Causes and Implications of Fox Population Dynamics in Central Southern England

Nathan Fletcher Williams
The Department of Life and Environmental Sciences
Bournemouth University

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Supervisors: Dr Emilie Hardouin, Dr Demetra Andreou, Prof Richard Stillman, Dr Andrew Hoodless, Dr Tom Porteus, Mike Short

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“Good authors, too, who once knew better words,
Now only use four letter words
Writing prose, Anything goes”

Cole Porter, 1934
“*Anything goes*”

“There are known knowns. These are things that we know we know. There are known unknowns. That is to say, there are things that we know we don’t know. But there are also unknown unknowns. There are things we don’t know we don’t know.”

Donald Rumsfeld, 2002

“Whether in the context of livestock, or game, or wildlife, or sport, or welfare, or disease, or most of all, human values, prejudices and perceptions, I’ve never found any dimension of human-wildlife conflict anywhere in the world that wasn’t illustrated by red foxes.”

David Macdonald, 2023
International Conference on Human-Wildlife Conflict and Coexistence

Abstract

The red fox (*Vulpes vulpes*) is a generalist mesopredator and the world's most widespread terrestrial carnivore. As a major predator of game, livestock, and wildlife, foxes are culled throughout their range to limit their impact, including in the UK, where data suggests they occur at higher overall densities than many other European countries. However, owing to source-sink dynamics, numerous studies have demonstrated that individuals removed by lethal methods can be replaced rapidly through compensatory immigration. Therefore, given that culling is not a long-term solution, identifying the underlying causes of such high fox immigration pressure is needed to provide support for alternative, more sustainable means of controlling foxes. In this thesis, I investigated the population ecology of foxes in central southern England, a region identified as having exceptionally high fox densities in some areas. The region also boasts important areas for conservation, including the New Forest National Park (NFNP), where foxes are culled by professional wildlife managers to conserve threatened populations of ground-nesting wading birds, such as the Eurasian curlew (*Numenius arquata*).

Compensatory immigration is the primary mechanism that happens in response to culling in population sinks, and occurs because culling in restricted-areas generally fails to account for the spatial scale of dispersal. Due to extensive gene flow, the areas contributing to compensatory immigration are expected to show no genetic differentiation to the population sink, together forming part of the same 'management unit'. The first objective of this study was to provide an initial investigation into the extent of the management unit relevant to the NFNP using a population genetic analysis. As foxes are highly mobile, genetic structure was not expected on mainland locations surrounding the NFNP, whereas differentiation was expected between these populations and an adjacent insular population on the Isle of Wight, given the relative isolation of the latter. A 653 base-pair fragment of mitochondrial DNA (mtDNA) was obtained from 53 foxes sampled throughout the study region and aligned to a database of published homologous sequences across Europe. These data were used to provide insight

into the geographic origins of foxes on the Isle of Wight and test for differences in haplotype frequencies using pairwise F_{ST}. The findings showed that foxes on the Isle of Wight are the only population consistently differentiated from discrete areas on the mainland, supporting previous findings that foxes exhibit a general lack of population genetic structure across large swaths of mainland areas, although large bodies of water such as The Solent can isolate individual populations.

Compensatory immigration undermines the effect of culling on fox populations, therefore the factors that could potentially exacerbate the rate of replacement into population sinks are important to understand from a management perspective. One example is anthropogenic subsidisation. Population sinks can function as 'ecological traps' due to dispersers being deceived by an attractive feature of sinks that belies the true reduction in fitness incurred by inhabiting them. For instance, anthropogenic subsidisation could increase the productivity and carrying capacity of the sink, promoting higher rates of immigration, despite the high mortality rate caused by culling. Accordingly, the second main objective was to examine the diet of foxes for evidence of anthropogenic subsidisation in the population sink (i.e., the NFNP). The occurrence of anthropogenic subsidisation here was postulated given the absence of secure wheelie bins in the waste disposal system, potentially providing foxes with easier access to human food waste. To identify the local food resources supporting foxes in the NFNP, a stomach content analysis of 447 culled foxes was conducted. Stomach contents were separated into broad categories and quantified using electronic weighing scales. Foxes exhibited a highly varied diet, including anthropogenic food, which comprised at least 14% of overall stomach volume. Access to this anthropogenic food was associated with human infrastructure. The volume of anthropogenic food consumed annually and the number of foxes this could support in isolation was estimated, using Monte Carlo simulations to handle uncertainty. The output of these simulations equated to a significant proportion of the annual number of foxes culled in the NFNP. The conclusion was that that improved waste management should be included as a more holistic conservation strategy.

The size of adjacent source populations contributes to the rate of compensatory immigration into population sinks. Access to food resources is a limiting factor for population growth among all organisms (i.e., bottom-up control) including mesopredators, especially in the absence of top, apex predators. Therefore, large-scale anthropogenic subsidisation of source populations could also exacerbate the rate of compensatory immigration by elevating regional average fox density. A potentially widespread and prevalent form of anthropogenic subsidisation of source populations is the release of free-roaming gamebirds that lack anti-predator behaviours having been reared in captivity. Nevertheless, there has been a paucity of studies examining fox diet on a management unit scale. Stable isotope analysis is one method that could be utilised, which quantifies the assimilated diet of consumers and overcomes some of the disadvantages of traditional macroscopic analyses. Using stable isotope analysis of 162 fox ear hair samples and potential food items, the diet of foxes throughout the study region was quantified using Bayesian Stable Isotope Mixing Models (BSIMMs). However, these BSIMMs did not produce precise estimates of fox diet owing to the large number of overlapping source categories, such that firm conclusions regarding anthropogenic subsidisation could not be made. The limitations of this method are highlighted and ideas for future work are suggested.

The impact of compensatory immigration means that the effectiveness of restricted-area fox control could be negated to a large extent, therefore such a programme needs to be rigorously evaluated and alternatives tested to support its implementation. Hitherto, a tool that can be readily used to examine how varying the intensity and timing of fox control by lamping has been missing. The final objective was to adapt and parameterise an agent-based model (ABM) to simulate several alternative management strategies that could be implemented in the NFNP or elsewhere where lamping is the principal mode of fox control. An existing, spatially explicit ABM – 'FoxNet' – was used to investigate how different management scenarios at local and regional scales might influence fox density within the NFNP, testing how the number of hours spent shooting foxes at night during the culling season, and the timing of the culling season, affected the resulting fox density during the breeding season for ground-nesting birds (March-July). To build on the existing model framework, a lamping procedure was written into the underlying code, with its efficiency determined by a modifiable log-normal distribution for the rate of successful search. These simulations showed that intensifying fox control effort above existing levels, or extending it back into the fox dispersal season, would not necessarily reduce spring fox density any further in the long-term. Instead, reducing regional habitat productivity would be useful.

Overall, these findings support that the prolific mobility of foxes undermines the long-term efficacy of restricted-area fox culling in the NFNP, potentially exacerbated by local anthropogenic subsidisation. The results are not in favour of more intense fox control in the NFNP, instead highlighting that a change of land management should be considered to contribute to more sustainable fox control and enhance species conservation. In striving for sustainability and ethical responsibility, the results of this thesis have direct implications for the management of foxes in the UK lowlands.

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I (NW) confirm that the research presented in thesis is my own. This thesis includes reformatted versions of research papers that have been published (Chapters two and three) or written for publication (chapters four and five) in collaboration with Emilie Hardouin (EH), Demetra Andreou (DA), Richard Stillman (RS), Tom Porteus (TP), Andrew Hoodless (AH), Mike Short (MS), Jodie Case (JC), Elli Rivers (ER), and Rona McGill (RM). Chapter two: NW, MS, DA, AH and EH conceived the ideas; NW and EH processed the samples; NW analysed the data; NW led the writing with assistance from NW, MS, DA, TP, RS, AH and EH. Chapter three: NW, TP, EH and MS conceived the ideas; JC and MS collected the samples; NW, JC and ER processed the samples; NW analysed the data; NW led the writing with assistance from TP, EH, DA, AN, RS and MS. Chapter four: NW, TP, EH, and MS conceived the ideas; NW and EH secured the funding; NW and MS collected the samples; NW and RM processed the samples; NW analysed the data; NW led the writing with assistance from TP, MS, DA and EH. Chapter five: NW conceived the ideas with input from TP, RS and EH; NW ran the simulations; NW analysed the data; NW led writing the manuscript with assistance from TP, RS, EH, RM, DA and MS.

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1. Introduction

1.1. Mesopredators

i. The age of mesopredators

The interests of humans are often in conflict with that of large ‘apex’ predators that typically require extensive home range sizes (Gittleman et al., 2001), leading to persecution through human-wildlife conflict and sometimes their extirpation (Woodroffe & Ginsberg, 1998). Predators with slower reproductive rates, inhabiting areas with higher human population densities generally suffer the highest risk of extinction (Cardillo et al., 2004). However, apex predators play a vital role in structuring and regulating their ecological communities, disproportionate to their overall abundance (Ripple et al., 2014). Therefore, the removal of large apex predators by humans across the world – so-called ‘trophic downgrading’ (Estes et al., 2011) – has propagating impacts known as ‘trophic cascades’, fundamentally restructuring ecological communities (Beschta & Ripple, 2009; Ripple & Beschta, 2006). In particular, the loss of apex predators is associated with the removal of top-down control and a corresponding increase in the abundance of subordinate ‘mesopredators’ (Newsome & Ripple, 2015; Ritchie & Johnson, 2009; Prugh et al., 2009) – a phenomenon known as ‘mesopredator release’ (Crooks & Soulé, 1999; Soulé et al., 1988). Although no absolute body size range defines them, mesopredators are characterised by their medium build, usually occupy mid-ranking trophic levels in the presence of apex predators, and are ‘generalists’ capable of exploiting a broad range of habitats and food sources (Prugh et al., 2009). Whilst being a phylogenetically diverse ‘guild’, some examples of mammalian mesopredators include raccoons (*Procyon lotor*), feral cats (*Felis catus*), and – the focus of this thesis – red foxes (*Vulpes vulpes*) (Prugh et al., 2009).

Access to food resources plays another fundamental role in determining the survival and abundance of vertebrates. Sinclair & Krebs (2003) stated that “population growth rate is determined in all vertebrate populations by food supplies, and we postulate bottom-up control as the universal primary standard". Consumers display a numerical response to changes in food supply, such that their population growth rate increases with the total abundance of prey until a positive asymptote is reached at carrying capacity, when other factors limit the population such as interspecific competition for space (Sinclair & Krebs, 2003). Population regulation determined by finite food resources is known as bottom-up control, from which mesopredators can be released by human activity. The types of food resources made available to predators by humans – collectively termed 'anthropogenic food subsidies' – are myriad and include food waste, livestock, free-roaming game animals or leftover carcasses, and crops (Plaza & Lambertucci, 2017; Newsome et al., 2015a; Oro et al., 2013). Mesopredators normally have a varied and flexible diet so are well-adapted to exploit these resources. Globally, the utilisation of anthropogenic food subsidies has been recorded in at least 36 terrestrial mammalian predator (> 1kg) species, coinciding with a documented increase in their abundance (Newsome et al., 2015a).

ii. Consequences of mesopredators outbreaks

One of the deleterious side-effects of releasing generalist mesopredators from top-down and bottom-up control is the decline of prey species triggered by an increase in the rate of predation (e.g., Letnic et al., 2009). In ordinary circumstances, consumers respond to diminishing prey abundance by switching to alternative, more abundant prey. However, 'hyperpredation' can occur when a predator continues to predate a prey species at low abundance due to persistent subsidisation from another less depletable resource that boost their population density, such as reliable anthropogenic food subsidies (Oro et al., 2013), potentially causing local extirpation (Taylor, 1979).

Given the typically generalist nature of a mesopredator's diet, multiple prey species are likely to be adversely affected (Ripple et al., 2013; Crooks & Soulé, 1999). The species identified as being most susceptible to limitation by mesopredators are characterised by slower paces of life; for instance, among birds those that brood single clutches, have longer pre-breeding life-history stages and have overall longer lifespans (Roos et al., 2018). Other factors that predispose species to limitation by predators more often than expected by chance include the specific nesting strategy (i.e., ground-nesting) and breeding in agricultural settings (McMahon et al., 2020; Roos et al., 2018).

In certain cases, prey species may be held at an equilibrium of low overall population size with predator abundance limiting their recovery (the ‘predator pit’) (Clark et al., 2021). A reduction in population size due to predation also increases vulnerability to factors such as inbreeding depression, demographic, and environmental stochasticity, potentially driving populations into a mutually-reinforcing, downward spiral to extinction (the ‘extinction vortex’) (Blomqvist et al., 2010; Fagan & Holmes, 2006; Gilpin & Soulé, 1986).

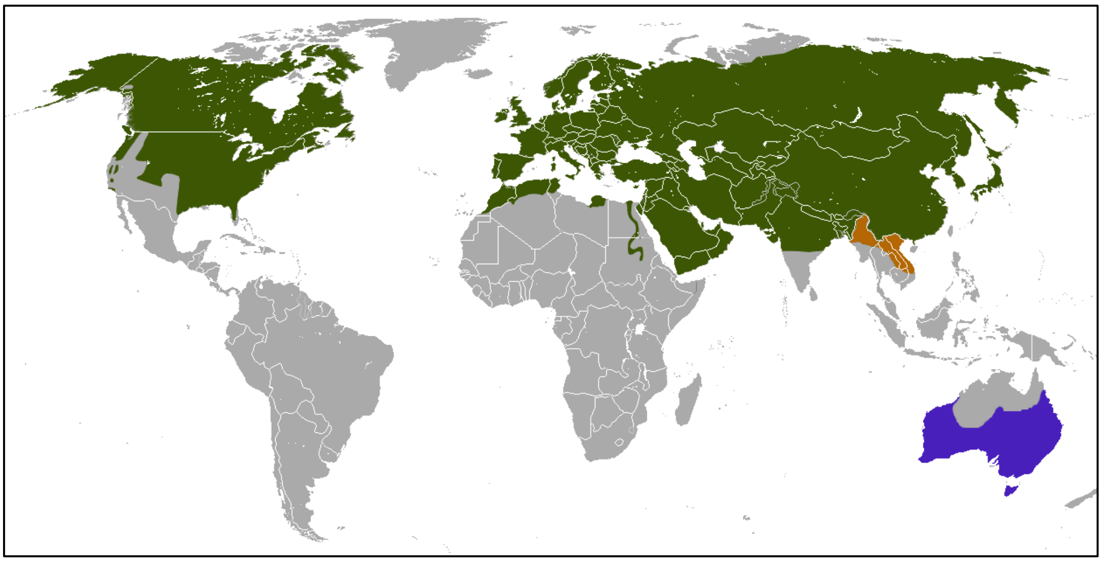
1.2. The red fox

i. Biogeography and habitat

The red fox (hereafter ‘fox’) is the most widespread of all carnivores (Schipper et al., 2008), with a geographic range covering Europe, most of North America, northern parts of Africa and much of Asia (Larivière & Pasitschniak-Arts, 1996) (Figure 1.1). It is also an established invasive species throughout Australia (except the northern tropical region) (Rolls, 1969). The success of the fox can be illustrated by its ability to withstand environments as distinct as tundra, semi-arid deserts, and both temperate and tropical forests (Macdonald & Reynolds, 2004). The fox’s medium-sized build (3-14kg; Nowak, 2005) is ideal for life in such a rich variety of habitats: whereas a smaller canid would lack sufficient mobility in less productive ecosystems, a larger canid would require a greater quantity of resources (territory, food etc.,) and be less tolerant to the presence of humans (Crees et al., 2019).

The species has proven adept at living alongside humans, with many established urban fox populations known in cities across the world (Hofer et al., 2000; Adkins & Scott, 1998; Harris, 1981; Saunders et al., 1993), facilitated by specific morphological (Parsons et al., 2020) and behavioural (Gil-Fernández et al., 2020) adaptations to these environments. In common with other generalist predators, they attain higher population densities and reduced home range sizes in urban areas than more natural habitats (Kobryn et al., 2023; Bateman & Fleming, 2012). As well as being an influential predator, its plasticity in the face of rapid anthropogenic transformations to the biosphere (Lewis & Maslin, 2018), which typically allow generalist human-commensals to thrive (Otto, 2018), make the fox an especially relevant species to study for anticipating changes to the structure of ecosystems in the future.

a)



b)

Figure. 1.1. a) extant native (green), introduced (blue), and vagrant (orange) geographic range of the red fox. b) The red fox in its natural habitat in the UK. Images obtained from Wikipedia (available under CC BY-SA 3.0).

Table 1.1. Profile of the red fox including selected physical characteristics, behavioural traits, and life history parameters. Ranges are minimum and maximum mean values from individual studies. Values for different geographic perspectives - the UK and across the geographic range of the fox - are given where known or applicable.

	UK	Reference	Range wide	Reference
Physical characteristics				
Adult body mass	Male: 6.5 kg; Female 5.5 kg	Corbet & Harris (1991)	3-14 kg	Nowak (2005)
Behavioural traits				
Home range size	0.14-2.7 km^2	Main et al. (2020)	0.14-45 km^2	Main et al. (2020)
Social group structure	-	-	Monogamous breeding pair, subordinate 'helpers', & cubs	Iossa et al. (2008)
Life history				
Maximum longevity	9 years	Kolb & Hewson (1980)	14 years	Maekawa et al. (1980)
Generation time	-	-	0.9 – 3.13 years	Devenish-Nelson et al. (2013)
Gestation length	-	-	52 – 53 days	Lloyd (1980)
Age at maturity	-	-	8 – 10 months	Lariviére & Pasitschniack-Arts (1996)
Sex ratio at birth	1:1	Heydon & Reynolds (2000b)	1.5:1 – 0.9:1	Devenish-Nelson et al. (2013)
Litter size (mean across all ages)	5.55	Heydon & Reynolds (2000b)	3.1 – 7.1	Devenish-Nelson et al. (2013)
Litters per year	-	-	1 per year	Lariviére & Pasitschniack-Arts (1996)

ii. Motivation for fox control

Despite benefiting from human activity to a large extent, the ecology of the fox lead many to consider the species as a pest (Macdonald & Reynolds, 2004). Although synanthropic foxes provide some benefits, such as the regulation of other pests (e.g., small rodents and ticks; Levi et al., 2012) and a connection to the natural world for urban-dwelling people otherwise deprived of such experiences (Moesch et al., 2024), they are also vectors of numerous infectious diseases and parasites such as *Sarcoptes scabiei* (a mite that causes scabies) (Corricondo-Sanchez et al., 2017), *Toxocara canis* (Saeed & Kapel, 2007), *Rabies lyssavirus* (Macdonald & Voigt, 1985) and *Echinococcus multilocularis* (a tapeworm that causes alveolar echinococcus) (Learmount et al., 2012), meaning that their occurrence in anthropogenic landscapes represents a potential hazard to the health of humans and their domestic pets (Plumer et al., 2014). As a major predator of livestock, game, and wildlife such as ground-nesting birds (Roos et al., 2018; Reynolds, 2000), it is also the target for control by farmers, estate gamekeepers, and wildlife conservationists across its range (Muller et al., 2015; Shwiff et al., 2011; McLeod, 2004; Heydon & Reynolds, 2000a).

iii. Foxes in the UK

Foxes native to the UK are believed to have derived from central Europe prior to end of the last glacial maximum, becoming isolated from their ancestral population following the formation of the English channel around 8,200 years before present (McDevitt et al., 2022; Statham et al., 2018; Edwards et al., 2012). Today, foxes are found in abundance throughout the UK, with an estimated population size of around 357,000 individuals (Mathews et al., 2018) and an increasing trend in urban areas (Sainsbury et al., 2019). While population densities vary according to landscape productivity (Webbon et al., 2004), a recent review suggested that population densities of the fox (as well as the carrion crow *Corvus corone*, another generalist predator) are greater on average in the UK than those elsewhere in Europe (Roos et al., 2018).

The underlying reasons for this probably include the extirpation of apex predators (e.g., Eurasian lynx *Lynx lynx*, and golden eagle *Aquila chrysaetos*) in past centuries resulting in mesopredator release (Pasanen-Mortensen & Elmhagen, 2015; Pasanen-Mortensen et al., 2013; Elmhagen et al., 2010; Ritchie & Johnson, 2009; Elmhagen & Rushton, 2007; Helldin et al., 2006), compounded by the opportunities presented by intensified and fragmented agricultural landscapes in the UK (Pasanen-Mortensen & Elmhagen, 2015; Kurki et al., 1998), the introduction and proliferation of prey species (e.g., European rabbits *Oryctolagus cuniculus* and gamebirds such as the pheasant *Phasianus colchicus* and red-legged partridge *Alectoris rufa*) (Pringle et al., 2019), and various other forms of anthropogenic subsidisation including access to human-derived waste (Waggershauser et al., 2022; Saunders et al., 1993).

Given the abundance of foxes and other generalist mesopredators in the UK, there are concerns about their impact on threatened prey species. Specifically, ground-nesting wader populations are a group acutely sensitive to the impact of predation (Roos et al., 2018; Macdonald & Bolton, 2008). Across Europe, they are significantly more likely to be declining than other species, with this pattern being especially pronounced in the UK, perhaps due to higher relative densities of mesopredators (McMahon et al., 2020). Indeed, the observed rate of population decline for ground-nesting birds in the UK over recent decades has been linked to a variety of factors (Harris et al., 2020), including the abundance of generalist mesopredators (Franks et al., 2017).

1.3. Fox control in the UK

i. Historical aspects of fox control in the UK

Predator control has a long history in the British Isles, with efforts to reduce fox numbers having taken place since at least the time of the Anglo-Saxons, largely for the benefit of animal husbandry (Reynolds & Tapper, 1996). Although the fox has persisted, unlike larger predators that were eradicated pre-1900, fox numbers in Britain were reportedly low by the late 18th and early 19th centuries, attributable to the popularity of fox hunting and widespread fox control to reduce predation on human food sources such as rabbits (Lloyd, 1980). Efforts to maintain fox numbers as sporting quarry for fox hunts included translocating them from the European continent (Carr, 1976), a trade that grew to considerable proportions such that certain markets in London (e.g., Leadenhall) are reported to have handled hundreds of foxes per year (Bovill, 1959). The historical legacy of these translocations has been revealed by the examination of microsatellite DNA sequences across Britain and north-east France, showing evidence of recent mixing between foxes in south-east England and Calais (Atterby et al., 2015).

The activity of fox control in Britain with the aim of reducing their numbers for the preservation of game originated in the 19th century on private game reserves (Reynolds & Tapper, 1996; Tapper, 1992). However, this practise was greatly reduced following WWII as fewer gamekeepers were employed for this purpose, probably accounting for a rapid increase in their abundance throughout the country during the latter half of the 20th century (Aebischer, 2019). Existing legal methods of fox control in England include: i) shooting with a firearm, often with a spotlight or other optical device such as a thermal imager at night ('lamping'), ii) killing live foxes captured with non-locking passive or mechanically propelled neck snares, and iii) killing live foxes captured in cages or pipe traps (Reynolds, 2000). The use of packs of dogs to hunt foxes was outlawed in Britain after the Hunting Act 2004 came into force (http://www.legislation.gov.uk), however it remains lawful to use up to two dogs to flush foxes from cover and shoot them with a firearm.

ii. Non-lethal approaches to predation management

Non-lethal forms of predation management for conservation, such as predator exclusion, predator diversion, and 'headstarting' (i.e., raising chicks to independence *ex situ* before releasing into the wild), have all been implemented in different situations with varying degrees of success, although none of these methods are completely effective (Laidlaw et al., 2021). One of the underlying causes of elevated fox densities in the UK is the absence of apex predators (Maroo & Yalden, 2000). In general, management by humans often fails to emulate the order and suite of influences maintained by apex predators (Lennox et al., 2022; Prugh et al., 2009), therefore the reintroduction of top predators to limit populations of mesopredators is a potential mechanism to restore degraded ecosystems (Ritchie et al., 2012), as demonstrated by the return of the grey wolf (*Canis lupus*) to Yellowstone National Park in the 1990s (Ripple & Beschta, 2012). However, despite the likely huge environmental and economic benefits (Spracklen et al., 2025), this remains a highly controversial topic in the UK, with major obstacles including the provision of sufficient habitat to support viable and ecologically functional populations of large predators, whilst reconciling the interests of conservation with that of the safety and livelihoods of people in rural and urban communities (Zanni et al., 2023; Wilson, 2004). A formal proposal to reintroduce the lynx to Kielder Forest, Northumberland, was rejected by the UK government in 2019 (Hawkins et al., 2020). Overall, the prospect of reintroducing apex predators to control populations of foxes in the UK appears to be out of reach for the foreseeable future.

1.4. Challenges to restricted-area fox control in the UK

i. Source-sink dynamics and compensatory immigration

Lethal control of species such as the fox does not occur without significant economic and ethical considerations, such as the high cost of wages for gamekeepers and other fox control practitioners (£19k-30k per annum; National Careers Service, 2024) or the risk of causing unacceptable animal suffering (e.g., by orphaning cubs; Laidlaw et al., 2021). This practice is hard to justify unless demonstrably effective in achieving the desired outcome (Lennox et al., 2018), yet the efficacy of fox culling in the way that it is commonly implemented is questionable.

The rural UK countryside is characterised by a mosaic of small to medium-sized landholdings, such as private estates, farms, and nature reserves, more than half of which do not engage in control practises (Defra, 2012). Instead, lethal fox control is usually confined to restricted areas leading to heterogeneous culling intensities throughout the landscape (Porteus, 2015), which is associated with the emergence of source-sink dynamics (Novaro et al., 2005; Reynolds et al., 1993). In this situation, there is an increase in the rate of dispersing individuals from surrounding unculled areas (the ‘sources’) immigrating into the culled area (the ‘sink’) to acquire vacant territories (Pulliam, 1988), so-called ‘compensatory immigration’, coinciding with a shift in the demographic structure of the source and sink populations (Oliver et al., 2016; Robinson et al., 2008).

With the outcome of compensatory immigration being a rebound in the culled population towards pre-culling abundance, often within a short timeframe (Lieury et al., 2015), it is contrary to the objectives of restricted-area control. Consequently, while seasonal suppression of fox density below carrying capacity can be achieved (Porteus et al., 2019a), alongside a corresponding increase in breeding densities of prey species (Reynolds et al., 2010; Tapper et al., 1996), the effects of local-scale culling are short-lived and can also prove unsuccessful in reducing overall predation rates (Kämmerle et al., 2019a; b). A more effective control strategy would overcome the impact of compensatory immigration by accounting for the spatial scale of replacement (Oliver et al., 2016), although without additional information it is likely unclear precisely what area this encapsulates.

ii. Impact of anthropogenic subsidisation

While the positive relationship between food availability and abundance can be tempered or decoupled by apex predators as they exert strong top-down control on mesopredator populations (Feit et al., 2019; Pasanen-Mortensen et al., 2017), this is not relevant to the UK given the absence of apex predators. Although data is lacking for mammalian predators, Pringle et al. (2019) showed broad landscape-scale correlations between the abundance of gamebirds and several generalist avian predator species in the UK. Given that the surrounding population density is important in determining the rate of replacement into population sinks (Porteus et al., 2018a; Lieury et al., 2015; Turgeon & Kramer, 2012), artificially increasing the size of source populations of foxes could amplify the rate of compensatory immigration.

Anthropogenic subsidisation within sinks themselves could also enhance immigration rates. The term ‘ecological trap’ is used to describe a habitat that is disproportionately attractive compared to its value for fitness (Robertson et al., 2013). For example, the increase in prey abundance following the release of gamebirds might increase the rate of fox immigration onto gamebird estates. Indeed, Porteus (2015) showed positive correlations between fox immigration rate and the density of gamebird releases on a small sample of shooting estates. Foxes experience higher mortality on these estates due to culling, which is a form of habitat degradation that foxes cannot perceive (Delibes et al., 2001).

Accordingly, anthropogenic food subsidisation within source and sink areas has the potential to exacerbate the challenge of conducting effective restricted-area fox control in the face of rapid replacement through compensatory immigration. Using diet information to assess the degree of anthropogenic subsidisation in both source and sink populations can therefore reveal conflicts between human activity and management objectives (Kirby et al., 2017).

iii. Testing alternative control strategies

The action of lethally controlling predators to reduce predation on prey species is controversial, so evaluating the success of a culling program is crucial for its justification (Lennox et al., 2018). Experimental approaches have previously been used, for example, to examine the impact of removing predators on the breeding success of prey species (Baines et al., 2023; Fletcher et al., 2010; Bolton et al., 2007; Tapper et al., 1996). However, these studies are often costly, time consuming, and their findings cannot necessarily be applied to different situations. Sampling a limited range of certain variables curtails insight regarding the factors that contribute to the success or failure of a respective program. Such limitations compromise their ability to inform adaptive fox management at any given location.

Given its relation to the risk of predation for prey species (Fletcher et al., 2010; Tapper et al., 1996), the change in local fox density in response to culling is one aspect of a culling program that is important to monitor and, given the effect of compensatory immigration, this is not trivial. Traditional field-based techniques such as capture-mark-recapture to estimate population density are not suitable for the dynamic nature of culling systems, whereby marked individuals might be culled before generating useful data, nor do they take advantage of potentially informative culling data. Porteus et al. (2019a) developed a Bayesian state-space population dynamics model that uses culling data to reconstruct within-year (weekly, biweekly etc.) fox population density on a given estate. The ability to fit site-specific parameters rather than relying on parameter estimates from external sources (e.g., published literature) is arguably the primary advantage of these models over previous modelling of culled populations (Lieury et al., 2015; McLeod & Saunders, 2014; Harding et al., 2001). However, at least three years of culling data is required to produce robust density outputs, and alternative fox culling programs cannot be evaluated readily using these models in a manner that is spatially explicit (Porteus, 2015). Developing novel tools that can be used to predict how the fox density might respond to alternative strategies would be a valuable asset to wildlife managers aiming to maximise their efficiency.

1.5. Potential methods to study managed fox populations

i. Using population genetics to identify ‘management units’

As highlighted above, source-sink dynamics leading to compensatory immigration is the primary challenge confronted by restricted-area fox control (Porteus et al., 2019a). The scale of the surrounding source area contributing to immigration into the sink is governed by the extent of the ‘management unit’, defined as a “demographically independent population whose population dynamics (e.g., population growth rates) are determined by local birth and death rates” (Palsbøll et al., 2007). Given its dependency on the scale of dispersal, the proportion of the management unit where fox control is implemented will determine the extent of a core area within which immigration is successfully minimised. In other words, the outer edges of the managed area effectively serve as an immigration buffer to the core area (Francis et al., 2020). Hence, delineating the overall management unit is necessary to determine the relevant geographic area where population control would help to pre-empt compensatory immigration.

