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**Demography of a carnivore, the red fox, Vulpes vulpes: what have we learnt from 70 years of published studies?**

**Devenish-Nelson et al., 2012**

the demography of populations within a species has been shown to be highly variable

The red fox Vulpes vulpes, a widely-studied, widespread and economically important species, offers an opportunity to consider the degree of intraspecific variability in the demography of a carnivore and to test the consequences of interpopulation data substitution

Modelled populations have a tendency towards positive population growth, with survival and fecundity of the youngest age class contributing most to that growth.

Despite 70 years of published studies, we were unable to examine the effects on demographic parameters of harvesting regimes, density and weather.

Moreover, demographic parameters are often missing for a focal population, requiring modellers to rely on surrogate data from other populations of the same species (Pech et al. 1997, 2008)

Nilsen et al. (2009) showed population-specific demography of roe deer Capreolus capreolus resulting from distinct climatic conditions, predation and harvest levels, and Servanty et al. (2011) found variation along the fast–slow continuum among wild boar Sus scrofa populations facing different hunting pressure. Similarly, Johnson et al. (2010) demonstrated substantial differences in vital rate contributions between populations of Sierra Nevada bighorn sheep Ovis canadensis sierra in various phases of population growth.

Red foxes are the most widespread, extant, terrestrial mammal (Schipper et al. 2008) and are also a species of great economic, cultural and disease importance (Baker et al. 2008).

Recent deterministic models of red foxes have suggested that demographic traits, particularly age-specific contributions to population growth, are highly consistent across a sample of populations (McLeod and Saunders 2001)

Foxes are found across many habitats, from tundra to arid environments, and with rural and urban populations (Pils and Martin 1978, Harris and Smith 1987, Lindström 1989, Saunders et al. 2002).

Age-specific models are appropriate for modelling fox population dynamics because attributes such as litter size have been shown to vary significantly with female age (Harris 1979, McIlroy et al. 2001).

Females are able to mate when they are about 10 months old and produce one litter per year thereafter (Englund 1970)

Life-history ‘speed’ is determined by how a species resolves the evolutionary tradeoff between reproduction and survival, in response to extrinsic mortality and environmental stochasticity (Bielby et al. 2007)

Perturbation analyses provide a ranking of the relative importance of demographic rates, in the context of their effects on the population growth rate (l) (Caswell 2001).

Traditional perturbation methods do not account for variability and uncertainty in vital rates, potentially masking the true importance of life stages (Mills et al. 1999).

Relative to many other carnivores, red foxes mature early, are fairly short-lived and, as is typical of canids, have larger than average litter sizes; consequently, theory predicts that they should fall towards the fast end of the spectrum (Heppell et al. 2000).

Life-history theory suggests that relatively early-maturing mammals, such as the fox, should have higher elasticity of fecundity than survival (Heppell et al. 2000). Elasticity analysis and LSA reveal two main points: that the youngest age class makes the largest contribution to l, and that, generally, fecundity is as important as survival

we found that fecundity is more variable than survival, possibly because fecundity is influenced more than survival by complex factors, which include food limitation, body mass, and social factors (Cavallini 1996, Iossa et al. 2008).

At the moment, for instance, it is unclear how samples taken by driven shoots, night shoots, snaring, leghold traps or digging out of dens differ: data from different collection methods should be presented separately and by time of year to facilitate analyses on the impact of sampling method on demographic parameters

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

**Delcourt et al., 2022**

Over several decades, Western Europe experienced an outbreak of sylvatic rabies, eliminated through an EU programme involving large-scale red fox vaccination campaigns.

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.

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.

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.

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 front is now located at the eastern limit of the EU, from Estonia to Romania (Robardet et al. 2019).

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.

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

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

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.

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).

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).

In every case, the number of fox rabies cases drastically decreased with the ongoing vaccination effort.

Everywhere, the number of foxes hunted increased remarkably during the vaccination period

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

records suggest a population increase in the UK from the 1960s, followed by stabilisation after the 1990s

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).

