contrast, hares and black grouse populations in Scandinavia increased by 40–100% during the fox mange epidemic, and their populations dropped when the fox populations recovered. Another case is noted in a Belgian Natural Park with fox rabies and black grouse (Fig. 6). After natural variation around a relative equilibrium was observed throughout the 1970s-1990s, the black grouse population has suffered from a constant decline since 1994, during a period that corresponds exactly with the fox demographic explosion consecutive with the vaccination against rabies.

In Western and Central Europe, due to its opportunistic predatory behaviour, the diet range of the red fox overlaps that of other predators, be they native (such as Mustelidae, including the European badger and wild cat), invasive (raccoon, raccoon dog), or even new arrivals (golden jackal) or returning species (grey wolf and Eurasian lynx); at high densities, the fox could become a competitor for food resources to these species. The red fox supplements its diet with some invertebrates and fruits (mainly drupes and berries). If the impact on invertebrates is probably limited, the red fox can potentially increase its role in the dispersion of numerous seeds, notably by endozoochory (i.e. D'hondt et al. 2011).

Finally, some wild species can be impacted by fox epizootic diseases, via vulpine rabies in badgers (Smith 2002, Smith & Wilkinson 2002) and CDV in other canids and some mustelids. However, the connection between fox density and the probability of other wild species being

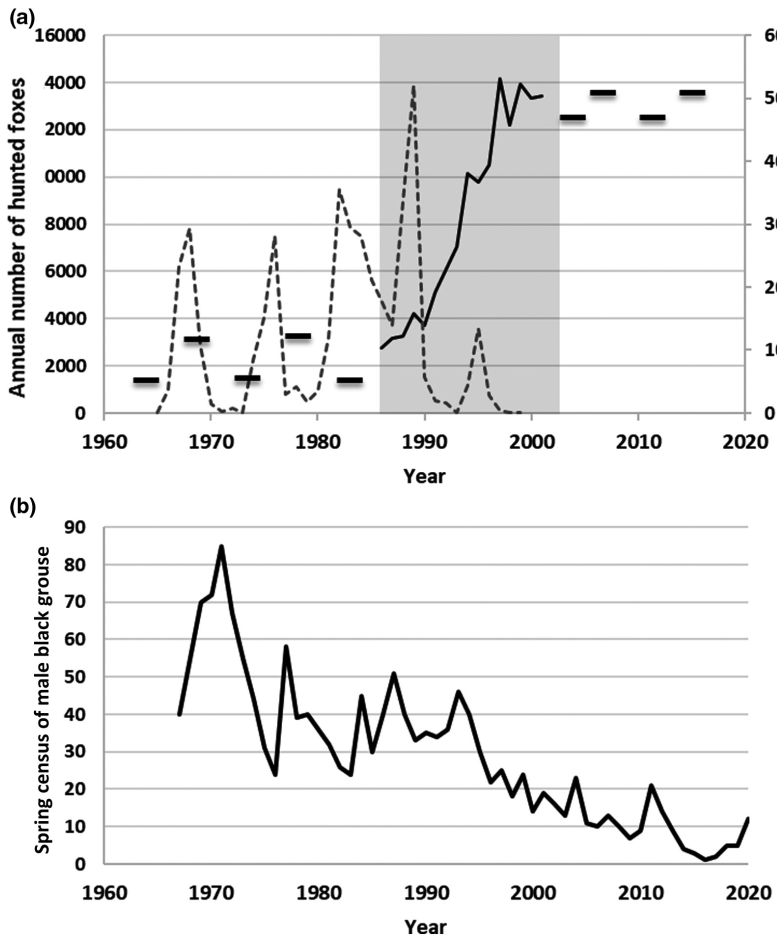

Fig. 6. (a) Numbers of red fox *Vulpes vulpes* rabies cases (dashed line, y-axis on right), period of vaccination (shaded time period), annual number of red foxes killed in Wallonia (southern Belgium; continuous line, y-axis on left). The horizontal dashes indicate estimated numbers of foxes killed before and after the period of vaccination. (b) Spring census of male black grouse *Lyrurus tetrix* in High Fens Natural Reserve in south-east Belgium; data from the north-eastern part of the reserve are not included here because of a confounding effect due to graduate closing of vegetation.

affected by these diseases is not well understood. Moreover, vulpine rabies is currently eradicated in Western Europe.

CONCLUSIONS

Previous research has been focused on the prevalence of fox rabies after the vaccination campaign. Our aim was to review the impact of rabies and the vaccination campaigns on the fox population during the epidemic and, significantly, after the official eradication of the disease. We underline that rabies negatively impacted fox populations, and the vaccination campaigns were directly followed by a demographic explosion. However, rabies vaccination was not the direct cause of this demographic explosion, as rabies-free areas experienced it also. The causes of this demographic explosion are more to be sought in the environmental modifications induced by humans. Around the 2000s, rural fox populations probably reached densities close to carrying capacity and populations stabilised. However, subsequently, with some exceptions, rural Western European populations seem to be experiencing a recent moderate decline. The very large majority of available data come from hunting statistics; we encourage the diversification of the sources, including data from camera-traps, road traffic casualties or large-scale kilometric index. These data will help us to understand fox population trends at large spatial scales and over long time periods. Understanding trends in the fox population is imperative for improving the future management of this species and for the conservation of its prey populations, particularly if the latter are sensitive to fox density. It will also help us to understand the ecological impact of variations in fox density, as this mesopredator has numerous connections with a large number of species (prey species, competitors, and apex predators) and has a role in the transmission of some diseases to other species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Correlations between the relative trends of foxes hunted (since 2000, the reference year 2003 = 1; *P*-value and r^2 of the correlation are shown).