Population genetic data can be used to identify putative management units (Palsbøll et al., 2007), because the pattern of dispersal across landscapes dictates the amount of gene flow between individuals (Hamilton, 2021). Unrestricted gene flow is expected to result in one continuous randomly mating population that exhibits little or no population genetic structure (‘panmixia’) (Hamilton, 2021). Alternatively, population genetic structure can arise when gene flow is restricted due to physical geographic barriers causing dispersal to become spatially limited, leading to genetic differentiation between populations over time through random changes in allele frequencies (‘genetic drift’) (Hamilton, 2021). In the latter scenario, genetic distance is also expected to be correlated with geographic distance, whereas in the former, factors dictating gene flow other than distance cause this correlation to breakdown (Wright, 1946).

An assessment of population structure can be achieved by analysing highly variable (polymorphic) fragments of mitochondrial DNA (mtDNA; e.g., D-loop or cytochrome b) or short tandem repeats within nuclear DNA ('microsatellites'). Targeted amplification and sequencing of these polymorphic loci facilitates insights into population structure based on the amount of allelic differentiation between clusters of individuals across space (Hamilton, 2021). Foxes have relatively short generation times (Devenish-Nelson et al., 2013) and high dispersal capabilities (Gosselink et al., 2010), with movements of up to 1000 km over a matter of days to months being recorded in some parts of their range (Walton et al., 2018), highlighting the potential for fox management units to cover wide areas. Indeed, previous applications of mtDNA fragments or microsatellites among fox populations have generally found a tendency for limited population structure across large swathes of mainland areas (Atterby et al., 2015; Galov et al., 2014; Mullins et al., 2014; Kirschning et al., 2007), implying that foxes can disperse relatively unimpeded by potential barriers. In cases where differentiation has been detected, it is typically between insular populations (Langille et al., 2014) or those connected by narrow land bridges (i.e., peninsulas; Amaike et al., 2018), which do seem to restrict the movement of this terrestrial carnivore. However, whilst the targeted amplicon sequencing of highly polymorphic regions can provide insights into the population structure of the organism in question, the relatively short sequences involved can result in a low number of polymorphic sites, potentially thwarting the ability to detect genetic differentiation between distinct populations on a regional scale (Kirschning et al., 2007). To enhance the power and flexibility of analyses, techniques covering a much greater proportion of the genome are required.

Whole genome sequencing is becoming increasingly affordable (Snyder et al., 2010), although this is not commonly deployed by population ecologists (Peterson et al., 2012). Assembling whole genomes for the typically large numbers of individuals included in population ecological studies would normally be unattainable owing to limits to computing power, especially for eukaryotes with genome sizes over 10^9 base pairs in length. The use of polymorphic loci distributed throughout the genome ('Single Nucleotide Polymorphisms'; SNPs) is an effective means of overcoming these issues. To this end, a set of approaches known as 'reduced representation genome sequencing' can be implemented, whereby a representative portion of the whole genome is sequenced, permitting high-coverage genotyping of many individuals at thousands of markers in a cost-effective manner. One such method, known as restriction-site associated DNA sequencing (RAD-seq), utilises restriction enzymes to shear genomic nuclear DNA at enzyme-specific recognition sites (restriction sites), producing fragments interspersed throughout the genome (Davey & Blaxter, 2010). In the original RAD-seq protocol (Baird et al., 2008), preparing libraries for sequencing involved ligating adapters with ends complementary to the restriction site. These adapters also contained an amplification primer and a unique barcode to allow for multiplexing of many samples. The hybrid DNA was then randomly sheared using a sonicator, with the resulting fragments size-selected in accordance with the read length of the sequencer. A Y-shaped adapter containing the reverse primer sequence were subsequently ligated to the sheared end of the DNA fragments, with only fragments containing both adaptors being amplified.

A drawback of the original RAD-seq protocol was its reliance on sonication to fragment the DNA, which is an entirely random process, resulting in fragment lengths varying greatly in size. The sonication also fragmented DNA with varying degrees of efficacy, compounding the risk of losing informative loci during the size-selection stage. The ddRAD-seq protocol negates the need to use a sonicator by using two restriction enzymes to digest the template DNA simultaneously, giving homologous fragments between samples derived from the same taxon (Peterson et al., 2012). The enzyme combination typically includes a rare and a common cutter, with alternative combinations of enzymes producing a different number of fragments of the desired length, thereby affording practitioners greater control in terms of genomic representation than the original RAD-seq protocol.

The introduction of ddRAD-seq was an important step forward, although there were still some limitations. The need to enrich libraries using PCR inevitably leads to ‘PCR duplicates’ – identical sequences of DNA cloned from the same sample. These are problematic as they can lead to inflated estimates of homozygosity (Pompanon et al., 2005). In the original protocol that used only one restriction enzyme, PCR duplicates could be more readily identified due to the random shearing process creating fragments of different size. However, in ddRAD-seq, fragments containing the same loci are of the same length, given the predictability of the double digest, compromising the ability to identify PCR duplicates without further modification. The incorporation of a short (four base) degenerate sequence within the adaptors is one way to identify PCR duplicates and was adopted by Franchini et al. (2017), who introduced the quaddRAD-seq protocol. This protocol is also distinguished by the use of four barcode sequences (hence ‘quadd’), increasing the multiplexing capacity up to 192 samples up from 92 in ddRAD-seq.

ii. Measuring consumer diets to quantify anthropogenic subsidisation

The issue of compensatory immigration is potentially compounded by the effects of anthropogenic subsidisation, but an examination of diet is required to assess the extent of the issue. Among the numerous ways of studying the diet of consumers, ‘macroscopic’ analyses refer to methods in which food items in the stomachs of deceased individuals or their faeces (scats) are quantified according to their abundance (Reynolds & Aebischer, 1991). This strategy has been widely employed and is considered a conventional approach to the study of consumer diets (Castañeda et al., 2022). However, macroscopic analyses are burdened by certain shortcomings. Aside from being relatively labour intensive, time consuming, and hampered by observer error, the contents of stomachs or scats represents a snapshot in time, which does not necessarily correspond to the consumers long-term dietary habits. There also seems to be an inherent bias towards detecting foods consisting of indigestible material, such as keratinaceous tissue and bones (Reid & Koch, 2017; Meckstroth et al., 2007; Stapp 2002), with this limitation being especially apparent for analyses of scat (Balestrieri et al., 2011). In general, foxes will consume more indigestible material from smaller prey items (Ferraras & Fernandez-de-Simon, 2019). In a meta-analysis of fox diet across Australia, the frequency of occurrence of large mammals was greater in studies that analysed stomach contents compared to those that analysed scat contents (Fleming et al., 2021), whilst the opposite was found for small and medium-sized mammals. These results were supported by the findings of a global scale meta-analysis of fox diet (Castañeda et al., 2022). Peterson et al. (2021) found no evidence of anthropogenic food in fox scat sampled in the suburbs of New York, USA. However, processed anthropogenic food generally lacks indigestible components, making it impossible to conclude an absence of anthropogenic food in their diet.

Stable isotopes offer a powerful alternative to traditional methods in the study of diet, with their utility being grounded in the fact that, with some degree of fractionation, the stable isotope composition of a consumer's tissues corresponds to its diet during the period of tissue synthesis ("*you are what you eat*") (DeNiro & Epstein, 1981, 1978). The temporal coverage for which this method provides dietary information will depend on the isotopic turnover rate of the tissue being used, as this determines the time taken for the tissue-specific stable isotope composition to equilibrate to the present diet (Ben-David & Flaherty, 2012). For example, red blood cells have a relatively rapid turnover rate and therefore their stable isotope composition would show the average diet over approximately the past two weeks (Carter et al., 2019), whereas that of bone collagen would indicate the average dietary habits over the course of an individual's life (Carbonell Ellgutter et al., 2020). As such, unlike macroscopic or DNA-based metabarcoding analyses, stable isotope analysis can provide an insight into the long-term use of broad food categories by consumers (Ben-David & Flaherty, 2012).

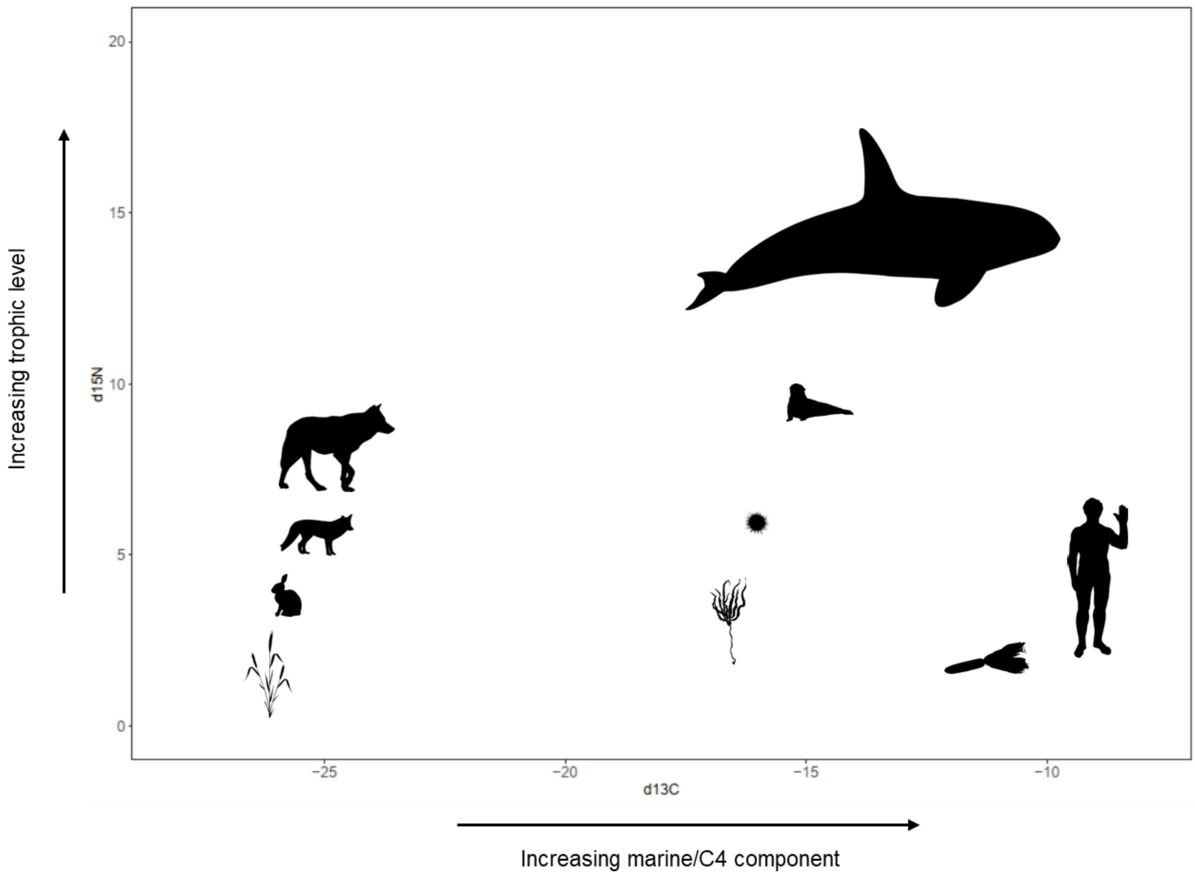


Figure 1.2. A simplified stable isotope biplot depicting stable isotope values for marine and terrestrial ecosystems, adapted from Schulting (1998). Trophic enrichment of δ^{13}C and δ^{15}N occurs from primary producers to herbivores, to meso- and apex predators, as well as from terrestrial to marine ecosystems. Enrichment in δ^{13}C also occurs from ecosystems based on C3 plants (e.g., wheat) to ecosystems based on C4 plants (e.g., maize) (Ben-David & Flaherty, 2012). Humans with diets based on C4 plants (e.g., North Americans) have enriched δ^{13}C (Valenzuela et al., 2012). Organism silhouettes were obtained from PhyloPic (available under CCO 1.0 Universal).

Using the ratio of heavy to light stable isotopes of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N) in the tissues of a consumer and their potential prey sources relative to international standards (expressed as δ^{13}C and δ^{15}N) (Ben-David & Flaherty, 2012), Bayesian stable isotope mixing models (BSIMMs) quantify the proportion of each source in a consumer's diet (Phillips et al., 2014). BSIMMs are commonly used to quantify the importance of various food categories in the assimilated diet of a consumer (Phillips et al., 2014). BSIMMs provide posterior distributions of diet composition by allowing for the inclusion of ‘informative priors’ to facilitate model fit and improve performance, thereby incorporating uncertainty in model parameters (Parnell et al., 2013; Moore & Semmens, 2008). These priors can be particularly useful where BSIMMs are limited by their inability to discriminate between food items with similar isotopic signatures (Lerner et al., 2018). Such priors may be derived from complementary studies of prey abundance in the field or in the stomachs or scats of the consumer in question. However, as discussed, traditional macroscopic methods are typically hampered by their bias towards certain food items. Consequently, there is a risk that such biases are propagated to BSIMMs when used as the basis for informative priors, leading to erroneous conclusions (Swan et al., 2020a).

An additional complication with respect to BSIMMs is that the stable isotope ratios are altered by metabolic processes during the assimilation of food into the tissues of consumers, a process known as ‘trophic discrimination’. To account for this nuance, trophic enrichment factors (TEFs) – the increase in values of $\delta^{13}C$ and $\delta^{15}N$ due to the heavier isotope being preferentially assimilated – need to be applied to raw stable isotope measurements (Phillips et al., 2014). TDFs are commonly sought from pre-existing feeding-experiments or phylogenetically similar species (Caut et al., 2009). Nevertheless, TEFs are known to vary between ecologically similar species (Kelly et al., 2012), and within a given organism according to a number of factors, including tissue type (Roth & Hobson, 2000). Therefore, it is necessary to incorporate uncertainty in TEFs when formulating a BSIMM (Phillips et al., 2014).

Despite its advantages, stable isotope analysis is not entirely devoid of limitations. In general, it can be used to inform about the broad resource types utilised by a consumer, but it does not normally indicate the precise food items that are consumed. As such, macroscopic methods could serve as a useful complement to stable isotope analyses when used simultaneously, providing a more complete inquiry of a consumer's diet. In fact, *a priori* knowledge of the important food items resourcing a consumer in an area is a necessary precondition for selecting which source categories to include within a BSIMM, as avoiding the inclusion of uncommon food items improves model accuracy (Phillips & Gregg, 2003). In certain situations, a high taxonomic resolution of identified prey items is desired, requiring researchers to implement more advanced approaches such as DNA metabarcoding, which have also been shown to identify more species than conventional surveying techniques (Siegenthaler et al., 2018; Berry et al., 2017). Indeed, the faecal matter of generalist predators, including the fox, has been demonstrated to act as 'biodiversity capsules' with potential utility in improving biodiversity assessments (Nørgaard et al., 2021).

A possible application of stable isotope analysis is to assess the importance of anthropogenic food in the diets of consumers more accurately, due to differences in the stable isotope composition of anthropogenic food compared to natural foods (Murray et al., 2015; Newsome et al., 2015b; Bentzen et al., 2014; Savory et al., 2014; Mizumkami et al., 2005). For instance, in North America livestock reared for human consumption are normally fed a diet rich in corn, a C4 plant characterised by enriched quantities of ^{13}C compared to C3 plants (Figure 1.2). Moreover, many anthropogenic foods are derived from low trophic levels, containing lower levels of ^{15}N (Gannes et al., 1998) as the lighter isotope is more readily excreted by consumers (DeNiro & Epstein, 1981). Newsome et al. (2010) demonstrated higher ^{13}C values and lower ^{15}N values in the hairs of urban San Joaquin kit foxes (*Vulpes macrotis mutica*) compared to those from rural areas, with an isotopic composition of the former closely matched to the hairs of humans residing in the same urban area, leading to the conclusion that urban kit foxes were primarily being resourced by anthropogenic food. However, analogous studies carried out in western Europe may be complicated by the fact that far less corn is used in the food production industry compared to North America, as reflected by the divergent ^{13}C values in scalp hair between North American and European individuals (Valenzuela et al., 2012). Indeed, isotopic analysis of fox diet has seldom been conducted in the UK, therefore it is unclear whether it can be usefully applied here to distinguish between natural food sources and those provisioned by humans.

iii. Using agent-based models to ask ‘what if…?’

In the past, the scientific models used to solve real-world problems such as differential calculus have been restricted in terms of complexity – they must be simple enough to solve mathematically (Railsback & Grimm, 2019). However, the advent of computer simulations has enabled researchers to formulate more sophisticated models that better represent the components of a given system. Agent-based models (ABMs) are used to investigate how bottom-up processes, such as individual behaviours and interactions, result in emergent properties of a system, such as population dynamics (Railsback & Grimm, 2019). ABMs have particular applicability to ecology, where complex agent-based systems abound. In a pattern-oriented modelling approach, multiple patterns observed in real systems can be used to inform model structure and pit alternative theories against each other (Grimm et al., 2005). Validating *in silico* predictions against those observed in real life increase a model’s credibility and serve to justify using it to address other questions.

Along with their tantalising ability to model extremely complicated systems, beyond the reach of traditional methods, this ability does not come without cost as implementing agent-based models requires us to acquire advanced software skills and an understanding of novel concepts. Therefore, in formulating ABMs, an intermediate level of complexity is generally sought – the so-called ‘Medawar zone’ – the minimum level of complexity that can reconstruct multiple observed patterns (Grimm et al., 2005).

Hradsky et al. (2019) recently introduced a customisable ABM framework, known as ‘FoxNet’, providing a unique opportunity to model population dynamics of foxes in distinct areas across the world. Preexisting fox ABMs provided insightful perspectives on alternative management approaches, such as the relative merits of fertility control versus direct culling (Rushton et al., 2006), yet they were often also developed for generic spatial landscapes without the option to apply them to specific locations. In contrast, a custom landscape raster can be readily loaded into the FoxNet framework via a GIS extension, allowing users to apply the model seamlessly to their own region of interest. The authors ‘evaludated’ the model’s ability to reconstruct multiple patterns observed within fox populations in different parts of the world, including population structure and density, justifying its use as a tool to show the effect of alternative strategies for culling programs across the state of Victoria, Australia (Francis et al., 2020).

Hitherto, FoxNet has not been used in a UK-based fox culling system, where lamping is the primary method of control (Porteus, 2015), rather than the use of poison baits. The underlying FoxNet code could be adapted for this purpose, but for this to be achieved, additional parameters would need to be accounted for. For instance, a plausible distribution is needed for the rate of successful search (km^2 hr^{-1}), a coefficient (scaling factor) that scales the relationship between the density of foxes (foxes km^{-2}) within the search area with the duration of a lamping outing (hr), to give the total number of foxes seen during the outing (Porteus et al., 2019b), as well as a measure of the average kill success – the proportion of foxes successfully culled among those that were seen.

1.6. The study region – central southern England

The focus of this thesis is on the region of central southern England, encompassing parts of four English counties: Dorset, Hampshire, Wiltshire, and the Isle of Wight (Figure 1.3). The region is characterised by a diverse patchwork of rural land uses, including agricultural farmland, managed woodland, and heathland and natural grassland managed for conservation purposes. This region also includes large towns and cities from Dorchester in the west, Southampton in the east, Salisbury in the north, and Bournemouth, Christchurch, and Poole in the south (Figure 1.2b).

The New Forest National Park (NFNP), Hampshire, is a focal point in the region for conservation. Several species of red-listed ground-nesting birds breed in this area, including Northern lapwing (*Vanellus vanellus*), common redshank (*Tringa totanus*), Eurasian oystercatcher (*Haematopus ostralegus*), and Eurasian curlew (*Numenius arquata*), the latter being the UKs highest conservation priority bird species (Brown et al., 2015). The local curlew population is of particular national importance with the NFNP being one of the final strongholds in the south of England (Rivers et al., 2025). The loss of the population would represent a significant range contraction. However, the population is showing a declining trend (ca. 40-45 breeding pairs) and poor breeding success due to a high rate of nest predation, especially by foxes, remains an existential threat. The importance of fox predation as a contributor of poor breeding productivity is evidenced by trail camera monitoring of 429 wader nests between 2021 and 2024, showing 151 predation events of which 54% were attributed to foxes, although this is likely an underestimate as there were a further 29 predation events where the predator responsible was unknown (GWCT, unpubl. data). Efforts to save these breeding wader populations from extirpation primarily involves the lethal control of foxes by local wildlife managers. Currently this is their only viable option, as alternative methods of nest protection, such as the use of electrified fencing around nests, are not permitted.

Recent studies have indicated that fox densities are locally high in parts of central southern England adjacent to the NFNP. Porteus et al. (2024) demonstrated the highest densities of foxes ever recorded outside of urban areas on a rural landholding in Britford on the edge of the NFNP (> 10 fox km^{-2}). Also, foxes can occur at high densities in urban areas (Bateman & Fleming, 2012), and the NFNP is flanked on either side by two large urban centres, Bournemouth and Southampton; the available data suggests high fox densities in Bournemouth in particular (Scott et al., 2018). These areas could therefore be acting as potent source populations of foxes for the NFNP. Interestingly, state-space models of fox population dynamics on 22 small private estates across the country revealed that an estate bordering the NFNP (near Christchurch) had the highest rate of fox immigration (29 fox km^{-2} yr^{-1}), and consequently, achieved only relatively minor suppression below carrying capacity despite prodigious effort to control foxes (Porteus et al., 2019a). The impact of fox predation on breeding wader productivity, combined with the evidence of locally high fox population densities, make the study region a particularly interesting place to study fox population ecology from a management perspective.

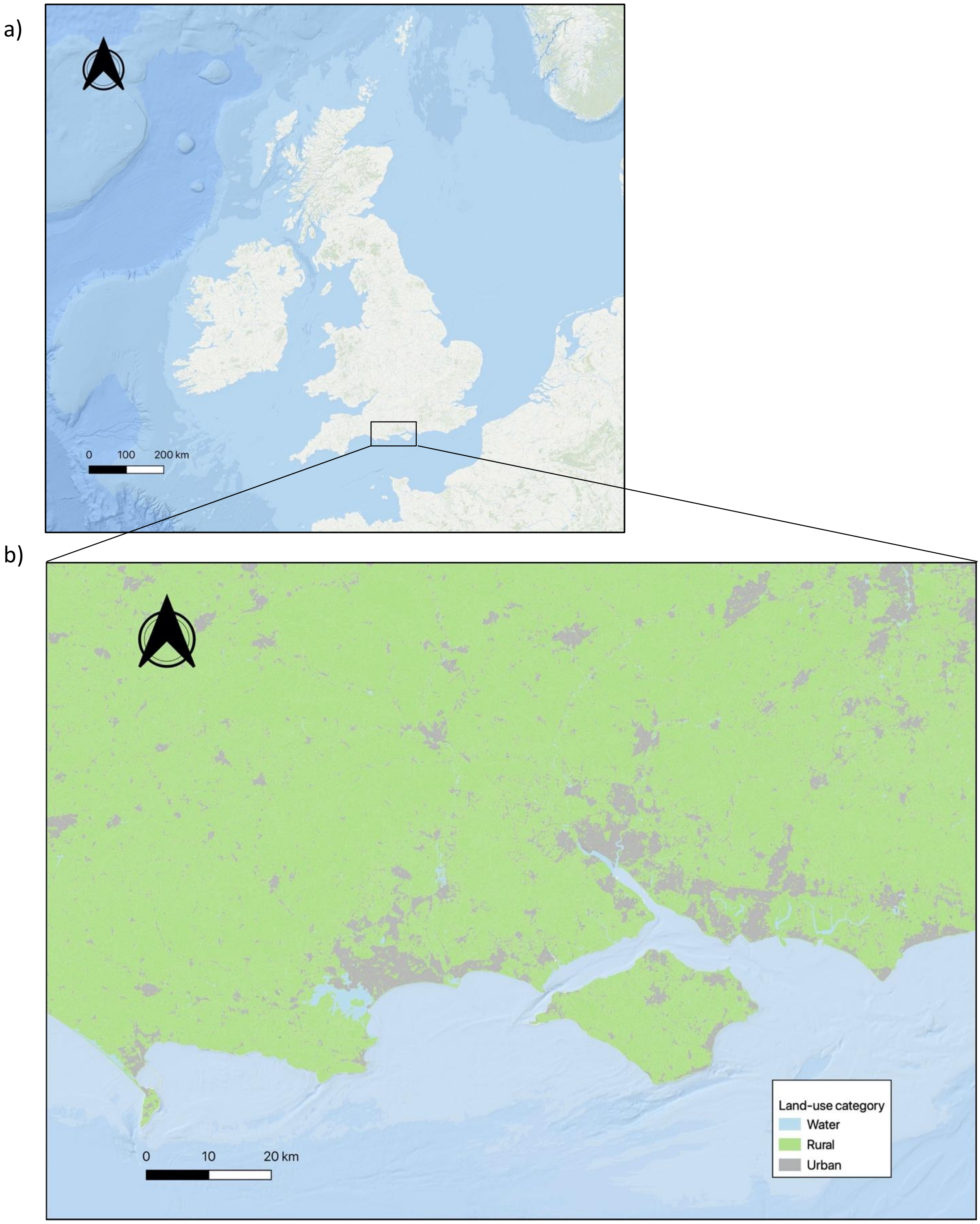


Figure 1.3. a) Position of the study region in the British Isles. b) Distribution of broad habitat in the study region, including water, rural (woodland, grassland, and heathland etc.) and urban (built-up areas). Data from the 2007 UKCEH landcover map (Bunce et al., 2007).

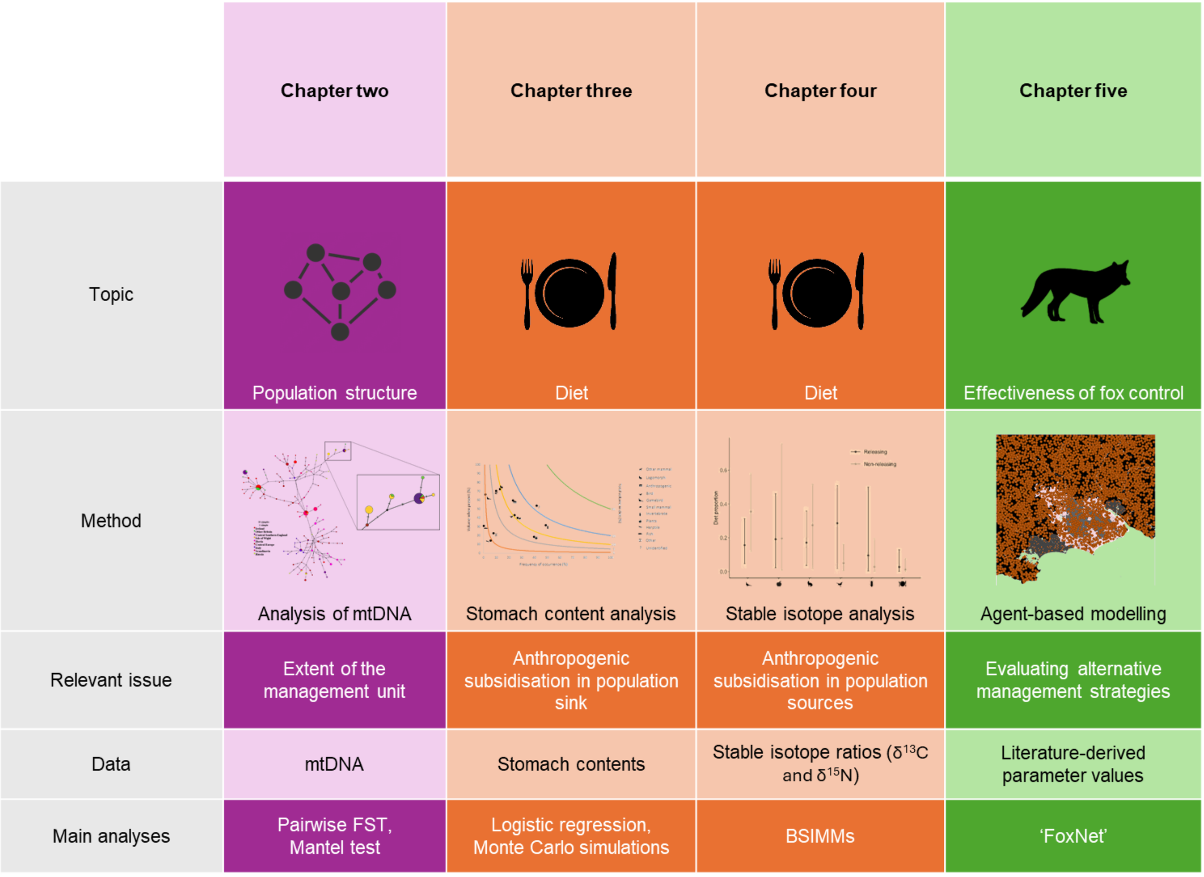
1.7. Thesis aims and structure

The objective of this thesis is to explore the ecological factors that challenge restricted-area fox control in the NFNP, and develop a tool to facilitate adaptive fox management in the NFNP as well as elsewhere in the UK where restricted-area fox control takes place. This thesis will aim to achieve these objectives using an array of methods frequently used in population ecology. Specifically, the main goals are to 1) investigate the extent of the management unit relevant to the NFNP using a population genetic analysis, 2) examine the diet of foxes for evidence of anthropogenic subsidisation in the population sink (i.e., the NFNP) and the probable source areas (i.e., surrounding region), and 3) adapt and parameterise an agent-based model to simulate several alternative management strategies that could be implemented in the NFNP or elsewhere where lamping is the principal mode of fox control. Although the fox garners specific interest in this region of the UK as the dominant predator of ground-nesting bird nests, the issues highlighted above (source-sink dynamics, anthropogenic subsidisation) can apply to mesopredators in general. Therefore, the knowledge acquired from studying foxes in this region and the implications for their control could be applied to other parts of the world where mesopredator species are problematic.

This thesis comprises four analytical chapters and one concluding chapter:

- Chapter two analyses the population genetic structure of foxes sampled throughout central southern England using hypervariable fragments (D-loop & cytochrome-b) of mtDNA.
- Chapter three quantifies the diet of foxes sampled within the NFNP using stomach content analysis.
- Chapter four evaluates the use of stable isotope analysis to identify the broad food sources that support fox population growth across the region.

- Drawing on some of the findings from previous chapters, chapter five adapts FoxNet to assess how management decisions at the local scale could affect fox population density during the ground-nesting bird breeding season.
- Chapter six brings the findings of the preceding chapters together in a summary.