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

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. 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).

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).

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

However, many of the foxes that were killed were left in the field and not reported, particularly when incentives were absent.

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.

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.

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

Other diseases can also induce a high mortality rate in foxes, in particular, sarcoptic mange and the canine distemper virus (CDV).

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.

humans have provided supplementary available prey: road kills, poultry, and release of reared small game

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)

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.

The first hypothesis would be that the targeted hunting effort on the fox has recently declined.

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.

During years with low micromammal densities, foxes take more groundbreeding birds (e.g. Marcström et al. 1988).

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.

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).

**Efficient use of harvest data: a size-class-structured integrated population model for exploited populations**

**Gamelon et al., 2021**

Despite their relevance for management decisions, structure and size of exploited populations are often not known, and data limited

joint analysis of different types of demographic data, such as population counts, reproductive data and capture–mark–recapture data, within integrated population models (IPMs) has gained much popularity as it may allow estimating population size and structure, as well as key demographic rates, while fully accounting for uncertainty. IPMs built so far for exploited populations have typically been built as age-structured population models. However, the age of harvested individuals is usually difficult and/or costly to assess and therefore often not available. Here, we introduce an IPM structured by body size classes, which allows making efficient use of data commonly available in exploited populations for which accurate information on age is often missing.

Models designed to assess interactive effects of harvest and other stressors on population dynamics and to predict sustainability of harvest management typically require detailed information on demographic parameters (e.g. survival, reproduction) and population size. Nonetheless, these quantities are challenging to estimate in absence of detailed long-term data (Clutton-Brock and Sheldon 2010). When demographic information is limited, the challenge lies in making efficient use of available data to gain an understanding of the dynamics of exploited populations that is sufficient to provide appropriate management recommendations.

Our model differs from traditional IPMs applied to vertebrate populations in two ways. First, it integrates CMRR data and an individual trait recorded at death (body size) into a size class-structured population model.

Second, the model makes inference on population size using size-specific counts of individuals that have died due to harvesting. For each size class, the model allows us to get annual estimates of demographic parameters and of the number of alive individuals

We illustrate the usefulness of this IPM for assessing population dynamics based on the case study of an economically important game species, the wild boar Sus scrofa.

contrary to large herbivores, age is not a structuring factor of survival in wild boar (Focardi et al. 2008).

Moreover, contrary to age, size information is routinely collected by hunters, making size-structured model relevant for modeling many game species.

Three types of demographic data were thus available (Fig. 1): CMRR data (with live recaptures between March and September, and harvest recoveries between October and February), size-at-harvest data (from October to February) and reproduction data (from October to February)

Integrated population models consist of two components, a population process model and a set of different data likelihoods (Besbeas et al. 2002), both of which are combined and analyzed under a joint likelihood (Schaub and Abadi 2011, Zipkin and Saunders 2018).

CMRR data were analyzed using a multistate model (reviewed by Lebreton et al. 2009) that allows separating estimation of size-class-specific parameters associated with growth, natural mortality and hunting mortality (Lebreton et al. 1999, Gamelon et al. 2012).

Both natural and hunting mortalities varied among size classes (Fig. 3A, D) and across time

Hunting mortality was therefore substantially higher than natural mortality for all size classes.

Low natural mortality is common among ungulate species, for which average natural adult survival probability often exceeds 0.90 for females (Gaillard et al. 2000).

Generation time is around two years for hunted wild boar, whereas it is close to six years for other, similar-sized ungulates (Servanty et al. 2011, Gamelon et al. 2021).

Acorn mast events vary in intensity and frequency over years and are major determinants of breeding proportions in wild boar (Servanty et al. 2009, Gamelon et al. 2017, Touzot et al. 2020).

Management recommendations based on body mass classes – instead of exact body mass itself – may thus be more realistic to implement in the field.

demographic parameters of a variety of exploited species are strongly dependent on body size and it is thus particularly relevant to use size-class-structured models.