	Chapter two	**Chapter three**	**Chapter four**	**Chapter five**
Topic	Population structure	Diet	Diet	Effectiveness of fox control
Method	Analysis of mtDNA	Stomach content analysis	Stable isotope analysis	Agent-based modelling
Relevant issue	Extent of the management unit	Anthropogenic subsidisation in population sink	Anthropogenic subsidisation in population sources	Evaluating alternative management strategies
Data	mtDNA	Stomach contents	Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$)	Literature-derived parameter values
Main analyses	Pairwise FST, Mantel test	Logistic regression, Monte Carlo simulations	BSIMMs	'FoxNet'

Figure 1.4. An overview of the issues, methods, data types and analyses utilised in this thesis, chapter-by-chapter.

Animal welfare is a primary concern when carrying out research and their humane use is guided by 'the three Rs': i. the use of animals should be avoided altogether where possible (replace), ii. the number of animals used should be kept to a minimum (reduce), iii. the amount of suffering experienced by animals should be minimised (refine). While studying the population genetics and diet of consumers (chapter two-four) necessitated the use of animal samples, the computer simulations used in the final data chapter (chapter five) avoided the use of animal samples altogether. To reduce the number of individual samples used across all studies, DNA was extracted for genetic sequencing from samples that were also used to obtain ear hair for use in stable isotope analysis, where possible. No live animals were used for this research, but it was important to consider how samples were obtained from the field. Samples were obtained opportunistically from carcasses found dead for unknown reasons (e.g., RTAs, intraspecific aggression, disease etc.) or from professional fox controllers and wildlife managers who ran a fully justified culling program using legal, humane methods. For instance, fox culling in the NFNP is commissioned by Forestry England and is only conducted during the wader breeding season for conservation. No samples were taken solely for the purpose of this research.

This is an accepted version of the published manuscript available at: Williams, NF., Short, MJ., Andreou, D., Porteus, TA., Stillman, RA., Hoodless, AN. & Hardouin, EA. (2024). Ancestry and genetic differentiation of red foxes (Vulpes vulpes) on the Isle of Wight. *Mammal Communications*, 10, 8-14. http://dx.doi.org/10.59922/AJXF9454

2. Ancestry and genetic differentiation of red foxes (*Vulpes vulpes*) on the Isle of Wight.

2.1. Abstract

Foxes were presumed absent from the Isle of Wight, UK, until their introduction for sport hunting in the 19th century. The ancestry of red foxes on the Isle of Wight, UK, was investigated by generating a dataset of 53 concatenated D-loop and cytochrome-b mitochondrial DNA sequences which was then compared to a previously published database of European sequences. Genetic differentiation between the Isle of Wight and other populations throughout Europe was also tested. There was evidence that red foxes on the Isle of Wight likely originated from mainland Britain, but that the Isle of Wight population is genetically differentiated from adjacent populations in mainland central southern England. At >1 km across, The Solent serves as a natural barrier to gene flow between the mainland and the Isle of Wight.

2.2. Introduction

Although widespread across Great Britain, red foxes (*Vulpes vulpes*) are absent from many islands surrounding the mainland (Reynolds & Short 2003; Harris & Lloyd 1991). However, there are several islands where they have been introduced by humans, including the Isle of Wight. According to the hunting-with-hounds literature, foxes of unknown origin were introduced to the Isle of Wight during the mid-1800s for sport hunting (The Leverets 2012), where they are now common. Although there are no records of the transactions, foxes introduced to the Isle of Wight may have come from mainland Britain as well as imports from continental Europe (Carr 1976; Introduction section 1.3).

Regional fox populations typically exhibit low levels of genetic structure across mainland areas, with physical barriers such as rivers and small mountain ranges having relatively little or no isolating effects (Atterby et al., 2015; Galov et al., 2014), a testament to the species' ability to occupy a range of habitats and disperse over large distances (Walton et al., 2018). However, there is a consistent effect of peninsularity and insularity in creating genetically differentiated fox populations (Amaike et al., 2018; Galov et al., 2014), indicating a limited ability for this species to traverse narrow land bridges and large bodies of water. Having been present on the island for nearly two centuries and separated from mainland Britain by 1.2 km of open water, the Isle of Wight provides an interesting case study for investigating the long-term effect of insularity in promoting genetically differentiated fox populations. This question could be addressed using hypervariable fragments of mtDNA, comparing the allele frequency between populations on the mainland and the Isle of Wight (Introduction section 1.5).

In this study, two aspects of the foxes on the Isle of Wight were investigated, i) the geographic origins of foxes inhabiting the Isle of Wight, and ii) whether they are genetically differentiated from foxes at nearby locations on the mainland in central southern England. To achieve this, two fragments of the mitochondrial genome were used, the D-loop and cytochrome-b (Cytb) gene. Given its geographic position haplotypes sampled on the Isle of Wight were expected to be shared with mainland Britain, although perhaps not exclusively given historical translocation of foxes from central Europe to Britain. Its isolation might also facilitate the emergence of haplotypes unique to the island. This factor is also expected to lead to the differentiation of allele frequencies between the population on the Isle of Wight and those in on the mainland.

2.3. Methods

Ear tissue samples were collected opportunistically from 57 wild foxes culled from 2018-2021 on the Isle of Wight and across six locations in central southern England (section 1.6; Figure 2.1) by professional wildlife managers during their routine fox control activities to protect ground-nesting bird populations (i.e., not culled specifically for use in this study). Samples were stored in individually labelled plastic wallets in a -20°C laboratory freezer. Mitochondrial DNA (mtDNA) was extracted using the QIAGEN DNeasy® Tissue Kit. A 305 base pair (bp) fragment of the D-loop was amplified using primers and protocol from Aubry et al. (2009). A 348 bp fragment of the Cytb gene was amplified using the primers and protocol from Perrine et al. (2007). Samples were sequenced in both directions using Sanger sequencing technology. Reactions were outsourced to GENEWIZ®.

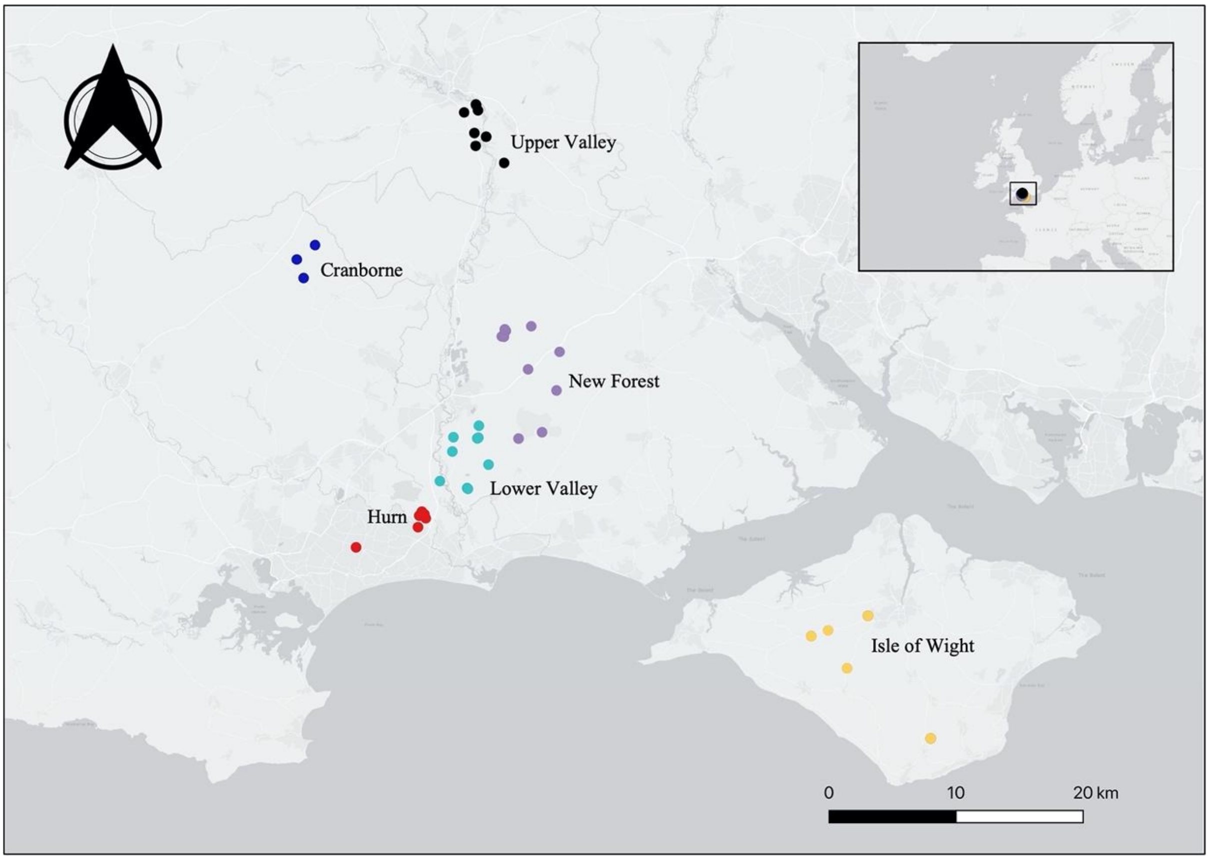


Figure 2.1. Map of central southern England with circles representing the locations of the 53 fox samples successfully sequenced.

D-loop and Cytb sequences were concatenated to a final alignment of 653 bp. To provide phylogenetic context with foxes across Europe, these sequences were aligned to a previously published dataset of 286 sequences from 14 countries (Statham et al., 2014), using the 'MUSCLE' algorithm (Edgar 2004) in MEGA v11.0.10 (Tamura et al., 2021). Final alignment was inspected visually. To evaluate the adequacy of the sample size, a rarefaction curve based on 1000 permutations was fitted to the Isle of Wight allelic richness data using 'vegan' (Oksanen et al., 2022) in R (R Core Team 2022). Two and three-parameter asymptotic exponential models were fitted to the rarefaction curve, with the better-fitting model used to estimate the asymptotic number of haplotypes (Pacioni et al., 2015). A median-joining haplotype network was constructed using PopART (Leigh & Bryant 2015) and pairwise F_{ST}

between populations represented by ≥ five samples were calculated using Arlequin v3.5.2.2. (Excoffier & Lischer 2010). The interpretation of significant pairwise F_{ST} results is that allele frequencies differ more than expected by chance.

2.4. Results

D-loop and Cytb sequences were successfully obtained from 53 out of 57 fox samples available in the study region. Four haplotypes were found on the Isle of Wight, of which two were private to the island considering the full European dataset, and both only a single mutational step away from their closest haplotypes (Figure 2.2). When fitted to the Isle of Wight rarefaction curve, the three-parameter model had a significantly better fit than the two-parameter model ($P < 0.0001$). The expected asymptotic number of haplotypes was 4.48 (95% CI: 4.37 – 4.59), indicating that additional sampling would not reveal many additional haplotypes. There were two non-private haplotypes on the Isle of Wight, one of which was shared only with central England and the other with several locations in central southern England (Hurn, Cranborne, and the Lower Avon Valley) (Figure 2.2).

Pairwise F_{ST} values were relatively high (0.30-0.84; Mean: 0.59) between the Isle of Wight and all European populations (Figure 2.3). The pairwise F_{ST} values were significantly different between the Isle of Wight and adjacent populations in central southern England (mean pairwise $F_{ST} = 0.53$, SD = 0.16; Figure 2.3).

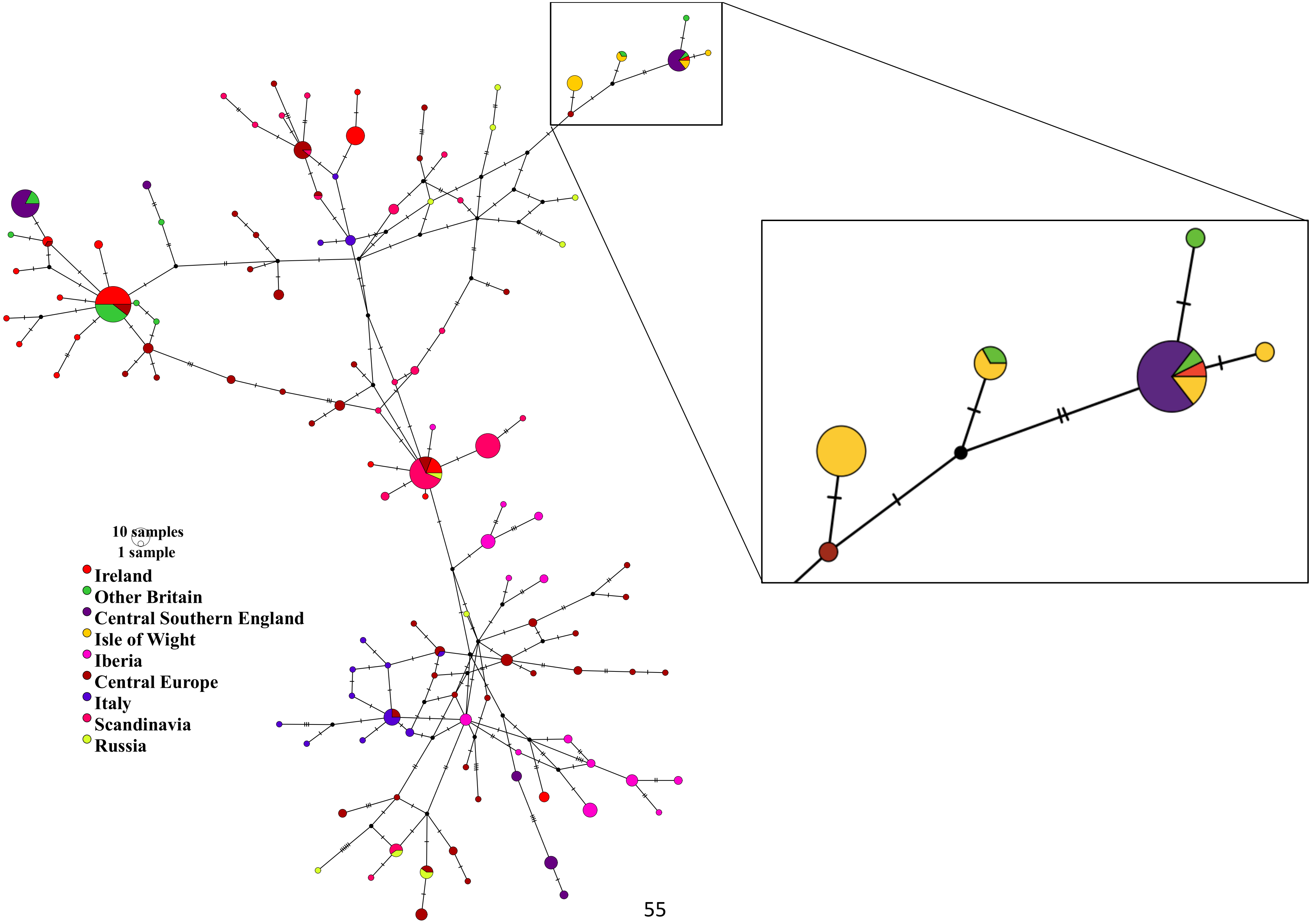

10 samples
1 sample
Ireland
Other Britain
Central Southern England
Isle of Wight
Iberia
Central Europe
Italy
Scandinavia
Russia

Figure 2.2. Concatenated D-loop and Cytb median-joining haplotype network for the entire dataset and an enlarged view of the branch with all the haplotypes sampled from the Isle of Wight. The size of the circle represents the frequency of the respective haplotype based on the 653 bp alignment, and the colours represent the populations of the individuals carrying a particular haplotype. ‘Other Britain’ refers to locations in Britain outside of the focal study region (Wiltshire, Hampshire, Dorset, and the Isle of Wight). Dashed lines represent number of base pair differences between haplotypes. Black circles represent internal nodes.

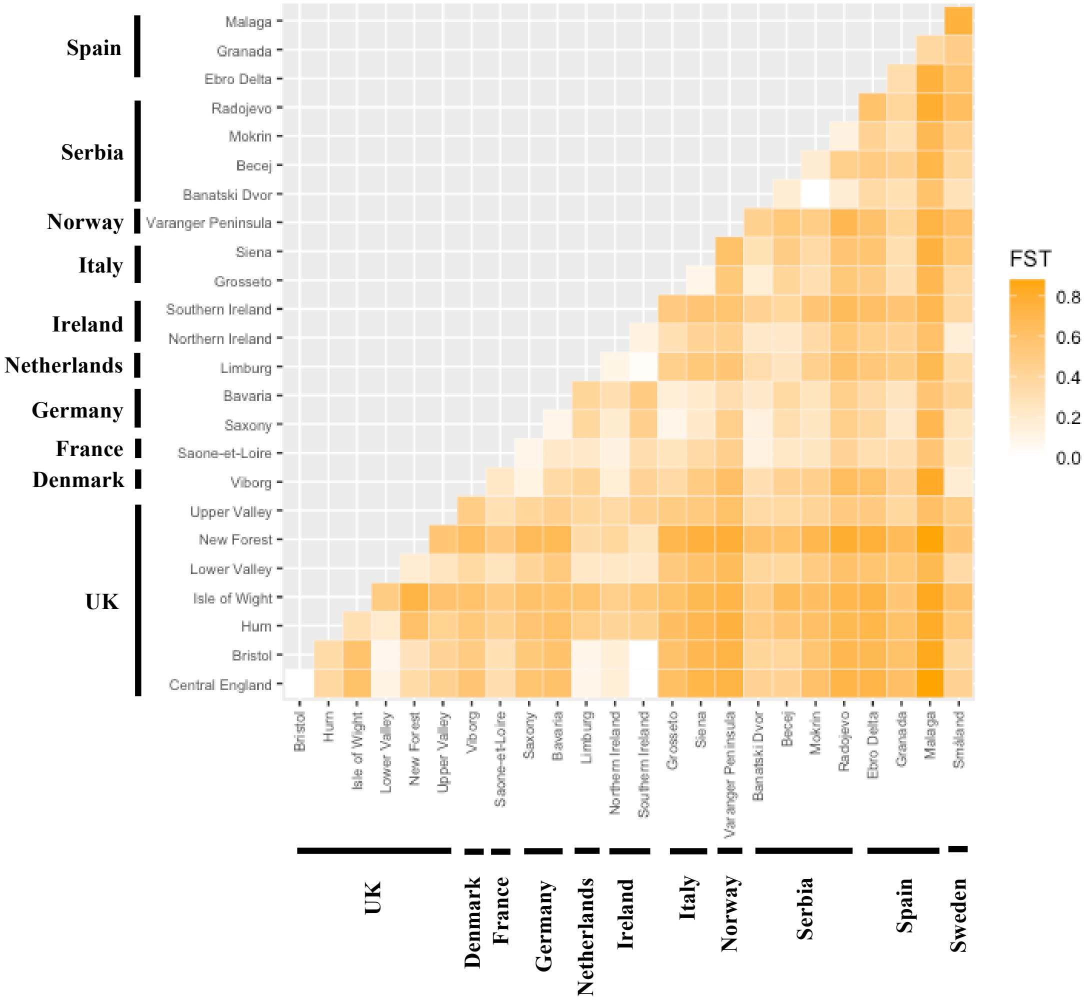


Figure 2.3. Pairwise F_{ST} heatmap for the populations across Europe with ≥ five samples.

2.5. Discussion

This analysis of fox mtDNA sequences provides insight into the geographic origins of foxes on the Isle of Wight and the population genetic structure of the species in this region. The results indicate that while the current population of foxes on the Isle of Wight were likely derived from mainland Britain, they are genetically differentiated from foxes in mainland central southern England.

There is no mention in the literature of foxes on the Isle of Wight until their introduction in the mid-19th century for sport hunting (The Leverets 2012). Inferring the geographic origins of these foxes is complicated given that foxes in Europe show a lack of phylogeographic structure based on mtDNA (Teacher et al., 2011), possibly due to relatively short periods of isolation during glacial maxima with gene flow occurring between regions during temporary warm phases (Kutschera et al., 2013). Nevertheless, this analysis indicates that the ancestry of the foxes sampled on the Isle of Wight can be pinpointed to mainland Britain. The non-private haplotypes recorded on the Isle of Wight are only shared with central southern England and the Midlands.

It is surprising not to find more diverse haplotypes on the Isle of Wight, given the historically large numbers of foxes thought to have been imported from the continent (Carr 1976). It is possible that foxes from mainland Europe were introduced to the Isle of Wight but have gradually been supplanted by other lineages from mainland Britain due to the popularity of fox hunting on the island alongside other methods of population control. Additionally, despite indications that the sample size was adequate, samples were only collected from a relatively small part of the island; greater phylogenetic diversity might be uncovered through more widespread sampling. Interestingly, the fox on the Isle of Wight shares a similar pattern to red squirrels (*Sciurus vulgaris*). Genetic analysis of red squirrels revealed a British origin for haplotypes sampled on the island despite the widespread presence of Scandinavian haplotypes on the mainland, indicating that in this case the existing population represents the remnants of the original British red squirrel population (Hardouin et al., 2019).

There was convincing evidence for genetic differentiation between the Isle of Wight and all mainland areas in central southern England. Elsewhere, genetic differentiation between mainland and insular fox populations, or those connected to larger areas via narrow land bridges, has been observed (Amaike et al., 2018; Langille et al., 2014). Foxes are capable swimmers; for example, a male fox was reported to have swum over 125 metres across a Danish fjord in flowing water (Olesen, 2016). However, the minimum distance between the island and the mainland (1.2 km) in the strongly tidal waters of The Solent almost certainly represents a restrictive boundary to natural migration. Differences in haplotype frequencies between the Isle of Wight and mainland Britain are expected given that the island was likely founded by a relatively small number of individuals, with the barrier to gene flow preserving these genetic differences over time. In future work, a genome-wide approach will likely help to resolve the population genetic structure and biogeographic history of foxes in the region in more detail (McDevitt et al., 2022; Walton et al., 2021).

Table 2.1. Genetic variability of fox samples and pairwise F_{ST} values calculated using Arlequin between sites in the present study.

Area	Location	No. samples	No. haplotypes	Haplotype diversity	Nucleotide diversity	Pairwise F_{ST}				
						Lower Avon Valley	Upper Avon Valley	New Forest	Hurn	Cranborne
Central southern England		41								
	Lower Avon Valley	10	4	0.80	0.010	-				
	Upper Avon Valley	9	3	0.67	0.009	0.25	-			
	New Forest	10	2	0.20	0.004	0.74	0.55*	-		
	Hurn	9	2	0.39	0.006	0.20	0.44*	0.60*	-	
	Cranborne	3	2	0.67	0.010	0.00	0.34*	0.03	0.18	-
Isle of Wight		12	4	0.65	0.004	0.49*	0.57*	0.74*	0.30*	0.53*

* $p < 0.05$

This is an accepted version of the published manuscript available at: Williams, NF., Porteus, TA., Hardouin, EA., Case, J., Rivers, E., Andreou, D., Hoodless, AN., Stillman, RA. & Short, MJ. (2024). Evidence of anthropogenic subsidisation of red foxes in a national park important for breeding wading birds. *Mammal Research*, 70, 61-73. https://doi.org/10.1007/s13364-024-00769-8

3. Evidence of anthropogenic subsidisation of red foxes in a national park important for breeding wading birds

3.1. Abstract

The red fox (*Vulpes vulpes*) is a generalist mesopredator found throughout the UK. It has been linked to national declines in native wildlife, especially ground-nesting birds such as waders. In the New Forest National Park, nest predation and poor chick survival is primarily responsible for low breeding success of Eurasian curlew (*Numenius arguata*), a species of high conservation concern. To reduce predation losses, foxes are lethally controlled by wildlife managers. Here, the major food resources that are being exploited by foxes in the New Forest area were identified and temporal and spatial patterns in the presence of specific food categories were examined, with special reference to anthropogenic food. Stomachs from foxes culled in curlew breeding areas were collected from April 2021 - July 2022 and the contents of these stomachs were quantified. Foxes exhibited a highly varied diet with no single food category predominating. Anthropogenic food comprised 14% of the overall diet, with its presence predicted by proximity to human settlements and other infrastructure. The total annual volume of anthropogenic food consumed by the fox population and by extension how many individual foxes this volume of food could support in isolation was estimated. According to these calculations, at present the number of foxes subsidised by anthropogenic food is approximately 64.8% (50.2-79.7%) of those removed by culling per year. These findings

highlight that better local food sanitation and education should become important parts of a more holistic management approach to reduce the burden of fox predation experienced by breeding waders.

3.2. Introduction

The red fox (*Vulpes vulpes*; henceforth ‘fox’) is a medium-sized mammalian predator, widespread across North America, Eurasia, and Australia (Macdonald & Reynolds, 2004). Like many aspects of its ecology, fox diet has been the subject of many studies throughout its native and invasive geographic range (Castañeda et al., 2022; Fleming et al., 2021; Soe et al., 2017; Diaz-Ruiz et al., 2013; Reynolds & Tapper, 1995). In broad terms, the fox is defined as a dietary generalist, capable of exploiting a wide-variety of food items including small and medium-sized mammals, invertebrates, birds, plant-based foods, herptiles and even fish (Castañeda et al., 2022). The fox diet is also highly flexible, with the relative importance of each prey item changing according to spatial and seasonal variation in availability (Balestrieri et al., 2011 Leckie et al., 1998).

Although natural prey are more important components of the fox diet from a global perspective (Castañeda et al., 2022), humans can locally subsidise fox populations via unmanaged food waste (Reshamwala et al., 2018; Ghosal et al., 2016), leftover viscera and carrion from hunting (Schwegmann et al., 2023; Tobajas et al., 2022), livestock, free-roaming game animals, and cultivated crops (Reshamwala et al., 2021; Jacquier et al., 2020; Dell’Arte & Leonardi, 2005), and food left out for pets and wildlife (Harris, 1981). Diversionary feeding might also subsidise populations (Kubasiewicz et al., 2016), but evidence is equivocal for foxes (Finne et al., 2019). Anthropogenic food subsidies are characterised by low foraging costs with the effect of driving higher productivity and population densities of wild canids (Newsome et al., 2015a). Given their opportunistic nature, foxes are one of several predator species worldwide that thrive in human-dominated landscapes to attain often exceptionally high population densities (Scott et al., 2018; Bateman & Fleming, 2012) with smaller individual home range sizes (Main et al., 2020). In common with other predators, foxes provide important benefits to ecosystems (O’Bryan et al., 2018). However, the artificial overabundance of canid species can have a suite of detrimental effects, including an increased risk of disease transmission, and elevated predation pressure on their prey species (Plaza & Lambertucci, 2017; Newsome et al., 2015a).

Roos et al. (2018) demonstrated that the fox and another generalist mesopredator, the carrion crow (*Corvus corone*), have larger population densities in the UK than in most other European countries. Contributing factors might include a favourable landscape composition for foraging (e.g., Kurki et al., 1998), the long-term absence of apex predators (i.e., '*mesopredator release'*) (Prugh et al., 2009; Ritchie & Johnson, 2009; Maroo & Yalden, 2000), and high food supplementation (Pringle et al., 2019; Harris, 1981). Foxes are one of the most important predators of ground-nesting birds (MacDonald & Bolton, 2008) and, concomitant with their high population densities, they have been implicated in national declines of multiple species such as the Eurasian curlew (*Numenius arguata*) (Franks et al., 2017), the UKs highest conservation priority bird species (Brown et al., 2015). Accordingly, understanding ways to reduce predation pressure by foxes on breeding birds is considered an urgent priority for conservation (Laidlaw et al., 2021).

The New Forest National Park (henceforth: 'New Forest') is in the county of Hampshire, central southern England. Spanning an area of 566 km^2, landcover in the New Forest consists of a mix of broadleaved woodland, heathland, and grassland, and the park forms a coastline. Home to around 34,000 residents, the New Forest is also flanked by key urban centres such as Southampton and Bournemouth, Christchurch and Poole (BCP) and receives over 15 million day-visits each year (New Forest National Park Authority, 2022), among the highest of any national park in the UK. Consequently, the prominence of human activity in the New Forest area is likely to provide ample opportunity for foxes to scavenge on anthropogenic waste. As a designated Special Protection Area (SPA) for birds, a site of Special Scientific Interest (SSSI), and a Ramsar Site, the New Forest is also an important area for conservation. Despite this, it faces a multitude of challenges, including the unfavourable status of its resident breeding wader populations (Hampshire Ornithological Society, 2021), in common with nationwide population trends (Harris et al., 2020). The New Forest has one of the most significant populations of Eurasian curlew in the southern lowlands, however poor breeding success, in-part due to high predation rates, is the most urgent threat to their persistence. As part of an ongoing wader nest monitoring project across the New Forest, between 2021-2024, trail cameras were used to monitor the fate of 429 wader nests of high conservation concern (mainly curlew and lapwing nests), and out of 151 recorded nest predation events, 54% were attributed to foxes (Case et al., 2022). To improve the reproductive performance of curlew, foxes are lethally controlled by professional wildlife managers in the New Forest. However, anthropogenic subsidisation could be undermining the efficacy of culling. Therefore, quantifying the degree of anthropogenic subsidisation of foxes in the New Forest is highly relevant to local conservation efforts.

Although studying the diet of foxes is complicated by their nocturnality and elusive behaviour, making direct observations of their feeding behaviour difficult, macroscopic analyses (i.e., stomach and scat contents) have provided valuable insights into the diet of fox populations (Peterson et al., 2021; Reynolds & Tapper, 1995; Reynolds & Aebischer, 1991; Harris, 1981). This study sought to examine the degree of anthropogenic food subsidisation of the fox population in the New Forest using stomach content analysis of individuals culled by professional wildlife managers. Using these non-spatial results of stomach content, the occurrence of broad food categories were modelled according to key variables, including period of the annual fox cycle and proximity to human infrastructure, with the aim of identifying general temporal and spatial patterns. This, alongside supplementary data, was used to estimate the theoretical number of foxes subsidised by anthropogenic food each year, thus illustrating the potential influence of anthropogenic subsidisation on local fox abundance.

3.3. Methods

i. New Forest stomach samples

447 fox stomachs were obtained from individuals culled by professional wildlife managers within the area of the New Forest managed by Forestry England (Figure 3.1), during routine fox control activities to reduce predation around wader nesting sites (i.e., not directly for use in this study) from April 2021 through July 2022. Many of the foxes culled by wildlife managers were baited to safe shooting locations with dog biscuits following initial detection by trail cameras. Hence, dog biscuits were expected to be present in the stomachs of foxes shot over bait sites. The location (UK grid reference), sex and date of each culled individual was recorded by the wildlife managers and the stomachs were extracted, placed into plastic bags and frozen before being sent to the laboratory immediately. All stomachs were stored at -20°C in laboratory freezers and defrosted prior to dissection.

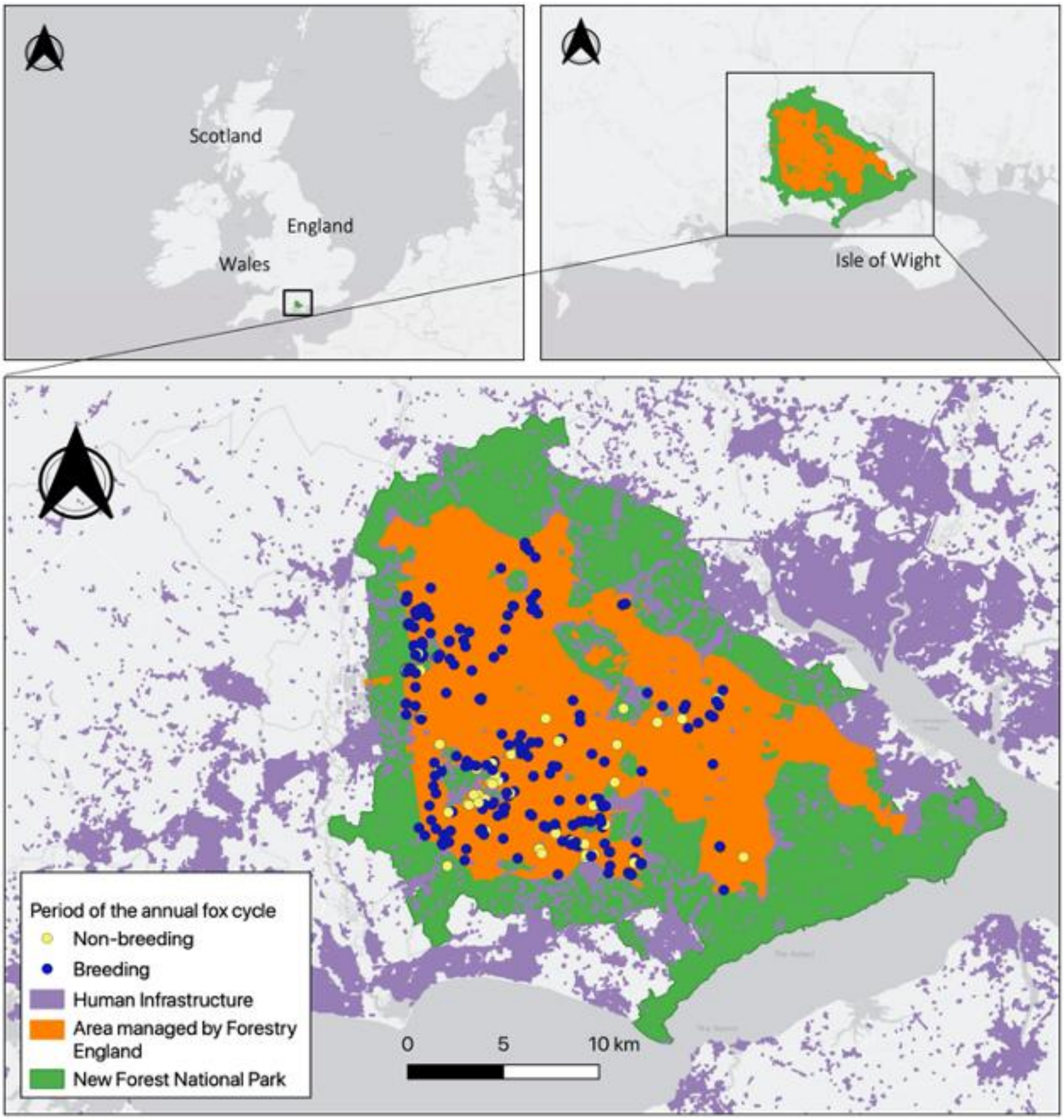


Figure 3.1. Distribution of non-empty fox stomachs sampled across the New Forest Forestry England-managed area for which date of collection and sample location was recorded (N = 363).

ii. Laboratory methods

The contents of each stomach were grouped according to several main categories: i. small mammal, ii. lagomorph, iii. other mammal (deer gralloch and grey squirrel *Sciurus carolinensis*), iv. fish, v. non-game bird, vi. gamebird, vii. herptile, viii. plant material, ix. invertebrate, x. anthropogenic (remains of cooked meat and fish, bread, pasta, vegetables, nuts and seeds; Figure S3.1), xi. indigestible material (human-derived materials such as fabric or plastic, other non-food items such as stones, intestinal worms, and mud), and xii. unidentified. The mass (g) of each category was taken using electronic weighing scales. All analyses were based on non-empty stomachs.

iii. Stomach content composition of foxes

The absolute frequency of occurrence (FO = number of samples containing a specific category/total number of samples x 100) and the relative volume (V = total estimated volume of each category as ingested/number of samples containing that category) of each category was taken whenever it was ingested. These values were compared on a Kruuk graph to evaluate the mean volume (mV = FO*V/100), the proportional contribution of each category to the stomach contents, with isopleths connecting points of equal mV (Kruuk & Parish, 1985). Categories occurring in negligible proportions within a given stomach (<1% overall volume) were treated as not being present. To examine whether there were differences in stomach content during distinct periods of the annual fox cycle, stomachs collected during two distinct periods were analysed separately: 1) February 1st – August 31st, the breeding period during which gestation and the rearing of cubs occurs, and 2) September 1st – January 31st, the non-breeding period (Lloyd, 1980). Changes in niche breadth were assessed by calculating Levin's standardised index for each period (Krebs, 1999):

$$B = \frac{1}{(n-1)}\left[\frac{1}{(\sum_i {p_i}^2)} - 1\right] \qquad [1]$$

where *B* = standardised index of niche breadth, p_i = proportion of stomach content (mV) of predator on prey i, and *n* = total number of categories. *B* values can range from 0 (predator subsists on single category) to 1 (predator exploits all available categories in equal proportion).

The adequacy of the sample size was evaluated using a rarefaction curve analysis to determine how the difference in proportion of each food category changes with increasing sample size (McQueen & Griffiths, 2004). In brief, the difference in mV of anthropogenic food (*D*) between consecutive sample size classes was calculated, increasing in increments of 5, and repeated using 1000 permutations. When the median *D* reached ≤ 0.01 the sample size was adequate. A more detailed description is provided in the Appendix.

iv. Factors influencing stomach contents

Binomial logistic regression was used to model the presence of each category according to the period in which the stomach was collected, and the distance to the nearest urban or suburban land parcel. For the latter, urban and suburban land parcels were extracted from the Centre for Ecology and Hydrology Land Cover Map 2020 vector layer (Morton et al., 2021). Use of both urban and suburban land parcels (henceforth: 'human infrastructure') encompasses houses, domestic gardens and allotments, and other man-made structures such as farm buildings, caravan parks, dock sides, car parks, industrial estates, and urban parkland. The distance (m) from the location where each fox stomach was collected to the nearest human infrastructure boundary was calculated using the R package 'sf' (Pebesma, 2018). Samples that were contributed without the date of collection and/or precise geographic coordinates were excluded from this analysis (N = 29).

For each food category, models were constructed with the presence in fox stomachs as the binary response variable (present/absent), and five different combinations of the explanatory variables: i. period of the annual fox cycle, and ii. distance to nearest human infrastructure boundary. Uniformity and overdispersion of the residuals were tested using the R package

‘DHARMa’ (Hartig, 2022), finding that model assumptions were met in all cases. Where there was no clear best performing model from the list of competing models, the top models were averaged (cumulative sum of AIC weights ≤0.95) and the coefficients of this averaged model were taken (Burnham & Anderson, 2002) using the R package ‘MuMIn’ (Bartoń, 2022).

v. Number of foxes subsidised by anthropogenic food

To illustrate how the observed proportions of anthropogenic food consumed by foxes might be influencing their abundance in the New Forest, the annual number of foxes being subsidised by this resource was modelled. To do this, the total number of adult males, adult females, and cubs in the New Forest was estimated according to different population density scenarios and supplementary data on breeding productivity, combined with information on their annual food requirements from the literature to calculate the number of foxes subsidised based on the observed contribution of anthropogenic food to fox diet in the New Forest. Monte Carlo simulations were used to represent the plausible range of input parameters, thus accounting for uncertainty (Figure 2a, b). Full details of how estimates were derived are provided in the Appendix and distributions of input parameters are provided in Table 3.1. All analyses were carried out in R v4.2.2 (R Core Team, 2022) using a custom script.

Pre-breeding adult population density was a key input parameter for the simulations, however contemporary measures of adult fox density in the New Forest are not available, with the most recent estimate dating back to 1974 (0.75 adult foxes km^{-2}: Insley, 1977). Therefore, several potential population densities were considered based on i) landscape-based estimates of fox densities recorded across different habitat categories (Webbon et al., 2004), and ii) local-based estimates of fox density arising from a recent fox GPS-tagging study in the Avon Valley, immediately west of the New Forest; on a landholding at Britford – an area of pastoral farmland with a high fox population density and no predator management, and Somerley Estate – an area with a more moderate fox population density with some predator management (Porteus et al., 2024; GWCT, 2020). At Somerley, some tagged-fox territories encompassed parts of the New Forest, immediately adjacent to important curlew breeding sites.

Table 3.1. Input variable estimates and coefficient of variation (CV) used in the Monte Carlo simulations.

Variable	Population density scenario	2.5% tail	Median	97.5% tail	CV
Adult population density	Landscape prediction	0.79	1.09	1.38	0.14
	Somerley	1.87	2.37	2.87	0.13
	Britford	8.83	10.49	12.16	0.10
Male body mass (kg)		6.17	6.72	7.26	0.04
Female body mass (kg)		5.16	5.46	5.76	0.03
Adult sex ratio		-	0.50	-	-
Proportion breeding females		0.84	0.90	0.96	0.03
Litter size		3.98	4.22	4.47	0.03
Proportion diet anthropogenic		-	0.14	-	-

3.4. Results

Out of the 447 fox stomachs collected, 33 were empty. Dog biscuits were found in 110 (26.6%) of the remaining 414 stomachs, comprising 73.2% of stomach volume on average when present. Dog bait biscuits are not expected to be an important component of the regular fox diet and therefore were excluded from stomach volumes in all subsequent analyses. After excluding dog biscuits, 392 stomachs remained (i.e., as some stomachs contained dog biscuits exclusively), of which 333 (84.9%) were from the breeding period and 52 (13.3%) were from the non-breeding period. Date of collection was not recorded for seven (1.8%) of these stomachs. Of the stomachs that were non-empty, the mean number of food categories per stomach was 2.43 (±1.25 *SD*). Only 72 (18.4%) stomachs contained four or more categories. For the breeding period, the mean number of food categories per stomach was 2.46 (±1.26 *SD*), with 64 (19.2%) stomachs containing four or more categories. For the non-breeding period, the mean number of categories per stomach was 2.29 (±1.14 *SD*), with eight (15.4%) stomachs containing four or more categories.

i. Description of fox stomach content

Several food categories contributed similar proportions to the overall mV of the populations' stomach content (9-15% mV), reflecting the high diversity of the fox diet, including small mammals, lagomorphs, non-game birds, invertebrates, and anthropogenic food (Figure 3.3). Specifically, anthropogenic food comprised 13.9% of mV (Table 3.2). There were alternative pathways to similar importance, reflecting the difference between small and 'common' (e.g., invertebrates) and large and 'occasional' (e.g., lagomorphs) items. Plant material and other mammals were of secondary importance (each ~8% mV; Figure 3.3). Herptiles, gamebirds, fish, and indigestible material were relatively uncommon items (≤2% mV; Figure 3.3). Additionally, 22.6% of the mV could not be unequivocally assigned to any specific category (Figure 3.3).

The mV for several food categories was similar (≤5% difference) during the breeding and non-breeding periods, including small mammals, other mammals, plant material, invertebrates, anthropogenic, and indigestible material, although there was some variation in stomach content between the two defined periods (Table 3.2). In general, the niche breadth was similar during the breeding (B = 0.55) and non-breeding (B = 0.52) periods (Table 3.2).

The median D for anthropogenic food for the breeding period fell below 0.01 after ~265 samples, indicating that the sample size (N = 333) for this portion of the year was adequate (Figure S3.2a). Given the smaller sample size for the non-breeding period, the median D marginally did not fall below 0.01 (Figure S3.2b), although the median D after 50 samples (0.015) was close to the threshold value, indicating that additional samples would not greatly change the inferences on the amount of anthropogenic subsidisation during this part of the year.

Table 3.2. Breakdown of the contents of all 392 non-empty fox stomachs from the New Forest, and of stomachs sampled within each period of the annual fox cycle. The three quantitative sub-columns correspond to the frequency of occurrence (%; FO), mean volume when present (%; V), and overall mean volume (%; mV = FO*V/100) of each category.

					Period					
Category	Sub-category	All stomachs (N = 392)			Breeding (N = 333)			Non-breeding (N = 52)		
		FO	V	mV	FO	V	mV	FO	V	mV
Small mammal		26.8	40.2	10.8	26.4	41.2	10.9	26.9	32.4	8.7
Lagomorph		13.0	72.6	9.4	11.1	69.3	7.7	26.9	81.1	21.9
Other mammal		9.9	70.6	7.0	9.6	72.1	6.9	13.4	64.1	8.6
	Sciurus carolininensis	2.8	56.5	1.6	2.7	57.5	1.6	3.8	52.1	2.0
Fish		0.3	31.1	0.08	0.3	31.1	0.09	-	-	-
Non-game bird		24.5	43.1	10.6	26.7	44.2	11.8	7.7	18.2	1.4
	Passeriformes (non-corvid)	8.4	45.2	3.8	9.3	47.3	4.4	1.9	6.4	0.12
	Corvidae	0.3	1.0	0.00002	0.3	1.0	0.00003	-	-	-
	Columbiformes	1.8	46.0	0.8	1.8	45.3	1.2	1.9	50.0	1.0
	Anseriformes	0.5	34.7	0.2	0.6	34.7	0.2	-	-	-
	Unidentified	11.7	37.7	4.4	12.6	38.2	4.8	3.8	8.3	0.3
	Eggshells	1.5	20.6	0.3	1.8	20.6	0.4	-	-	-
Gamebird		1.5	66.5	1.0	1.8	66.5	1.2	-	-	-
Herptile		5.6	14.4	0.8	6.3	12.2	0.8	-	-	-
	Lacertidae	3.3	8.7	0.3	3.9	8.7	0.3	-	-	-
	Anguis fragilis	0.5	0.3	0.2	0.3	1.9	0.00006	-	-	-
	Unidentified	1.8	20.2	0.4	2.1	20.2	0.4	-	-	-
Invertebrate		49.0	31.9	15.6	48.9	31.1	15.2	51.9	38.4	20.0
	Beetles	44.1	25.4	11.2	43.2	23.5	10.2	51.9	36.9	19.2
	Earthworms	3.3	19.6	0.6	3.0	22.2	0.7	5.8	10.5	0.6
	Unidentified	11.2	33.3	3.7	11.4	38.2	4.4	7.7	2.5	0.2
Anthropogenic		23.2	59.8	13.9	23.4	60.5	14.2	19.2	56.6	10.9
Plant material		39.8	18.8	7.5	39.6	17.9	7.1	42.3	25.4	10.7
	Grain	3.1	16.9	0.5	2.7	16.4	0.4	5.8	18.6	1.1
	Berries	1.3	25.7	0.3	0.6	28.3	0.2	5.7	23.9	1.4
	Other vegetation	38.3	17.3	6.6	38.4	16.9	6.5	38.5	21.5	8.3
Indigestible material		7.9	22.8	1.8	6.6	21.3	1.4	11.5	31.0	3.6
Unidentified		41.8	53.9	22.6	43.8	54.5	23.9	28.8	49.4	14.2
Levin's standardised index		0.57			0.55			0.52		

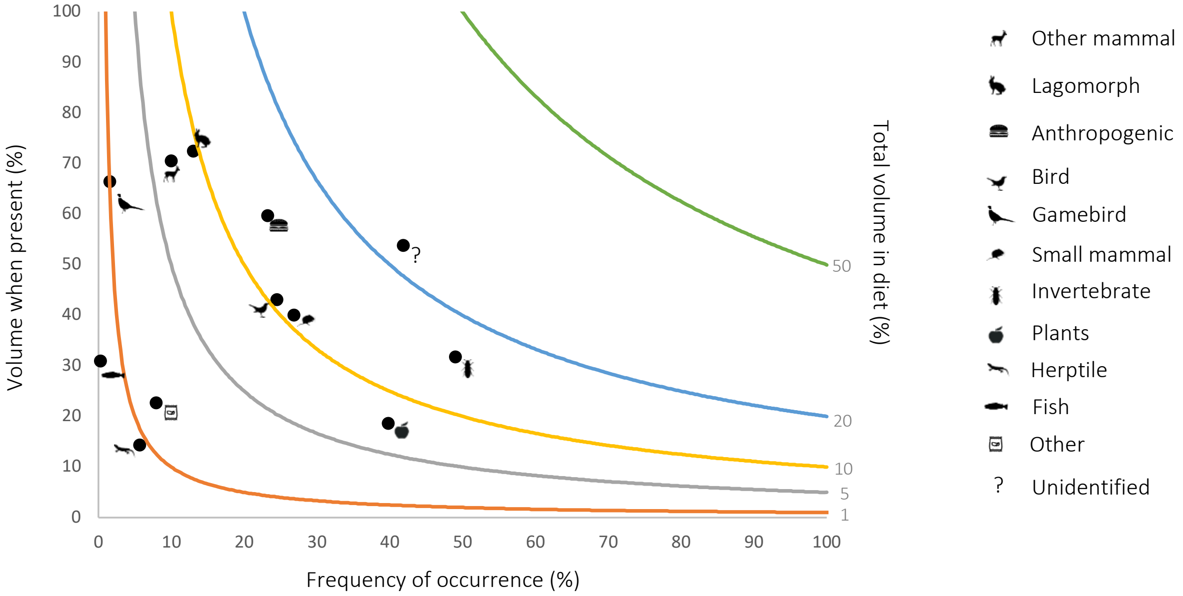


Figure 3.3. Diet habits of foxes in terms of volume of a given food category when present (V) against its frequency of occurrence (FO). Isopleths connect points with equal relative volume (mV).

ii. Factors influencing occurrence of food items

Overall, 363 stomach samples were obtained with both date of collection and precise geographic coordinates. A significant negative relationship was found between the occurrence of anthropogenic food in fox stomachs and distance to the nearest human infrastructure boundary (-0.0013 ± 0.00039 SE; *p* < 0.001; Table 3.3). The occurrence of non-game birds in fox stomachs was greater during the breeding period (1.53 ± 0.54; *p* < 0.01; Table 3.3), whereas the occurrence of lagomorphs was greater during the non-breeding period (-1.09 ± 0.36; *p* < 0.01; Table 3.3).

Table 3.3. Coefficient values (± standard error) for the average model predicting the occurrence of category according to period of the annual cycle (PAC) and distance to nearest human infrastructure boundary (DNU), in 363 fox stomachs. Values in bold are significant at the 0.05 α value. Note that period of the annual cycle is a categorical variable with values here representing change in log odds for the breeding period. There is no coefficient for model terms where it was not included in at least one of the constituents of the average model.

Model	Intercept	PAC (breeding)	DNU
Small mammal	**-1.03 (± 0.19)**	-0.0060 (± 0.16)	0.000015 (± 0.00013)
Lagomorph	**-1.00 (± 0.31)**	**-1.07 (± 0.36)**	
Other mammal	**-2.11 (± 0.31)**	0.19 (± 0.94)	0.000096 (± 0.00025)
Herptile	-19.67 (± 1490)	16.90 (± 1490)	0.00017 (± 0.00017)
Non-game bird	**-2.48 (± 0.52)**	**1.51 (± 0.54)**	
Anthropogenic	**-0.66 (± 0.19)**		**-0.0013 (± 0.00039)**
Invertebrates	-0.20 (± 0.22)	-0.0055 (0.14)	0.00043 (± 0.00030)
Plant material	**-0.41 (± 0.18)**	-0.014 (± 0.13)	0.000091 (± 0.00019)
Indigestible material	**-2.37 (± 0.42)**	-0.27 (± 0.46)	-0.000038 (± 0.00023)
Unidentified	-0.76 (± 0.36)	0.47 (± 0.39)	-0.000027 (± 0.00013)

iii. Number of foxes subsidised by anthropogenic food

The output of the Monte Carlo simulations used to estimate the annual number of foxes subsidised by anthropogenic food is provided in Table 3.4. For context, 261 foxes were culled by wildlife managers between 1st April 2021 – 31st March 2022. Under the landscape-based scenario, the median input of anthropogenic food into the system would support 77 foxes, corresponding to 29.5% of the foxes removed by predator control. Under the Somerley scenario this rises to support 169 foxes over the course of a year, 64.8% of those removed by culling. Under the Britford scenario the median would support 751 foxes, 287.7% of those removed by culling.

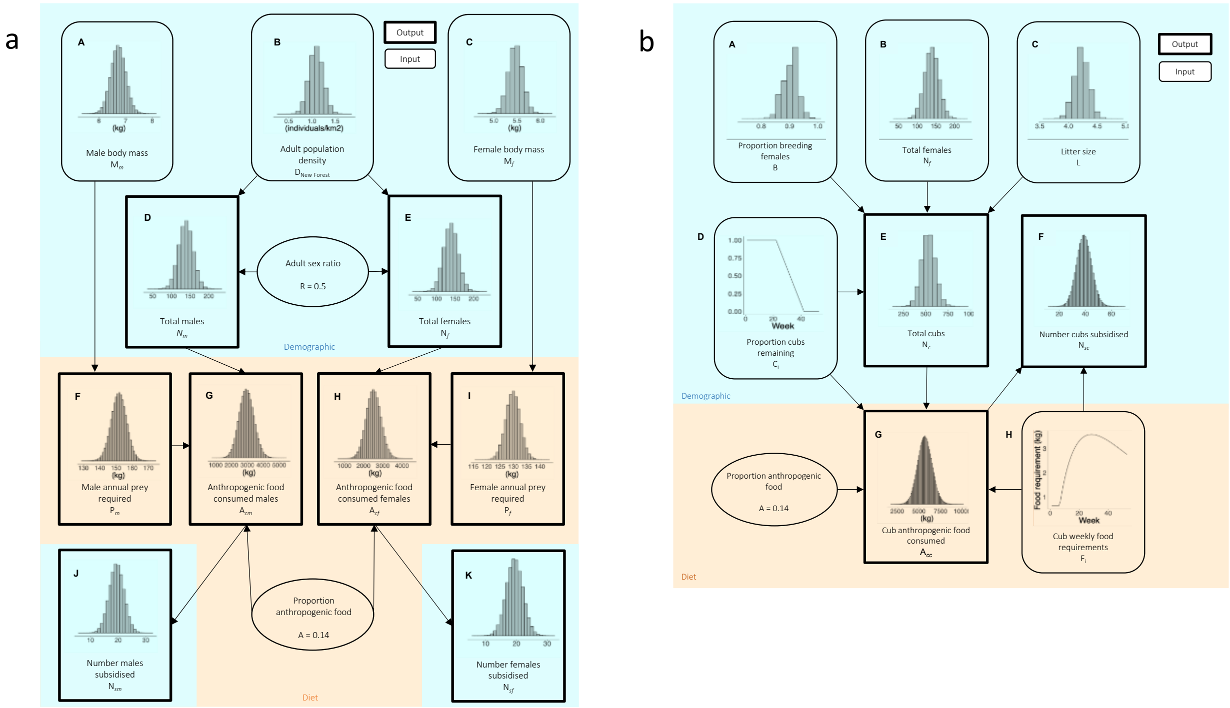


Figure 3.2. a) Schematic representation of the data used to estimate the number of adult foxes supported by anthropogenic food. The landscape-based scenario of adult population density is depicted for illustration. (A) Male body mass distribution. (B) Adult population density distribution. (C) Female body mass distribution. (D) Inferred total number of adult males. (E) Inferred total number of adult females. (F) Inferred annual prey requirements for an adult male. (G) Estimated anthropogenic food consumed by adult males annually. (H) Estimated anthropogenic food consumed by adult females annually. (I) Inferred annual prey requirements for an adult female. (J) Estimated number of adult males subsidised by anthropogenic food annually. (K) Estimated number of adult females subsidised by anthropogenic food annually. b) Schematic representation of the data used to estimate the number of cubs supported by anthropogenic food. (A) Distribution of the proportion of females that are breeders. (B) Number of adult females' distribution (based on the landscape-based scenario of adult population density for illustration). (C) Litter size distribution. (D) Proportion of cubs remaining versus week of the year plot. (E) Inferred number of cubs produced during the breeding season. (F) Estimated number of cubs subsidised by anthropogenic food annually. (G) Total anthropogenic food consumed by all cubs annually. (H) Food requirements of a cub versus week of the year.

Table 3.4. Output variable estimates and coefficient of variation (CV) derived from Monte Carlo simulations, based on different fox density scenarios.

Population density scenario	Variable	2.5% tail	Median	97.5% tail	CV
Landscape prediction	Male annual prey consumption (kg)	142	152	161	0.03
	Female annual prey consumption (kg)	124	130	135	0.02
	Total males	101	138	176	0.14
	Total females	101	138	176	0.14
	Total cubs	379	527	682	0.15
	Number males subsidised	14	19	25	0.14
	Number females subsidised	14	19	25	0.14
	Number cubs subsidised	28	39	50	0.15
	Male annual anthropogenic food consumed (kg)	2053	2939	3891	0.16
	Female annual anthropogenic food consumed (kg)	1781	2516	3288	0.15
	Cub annual anthropogenic food consumed (kg)	4087	5682	7344	0.15
Somerley	Male annual prey consumption (kg)	142	152	161	0.03
	Female annual prey consumption (kg)	124	130	135	0.02
	Total males	238	302	366	0.13
	Total females	238	302	366	0.13
	Total cubs	889	1151	1436	0.14
	Number males subsidised	33	42	51	0.13
	Number females subsidised	33	42	51	0.13
	Number cubs subsidised	65	85	106	0.14
	Male annual anthropogenic food consumed (kg)	4998	6410	7904	0.13
	Female annual anthropogenic food consumed (kg)	4306	5490	6710	0.13
	Cub annual anthropogenic food consumed (kg)	9575	12 398	15 469	0.14
Britford	Male annual prey consumption (kg)	142	152	161	0.03
	Female annual prey consumption (kg)	124	130	135	0.02
	Total males	1126	1338	1551	0.10
	Total females	1126	1338	1551	0.10
	Total cubs	4175	5097	6106	0.11
	Number males subsidised	158	187	217	0.10
	Number females subsidised	158	187	217	0.10
	Number cubs subsidised	309	377	451	0.11
	Male annual anthropogenic food consumed (kg)	23 526	28 389	33 561	0.10
	Female annual anthropogenic food consumed (kg)	20 314	24 312	28 460	0.10
	Cub annual anthropogenic food consumed (kg)	44 971	54 906	65 770	0.11

3.5. Discussion

Stomach content analysis was used to examine the diet of foxes in the New Forest and spatial variation in stomach contents with respect to human infrastructure was examined. The theoretical number of foxes supported by anthropogenic food within the managed area of the New Forest was also estimated. Foxes exhibited a highly varied diet overall with no food category predominating, although anthropogenic food was an important component comprising around 14% of mean volume, similar in importance to other key food categories such as invertebrates, small mammals, lagomorphs, and non-game birds (Table 3.2). Notably, the findings suggest that foxes were readily exploiting anthropogenic food subsidies associated with human settlements and other infrastructure throughout the year. The output from the Monte Carlo simulations suggests that the number of foxes theoretically supported by anthropogenic food annually represents a non-trivial proportion of the number of foxes removed by culling over the course of a year.

The presence of anthropogenic food in the diets of foxes is not a new phenomenon (e.g., Ghoshal et al., 2016; Harris, 1981), though it is a cause for concern for several reasons (Newsome & van Eeden, 2017). The physiology of carnivores could be adversely affected by anthropogenic foods, which are typically of lower in protein than natural prey items (Ng et al., 2023), and can cause additional harm by increasing exposure to inedible items such as plastics (Newsome & van Eeden, 2017). Foxes are also known to limit populations of ground-nesting birds via depredation of nests and chicks (Roos et al., 2018), and anthropogenic subsidisation of foxes might serve to bolster their local population numbers, resulting in increased nest and chick predation in the surrounding area (Harju et al., 2021; Selva et al., 2014; Esque et al., 2010; Kristan & Boarman, 2003). Subsidisation thus leads to an ethical issue where foxes are culled to reduce this predation risk; lethal control is a controversial practice, and it is necessary to evaluate the benefits of culling foxes against welfare costs (Fall & Jackson, 2002).

Aside from suburban areas (Saunders et al., 1993; Doncaster et al., 1990; Harris 1981), anthropogenic food has not normally featured in previous analyses of rural fox diet in the UK (Webbon et al., 2006; Leckie et al., 1998; Reynolds & Tapper, 1995), although the use of scat to analyse diet in these studies could have prevented its detection (Peterson et al., 2021). The finding of an overall FO for waste anthropogenic food of 23% aligns closely with the Europe-wide average of 17% (Castañeda et al., 2022). It is plausible that the negative consequences of anthropogenic subsidisation of foxes on breeding waders in the New Forest are exacerbated by the fact that it contributes to the overall diet but does not predominate. Where anthropogenic subsidies are the dominant component of predator diet, as observed in large metropolitan areas (e.g., foxes in Zurich, Contesse et al., 2004), the relationship between predation rates and prey survival can be disarticulated, by diverting predators away from their usual prey (Reshamwala et al., 2018; Rodewald et al., 2011).

Although the output from the Monte Carlo simulations is subject to a great deal of uncertainty, the findings suggest that anthropogenic subsidisation could be adding to the burden of predation pressure experienced by ground nesting birds in the New Forest. Previous work has demonstrated that landscape-based metrics are not necessarily reliable predictors of fox density (Heydon & Reynolds, 2000b). Evidence of extreme population densities in Britford – among the highest ever recorded in mainland Britain outside of urban areas might be attributable to a fish farm operation providing a plentiful and easily accessible food resource coupled with a lack of population control (Porteus et al., 2024). Therefore, this almost certainly does not represent the general situation across the New Forest but might at the local scale where intentional feeding occurs. A less extreme adult population density with evidence of fox home ranges overlapping with human settlements, means that Somerley Estate probably serves as the best analogue for the New Forest study area, with the annual median number of foxes subsidised by anthropogenic food being around 65% of those removed by culling (Table 3.4). It is worth emphasising that foxes are an important component of the ecosystem, serving to control small mammal populations, and thus potentially reduce tick-borne infections (Levi et al., 2012) and promote timber production (Chadwick et al., 1997). The objective of intensive seasonal culling by its wildlife managers is not to extirpate foxes but to reduce predation risk during critical time windows for breeding waders (Baines et al., 2023).