For example, the collection of wings of shot ducks makes it possible to differentiate both between sexes and between juvenile and adult individuals in the harvest

Furthermore, once fitted, the IPM may lend itself to a variety of follow-up analyses with high relevance to population management. Retrospective perturbation analyses, such as transient life table response experiments, can be run on IPM outputs to determine the relative importance of different drivers of past population dynamics at the levels of demographic rates, population structure, trait dynamics and environmental influences (Koons et al. 2016, 2017, LaytonMatthews et al. 2021). Future population dynamics, on the other hand, can be explored using prospective perturbation analyses

**An integrated population modelling workflow for supporting mesopredator management**

**Nater et al., under review**

Lethal control through harvest is commonly implemented as a mitigation measure, yet the effects of harvest and its interaction with environmental conditions on mesopredator population dynamics have rarely been assessed quantitatively due to data constraints.

applied it to an expanding population of red 12 foxes in Arctic Norway.

data on age, reproductive status, and genetic variation from >3600 harvested red foxes with opportunistic field observations and information published on red foxes elsewhere. This allowed us to quantify 15 population dynamics over a period of 18 years, and to identify the drivers of changes in 16 population growth rates using retrospective (Life Table Response Experiments, LTREs) and 17 prospective (population viability analyses, PVAs) perturbation analyses.

population growth and range expansion of predators that occupy mid-ranking positions 38 in the food-web (mesopredators) are particularly problematic (J. H. Moore et al. 2023; Prugh 39 et al. 2009). Mesopredators of concern are often generalists

increased food availability in human41 dominated landscapes relaxes bottom-up constraints on mesopredators (Larivière 2004; 42 Pasanen-Mortensen and Elmhagen 2015).

mesopredators face less top-down 43 constraints following the eradication of many apex predator populations (Elmhagen and 44 Rushton 2007; Prugh et al. 2009).

leading to high predation pressure 46 on their prey and causing negative cascading effects down the food chain (Prugh et al. 2009; 47 Roos et al. 2018).

the expansion of 52 mesopredators can also pose a threat to human health as some mesopredators (e.g. red foxes, 53 Vulpes vulpes) are vectors for zoonotic diseases such as rabies and alveolar echinococcosis 54 (Holmala and Kauhala 2006; Laurimaa et al. 2016).

Population growth, human spread, and climatic changes also help mesopredators 50 expand into new habitats, become invasive, and displace native species (Salo et al. 2008; 51 Elmhagen et al. 2017).

the effect of harvest is difficult to quantify and often unclear (Conner and Morris 58 2015)

compensate for increased morality (Salo et al. 2010; Minnie, Gaylard, and Kerley 2016).

Data obtained from harvested animals, on the other hand, are readily available 68 but traditional methods of analysing them (e.g. life table analysis) are prone to bias and unable 69 to reliably estimate demographic parameters (Williams, Nichols, and Conroy 2002).

we develop a versatile IPM workflow for studying mesopredator population 94 dynamics under different harvest regimes and apply it to a case study of an expanding red fox 95 population in the tundra of Northern Norway.

over the last 18 years (2005-2022) of intense harvest

investigate the potential role of environmental conditions (food availability via the 101 abundance of small rodents and reindeer carcasses) for population regulation and identify the 102 key demographic drivers of population change through transient life table response 103 experiments (tLTREs, Koons et al., 2016, 2017)

we couple our IPM with a population 104 viability analysis (PVA, Morris & Doak, 2002; Saunders et al., 2018)

Red foxes are one of the most widely distributed mesopredators in the world (Larivière and 116 Pasitschniak-Arts 1996) and their influx into tundra regions of Eurasia and North America

The red fox’s success in colonizing and thriving in new habitats stems from its opportunistic diet and relatively fast life history: red foxes can reach sexual maturity towards the end of their first year of life and females typically give birth to 3-6 pups (range 1-12) per year. Survival beyond 5 years of age is rare in the wild (Larivière and Pasitschniak-Arts 1996).