Evidence was found that fox diet in the New Forest changed slightly during different periods of the annual fox cycle. For example, the occurrence of non-game birds was higher during the breeding period when there is an abundance of vulnerable nestlings and fledglings (Table 3.2). The occurrence of lagomorphs was higher during the non-breeding period where the longer nights could make them more susceptible to predation (Lloyd, 1980) (Table 3.2). However, the overall contribution of anthropogenic food did not change according to period of the fox cycle, despite the breeding period coinciding with a peak in visitation to the New Forest during the spring and summer months (Liley et al., 2019). Accordingly, human settlements appear to be providing reliable sources of anthropogenic food year-round. Rather than the use of secure bins, household waste disposal in the New Forest involves rubbish bags placed on the edge of properties, potentially providing easier access to organic rubbish. Plans to introduce wheelie bins to the New Forest area as of 2025 have been announced (New Forest District Council, 2023). The response of predators to changes in prey availability can be functional or numerical (Angerbjorn et al., 1999). As generalist consumers, foxes can be buffered against a numerical response by switching to alternative food sources (Kjellander & Nordström, 2003). However, a rapid reduction in survival of foxes following the removal of anthropogenic subsidies has been demonstrated (Bino et al., 2010). It would be useful to carry out a similar study following the introduction of wheelie bins to assess the impact of this policy change (Newsome & van Eeden, 2017).

Anthropogenic food was more likely to be found in fox stomachs sampled closer to human settlements, but it cannot be determined whether foxes with territories situated closer to human settlements consume a larger amount of anthropogenic food over the long-term.

According to the ‘Resource Dispersion Hypothesis’, aggregated food sources can facilitate space sharing in otherwise non-cooperative species. Alternative means of assessing diet would help to investigate this further. For example, Maeda et al. (2019) used stable isotope analysis to show that both feral and stray domestic cats (*Felis catus*) were exploiting anthropogenic food on the island of Tokunoshima, Japan, with feral cats living in the nearby forest making forays into built-up areas to access anthropogenic food subsidies. GPS-tracking data in Australia has shown that individual foxes commute large distances (~ 5 km) at night from the interior of forests to farms and townships, likely to access anthropogenic resources (Hradsky et al., 2017).

The use of stomach contents herein does not necessarily provide a completely unbiased overview of fox diet. Obtaining samples via culling can lead to an overrepresentation of young inexperienced foxes, thereby inflating the frequency of less preferred prey items like invertebrates and plant material (Cavallini & Volpi, 1995). Given the nature of macroscopic methods such as stomach content analysis, there is a potential bias towards food items with indigestible components, which are easier to visually identify. Waggershauser et al., (2022) recently showed using a metabarcoding approach that domestic dog (*Canis familiaris*) faeces are a prevalent component of fox diet in the Cairngorms National Park, present in 39.1% of sampled fox scats. Faeces are not typically identifiable using macroscopic methods but given the abundance of dog walkers in the New Forest (Liley et al., 2019), it would not be surprising to find similar or higher rates of coprophagia by foxes in the New Forest. This reflects an additional anthropogenically-derived food resource that could result in the extent of subsidisation being higher than the results suggest.

Resources supporting foxes outside the boundaries of the New Forest are also relevant as foxes removed by culling are replaced by itinerants (Kämmerle et al., 2019a, b; Porteus et al., 2019a). Immigration rates in the region are particularly high (Porteus et al., 2019a), possibly because the area is adjacent to two large urban conurbations (Bournemouth, Christchurch, Poole to the west and Southampton to the east). These areas have particularly high densities of foxes (Scott et al., 2018), where anthropogenic subsidisation can be particularly prevalent (Handler et al., 2020; Contesse et al., 2004). Furthermore, although gamebird shooting is not an important land-use within the study area, gamebirds are typically released on shooting estates (Madden & Sage, 2020) of which there are several around the boundaries. There was scant evidence of gamebirds in this fox stomach analysis, and there is currently little evidence to support the notion that gamebird releasing drives local increases in fox abundance (Sage et al., 2020); in fact, there is evidence to the contrary, likely due to the association with the activities of gamekeepers (Madden et al., 2023).

This study has shown that anthropogenic food is a prevalent component of fox diet in the New Forest. It remains unclear what role this is playing in terms of influencing the local fox population dynamics and their prey species. Nevertheless, the findings indicate that foxes are readily exploiting human infrastructure to access this potentially important resource. Improved food sanitation could help to reduce fox densities and predation pressure, thereby helping to preserve the remaining breeding wader populations in the New Forest.

4. Evaluating the use of stable isotope mixing models to infer the feeding ecology of rural red foxes in the UK

4.1. Abstract

Anthropogenic subsidisation through the scavenging of organic refuse and the consumption of gamebirds that are released annually in the tens of millions could be related to the relatively high population densities of foxes found in the UK compared to Europe. However, there have been no studies to measure the consumption of these food resources at a regional scale. To address this, stable isotope analysis of ear hair from 162 predominantly rural foxes culled or found dead between 2018-2023 in central southern England was used, along with tissue from a variety of common prey items. Using the $\delta^{13}C$ and $\delta^{15}N$ values, Bayesian stable isotope mixing models (BSIMMs) were formulated to estimate the relative proportions of six source categories. Using generalist priors, BSIMMs were poorly resolved with broad overlap between 95% credibility intervals. Human food waste was suggested to be of little importance, although sampling was limited around large conurbations where this resource is likely mostly available. Using BSIMMs to estimate the diet in this generalist predator is challenging given the broad isotopic overlap between numerous source categories.

4.2. Introduction

Evidence suggests that red foxes ('foxes') occur at higher densities in the UK than many other European countries (Roos et al., 2018), with an apparent increase in abundance by an order of magnitude since the Mesolithic (Maroo & Yalden, 2000). Multiple anthropogenic impacts are postulated to have contributed to this over time including the eradication of apex predators, habitat fragmentation, and high food supplementation (Roos et al., 2018). Pertinent to the latter, humans can provide food subsidies to foxes in a variety of ways, including from human food waste, livestock, the rearing and release of free-roaming gamebirds, roadkill, and leftover hunting offal (Schwegmann et al., 2023; Jacquier et al., 2020; Ghosal et al., 2016).

Increased population densities of foxes and other predators can have a suite of unfavourable impacts on ecosystems (Manlick & Pauli, 2020; Kirby et al., 2017; Plaza & Lambertucci, 2017; Newsome et al., 2015a). The high abundance of foxes in the UK has caused concern amongst conservationists given that they are a key predator of numerous species (Laidlaw et al., 2021; Roos et al., 2018). Foxes limit populations of their prey species predisposed to high predation rates, notably ground-nesting birds, via depredation of nests and chicks (McMahon et al., 2020; Roos et al., 2018; MacDonald & Bolton, 2008), and these effects may be exacerbated in areas of artificially high fox abundance. The decline of several wader species in the UK, such as Eurasian curlew (*Numenius arquata*), has been linked to predation by mesopredators, especially foxes (Rivers et al., 2025; Franks et al., 2017).

Efforts to improve wader breeding success include local culling of foxes by wildlife managers (Laidlaw et al., 2021), nevertheless, understanding the drivers of fox population dynamics such as diet on a regional scale is relevant to the conservation of threatened prey species in specific areas of conservation interest. For instance, widespread subsidisation could elevate regional fox abundance and enhance the immigration pressure of foxes into places where culling takes place (i.e., 'population sinks'), compromising its efficacy (Porteus et al., 2019a).

Insights into the feeding ecology of foxes can provide the evidence required to modify management policies to reduce fox access to anthropogenic-derived resources (Jacquier et al., 2020), and potentially regulate their abundance more sustainably (Bino et al., 2010).

In the UK, fox diet studies have typically involved macroscopic analyses of scat and stomach contents (chapter three; Mason et al., 2020; Reynolds & Tapper, 1995), methods that are hindered by several key drawbacks: providing only a snapshot in time, influenced by the method of diet estimation (i.e., frequency of occurrence vs volume), often biased towards larger prey items or those with indigestible components, and hampered by observer error (Castañeda et al., 2022; Nørgaard et al., 2021; Ferreras & Fernandez-de-Simon, 2019; Reynolds & Aebischer, 1991). Stable isotope analysis (SIA) provides an alternative means of assessing diet that, although bringing its own complexities, can help to overcome some of the various limitations of macroscopic methods (Reid & Koch, 2017). The increased efficiency of SIA at larger sample sizes can also facilitate a dietary assessment of consumers across broad geographic scales (e.g., Manlick & Pauli, 2020). The utility of SIA is grounded in the fact that the carbon and nitrogen stable isotope composition of tissues (e.g., blood, bone or hair) serves as a record of an animal's diet during the period of tissue synthesis, with the temporal coverage varying according to the tissue-specific turnover rate (Ben-David & Flaherty, 2012). Using the ratio of heavy to light stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in the tissues of a consumer and their potential prey sources relative to international standards (expressed as $\delta^{13}C$ and $\delta^{15}N$) (Ben-David & Flaherty, 2012), Bayesian Stable Isotope Mixing Models (BSIMMs) quantify the proportion of each source in a consumer's diet (Phillips et al., 2014).

Previous studies have used SIA to infer foraging behaviours and to quantify the diet of foxes and other canids (Handler et al., 2020; Jacquier et al., 2020; Scholz et al., 2020), although this technique has seldom been applied in the UK until recently (Fletcher et al., 2025). The objective in this study was to evaluate the ability of BSIMMs to provide high confidence estimates of fox diet across a region of the UK. Accordingly, the primary aims of this study were to quantify the SI values of foxes and their potential food items, and use these data in BSIMMs to estimate the diet composition of foxes across a large region in the UK.

4.3. Methods

i. Study region and sampling

The study region was situated within central southern England (~10 000 km^2) including parts of the counties Wiltshire, Hampshire, and Dorset (Figure 4.1). The most recent population census shows a total human population size of around 3.4 million (Office for National Statistics, 2022), with major urban centres including Salisbury, BCP (Bournemouth, Christchurch, and Poole), and Southampton. The region also encompasses important areas for conservation, including the New Forest National Park, a designated Site of Special Scientific Interest (SSSI) and a Ramsar Site (Hampshire Ornithological Society, 2021), and the Avon Valley Special Protection Area, a 14 km^2 riverine habitat corridor that runs between Salisbury and Christchurch (GWCT, 2020; Wilson et al., 2005).

Keratinaceous tissues such as fur and vibrissae are metabolically inert and provide an indefinite record of diet at the time of synthesis (Phillips et al., 2014). They have been widely used to analyse aspects of fox dietary behaviour in North America and Europe (Handler et al., 2020; Jacquier et al., 2020; Manlick & Pauli, 2020; Scholz et al., 2020). Between 2018-2023, fox ears were obtained opportunistically from foxes found dead from natural or accidental causes (e.g., RTAs) and those killed by gamekeepers and professional wildlife managers throughout the region during their routine population control activities (i.e., not directly for use in this study), along with the location (UK grid reference), sex and date of collection (Table 4.1; Fig 4.1).

Foxes undergo two annual moults that commences with the growth of new guard hair in early April, progressing upwards from the animal’s limbs until September. Then, from October their coat thickens with underfur until December, also progressing upwards, with no growth occurring between December – March (Maurel et al., 1986). During these two annual moults, the ears are the final part of the animal to grow new hair (Maurel et al., 1986). According to this pattern of moulting, it can be anticipated that ear hair obtained from samples collected between August – November likely represents their summer diet, whilst ear hair obtained from samples collected between December – July likely represents a mix of both summer and autumn/winter diets. Overall, 52 samples were taken during months representing the first moulting period (summer; August – November) and 110 were taken during months representing the second moulting period (autumn/winter; December – July) (Fig. S2; Table S2).

Samples from a range of potential diet items were collected within the study region (Table 4.1), based on previous diet studies conducted in the area (chapter three; Reynolds & Tapper, 1995). European rabbit (*Oryctolagus cuniculus*) were the notable omission from the prey library, though it was assumed that they are represented by species with shared ecology that were included (i.e., other grazing mammals including European hare *Lepus europeus*). Human scalp hair samples were also obtained from local permanent residents in the region, to reflect the isotopic signature of combined human food waste (i.e., human diet) that might be available to foxes in waste not secured in a bin or deliberately fed to wildlife (Orros & Fellowes, 2014). The first 1-2 cm of scalp hair measured from the root was used, representing up to approximately the past eight weeks of growth (O'Connell & Hedges, 1999). Fox ears and soft tissue samples of potential prey items were stored in individually labelled plastic bags in a -20°C freezer and defrosted prior to laboratory preparation. Keratinaceous samples were stored in individually labelled plastic wallets.

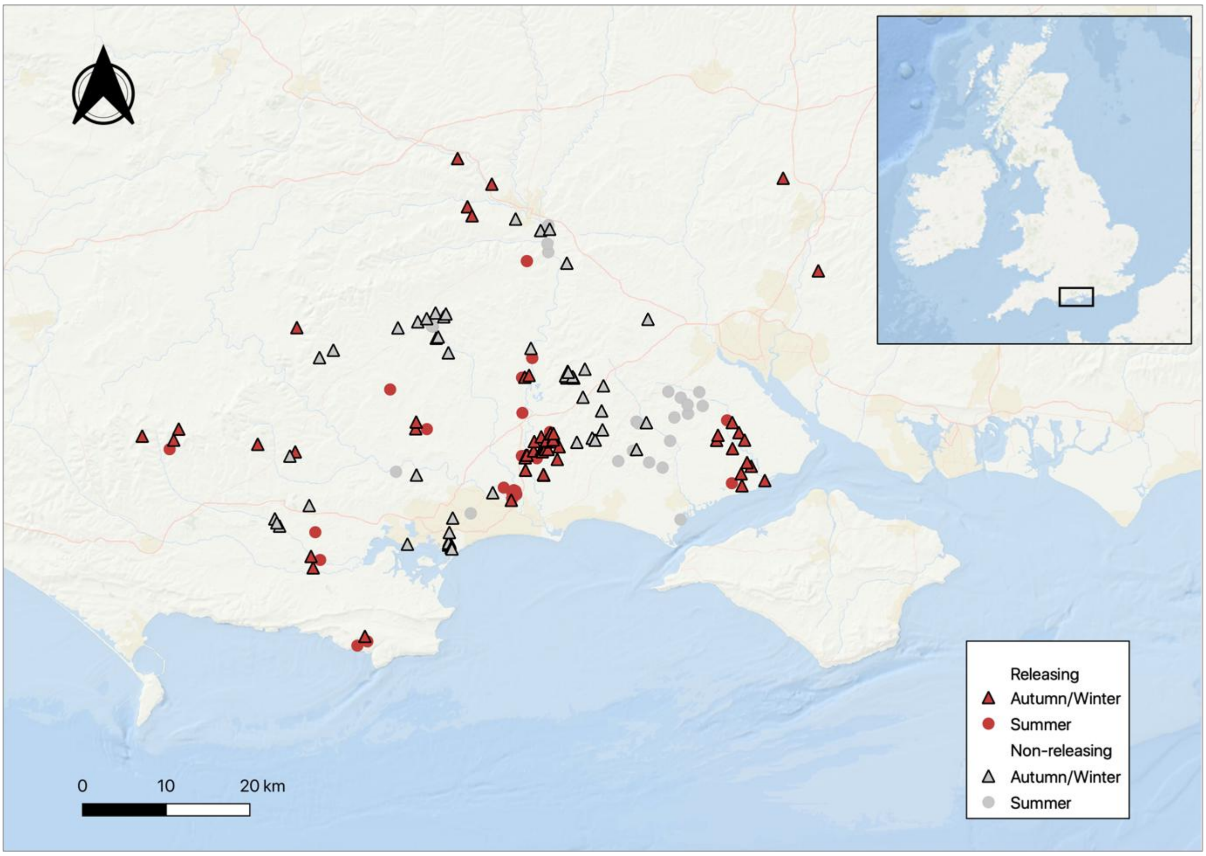


Figure 4.1. Distribution of 162 hair samples used to assess the assimilated diet of foxes across central southern England, 2018-2023. The darker shade on the landmass indicates conurbations.

ii. Sample preparation

A small quantity of dorsal-ear hair from each fox sample was taken and placed it in 2 ml microcentrifuge tubes. These and all the other keratinaceous samples were cleaned using a 2:1 chloroform:methanol solvent to remove surface contaminants, followed by rinsing with deionised water. Soft tissue samples were freeze-dried for 48 hours before being ground to a fine powder. For keratinaceous and soft-tissue samples, ~0.7 mg of each sample was weighed and placed individually into tin capsules. For nitrogen-depleted plant samples, ~10 mg was used for isotopic characterization. All samples were stored in 96-well plates prior to stable isotope analysis. The full protocol of sample preparation is provided in the Appendix (Table S4.1).

iii. Stable isotope analysis

Stable isotope analysis was carried out at the Natural Environment Isotope Facility (East Kilbride, Scotland, UK) using continuous-flow isotope mass spectrometry. Samples were analysed using an elemental analyser (vario PYRO cube; Elementar, Langenselbold, Germany) with a Delta Plus XP isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Stable isotope data are reported in delta notation (δ):

$$\delta = ((R_{sample}/R_{Standard}) - 1) \times 1000,$$

where $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$. To correct for instrument linearity and drift, three internal laboratory standards were analysed for every 10 samples. Following convention, delta values are expressed per thousand (‰) relative to the ratio of international reference standards of atmospheric N_2 and Vienna PeeDee Belemnite for nitrogen and carbon, respectively.

iv. Fractionation adjustments

The stable isotope values of consumer tissues reflect their diet with some degree of tissue-specific fractionation (Phillips et al., 2014). Following Jacquier et al. (2020), the difference in $\delta^{13}C$ and $\delta^{15}N$ values of keratin and muscle were corrected, as foxes do not assimilate the keratin of their prey. For mammal hair, 1.5 was subtracted from the $\delta^{13}C$ values to reflect mammal muscle, and for bird feathers, 1.0 were subtracted from the $\delta^{13}C$ and $\delta^{15}N$ values to reflect bird muscle (Caut et al., 2009). For human hair, 2.0 and 3.5 were subtracted from the $\delta^{13}C$ and $\delta^{15}N$ values, respectively, to represent human diet, following Newsome et al. (2015b).

v. Statistical analysis of diet composition

Mixing equations have multiple solutions when the number of sources is greater than or equal to one plus the number of tracers (Stock et al., 2018). BSIMMs enable the probability distributions of multiple source contributions to be estimated, accounting for multiple sources of uncertainty (Phillips et al., 2014). The discriminatory power of BSIMMs generally declines with increasing number of sources, and where the isotopic separation between sources is low (Phillips et al., 2014). Acknowledging these issues, potential prey species were aggregated into logical source categories *a priori* (Harju et al., 2021; Carbonell-Ellgutter et al., 2020; Jacquier et al., 2020; Swan et al., 2020a; Phillips et al., 2005): i. human diet, ii. mammals, iii. Galliformes, iv. other birds, v. invertebrates, and vi. fruit (Table 1). The mean isotope ratios of rainbow trout (*Oncorhynchus mykiss*), brown rat (*Rattus norvegicus*) and grey squirrel (*Sciurus carolinensis*) were far from the consumer data (Figure S4.1); therefore, these samples were excluded from all subsequent analyses. Stable isotope values of sources were characterised by an average (tissue adjusted mean ± SD) from the samples.

Correct tissue-specific trophic enrichment factors (TEFs) – the amounts by which values of $\delta^{13}C$ and $\delta^{15}N$ increase by during tissue synthesis owing to preferential assimilation of the heavier isotope – are required for BSIMMs to produce reliable estimates (Phillips et al., 2014). The TEFs for fox hair from Roth and Hobson (2000) were used, based on captive foxes raised on a commercial pellet feed ($\delta^{13}C$: 2.6 ± 1.0; $\delta^{15}N$: 3.4 ± 0.5 mean ± SD). As foxes are omnivores and the contribution of both animal and plant sources to assimilated diet were being estimated, the digestible elemental concentration of each tracer for each source was included to account for the differences in stoichiometry and digestibility of sources (Koch & Phillips, 2002; Phillips & Koch, 2002; Table S1).

Fox samples were obtained predominantly from rural areas where sites covered a wide variety of land-uses. The rural samples included many from gamebird-releasing estates, where habitat management designed to limit the dispersal of gamebirds is known to influence the structure of the ecological community on these estates relative to non-releasing sites (Madden et al., 2023). Thus, these practices could influence the range and abundance of different prey species available to foxes on gamebird-releasing estates (Swan et al., 2022). Based upon information provided by the gamekeepers and professional wildlife managers providing the samples, a binary estate status categorical variable was created, assigning values as ‘releasing’ or ‘non-releasing’ if the fox was sampled within the boundary of a known gamebird-releasing estate or not, respectively.

BSIMMs were formulated to estimate the proportion of diet for each source using MixSIAR (Stock et al., 2018) in R v4.2.3 (R Core Team, 2023). Based on the dataset assembled, a suite of mixing models with different covariate structures were considered, including a ‘Moult’ model with moult period (summer vs autumn/winter) as a fixed effect; an ‘Estate’ model with estate status (releasing vs non-releasing) of the landholding where the sample was collected from as a fixed effect; an ‘Individual’ model with individual ID as a random effect allowing offsets from the global mean for individuals, and the combinations ‘Moult + Estate’, ‘Moult + Individual’, ‘Estate + Individual’. It was hypothesised that including information on sampling location in the models would explain some of the variation in isotope ratios among foxes, for example, owing to individuals belonging to the same family or occupying territories with a shared availability of resources. Accordingly, the ID of the 1 km^2 grid square from which the sample was collected based on the British National Grid (BNG), was used as a random effect in a further set of models; ‘Grid’, ‘Moult + Grid’, ‘Estate + Grid’, closely matching the average home range size recently recorded for foxes in a rural area within the region (Porteus et al., 2024). As each model was fitted to the same mixture dataset, the leave-one-out information criterion (LOO$_{ic}$) was used to compare the relative fit across all models, selecting the model with the lowest LOO$_{ic}$ (McElreath, 2016). A Dirichlet prior on the global estimated proportions, which assigns equal weight prior probabilities to all sources (Stock et al., 2018). For all models, three simultaneous chains were run with 1,000,000 posterior draws each. The first 500,000 posterior draws were discarded as burn-in and thinned to every 500th draw, resulting in 1000 posterior draws per chain and 3000 total draws from the joint posterior distribution. A residual*process error structure was used meaning the consumer population can fall somewhere in between a perfect specialist and a generalist (Stock & Semmens, 2016). Model convergence was assessed using the Gelman-Rubin diagnostic and by visually examining trace plots. Diet composition was compared using posterior medians and 95% Bayesian credible intervals were used to summarise parameter precision.

Table 4.1. A summary of the samples collected between 2018-2023 for use in this study. Raw stable isotope values of samples are given (i.e., not corrected for trophic discrimination). Values in bold show means across each category.

Group	Major category	Species	Feather	Mean δ^{13}C	Mean δ^{15}N	Sample size
Predator						
		Vulpes vulpes	Hair	**-23.61**	**8.64**	**162**
Prey						
	Human diet	*Homo sapiens*	Hair	**-21.47**	**8.41**	**29**
	Mammal			**-24.28**	**5.82**	**102**
		Dama dama	Hair	-27.23	5.59	8
		Cervus elaphus	Hair	-27.25	6.14	8
		Muntiacus reevesi	Hair	-25.23	5.46	14
		Lepus europeus	Hair	-26.37	5.28	15
		Apodemus sylvaticus	Hair	-25.65	9.26	9
		Clethrionomys glareolus	Hair	-25.38	5.52	4
		Microtus agrestis	Hair	-27.14	4.74	13
		Sciurus carolinensis	Hair	-21.36	3.13	13
		Rattus norvegicus	Hair	-13.48	8.81	10
		Sorex araneus	Hair	-24.32	6.55	6
		Neomys fodiens	Hair	-24.28	4.39	2
	Fish	*Oncorhynchus mykiss*	Fin	**-19.24**	**7.96**	**10**
	Bird			**-24.31**	**6.86**	**75**
		Gallus gallus domesticus	Feather	-23.92	5.57	5
		Phasianus colchicus	Feather	-24.67	4.49	14
		Alectoris rufa	Feather	-22.38	5.88	5
		Alopochen aegyptiaca	Feather	-25.09	13.87	1
		Anser anser	Feather	-24.19	11.35	2
		Branta canadensis	Feather	-28.15	10.30	1
		Anas platyrhynchos	Feather	-23.21	8.32	1
		Anas crecca	Feather	-31.27	12.21	2
		Mareca penelope	Feather	-28.50	8.88	2
		Vanellus vanellus	Feather	-25.50	11.09	2
		Numenius arquata	Feather	-23.30	2.53	1
		Scolopax rusticola	Feather	-23.51	5.59	2
		Gallinago gallinago	Feather	-25.22	7.71	1
		Turdus pilaris	Feather	-22.51	-21.51	1
		Motacilla cinerea	Feather	-23.28	12.62	1
		Turdus philomelos	Feather	-24.66	5.64	1
		Corvus corone	Feather	-22.19	10.84	10

		Corvus monedula	Feather	-24.40	7.41	1
		Garrulus glandarius	Feather	-24.33	6.56	5
		Columba palumbus	Feather	-24.53	6.35	17
	Invertebrate			**-25.63**	**6.29**	**17**
		Lumbricus terrestris	Muscle	-25.11	6.39	5
		Carabidae spp.	Muscle	-26.72	6.70	8
		Oniscidea sp.	Muscle	-24.13	5.35	4
	Fruit			**-27.35**	**4.49**	**16**
		Malus sylvestris	Flesh	-27.95	3.53	5
		Prunus domestica	Flesh	-26.10	4.32	5
		Ribes uva-crispa	Flesh	-24.08	4.39	1
		Rubus idaeus	Flesh	-28.64	5.65	5
TOTAL						**411**

4.4. Results

i. Stable isotope values

The raw mean $\delta^{15}N$ and $\delta^{13}C$ values for foxes and prey items are presented in Table 4.1. The fox $\delta^{15}N$ values ranged from 5.57 – 12.27‰, and the $\delta^{13}C$ values ranged from -26.44 – 19.01‰ (Figure 4.2). There was no difference between the sexes in $\delta^{13}C$ (F(1, 155) = 0.029, p = 0.87) or $\delta^{15}N$ (F(1, 155) = 0.37, p = 0.55) values. Likewise, $\delta^{13}C$ (F(1, 160) = 0.036, p = 0.85) and $\delta^{15}N$ (F(1, 160) = 0.033, p = 0.86) did not differ by moulting period. After correcting the stable isotope values of sources for the actual tissue assimilated by foxes and trophic discrimination, the source isospace ranged from a mean $\delta^{15}N$ value of 7.40 – 12.2‰ and a mean $\delta^{13}C$ value of -25.0 – -16.7‰ (Figure 4.2).

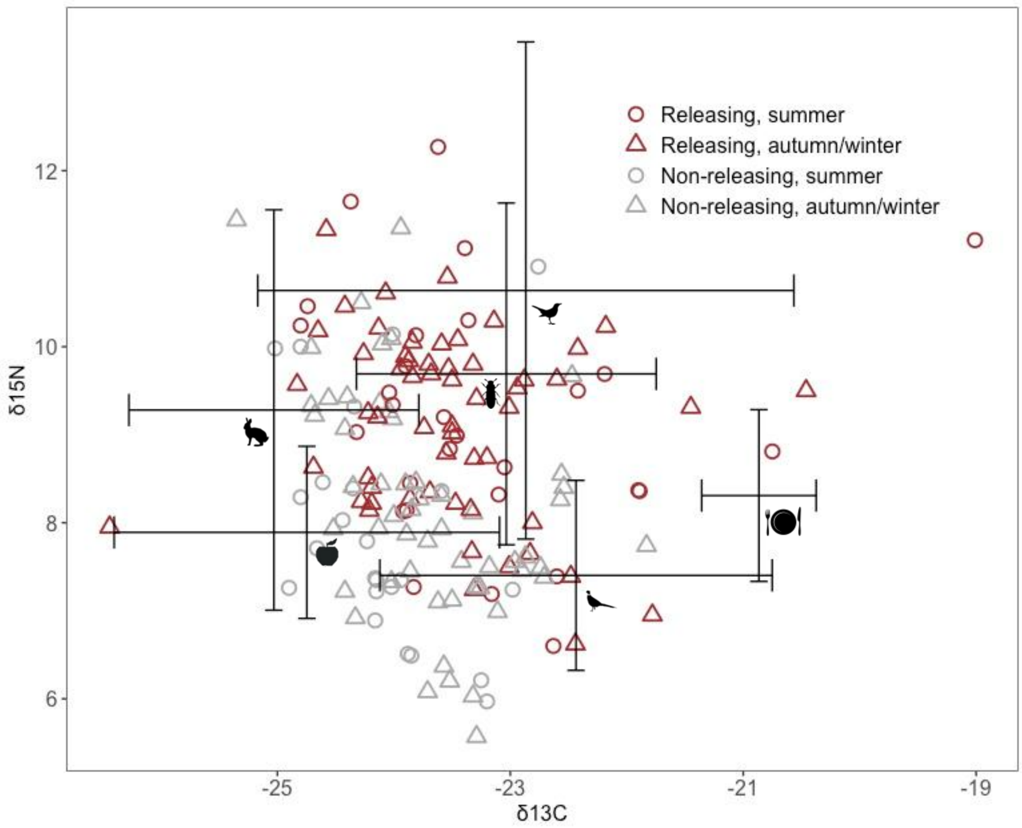


Figure 4.2. Biplot of $\delta^{15}N$ and $\delta^{13}C$ values of foxes and potential diet sources. Diet sources were adjusted to convert sampled tissue isotope ratios to the actual tissue of consumption, and by the trophic discrimination of fox hair. Bars indicate mean ±1 SD.

ii. Diet composition

The Gelman-Rubin Rhat values were < 1.05 for all variables in each model, confirming that they had converged. Full output for each model is provided in the Appendix (Table S4.4). Model selection results indicated that the model including estate status as a fixed effect and grid ID as a random effect was by far the most parsimonious and therefore preferred model ($\Delta LOO_{ic} \geq 19.9$; Table 4.2).

Table 4.2. Model selection of stable isotope mixing models to assess factors affecting the assimilated diet of foxes across central southern England (2018-2023). Factors in brackets correspond to random effects.

Model	LOO_{ic}	SE LOO_{ic}	ΔLOO_{ic}	SE LOO_{ic}	Weight
Estate + (Grid)	399.6	32.3	0.0	NA	1
Moult + (Grid)	419.5	31.1	19.9	8.2	0
(Grid)	426.5	32.6	26.9	9.1	0
Estate	430.2	37.1	30.6	15.4	0
Estate + (Individual)	431.6	31.7	32.0	11.6	0
Estate + Moult	432.7	37.2	33.1	14.7	0
(Individual)	461.0	35.1	61.4	17.0	0
Moult + (Individual)	462.7	34.5	63.1	16.4	0
Moult	464.4	38.3	64.8	18.7	0

LOO_{ic}: LOO information criterion; SE LOO_{ic}: standard error of LOO_{ic}; ΔLOO_{ic}: difference between each model and the model with lowest LOO_{ic}; SE ΔLOO_{ic}: standard error of the difference between each model and the model with lowest LOO_{ic}; Weight: relative support for each model, calculated as Akaike weights.

On releasing sites, the preferred model suggested that the bulk of assimilated diet consisted of five categories: other birds (median 0.29, 95% CIs 0.018-0.509), Galliformes (0.16, 0.047-0.313), fruit (0.19, 0.023-0.46), mammals (0.17, 0.036-0.358) and invertebrates (0.10, 0.003-0.501). Human food waste (0.03, 0.001 – 0.129) was a minor source (Figure 4.3). On non-releasing sites, the predominant categories were Galliformes (0.36, 0.119-0.582), mammals (0.27, 0.017-0.516) and fruit (0.20, 0.009-0.755), whereas minor sources were other birds (0.05, 0.005-0.16), invertebrates (0.028, 0.001-0.194), and human food waste (0.0011, 0.00-0.077) (Figure 4.3).

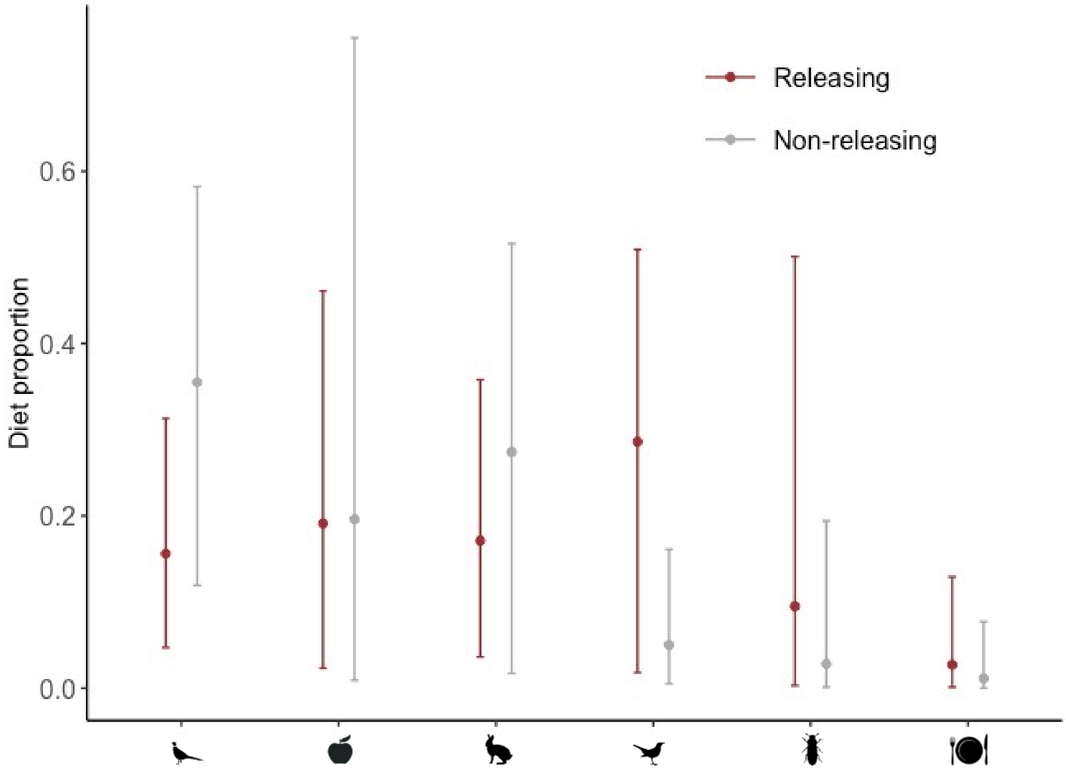


Figure 4.3. Distributions of posterior probabilities from the best performing model of proportion of assimilated diet for each source on releasing and non-releasing sites. Points indicate median estimates and bars indicate 95% CIs. Diet sources from left to right are Galliformes, fruit, mammals, other birds, invertebrates, and human diet.

4.5. Discussion

The isotopic signatures of 162 foxes were used to estimate dietary proportions of key source categories across a large and heterogeneous region in central southern England. Overall, foxes exhibited a varied diet throughout the region with stable isotope values of individual foxes spanning the entire source isospace (Figure 4.2). Several factors are known to complicate the estimation of the diets of consumers using SIA. For example, species-specific TEFs are required to obtain accurate estimates of prey proportions (Phillips et al., 2014), although this was not a concern here as TEFs for fox hair have already been determined (Roth & Hobson, 2000). However, when many source categories overlap isotopically, their source contributions often cannot be separated unambiguously, resulting in a diffuse posterior distribution; an issue commonly encountered when estimating the diets of generalists at the population level (Lerner et al., 2018), including in this study (Figure 4.3). In situations where BSIMMs exhibit low discriminatory power, dietary information from independent sources can be leveraged as informative priors to enhance their precision (Lerner et al., 2018), although such priors can also influence the results of mixing models by reflecting the inherent biases of the alternative methods (Swan et al., 2020a).

Although foxes are described as dietary generalists (Castañeda et al., 2022), previous research has shown evidence for specialist individuals within fox populations (Jacquier et al., 2020; Scholz et al., 2020), as suggested by the range of isotope values observed in this study (Figure 4.2). However, modelling diet at the population level misses the opportunity to study individual specialisation in diet. To estimate individual specialisation, multiple data points per individual are required, which can be achieved by sectioning vibrissae to produce a time series of stable isotope values. This has the added benefit of allowing temporal variation in diet to be traced more precisely (Jacquier et al., 2020; Scholz et al., 2020). Using these data, individual specialisation could be quantified using an index that compares population to inter-individual variance (e.g., Roughgarden's index). Individual diet could also be estimated using individual as a random effect in the MixSIAR framework (Harju et al., 2021).

There was little evidence for distinct differences in the proportion of different sources on releasing and non-releasing sites, including Galliformes (Figure 4.3). This is of interest because it is currently unknown to what extent gamebirds subsidise foxes in the wider countryside, beyond their immediate releasing locations (Mason et al., 2020). However, aside from the uncertainty inherent to the model, it is likely that SIA is a suboptimal tool to study fine-scale spatial variation in the diet of this species. Whereas macroscopic or metabarcoding methods provide a snapshot of diet, SIA represents diet over longer timeframes than conventional diet analyses (e.g., time since the last moult). However, rural foxes can exhibit relatively large home range sizes (2-4 km^2) that partially overlap with releasing sites (Reynolds & Tapper, 1995). Genetic analyses have demonstrated the high vagility of foxes (Atterby et al., 2015), and GPS-tagging has shown individuals dispersing long distances in relatively short periods of time (Porteus et al., 2024; Walton et al., 2018). This means that the diet of foxes inferred from SIA of fox hair does not necessarily represent food sources consumed local to sampling locations. For instance, gamebirds on release sites can be predated by foxes that were subsequently not killed within the boundaries of releasing sites, complicating the estate categorisation of fox samples. This is likely to be exacerbated by culling, promoting even greater movement by creating vacant territories for itinerant foxes from afar to move onto and acquire (Tuyttens et al., 2000).

SIA has recently been used to demonstrate differences in diet between foxes inhabiting urban and rural areas of Britain; much broader habitat types where fine-scale movement patterns are less of a concern (Fletcher et al., 2025). In their study, Fletcher et al. (2025) found evidence that human and pet food comprises a larger proportion of fox diet in urban areas. Here, there was no evidence for prevalent utilisation of human food waste, using human scalp hair isotope measurements as a proxy for the composite human diet. Consumption of human food waste has been noted on many occasions (Contesse et al., 2004; Saunders et al., 1993; Harris, 1981), including within the study region (chapter three), and is one of the primary factors thought to be driving population expansion and reduced home range sizes of foxes in heavily developed environments worldwide (Main et al., 2020; Scott et al., 2014; Bateman & Fleming, 2012). The dataset herein included relatively few samples (~8%) from highly urbanised areas where samples proved to be more difficult to obtain, so likely does not adequately represent the population of foxes that utilise human food waste. Furthermore, following previous studies (Harju et al., 2021; Newsome et al., 2015b), human hair was assumed to serve as an adequate representation of the array of edible material that can be gleaned from human food waste, although this is only valid if the different types of human food available from waste is consumed in similar proportions to the average human diet.

A further limitation of SIA is that it can only partition a small number of food sources with distinct stable isotope ratios, as opposed to individual food items. For example, in this study free-roaming gamebirds and domestic chickens (*Gallus gallus domesticus*) were combined into a single source category (Galliformes), yet the independent contribution of these prey items could have important management implications (Madden, 2021). Gamebird releasing is prevalent within the study region, with many gamebirds being artificially reared in pens and thus acquiring limited anti-predator behaviours (Whiteside et al., 2015). According to the latest APHA poultry and gamebird register (obtained on 14/03/2024; FOIA request reference: FOI2024/04449) – a compulsory register for flocks of ≥ 50 birds – a total of 1,347,969 partridge and pheasant were released for shooting across all postcode districts in the study region (BH, DT, SO & SP) in 2023. In comparison, the total number of chickens came to 4,301,721. Information on the management system was available for 76.5% of these chickens, of which 580,237 (17.6%) were free-range and therefore more susceptible to predation. This implies that the number of free-roaming gamebirds in the ecosystem is around double that of free-range chickens, making them much more available to foxes. Moreover, because free-range chicken flocks are commonly protected by anti-predator measures such as exclusionary perimeter fencing, predation accounts for a very small proportion of mortality (~0.5% of overall flock size for egg producers; Moberly et al., 2004). Chicken flock holders with < 50 birds are widely distributed but are not accounted for by the APHA register. As these are typically less protected than larger rearing operations this could increase the availability of chickens to foxes. Although tagged foxes have previously been observed spending a lot of time on smallholdings with domestic chickens (Porteus et al., 2024), there is no evidence that chickens are a significant source of food for foxes at a regional scale. By contrast, predation by foxes has been identified as one of the most common fates for free-roaming gamebirds (Madden et al., 2018); for example, accounting for 35% of individual pheasants released in July/August up until the end of the shooting season in February, averaged across six shoots in southern England (Sage et al., 2018). Previous analyses of fox diet support this finding of moderate proportions of fox diet comprising gamebirds on releasing sites (Mason et al., 2020; Reynolds & Tapper, 1996), and a preliminary analysis suggests the carrying capacity of an estate for foxes is positively associated with the number of gamebirds released there (Porteus, 2015). It can therefore be assumed that, on a regional scale, gamebirds contribute more significantly to fox diet than do domestic chickens. To address this, DNA metabarcoding of scat or stomach contents would be better suited to detect food items at a higher (species-level) resolution. Nevertheless, chicken could be consumed by foxes from multiple avenues including predation of live chickens, waste cooked chicken, or pet food, which would be complicated to disentangle unless consumed via coprophagia of dog faeces (Waggershauser et al., 2022).

The fox is controlled within restricted-areas throughout the country, usually to reduce their impact on prey species (Heydon & Reynolds, 2000a). Restricted-area fox culling forms population sinks whereby individuals are replaced rapidly through compensatory immigration (Robertson et al., 2008), especially in population sinks surrounded by higher densities of foxes (Lieury et al., 2015). Quantifying fox diet across the spatial scale of replacement (i.e., the management unit) is relevant to the success of fox control in population sinks. Regional subsidisation can release predators from bottom-up control and lead to population growth

(Kirby et al., 2017), especially in situations like the UK where there is an absence of apex predators, thereby potentially exacerbating the issue of compensatory immigration. However, this study has highlighted the limitations of using BSIMMs to study the feeding ecology of fox populations in the UK. As a generalist species, using BSIMMs to estimate the contribution of the array of isotopically similar food sources is particularly challenging (Lerner et al., 2018). This can be remedied with the use of informative priors based on complementary diet studies (e.g., scat analysis or direct observations) (Lerner et al., 2018; Robinson et al., 2018). Although informative priors could be used to improve model performance, care should be taken not to propagate bias into the BSIMM analysis (Swan et al., 2020a; Lerner et al., 2018); regardless, having already robust diet information would diminish the merits of using a BSIMM (Swan et al., 2020a). The results suggest that human food waste is a minor contributor of fox diet across the predominantly rural sampling area in agreement with previous findings (Fletcher et al., 2025; but see chapter three), although this resource is likely more important in urban areas where immigrants might also originate from. Alternative diet methods such as metabarcoding might lead to less ambiguous results, are more suitable to study fine-scale feeding patterns, and would improve the taxonomic resolution of consumed food items.

5. Optimising predation control in Great Britain to enhance species conservation: A case study in the New Forest using FoxNet

5.1. Abstract

Mesopredator overabundance is an emerging global conservation dilemma. In the UK, the red fox (*Vulpes vulpes*) has been linked to declines in native wildlife, especially ground-nesting wader birds. Lethal control methods (culling) such as shooting with a rifle at night, are commonly implemented to control fox populations. In the New Forest National Park (NFNP), fox culling is conducted by a team of wildlife managers to seasonally reduce fox densities during the spring and early summer (March-July) and limit nest predation on threatened waders. However, the development of flexible, predictive management tools to evaluate the efficacy of fox control in this context has been lacking. An existing agent-based model, known as FoxNet, was adapted to model the current fox control programme in and around the NFNP and test the effects of various alternative local and regional management scenarios. This included changing the weekly search time during the regular culling season, extending the culling season whilst keeping the total number of search hours per annum constant, introducing secure lidded bins to the New Forest area to reduce access to human food waste, and reducing regional rural habitat productivity. At equilibrium, models of the current management programme projected a reduction in pre-breeding fox density of 55% relative to a situation whereby no culling took place. The observed number of foxes culled per year (average during 2022 & 2023) fell just under the simulated distribution after five years of culling. More intense search effort did not reduce fox density any further in the long-term. In addition to maintaining the current culling efforts, reducing regional rural habitat productivity by 25%, by scaling back gamebird releases for example, was the only alternative management scenario that would have a significant effect, reducing pre-breeding fox density by 20%.

5.2. Introduction

Humans have controlled predators in the UK for hundreds of years (Reynolds & Tapper, 1996). Large-bodied 'apex' predators (e.g., grey wolf *Canis lupus* and Eurasian lynx *Lynx lynx*) were extirpated centuries ago, but targeted predator control continues for some of the mesopredator (medium-sized & occupying a mid-ranking trophic level) species that have persisted, including the red fox (*Vulpes vulpes*) (Reynolds, 2000). Estimates suggest that total fox population size in Great Britain has increased by an order of magnitude since the Mesolithic (~7 kya), when the island was predominantly covered by woodland (Maroo & Yalden, 2000), to around 375,000 individuals (Mathews et al., 2018). The elevated abundance of foxes in the present day has contributed to high rates of predation on livestock (Heydon & Reynolds, 2000a), economically valuable species (e.g., gamebirds such as pheasants *Phasianus colchicus and* red-legged partridge *Alectoris rufa*; Sage et al., 2018) and those of conservation concern, notably ground-nesting birds (McMahon et al., 2020; Roos et al., 2018; Franks et al., 2017). Reducing their impact on prey species is therefore one of the primary motivations for suppressing fox population densities via culling on farms, game-shooting estates, and conservation areas (Swan et al., 2020b; Heydon & Reynolds, 2000a).

Given the ethical concerns regarding the use of culling to control predator species (Laidlaw et al., 2021), and its substantial economic burden, such practises are justified only when supported by empirical analyses corroborating their effectiveness in supressing population densities of the targeted species and reducing their impact on the wider ecosystem (Lennox et al., 2018). In common with other target species (e.g., mink; Reynolds et al., 2013), a major challenge confronted by restricted-area fox culling is their rapid replacement in areas of high immigration pressure (Porteus et al., 2018a). Indeed, the relative effectiveness of culling in limiting local fox densities below carrying capacity can vary due to regional differences in population density (Porteus et al., 2019a; Lieury et al., 2015).

In the UK, shooting with a rifle and spotlight (or other device such as a thermal imager), also known as ‘lamping’, is often used as a method of controlling fox density in areas of conservation interest. This can be conducted from a vehicle high seat whilst intermittently driving along a transect between detections (Heydon et al., 2000). Alternatively, managers can be stationary allowing foxes to wander into view (‘sit & wait’) or pursue them on foot (‘foot stalking’). The effectiveness of this kind of fox management can be evaluated using an experimental approach, although these are costly, ethically controversial and typically need to take place over several years before reaching solid conclusions (Baines et al., 2023; Lennox et al., 2018; Tapper et al., 1996). Moreover, their generality to a range of situations is compromised by controlling for other variables that could influence the effectiveness of fox control (e.g., productivity of the surrounding landscape). The state-space modelling approach developed by Porteus et al. (2019a) uses culling data to reconstruct the population dynamics of fox populations on restricted areas where they are managed. Unlike previous modelling applications (McLeod & Saunders, 2014), these models fit demographic parameters to each population individually, rather than relying on literature-derived values, hence the output is highly informative to a given situation once fitted to specific cull data from an individual estate. However, these models similarly require at least three years of culling effort data to yield robust density outputs (Porteus, 2015), which can be costly to obtain, and such estimation models do not readily allow for alternative fox culling programmes to be evaluated in a spatially explicit format (Porteus, 2015).

An alternative approach to evaluate the potential impact of fox culling and advise conservation efforts that can effectively circumvent the disadvantages of the evaluation methods mentioned above is agent-based modelling (ABM), whereby the behaviour of individuals (i.e., ‘agents’) is programmed to study the emergent properties of a system based upon assumptions about input parameters (Railsback & Grimm, 2019). Hradsky et al. (2019) introduced a spatially explicit, agent-based model, ‘FoxNet’, as a modelling tool to simulate fox population dynamics, including their response to population control using toxic baits and changing habitat productivity. The ability to customise demographic parameters (Table 5.1) and incorporate uncertainty is an important advantage of FoxNet over previous fox ABMs (Hradsky et al., 2019). FoxNet has reproduced quantitative aspects of fox populations across different habitats - for example - the relationship between fox family density and home range size based on field data throughout the Northern Hemisphere (Hradsky et al., 2019). The model has since been used to evaluate a variety of existing fox control programmes in Australia involving the use of poison baits (Francis et al., 2020), illustrating its potential as a tool to refine management practises.

Parallel advances have improved understanding of aspects of lamping, notably an empirical range for the rate of successful search of fox control practitioners, a parameter that incorporates the detectability of foxes using this method (Porteus et al., 2019b). Alongside data on other parameters that the ABM uses to predict fox density, this information allows for a plausible distribution for the number of foxes killed for a given number of search hours to be specified.

Aside from culling intensity, food availability can also influence the survival rate of foxes (Bino et al., 2010). Prevalent food subsidisation is associated with extremely high fox densities in some cases (Porteus et al 2024; Main et al., 2020). Limiting access to these food subsidies could therefore be an effective alternative way to manage fox densities. In the New Forest National Park (NFNP) in central southern England, there is evidence that foxes are being subsidised by access to human food waste, which comprised at least 14% of overall diet, likely due to poor waste sanitation (chapter three). Region-wide, there is evidence of widespread consumption of Galliformes (domestic chickens *Gallus gallus domesticus*, pheasants, and red-legged partridges), of which the dominant contribution is likely to be from released gamebirds (chapter four).

Here, this information was integrated into the FoxNet framework (Figure 5.1), to test how a culled fox population in the NFNP would respond to potential local and regional management scenarios, including changes to the intensity and timing of the existing culling programme and reducing food availability to foxes. Two attributes of lamping strategy that can be manipulated to optimise its effectiveness were tested: the annual timing of lamping, and the number of hours spent lamping (search hours) per week. The effect of reducing habitat productivity at a local and regional scale was also tested.

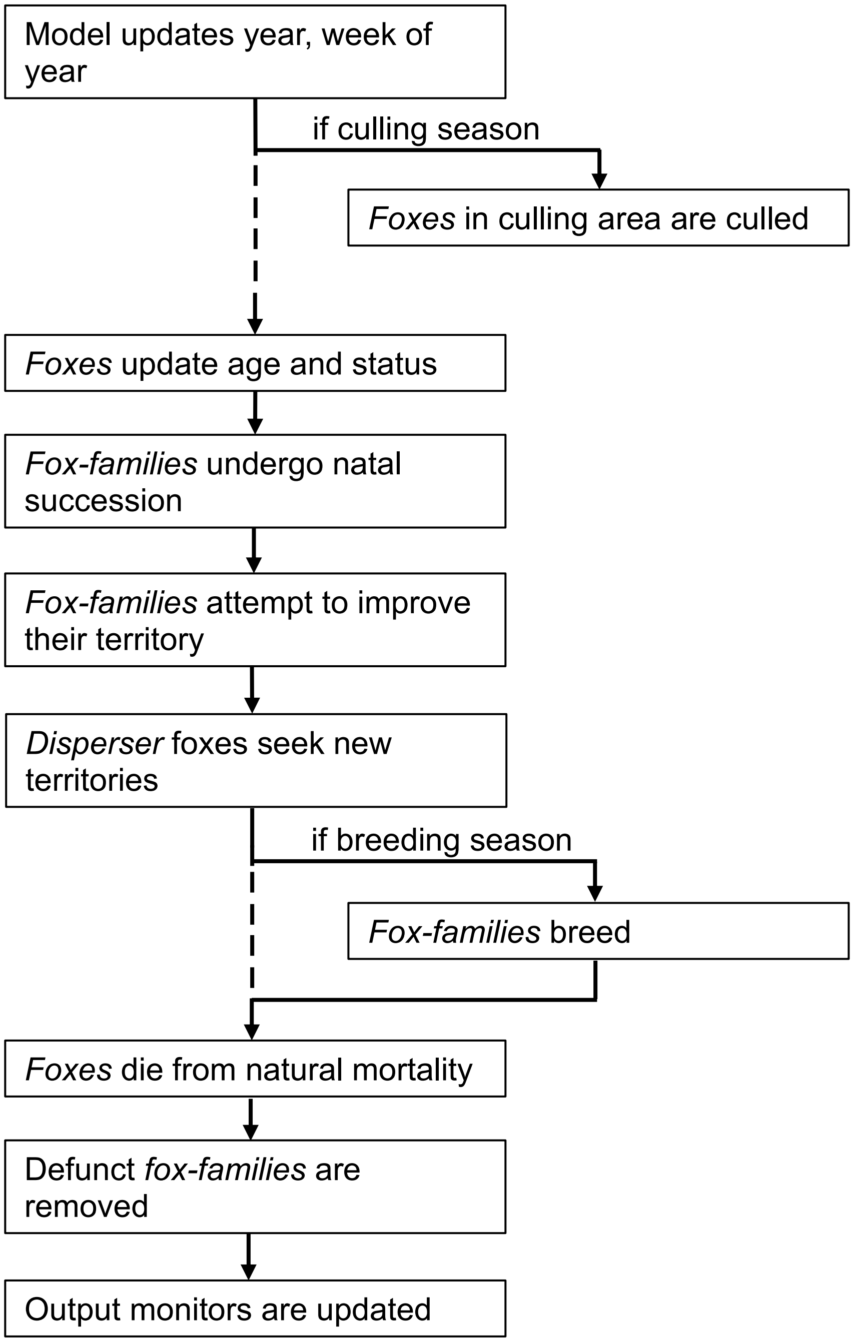


Figure 5.1. The sequence of processes in the FoxNet modelling framework, modified from Hradsky et al. (2019). This sequence repeats in each time step.

5.3. Methods

i. Study area

Fox control was modelled in a ~280 km^2 area managed by a team of eight wildlife managers within the NFNP, where the primary aim of fox control is to improve the local breeding productivity of threatened ground-nesting birds, such as Eurasian curlew (*Numenius arquata*) (A. Page, pers. comm.). Here, lamping in a vehicle along a transect in is the principal method of fox control, accounting for 67% and 64% of foxes culled in 2022 and 2023, respectively. Less widely used methods of lamping are 'sit & wait' (30% & 33%) and 'foot stalking' (3% & 2%). Lamping is typically conducted from the start of January to the end of July, coinciding with the reproductive season for ground-nesting birds (March-July), with little to no fox control outside of this period. In 2022, the average weekly (January 1st – July 31st) search time per wildlife manager was 4.93 hours (range: 1.38 – 12.82). In 2023, this was 2.21 hours (range: 0.75 – 6.01).

ii. FoxNet and model parameters

FoxNet was adapted to simulate fox population dynamics within the NFNP and surrounding region. An in-depth description of FoxNet is available elsewhere (Francis et al., 2020; Hradsky et al., 2019). In brief, a sequence of processes is repeated during each timestep (Figure 5.1):

1. Year and week counters are updated by the *weeks-per-timestep* (i.e., 1, 2 or 4 weeks).
2. The baiting procedure in the original FoxNet schedule has been replaced with a culling procedure that simulates lamping. If it is the culling season (i.e., weeks between *culling-season-begins* and *culling-season-ends*) a number of non-cub foxes are killed, determined by product of the *search-hrs-per-week*, *kill-rate*, fox density across the culling area, and the rate of successful search drawn from a lognormal distribution.
3. The age of each individual fox is updated by a number of weeks equal to the *weeks-per-timestep*. Cubs at *age-of-independence* become subordinates. During the dispersal season (i.e., weeks between *dispersal-season-begins* and *dispersal-season-*

ends), male and female subordinate foxes become dispersers with a sex-specific probability (*male-dispersers, female-dispersers*).

4. Natal succession occurs when fox families lack an alpha fox of a given sex. A subordinate in the fox family of the sex with no alpha representatives are promoted to alphas.
5. Territory improvement occurs whereby fox families maximise the productivity and efficiency of their territory.
6. If it is the dispersal season, disperser foxes leave their natal family.
7. If it is the *cub-birth-season*, fox families with both an alpha male and female produce a number of cubs drawn from a Poisson distribution with a mean equal to the *number-of-cubs*. The sex ratio of cubs produced is determined by the *propn-cubs-female*.
8. Background fox mortality occurs at rates determined by the age of the fox (*less1y-survival*, *from1yto2y-survival*, *from2yto3y-survival*, *more3y-survival*).
9. Cubs belonging to families without any alpha foxes die. Defunct fox families are removed from the model.
10. The model outputs (e.g., fox density) are updated. The model stops if no fox agents are alive at the end of the timestep or if the predetermined number of timesteps has elapsed (*duration*).

A custom landscape was divided into 1 hectare habitat cells (Figure 5.2). In FoxNet, fox dispersal distance is drawn from an exponential distribution with a mean proportional to the home range size (Trewhella et al., 1988), therefore the NFNP was buffered by 40 km to account for > 95% of foxes that are within dispersing range (Hradsky et al., 2019). A line shapefile was included to act as a barrier along the coastline to prevent unrealistic fox dispersal across open seawater. The landscape was built with QGIS (QGIS Development Team, 2023) and an existing shapefile was used to represent the NFNP. The Isle of Wight was excluded from the landscape, as a population genetic analysis suggested that those foxes were reproductively isolated from the mainland (chapter two).

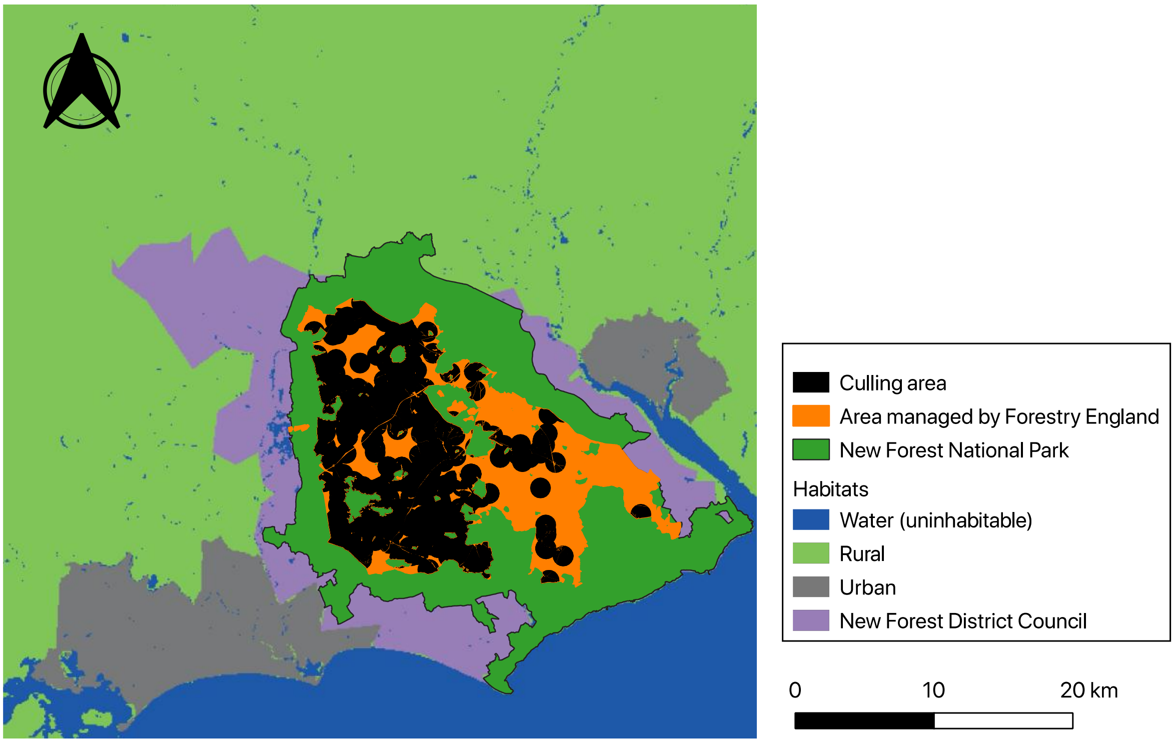


Figure 5.2. Regional landscape raster used in the present study, including the background landscape and the New Forest National Park.

Timestep length in FoxNet was set to one week (‘*weeks-per-timestep*’; Table 5.1), meaning that a full year corresponded to 52 timesteps with week 1 starting in January. Following Francis et al. (2020) the fox population was initialised at 0.5 fox km^{-2} (‘*initial-fox*-density’) and run for 10 years in each simulation, allowing it to reach equilibrium prior to the commencement of management (if applicable) for a further 10 years. FoxNet was originally developed to model the effects of a poison baiting programme on fox population dynamics, reflecting the culling method commonly implemented to control invasive foxes in Australia (Hradsky et al., 2019). To model culling by lamping in Britain this was replaced with an additional model procedure, which is described below (see ‘Culling’). Each model scenario was run for 10 iterations to capture variation in fox population dynamics owing to stochasticity. The FoxNet simulations were run using the software Netlogo (v6.2.2; Wilensky, 1999). As described below, the model input parameters were based on geographically relevant empirical data collected within the region wherever possible (Table 5.1).