Due 131 to rapid climate warming this tundra ecosystem is currently on trajectory to shift towards a 132 boreal climate (Pedersen et al. 2021)

Small rodents are the most important prey of red foxes on Varanger (Killengreen et al. 2011), and red foxes are known to exhibit strong 1-year lagged numerical response to rodent cycles (J. Henden, Ims, and Yoccoz 2009)

In addition, red foxes feed on reindeer carcasses, which are readily available in inland areas in winter due to widely practiced reindeer herding, and also exploit marine food subsidies along the coastline (Killengreen et al. 2011).

Intense red fox harvest has been implemented in our study area since 2005 to conserve 145 remaining populations of arctic foxes (Vulpes lagopus) and ground nesting birds (Hamel et al. 146 2013; Ims et al. 2017).

We inferred pregnancy rates from placental scars for females > 1 year and harvested from 170 July 1st until March 20th (n= 258).

**Demography, not inheritance, drives phenotypic change in hunted bighorn sheep**

**Traill et al., 2014**

Selective harvest, such as trophy hunting, can shift the distribution of a quantitative character such as body size.

we develop a size- and age-based two-sex integral projection model based on individual-based data from a long-term study of hunted bighorn sheep (Ovis canadensis)

We simulate the effect of trophy hunting on body size and find that the inheritance of body mass is weak and that any perceived decline in body mass of the bighorn population is largely attributable to demographic change and environmental factors.

Apparent shifts in the distribution of a quantitative character, however, may not occur through genetic mechanisms alone, because hunting can also alter age and sex structure, behavior, and social hierarchies (8–10), which may in turn interact with localized density-dependent and -independent factors to accentuate, or mask, a phenotypic response

**FoxNet: An individual-based model framework to support management of an invasive predator, the red fox**

**Hradsky et al, 2018**

FoxNet, a spatially explicit, individual- based model (IBM) framework that can be customised to predict red fox population dynamics, including responses to control and landscape productivity.

FoxNet models were largely successful in reproducing the demographic structure of two red fox populations in highly contrasting landscapes.

Future extensions could explore competitor and prey responses to red fox control and the effects of habitat disturbance on predator population dynamics.

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**Invasive predators and global biodiversity loss**

**Doherty et al, 2016**

Invasive species threaten biodiversity globally, and invasive mammalian predators are particularly damaging, having contributed to considerable species decline and extinction.

Invasive predators are implicated in 87 bird, 45 mammal, and 10 reptile species extinctions—58% of these groups’ contemporary extinctions worldwide.

Invasive mammalian predators endanger a further 596 species at risk of extinction, with cats, rodents, dogs, and pigs threatening the most species overall.

most impacted species are insular indicates that management of invasive predators on islands should be a global conservation priority.

Species such as cats (Felis catus), rats (Rattus rattus), mongoose (Herpestes auropunctatus), and stoats (Mustela erminea) threaten biodiversity through predation (4, 5), competition (6), disease transmission (7), and facilitation with other invasive species (8).

predation by feral cats and red foxes (Vulpes vulpes) has led to the decline or extinction of two thirds of Australia’s digging mammal species over the past 200 y (10, 11).

596 threatened and 142 extinct species (total 738) have suffered negative impacts from 30 species of invasive mammalian predators from 13 families and eight orders.

The 738 impacted species consist of 400 bird species from 78 families, 189 mammal species from 45 families, and 149 reptile species from 26 families

red foxes (48 species)

Introduced rodents and cats are major agents of extinction, collectively being listed as causal factors in 44% of modern bird, mammal, and reptile species extinctions.

The high extinction rates of ground-dwelling birds in Hawaii (28) and New Zealand (29)—both of which lack native mammalian predators—are cases in point.

we have documented the comparative severity of impacts of invasive mammalian predators, we note that the strength of evidence available to quantify predator impacts was often low

there remains an urgent need for research on the impacts of invasive predators relative to other threats (e.g., habitat loss).