- Reproduction

For the mean number of cubs per fox family (‘*number-of-cubs*’), the mean litter size (mean = 4.38, SE = 0.54) of vixens sampled between 1996-2000 (N = 21) within the study region (i.e., Hampshire, Wiltshire, Dorset) during the Fox Monitoring Scheme was used (‘FMS’, Porteus, 2015). Fox families annually produced a Poisson distributed number of cubs with a mean equal to the *number-of-cubs*:

$$\textit{number-of-cubs} \sim \textit{Pois}\ (\mu = 4.38) \tag{1}$$

For the week of the year when cubs are born (‘*cub-birth-season*’), the projected birth date from prenatal uteri samples (N = 10) opportunistically obtained from individuals culled in the NFNP from 2021-2022 was used, which was the 23rd March corresponding to week 12 in FoxNet. The proportion of cubs that were female (‘*propn-cubs-female*’) was set to 0.5 (Heydon & Reynolds, 2000b).

- Home range size

To represent the average home range size of rural foxes (‘*home-range-area*’), the mean estimate from a previous study on an 11 km^2 area of mixed farmland within the focal region was used (mean = 2.71 km^2; Reynolds & Tapper, 1995). There is evidence of anthropogenic subsidisation of foxes in the NFNP, where identifiable human food comprised 14% of the mean percent volume of fox stomachs (chapter three). The district council area that encompasses the NFNP is unique within the region, in that it does not yet use wheelie bins (lidded refuge bins) as part of its waste disposal system, instead utilising plastic refuse bags typically left on the roadside overnight, which could be providing foxes (and other wildlife) easier access to organic refuse. To model this increased food availability relative to areas outside the NFNP, a third habitat type was introduced defined by the jurisdiction of the New Forest District Council (https://geoportal.statistics.gov.uk/datasets/ons::local-authority-districts-may-2022-uk-bfe-v3-1/about), setting the productivity ratio between this habitat and rural habitat to 1.14:1 (‘*hab3:hab1*’).

The home range size of suburban foxes in Britain also varies, typically between 10-200 ha (Kobryn et al., 2023; Tolhurst et al., 2016). The fox family density recorded for Bournemouth (4.35 fox families km^{-2} or 0.22 km^{2} fox family^{-1}; Scott et al., 2018) was used to calculate the productivity ratio between urban and rural areas (12.32:1; ‘*hab2:hab1*’). Urban areas in the customised regional landscape covered the local authority districts of Bournemouth, Christchurch and Poole, and Southampton (https://www.planning.data.gov.uk/dataset/local-authority).

- Survival

The survivorship of foxes can differ markedly between populations depending on local circumstances, such as culling intensity (Heydon & Reynolds, 2000b). Culling in the NFNP was additive to background age-based ‘natural’ fox mortality, therefore using survival rate parameters from an exploited population would lead to culling mortality being applied twice to the population. As such, survival rates should reflect those from an unexploited population. Porteus et al. (2018b) used a Bayesian hierarchical model to predict total instantaneous mortality rate for unexploited British foxes according to maximum longevity, thereby accounting for intrinsic (e.g., genetic or degenerative disease) and extrinsic (e.g., road-traffic accidents, infectious disease, inter- and intraspecific competition) causes of non-culling mortality. Converting the median posterior estimate of total instantaneous mortality rate to a finite annual survival rate gives a value of 0.71 (i.e., $e^{-0.34}$). Adult foxes show little evidence of senescence, with negligible variation in survival rates between adult age-classes (Lloyd, 1980); therefore, this value was adopted for all adult age classes defined in FoxNet (‘*from1yto2y-survival*’, ‘*from2yto3y-survival*’, ‘*more3y-survival*’). For juvenile survival rate (0-1 years), a value of 0.65 (‘*less1y-survival*’) was adopted, equating to the same proportional difference in juvenile and average adult survival rates from an unexploited urban fox population in Bristol (Devenish-Nelson et al., 2013).

Age-based survival rates reported for the unexploited urban fox population in Bristol (0.48-0.54) are lower than the estimate from Porteus et al. (2018b), possibly due to greater incidences of density-dependent (e.g., disease & intraspecific aggression) and density-independent (e.g., road traffic collisions) causes of mortality (Harris & Smith, 1987). To account for this, a procedure was included to offset the natural survival rate for foxes inhabiting urban areas to match those recorded from Bristol (Devenish-Nelson et al., 2013).

- Dispersal

In the simulations, dispersal season began in week 37 (‘*dispersal-season-begins*’) and ended in week 9 of the following year (‘*dispersal-season-ends*’; Trewhella & Harris, 1988). In general, more males disperse from their natal territories than females, and dispersal rates seem to be lower in resource-rich habitats (Gosselink et al., 2010). As no regional estimates of sex-specific dispersal rates are available, the sex-specific dispersal rates recorded in Bristol were used: 0.758 (‘*male-dispersers*’) and 0.378 (‘*female-dispersers*’), respectively (Trewhella & Harris, 1988).

- Culling

In a gamekeeper-fox culling system, the number of foxes observed during lamping in week t, Y_t, is given by:

$$Y_t = s_t E_t D_t \tag{2}$$

where E_t is the search time (hrs), D_t is the fox population density (foxes km^{-2}), and s_t is the rate of successful search (km^2 hr^{-1}), a scaling factor given as follows:

$$s = p2rv \tag{3}$$

where p is the detection probability, r is the gamekeeper field of view radius (km; 2r representing the field of view diameter), and v is the speed of travel (km hr^{-1}). Porteus et al. (2019b) developed an informative prior for s based on a distance-sampling study of three different regional fox populations in Britain that used a spotlight to detect foxes, akin to lamping (Heydon et al., 2000). This prior can be updated using Bayesian state space models fitted to timeseries of fox sightings (Porteus et al., 2019a). Lamping is predominantly conducted by wildlife managers in the NFNP using a vehicle and a thermal imager, rather than a spotlight, to detect foxes. The posterior distribution for s from a model fitted to data from a privately managed estate adjacent to the NFNP using this culling method (T. Porteus, pers. comm.) was lognormally distributed with a mean of 0.348 and a standard deviation of 0.071:

$$s \sim Logn\ (\mu = -1.076,\ \sigma = 0.202) \tag{4}$$

This distribution for s was applied to a modified version of [2], to give the number of foxes removed by lamping in a timestep, L_t, as:

$$L_t = Ks_tE_tD_tT \tag{5}$$

where T is the number of weeks per timestep, and K is the kill success of wildlife managers in the NFNP; the proportion of foxes successfully killed out of the total number of foxes observed. Values of s were drawn from the lognormal distribution at each timestep during the culling season. In addition to the number of foxes killed, the wildlife managers in the NFNP also recorded the number of foxes seen during their lamping activities. During the culling seasons in 2022 and 2023, 640 foxes were seen and 356 were killed during lamping, giving an estimate for the long run average K of 0.56. Each wildlife manager recorded their cumulative search time on each night of lamping (Figure 5.3). Finally, D_t in the NFNP was monitored at the start of each timestep by default in FoxNet.

The number of foxes culled per week (L_t) was rounded to the nearest whole number, and a corresponding number of foxes inhabiting the NFNP of ≥ 8 weeks old (‘*age-at-independence’*; Lloyd, 1980) were then selected at random to die during each timestep in the culling season. Fox cubs (i.e., younger than the age at independence) have yet to emerge from their natal earths and therefore not directly susceptible to lamping. Nevertheless, cubs will be indirectly affected by lamping if all remaining adults in their family are killed, in which case they are also programmed to die (Hradsky et al., 2019). Lamping commenced in year 11 (‘*commence-culling-year*’) after 10 years of allowing the population to equilibrate and ended after year 20 (‘*stop-culling-year*’).

The culling intensity of foxes varies throughout the study region; restricted areas with fox control, contrasted with areas where no culling takes place. To account for background culling mortality, a culling procedure like that in the NFNP was applied to rural areas outside the NFNP (background landscape). To estimate the total number of search hours throughout background landscape per week, data from five estates in southern England where fox control data were collected from 1996 – 1999 as part of the FMS was extrapolated to the size of the wider region (Porteus, 2015). Based on these data, 119 search hours per week were estimated across this background landscape throughout the year. The same distribution of rate of successful search for the NFNP was used, although a separate estimate for kill rate was adopted (0.31) according to empirical data from the FMS (Porteus, 2015). An additional multiplier was included in equation 5 to predict weekly cull in the background landscape, the proportion of landholdings that practise fox control (0.43), to account for the proportion of rural areas where fox control is absent (Defra, 2012). No culling procedure was applied to urban areas.

There are some parts of the managed area in the NFNP that are more suitable for detecting and shooting foxes at night (e.g., open areas with good visibility and suitable backstops), whereby managers focus their search effort. To infer the distribution of these areas, the recorded locations of foxes culled from 2021 to 2024 were taken and buffered by 500 m. These buffers were exported as a shapefile and used in FoxNet as the area where fox culling by NFNP managers was restricted to (i.e., culling area).

iii. Model scenarios

- Changing weekly search hours: To represent the existing or ‘business-as-usual’ situation, the E_t was set equal to the average number of search hours per week during the regular culling season, according to the logbooks provided by the NFNP wildlife managers during the 2022 and 2023 culling seasons as these were complete annual records. The time spent lamping along a transect in a vehicle was combined with the time spent on ‘sit and wait’, which combined accounted for ~97% of foxes culled; assuming that a fox travels at a similar speed as a manager, the two methods are analogous (Porteus et al., 2019b). Few search hours occurred in January and February (< two hours per week), with more intense effort occurring between March – July. Therefore, the culling season was set to run from February 26th (week 9; ‘*culling-season-begins*’) – July 15th (week 28; ‘*culling-season-ends*’) (Figure 5.3). Across both years, the mean search hours per week during this time window was 45 hours (SD = 29.29) (‘*search-hrs-per-week*’). Changing the search time per week was tested in increments of 25 hours, ranging from 0 – 100. This provided scenarios ranging from where there was no lamping, to more than doubling the intensity of effort.

- Extending the culling season: A previous study showed that culling was only effective at reducing annual fox population growth rate when timed to coincide with the fox dispersal season (Lieury et al., 2015), by mitigating compensatory immigration during this period. It was considered that lamping at this time could help further reduce fox densities at the beginning of the wader nesting period. To maintain existing annual efforts, the effect of halving the search hours per week to 22.5 was tested, whilst doubling the length of the culling season by setting it to commence in week 41 (8th – 14th October; 4th week of the dispersal season) of the previous year and stopping in week 28.
- Introducing wheelie bins to the NFNP: While keeping the search hours per week and the culling season the same as the business-as-usual scenario, the impact of adjusting the productivity ratio of the two rural habitat types to 1:1 at the beginning of year 11 was tested to simulate the removal of the additional anthropogenic food resource.
- Reducing regional rural productivity: Using the same search hours per week culling season as the business-as-usual scenario, the impact of reducing the productivity of the two rural habitats by 25% was tested, while keeping the urban habitat productivity the same by increasing the hab2:hab1 ratio proportionately (15.40:1). The value of 25% is the approximate region-wide overall proportion of Galliformes to fox diet determined from a stable isotope analysis (chapter four).

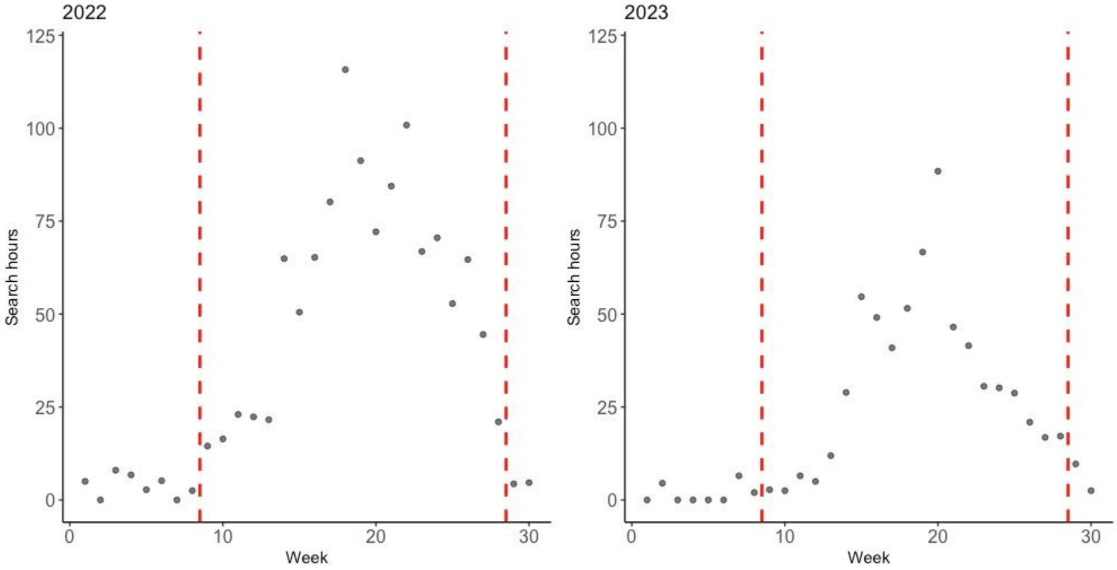


Figure 5.3. Search hours by week of year during the 2022 and 2023 culling season. Vertical dashed red lines show the regular culling season used in the present study (except model scenario ii; ‘Extending the culling season’).

Table 5.1. Parameters and data sources for the New Forest model in FoxNet model.

Model parameter	Unit	Value	Reference
duration	timesteps	1040	-
weeks-per-timestep	weeks	1	-
cell-dimension	ha	100	-
hab2:hab1	ratio	12.32:1	Scott et al. (2018)
hab3:hab1	ratio	1.14:1	Chapter three
Fox parameters			
initial-fox-density	no. km^{-2}	0.5	-
range-calculation	-	"1 kernel, 1 mean"	-
home-range-area	km^2	2.71	Reynolds & Tapper (1995)
less1y-survival	propn.	0.64	Porteus et al. (2018b)
from1yto2y-survival	propn.	0.71	Porteus et al. (2018b)
from2yto3y-survival	propn.	0.71	Porteus et al. (2018b)
more3y-survival	propn.	0.71	Porteus et al. (2018b)
cub-birth-season	week of year	12	GWCT (unpubl. data)
number-of-cubs	no. fox family^{-1}	4.38	GWCT (unpubl. data)
propn-cubs-female	propn.	0.5	Heydon & Reynolds (2000b)
age-at-independence	weeks	8	Lloyd (1980)
dispersal-season-begins	week of year	37	Trewhella & Harris (1988)
dispersal-season-ends	week of year	9	Trewhella & Harris (1988)
female-dispersers	propn.	0.378	Trewhella & Harris (1988)
male-dispersers	propn.	0.758	Trewhella & Harris (1988)
Barrier parameters			
propn-permeable-barrier	propn.	0	-
Culling parameters			
commence-culling-year	year	11	-
stop-culling-year	year	21	-
culling-season-begins	week of year	variable	GWCT (unpubl. data)
culling-season-ends	week of year	variable	GWCT (unpubl. data)
search-hrs-per-week	hours	variable	GWCT (unpubl. data)
search-hrs-per-week-background	hours	119	GWCT (unpubl. data)
kill-rate	propn.	0.56	GWCT (unpubl. data)
kill-rate-background	propn.	0.31	Porteus (2015)

5.4. Results

In the scenario with no lamping, from year 11 onwards the mean non-cub fox density (foxes km^{-2}) across iterations fluctuated annually between a minimum average of 3.08 and a maximum average of 4.68 coinciding with the recruitment of subordinates in week 20 (Figure 5.4). The mean pre-breeding fox density (week 11) in year 20 was 3.35 (range: 3.24 – 3.52) (Table 5.2). The results of the other scenarios were evaluated relative to this scenario at equilibrium.

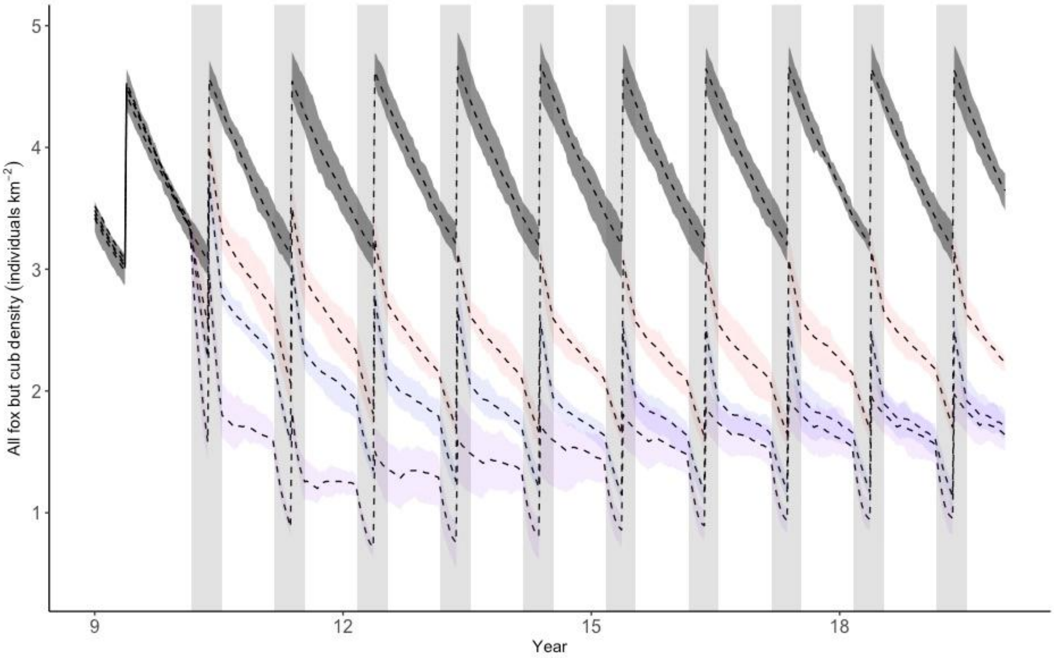


Figure 5.4. Simulated adult fox (i.e., excluding cub) densities for the NFNP according to weekly search time (hrs week^{-1}) during the culling season: 0 (grey), 25 (red), 45 (blue), and 100 (purple) hrs week^{-1}. Note that 50 and 75 hrs week^{-1} scenarios are omitted for clarity. Vertical grey bands indicate the duration of the culling season in each year for reference (weeks 9-28). Colour shaded areas are minimum and maximum densities across all 10 iterations for each scenario. Culling commenced in year 11 and continued until the end of the simulations.

i. Changing weekly search time

The model with 25 search hours per week during the culling season resulted in a continuous decline in average pre-breeding fox density before stabilising from year 15 onwards, with a 40% (mean = 2.04, range: 1.93 – 2.14) reduction relative to the scenario with no lamping in year 20 (Figure 5.4; Table 5.2). Similarly, models with 45 (business-as-usual) and 50 search hours week^{-1} during the culling season resulted in a decline in average pre-breeding fox density until year 15 onwards, with reductions of 57% (mean = 1.45, range: 1.34 – 1.55) and 59% (mean = 1.37, range: 1.21 – 1.48) relative to the scenario with no lamping in year 20, respectively (Figure 5.4; Table 5.2). Models with 75 and 100 search hours week^{-1} during the culling season resulted in an initial sharp decline in average pre-breeding fox density until year 12, after which it rebounded steadily until year 17, with reductions of 61% (mean = 1.31, range: 1.15 – 1.48) and 62% (mean = 1.26, range: 1.17 – 1.37) relative to the scenario with no lamping, respectively (Figure 5.4; Table 5.2). As such, fox densities converged in scenarios with 45 hours or more search hours per week during the culling season, resulting in non-significant differences in pre-breeding fox density by year 20.

The overall number of foxes culled during the culling season in each scenario responded to changes in fox density. In the scenarios with 25, 45, and 50 hours of culling during the culling season, the number of foxes culled declined each year before stabilising from year 15 onwards at a mean of 222 (range: 201 – 246), 298 (range: 261 – 332) and 305 (range: 259 – 346) foxes per year, respectively (Figure 5.5). The average number of foxes culled across the NFNP during the 2022/23 culling seasons (N = 271) was comparable to that from the business-as-usual scenario towards the end of the simulations, falling just below the range across all iterations, indicating that the model was reasonably well calibrated. In the scenarios with 75 and 100 hours of culling per week during the culling season, the number of foxes culled declined sharply with fox density in the first three years, before rising steadily each year with a mean of 435 (range: 361 – 520) and 578 (range: 513 – 636) in year 20, respectively (Figure 5.5).

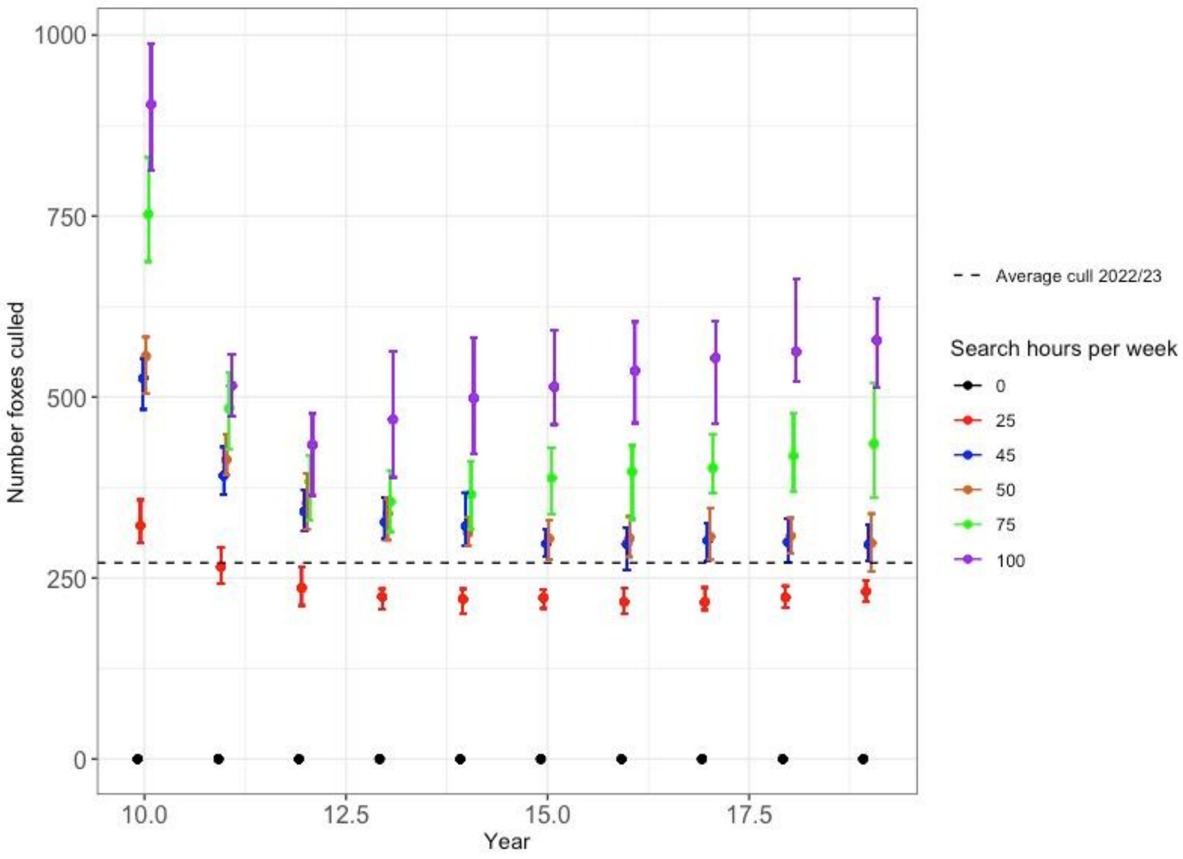


Figure 5.5. Number of foxes culled during each culling season according to the number of weekly search hours. Points show mean values and error bars show minimum and maximum values across all 10 iterations.

ii. Extending the culling season

The effect of doubling the length of the normal culling season by extending it back into the fox dispersal season was examined, while halving the number of search hours per week to 22.5 to give the equivalent number of total annual hours as the business-as-usual culling season. This resulted in a small reduction in pre-breeding fox density (mean = 1.26, range: 1.17 – 1.40; Table 5.2) relative to the business-as-usual scenario (13.1%). However, post-culling fox densities (mean = 1.90, range: 1.78 – 2.09) were slightly larger than the business-as-usual scenario (mean = 1.98, range: 1.85 – 2.23; Table 5.2).

iii. Introducing wheelie bins to the NFNP

The introduction of wheelie bins into the New Forest District council area by reducing the habitat productivity ratio down to 1:1 after 10 years was simulated, using the same culling season and search hours per week as the business-as-usual scenario. This resulted in a small reduction (5.1%) in pre-breeding fox density (mean = 1.38, range: 1.27 – 1.45; Table 5.2) relative to the business-as-usual scenario. Similarly, there was a small reduction in the number of foxes culled during the culling season, averaging 282 (range: 243 – 327) from year 15 onwards, 5.4% lower than the business-as-usual scenario.

iv. Reducing regional rural productivity

The impact of a 25% reduction in regional rural habitat productivity was simulated, using the same culling season and search hours per week as the business-as-usual scenario. This resulted in a significant reduction (20%) in pre-breeding fox density (mean = 1.16, range: 1.07 – 1.22; Table 5.2) relative to the business-as-usual scenario. The number of foxes culled during the culling season with a lower regional rural productivity, averaging 244 from year 15 onwards, was 18.1% fewer than the business-as-usual scenario.

Table 5.2. Modelled fox densities, mean foxes km^{-2} (min - max), in selected weeks during the 5th and 10th year of culling.

Model scenario	Search hours week^{-1}	Pre-breeding (week 11)		Post-culling (week 29)	
		Year 15	Year 20	Year 15	Year 20
Business-as-usual	45	1.47 (1.37 - 1.55)	1.45 (1.34 - 1.55)	1.93 (1.78 - 2.07)	1.90 (1.78 - 2.09)
Change weekly search time					
	0	3.39 (3.13 - 3.57)	3.35 (3.24 -3.52)	4.33 (4.08 - 4.53)	4.33 (4.12 - 4.53)
	25	1.95 (1.87 - 2.05)	2.04 (1.93 - 2.14)	2.54 (2.42 - 2.67)	2.61 (2.51 - 2.75)
	50	1.34 (1.26 - 1.43)	1.37 (1.21 - 1.48)	1.71 (1.26 - 1.43)	1.74 (1.57 - 1.87)
	75	1.18 (1.01 - 1.34)	1.31 (1.15 - 1.48)	1.57 (1.30 - 1.76)	1.80 (1.42 - 2.09)
	100	1.15 (1.00 - 1.28)	1.26 (1.12 - 1.37)	1.67 (1.44 - 2.00)	1.82 (1.63 - 1.99)
Extend the culling season	22.5	1.31 (1.18 - 1.41)	1.26 (1.17 - 1.40)	1.97 (1.75 - 2.20)	1.98 (1.85 - 2.23)
Introduce wheelie bins	45	1.44 (1.30 - 1.51)	1.38 (1.27 - 1.45)	1.81 (1.60 - 1.94)	1.76 (1.52 - 1.91)
Reduce regional rural productivity	45	1.21 (1.10 - 1.27)	1.16 (1.07 - 1.22)	1.58 (1.30 - 1.77)	1.51 (1.43 - 1.62)

5.5. Discussion

FoxNet was used to examine the impact of changes to an existing fox control programme in a National Park important for breeding waders in central southern England, in terms of the resulting fox density during the ground-nesting bird breeding season. The findings show that there is no long-term benefit to wildlife managers increasing their weekly hours spent searching for foxes to shoot during the culling season above the existing average, or from extending the culling season into the fox dispersal season. Likewise, improved waste management through the introduction of wheelie bins in the New Forest would have only a small impact on fox density. A regional change in the productivity of rural habitat would result in the most sustainable reduction in fox density in the NFNP under business-as-usual culling efforts.

Although all foxes in the culling area had an equal chance of being culled, there is an unequal chance that a vacant fox territory is recolonised by a disperser. The culling season in the NFNP occurs outside the dispersal season, whereby culled foxes are only replaced by itinerant foxes searching for vacant territories (or existing fox families with an alpha vacancy) towards the periphery of the NFNP, as dispersers search within a territory perception radius that is only three times the size of an average fox home range size (Hradsky et al., 2019). Therefore, vacant territories towards the core of the culling area can only be colonised by dispersers during the dispersal season, creating a gradient of fox density increasing towards the edge of the NFNP (Figure 5.6). After core fox densities have been reduced (i.e., in those areas at a distance greater than the territory perception radius from the edge of the NFNP culling area), a higher proportion of peripheral foxes constitute the cull during subsequent culling seasons, creating vacancies that are within range to be filled by dispersers just outside of the NFNP. Although higher search effort (i.e., 75 – 100 hours per week) instigates a more drastic reduction in core fox density, eventually the larger cull sizes become dominated by foxes on the periphery, which are replaced rapidly by background region dispersers moving onto vacant territories from just beyond the boundary of the NFNP.

According to these findings, where a reduction in fox density is desirable, managers might choose to invest more hours in the first few years of a management programme before scaling back their efforts to a maintenance level after fox densities in the core of the management area have been reduced. Continuing to invest heavily in search hours following this initial reduction is unlikely to have any impact on overall fox density despite higher cull sizes due to compensatory immigration, and therefore cannot be justified from an ecological, ethical, or economic standpoint. In any case, the current time of the NFNP wildlife managers also needs to be spent on various other duties and responsibilities, so it is unlikely that total search time during the culling season can be increased much beyond the existing amount without hiring additional staff. These results also suggest that the overall prospect of safeguarding wader nests from fox predation differs according to their location, being more feasible in core areas of the culling area where fox density can be held more persistently lower during the breeding season, in the absence of more intense background control (Heydon et al., 2000). These findings are probably more applicable to management areas that are of comparable size to the NFNP, or larger (Francis et al., 2020). Given sufficiently high regional fox abundance, compensatory immigration is likely to undermine culling in smaller management areas, where even the core areas are accessible to itinerants outside the dispersal season (Kämmerle et al., 2019a, b; Porteus et al., 2019a; Lieury et al., 2015; Newsome et al., 2014).

Extending the culling season into the fox dispersal season while halving weekly search hours resulted in a slightly lower pre-breeding fox density, although by the end of the culling season fox densities exceeded that of the business-as-usual scenario (Table 5.2). A modelling study of fox populations on five management units of comparable size to the NFNP (246 ± 53 km^2) in rural France found that the dispersal season was the only period in which culling rates were negatively associated with annual population growth rate (Lieury et al., 2015), indicating that autumn dispersal is the dominant factor underpinning how foxes can compensate for culling, as opposed to increased survival or recruitment. However, to the south and east much of the NFNP is bordered by coastline, limiting the areas from which itinerant foxes can arrive from, lowering the potential replacement rate during the dispersal season. Overall fox density did not return to pre-culling levels during the dispersal season, even with the lowest search effort tested during the culling season (i.e., 25 hours per week). Therefore, it is possible that compensation during autumn dispersal is less severe in this study area compared to other landscapes.

The introduction of wheelie bins had only a modest impact on fox density. Foxes were able to compensate for the reduction in productivity by increasing their average home range size, without causing a drastic reduction in fox density. Modelling this scenario is inherently speculative given the uncertainty regarding the exact contribution of anthropogenic food to fox diet in the NFNP; in a stomach content analysis, around 23% of the overall diet consisted of unidentified items so the true contribution could be higher (chapter three). There is also uncertainty whether the introduction of wheelie bins will cause the contribution of human food to fox diet to fall to 0%, and regarding the type of response of the fox population to the removal of this resource (i.e., numerical, or functional; Angerbjorn et al., 1999). Fox home range size is associated with habitat productivity such that more productive habitats promote smaller home range sizes (Main et al., 2020). A previous study demonstrated a rapid reduction in survival following improved sanitation in an area where foxes previously had access to poultry carcasses (Bino et al., 2010), although this likely reflects a situation of a more extreme reduction in food availability. Notwithstanding these findings, improved waste management is still advisable given the other adverse consequences of wildlife consuming human waste (Newsome & Van Eeden, 2017).

Reducing regional rural productivity caused a significant reduction in fox density in the NFNP relative to the business-as-usual scenario. Several previous studies have demonstrated the importance of adopting a regional perspective on fox population dynamics (Lieury et al., 2015; Heydon & Reynolds, 2000b). In the face of compensatory immigration (Porteus et al., 2018a), restricted-area fox culling can fail to achieve its purpose of a significant reduction in fox density (Francis et al., 2020; Newsome et al., 2014), especially in areas surrounded by high densities of foxes (Porteus et al., 2019a). Addressing the root cause of high regional fox densities will therefore lead to a more sustainable outcome (Roos et al., 2018). Although garnering widespread support and collaboration would be challenging, this might be partially achieved by limiting the number of gamebirds released into the countryside each year (Madden, 2021).

Although this study demonstrates the use of a valuable tool to fox control practitioners in a novel context, it is important to acknowledge some key limitations. The reliability of FoxNet in modelling fox control in the NFNP relies on the accuracy of the input parameters (Coulson et al., 2001). Fox demographic rates can vary considerably across their range (Devenish-Nelson et al., 2013), therefore geographically relevant parameter values were sought wherever possible although for some they were unavailable, and thus relied on limited information (e.g., dispersal rates, juvenile survival rate). Certain parameters are likely to be more influential to model output than others (e.g., home-range size), which could be explored further using a sensitivity analysis (Hradsky et al., 2019). This could, in turn, motivate data collection in the field to refine parameterisation and improve model performance. Some parameters will be inevitably more challenging to quantify than others, in which case information could be garnered from meta-analyses or directly from a panel of fox researchers. Alternatively, parameter values can be calibrated to observed data using Approximate Bayesian Computation (ABC). The basic principal involves specifying prior distributions for each unknown ABM parameter and sampling a parameter set from these to use in ABM simulations. The distance (d) from the synthetic data summary to the observed data is then calculated and the parameter set is retained if below a predefined tolerance threshold (i.e., $d \leq \varepsilon$). After repeating these steps many times, the accepted draws approximate the posterior distribution of parameters (De Visscher et al., 2024).

For ABMs such as FoxNet to support future management decision making, it is crucial to objectively evaluate model performance. The FoxNet model has been validated by reproducing fox demographic structure in disparate populations, as well as the association between home range size and fox family density. Here, model performance was assessed by comparing the number of foxes culled *in silico* in the business-as-usual scenario to the average cull size during the 2022 and 2023 culling seasons. The model seemed to perform satisfactorily with the actual cull falling just below the distribution generated from the simulations upon reaching stability in year 15 onwards (Figure 5.5). A distribution for the rate of successful search the rate of successful search from a nearby shooting estate was used, which might account for the observed number of foxes culled being slightly lower than the simulated distribution in the business-as-usual scenario. As such, more specific data on the rate of successful search in the NFNP would benefit model output. Additionally, various other factors might have contributed to this discrepancy, such as errors in the logbook data, the small number of hours invested outside of the 20-week period (week 9 – 28) adopted here for the culling season (Figure 5.2), and differences in the efficiency between hours invested in lamping and sit & wait. Ideally, model performance should be assessed against multiple patterns (Grimm et al., 2005). Another pattern that could be used to validate the model is the accuracy of population density predictions. Contemporary estimates of fox density in the NFNP is not currently available, although population dynamic models could be used to obtain estimates (Porteus et al., 2019a).

The measure of fox control success here is the change in fox density. Arbitrary reductions in fox density have previously been used as a basis to evaluate the success of fox control (e.g., > 65%; Francis et al., 2020). However, ultimately the goal of fox control in the NFNP and many other areas is to reduce predation rates. The relationship between fox density and predation rates are unknown but are likely to be context specific (Porteus et al., 2024). Controlled experiments have demonstrated the effectiveness of fox culling in improving the breeding productivity of ground-nesting birds in certain situations (Baines et al., 2023; Bolton et al., 2007; Fletcher et al., 2010; Tapper et al., 1996). However, these studies often demand a huge investment of time and economic resources. To complement FoxNet, it would be useful to develop models that predict the response of predation rates to changes in fox density (Francis et al., 2020). In the meantime, it is important to monitor the response of wader productivity to fox control. Given that the results herein suggest further reductions are unlikely to be achieved by increasing lamping effort alone, alternative control strategies would need to be considered.

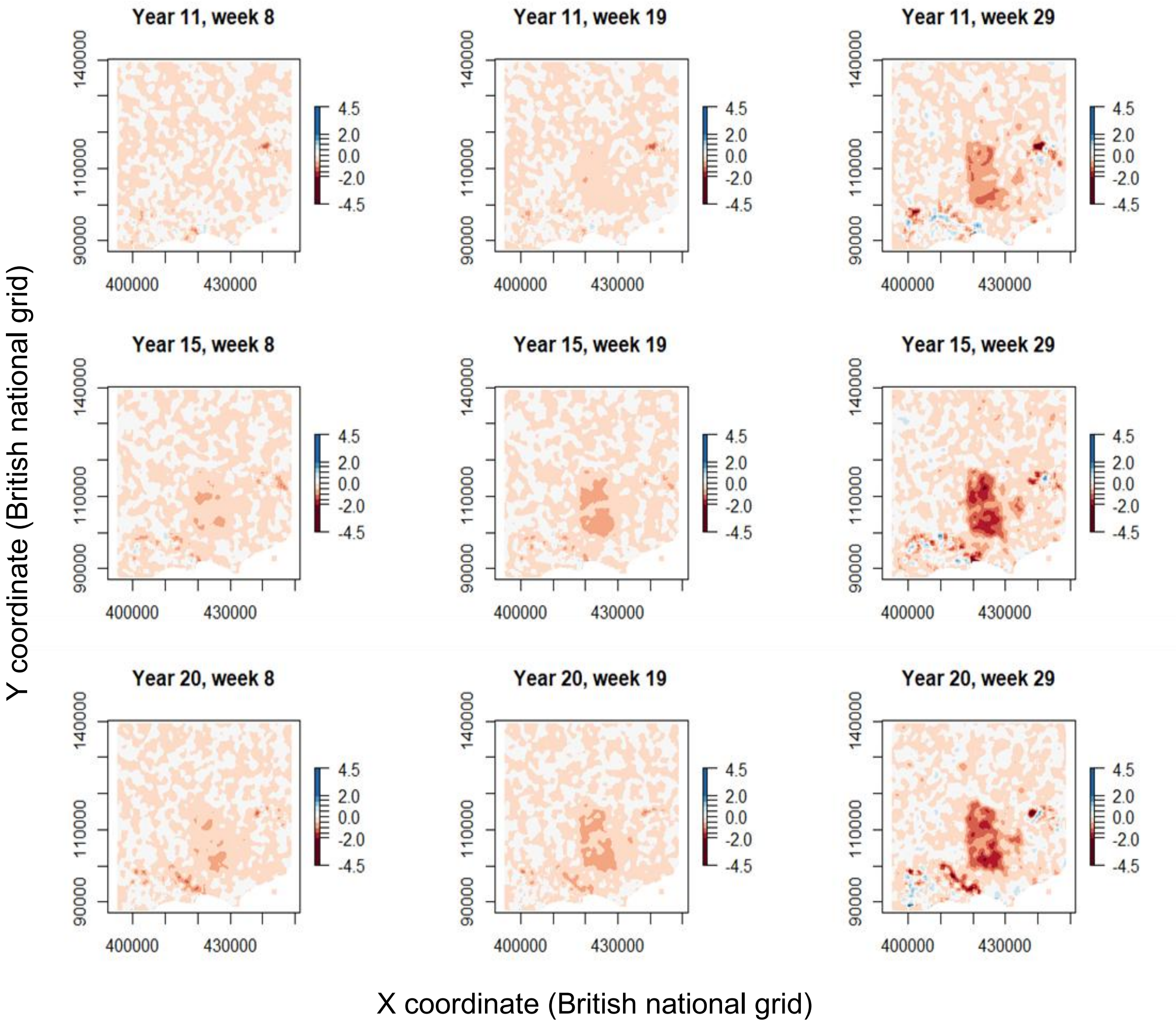


Figure 5.6. Heatmaps of change in non-cub fox density (individuals km^{-2}) for the business-as-usual scenario relative to the scenario with no fox culling in the NFNP during selected weeks in the 1st, 5th, and 10th year of fox culling. Weeks shown correspond to density in pre-culling (week 8), during culling (week 19), and post-culling (week 29) periods.

6. General conclusion

This thesis aimed to shed light on the drivers of fox population dynamics across a large region, with implications for the predation pressure experienced locally by breeding waders. In this chapter, the main findings of each thesis chapter in relation to the original aims are summarised and the implications for management and conservation are highlighted. Suggestions for further work are made that will further improve understanding of how drivers of fox population dynamics, including human activities, contribute to predation pressure of vulnerable prey species.

6.1. Summary of findings and limitations

i. Population genetics and the management unit

Fox populations can compensate for culling or other increased mortality factors by increasing the rate of immigration or recruitment (Pagh et al., 2018; Lieury et al., 2015), although the former is the predominant mechanism among foxes and other carnivores (Lamb et al., 2017; Lieury et al., 2015). Therefore, from a management perspective, compensatory immigration is the primary challenge to effective fox control (Porteus et al., 2019a; Lieury et al., 2015; Newsome et al., 2014). Population genetic structure refers to how genetic variation is spatially distributed among subpopulations of an organism. Using population genetic analysis to ascertain distinct subpopulations, or management units, the surrounding areas ('sources') where immigrants might originate from to repopulate the managed area ('sink') following culling can be identified (Palsbøll et al., 2007). This information could be used to inform the scale and spatial coordination required to mitigate source-sink dynamics and compensatory immigration.

Fox populations do exhibit population structure, although the scale of this varies according to the landscape and markers used to study them. A general conclusion among studies of fox population genetic structure is that foxes exhibit low regional genetic differentiation, due to their high mobility and extensive gene flow (Galov et al., 2014; Kirchning et al., 2007). This highlights their ability to overcome many geographic features that prevent dispersal in other species, homogenising fox populations over large areas. A microsatellite study in Britain showed limited differentiation throughout the country, although some distinct clusters were identified using STRUCTURE (Atterby et al., 2015), which seem to be the result of historical translocations and differences in habitat preferences between urban and rural foxes. These findings are supported by alternative study methodologies. For example, satellite-tagging of foxes within central southern England demonstrated instances of long-distance movements over short periods of time (Porteus et al., 2024), indicating the extensive scale of population processes such as dispersal. Such mobility seems to compromise the efficacy of local fox culling by facilitating the rapid replacement of individuals through compensatory immigration (Porteus et al., 2019a).

In chapter two, a population genetic analysis of fox samples collected throughout the study region was used to gain insight into regional population genetic structure. Two hypervariable mtDNA fragments – Cytb and the D-loop – were used to examine the broad scale fox population genetic structure across central southern England and the Isle of Wight. In accordance with previous studies, genetic differentiation on the mainland was markedly low, whereas the Isle of Wight was consistently differentiated from the mainland sampling areas, confirming The Solent is a natural barrier to dispersal, reproductively isolating individuals from the mainland.

The lack of population structure observed on the mainland implies an extensive management unit and broad coverage of source populations, with movement being limited by distance rather than by physical barriers. Hence, as restricted-area fox control in the New Forest National Park (NFNP) fails to account for the spatial scale of replacement, this helps to explain why culled foxes can be rapidly replaced by itinerants from neighbouring source populations. Given the short-term efficacy of fox control over small spatial scales, there is a sustainability issue associated with culling from practical and ethical standpoints – intense culling needs to take place indefinitely on restricted areas to maintain low fox densities during wader breeding seasons (Porteus et al., 2019a). Although coordinated fox control conducted over large networks of gamekeepered estates can suppress regional fox abundance (Heydon et al., 2000), thereby buffering important conservation areas from compensatory immigration, its implementation is most likely limited by feasibility and cost.

Although the population genetic analysis demonstrated a lack of broad scale genetic differentiation, the relatively short sequences inevitably resulted in a low number of polymorphic sites, preventing an examination of fine scale dispersal patterns between local sites within the study region. As introduced in section 1.5, a more sensitive analysis could utilise reduced representation genomic approach such as restricted-site associated DNA sequencing (RAD-seq) to obtain hundreds to thousands of single nucleotide polymorphic loci throughout the genome (Peterson et al., 2012). The multiplexing capacity of this method combined with next-generation sequencing technology would allow hundreds of polymorphic loci to be collected from several dozen individuals sampled throughout the region, simultaneously. To this end, a RAD-seq library following the protocol of Franchini et al. (2017) using 93 individual foxes sampled throughout the region has been constructed and sequenced, with the initial intention to include the findings as an additional thesis chapter. Due to unforeseen technical difficulties encountered in the laboratory at the library preparation stage of the protocol, this RAD-seq study was not completed in time to be included in this thesis. However, these data are expected to provide insight into population genetic structure in the region.

Given the absence of genetic differentiation observed on the regional scale, the geographic scope of sampling effort could also be expanded to the national scale where genetic structure is more likely to be observed using higher resolution genetic markers (Atterby et al., 2015). Another aspect that could be explored in more detail is the connectivity between foxes inhabiting urban and rural areas. Evidence for moderate genetic differentiation between urban and rural foxes has been noted on several occasions (Atterby et al., 2015; Magory Cohen et al., 2013; Wandeler et al., 2003), with contributing factors possibly including natal-biased habitat dispersal and the high mortality among dispersers on main roads on the periphery of urban conurbations (Oishi et al., 2011; Baker et al., 2007), or alternatively as an artefact resulting from the colonisation of urban areas by a small number of individuals followed by rapid population expansion rather than limited dispersal, *per se* (Wandeler et al., 2003). This is highly relevant to conservation efforts in population sinks, as urban areas are renowned for supporting high fox population densities (Main et al., 2020; Scott et al., 2014), likely due to the abundance of food resources (Contesse et al., 2004), and could thus serve as potent source areas. It is worth noting that obtaining fox tissue samples from urban areas, where culling is less prevalent, proved especially difficult in this project. Future work could overcome this problem using alternative, less invasive means of collecting DNA, for instance from fox scats (Amaike et al., 2018).

ii. Anthropogenic subsidisation in population sinks

Anthropogenic subsidisation within population sinks could drive compensatory immigration, by artificially increasing its attractiveness to dispersing foxes. Immigration is a density-dependent process, meaning that higher rates of immigration occur at lower densities relative to the carrying capacity. Therefore, by artificially raising the carrying capacity of a population sink there is a risk that anthropogenic subsidisation could exacerbate the rate of compensatory immigration, For instance, Porteus (2015) found positive correlations between the density of gamebird releases and both the carrying capacity and rate of immigration into shooting estates. Despite foxes incurring overall lower survival rates in the sink due to human-induced mortality, population sinks can act as ‘ecological traps’ (i.e., ‘attractive sinks’) owing to some feature of the sink such as abundant food resources promoting increased immigration of dispersers (Robertson et al., 2013; Delibes et al., 2001). Culling by humans is a relatively new phenomenon against which foxes have not evolved defensive behaviours. Predators might be particularly susceptible to ecological traps due to exhibiting lower vigilance against other predators (Lamb et al., 2017).

In chapter three, stomach content analysis from culled foxes was used to quantify the resources exploited by culled foxes within the NFNP. Although foxes exhibited a highly varied diet, anthropogenic food waste was one of the prevalent components of fox diet during breeding and non-breeding periods (~14% overall). Moreover, the occurrence of anthropogenic food in fox stomachs was negatively associated with distance to the nearest human infrastructure boundary. This suggests that poor waste sanitation is providing foxes with year-round access to this resource. Despite high mortality caused by culling, the presence of an easily accessible and reliable food resource, associated with low foraging costs, could increase the attractiveness of the NFNP for itinerants across the management unit to establish a home range, making the NFNP a putative ecological trap.

In some cases, access to anthropogenic food can divert predators away from their natural prey (Reshamwala et al., 2021); such 'diversionary feeding' can be used as a carefully managed conservation measure (Bamber et al., 2024; Finne et al., 2019). However, previous work has demonstrated the effect of unregulated anthropogenic subsidies leading to elevated local concentrations of mesopredators, resulting in increased 'spill-over' predation on prey species when predators still need to hunt (Shapira et al., 2008; Kristan & Boarman, 2003). Evidently the exploitation of anthropogenic food waste is failing to act as an effective diversionary feeding mechanism for foxes in the NFNP, given the rate of predation on breeding wader nests attributed to foxes observed from camera traps (GWCT, unpubl. data). In the absence of culling in the NFNP, the predation risk experienced by breeding waders would be even more severe.

Human infrastructure appears to be providing year-round access to anthropogenic food subsidies, possibly due to an inadequate waste disposal system. The data from this chapter are assumed to represent foods foraged and consumed locally. This is a reasonable assumption as stomach content analysis reflects a fox's most recent meal and experimental evidence shows the transit time of ingested biomass through the digestive system of foxes is less than 48 hours (Artois et al., 1987). In addition, fox home range sizes around this quite productive landscape are relatively small (~1 km^2; Porteus et al., 2024). This is further supported by the results, with the expected association between anthropogenic food and human infrastructure, as well as the scarcity of gamebird consumption (gamebirds are not released in the NFNP). However, people do feed wildlife deliberately, the prevalence of which cannot be evaluated based on this analysis. Questionnaire studies could be used to interrogate this further, similar to that carried out by Orros & Fellowes (2014) who found a strikingly high rate of supplementary feeding of reintroduced red Kites (*Milvus milvus*) by people living in Reading, demonstrating that such feeding alone could support a substantial number of red kites that visit the residential area each day (Orros & Fellowes, 2015). This information could provide the knowledge required for the design of future, targeted education programmes (Brunk et al., 2021).

The findings from chapter three also lead to speculation that the NFNP is operating as a kind of 'ecological trap' (Robertson et al., 2013), raising the carrying capacity and promoting higher rates of immigration into an area characterised by high mortality due to culling. The Monte Carlo simulations in chapter three aimed to illustrate the potential effect of anthropogenic food subsidies on the local fox abundance, yet these calculations are highly uncertain and make several simplifying assumptions. For instance, the models assume that adult population density is constant throughout the year when in reality there are likely to be fluctuations due to demographic stochasticity and culling, which would influence overall food requirements of the population. No differences in the diet of adults and cubs or juveniles were assumed, although young, inexperienced foxes might prefer items that require less proficient hunting skills (Cavallini & Volpi, 1995). The models assume a stable population, with no within-earth cub mortality before gradually emigrating or dying after emerging from earths to maintain a stable pre-breeding population by the following year, thus annual changes in population size are not considered. Anthropogenic food was also assumed to be equally nutritious as natural food, although this might also be a problematic assumption as the energy content might differ between these types of resources (Contesse et al., 2004), with human foods typically being of poorer quality (e.g., lower protein content; Ng et al., 2023). Finally, the response of the population is assumed to be strictly numerical, although prey switching behaviour might buffer foxes to a certain extent (Angerbjorn et al., 1999). A better measure of its effect could be achieved using the state-space model analysis developed by Porteus et al. (2019a). These models reconstruct the population dynamics of foxes in a restricted area using sighting rate data to parameterise a population dynamics model, including parameters such as the carrying capacity and immigration rate. It would be interesting to run these models before and after the introduction of wheelie bins to quantify its effect on carrying capacity and immigration rate.

Whilst macroscopic techniques such as stomach content analysis can facilitate a local dietary assessment at relatively low cost, it is hindered by several factors. The identifiability of stomach content items can be compromised depending on the extent of digestion. Also, designating items at the species level can be particularly challenging so some taxa are likely to be undetected (Nørgaard et al., 2021). However, the ability to identify species might be useful to inform conservation as hard-to-identify, or uncommon food items can include rare taxa that are similarly susceptible to predation pressure as wading birds. Herpetofauna are of relevance to the NFNP where all six indigenous species of reptiles in the UK can be found, including a nationally important population of smooth snake (*Coronella austriaca*) (Goddard, 1984). Unidentified herptiles were found in 1.8% of sampled fox stomachs, although 22.6% of mean stomach content volume was entirely unidentified. A more comprehensive dietary assessment would involve macroscopic methods used in concert with alternative approaches, such as DNA metabarcoding. Stomach contents from over 200 foxes have been preserved for use in a complementary metabarcoding study.

iii. Anthropogenic subsidisation in population sources

In common with other organisms, mesopredators are limited by the availability of food resources (bottom-up control) (Sinclair & Krebs, 2003). The provision of external food subsidies can release mesopredators from bottom-up control, allowing corresponding growth in their population sizes (Kirby et al., 2017; Newsome et al., 2015a), exposing prey species to a generally higher risk of predation (‘hyperpredation’) (Oro et al., 2013; Kristan & Boarman, 2003). Although the predation risk in protected areas can be mitigated through culling (Baines et al., 2023), as the population density of surrounding areas influences the intensity of compensatory immigration into population sinks (Porteus et al., 2018a; Lieury et al., 2015), widespread anthropogenic food subsidies that elevate population densities throughout the management unit could exacerbate the problem of compensatory immigration counteracting the effect of culling in population sinks and worsening the challenge faced by wildlife managers in controlling fox densities.

The widespread release of gamebirds is a prominent example of how humans could be increasing the availability of food to mesopredators in the UK (Rees et al., 2013). Humans have released reared gamebirds for centuries, but the ecological implications of this practice has only recently become an active area of research (Madden et al., 2023; Sage et al., 2021; 2020; Madden & Sage 2020; Mason et al., 2020; Mustin et al., 2018; Draycott et al., 2008). The scale in which gamebirds are released in the UK (~43 million year^{-1}; Madden, 2021), means that they could realistically support disproportionately high population densities of mesopredators in the countryside (Pringle et al., 2019), making this an important conservation issue nationwide (Mason et al., 2020). However, evidence for gamebirds supporting overall higher population densities of mammalian mesopredators in the UK is largely circumstantial (Mason et al., 2020). Gamebird releasing has been positively correlated with higher population densities of avian mesopredators (buzzard *Buteo buteo*, jay *Garrulus glandarius*, raven *Corvus corax*, magpie *Pica pica* and carrion crow) in the UK (Pringle et al., 2019), although the association with mammalian species has not been tested owing to a paucity of data. Porteus (2015) found a positive correlation between carrying capacity of foxes and the density of gamebird releases on shooting estates. Moreover, the fox index from the National Gamebag Census increased by 180% between 1966-2016, coinciding with a 588% and 6,395% increase in the index for pheasants and red-legged partridge releases, respectively (Aebischer, 2019).

The response of foxes to gamebird releases will largely be dictated by the overall importance of gamebirds to fox diet. Although there have been many studies on fox diet in the UK, they have tended to be confined to local areas; for instance, restricted to a single gamebird releasing site or network of mixed agricultural farmland (Reynolds & Tapper, 1995).

Consequently, while there is evidence that foxes do regularly predate released prey species such as gamebirds (Sage et al., 2018), it has not been determined how important these resources are on a broader, management unit scale. In chapter four, stable isotope analysis was used to estimate the relative importance of various prey groups to overall fox diet across the region, using the stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of ear hair from culled foxes and their known food groups in BSIMMs (Stock et al., 2018).

Ultimately, the information gleaned from the BSIMMs was limited as the posterior distributions were diffuse and provided little interpretive value. Generalist consumers exploit a wide variety of food sources that share similar isotopic ratios, whereas BSIMMs rely on distinct differences among sources to partition dietary contributions effectively (Phillips et al., 2014). Therefore, when the isotopic signatures of potential food sources overlap substantially, it becomes difficult for the model to discriminate among them, leading to increased uncertainty in the estimated proportions (Lerner et al., 2018). Although there was an indication that Galliformes could be an important source category, the findings from this study alone are too uncertain to inform potential changes in policy. Alternative methods should be used to help address this important ecological question.

In contrast to chapter three, the findings from the stable isotope analysis in chapter four suggest that anthropogenic food is only a minor component of rural fox diet throughout the wider region, indicating this is a local rather than a regional problem. However, the absence of wheelie bins for waste disposal is an unusual feature of the New Forest district area. Less secure food waste could explain the prevalent consumption of anthropogenic food waste by foxes in the NFNP relative to the wider region, although deliberate feeding by local residents could also be a factor. The recent introduction of wheelie bins could therefore play an important role in managing rates of fox immigration into the NFNP.

It is well-established that the performance of BSIMMs diminishes as the number of source categories increases (Phillips et al., 2014), yet an assumption of these models is that all important food items are accounted for in the prey library. The use of informative priors could be used to reconcile these conflicting truths (Lerner et al., 2018), although there is a risk that they would introduce bias into the analysis (Swan et al., 2020a). When the isotopic geometry is particularly unfavourable, BSIMMs can provide little additional information separate to the prior itself (Robinson et al., 2018). A pragmatic solution could be to select a small number of the most important individual prey items, rather than constructing aggregated source categories that are too variable to be discriminated. As BSIMMs estimate assimilated diet, food items that are more likely to be used in alternative metabolic pathways (e.g., fruit in respiration), and therefore not detected in hair (Hobson et al., 2009; Hobson & Stirling, 1997), could be omitted in favour of more proteinaceous food items (e.g., vertebrates). The most frequently consumed vertebrate prey could be inferred *a priori* using alternative dietary methods, namely metabarcoding of scat or stomach samples, as this method allows for the identification of prey at the species level (Nørgaard et al., 2021).

The SIA was also limited by the uncertainties relating to the period of tissue synthesis and the lack of data on fox movement. Given the samples available that had already been collected for a separate regional study, ear hair was used to provide the dataset with the broadest possible regional representation. However, the use of ear hair meant that the period of tissue synthesis could not be assigned with precision, hindering an analysis of dietary seasonality, even though some food items are expected to be highly seasonal. Given that gamebird releasing occurs in late summer, the fox tissue used probably accounts for the period whereby gamebirds are more abundant in the ecosystem as all the samples theoretically do not represent diet in spring and early summer. The manifold sources of mortality for gamebirds result in an overwinter decline in numbers following release (Madden et al., 2018). Accordingly, they might become a less important food resource for foxes in spring and early summer, although a stomach content analysis on a releasing estate within the region showed gamebirds still comprised approximately 32% of overall fox diet outside of the shooting season (March-August) (GWCT, unpubl. data). The composition of fox diet during late summer and winter is important as it determines the body condition and perhaps litter sizes of vixens in the lead up to reproduction in the late winter and early spring (Pagh et al., 2018; Winstanley et al., 1999). However, the diet of foxes in the spring and early summer when adults are rearing cubs, coinciding with the wader breeding season, is also of great interest as it could increase juvenile survival and future reproductive potential (Soulsbury et al., 2008). Nonetheless, the ear hair sampled between December-July will include guard hair grown during late summer of the previous year (Maurel et al., 1986), meaning the two growth periods could not be completely partitioned.

Previous studies have used vibrissae sectioned at equal lengths to pinpoint the time of synthesis according to mean growth rates and investigate dietary seasonality accordingly (Jacquier et al., 2020; Scholz et al., 2020). Obtaining multiple data points per individual would also facilitate an assessment of individual specialisation (Jacquier et al., 2020), which is likely more appropriate given that individuals of generalist species are known to specialise (Robertson et al., 2015; Araújo et al., 2011). Estimating diet at the population level misses the opportunity to examine this variation. This analysis could be augmented by simultaneously collecting data on fox movement, allowing for location and time of tissue synthesis to be synchronised. A given fox's precise location at the time of synthesis could be determined from GPS-tagging. For instance, a GPS-collared fox in the region was recorded to have travelled over 30 km in one night (Porteus et al., 2024). Given such prodigious movement, this highlights that the food assimilated into a fox's tissues could have been foraged far from their final sampling location. The joint application of these methods could therefore result in a highly informative and novel study.

iii. Effectiveness of fox control in the NFNP

Given the impact of rapid compensatory immigration, an inadequate culling program will not lower fox densities leading to the intended benefits failing to be achieved (Kämmerle et al., 2019a; b). Rigorous evaluation enables a determination on whether the management actions are actually resulting in a meaningful reduction, which is essential for maintaining confidence in the strategy and achieving the conservation objectives (Lennox et al., 2018). Fox population control can be evaluated in several ways, such as field experiments, demographic modelling, and population monitoring (Baines et al., 2023; Porteus et al., 2019b; Lieury et al., 2015; Newsome et al., 2014), using different performance metrics as an indication of success. A principal advantage of agent-based models is their ability to predict how alternative strategies would perform compared to an existing program, in a manner that other approaches are poorly suited. Answering these ‘what if’ questions helps to provide a basis for adaptive management allowing managers to adjust and fine-tune their control methods accordingly by modulating the intensity, spatial scale, and timing of culling efforts. This information is even more beneficial given the limited time and resources available to wildlife managers (Porteus, 2015).

The agent-based model ‘FoxNet’, introduced by Hradsky et al. (2019), has been used to evaluate the likely outcome of baiting programmes in Australia in terms of the change in fox density within local areas of conservation interest (Francis et al., 2020). In chapter five, FoxNet was adapted for this purpose but in the context of fox culling in the NFNP, which involves shooting at night with a rifle and an optical device (‘lamping’). The FoxNet model was adapted by incorporating a procedure that simulates lamping, with its efficiency being determined by the rate of successful search probability distribution (Porteus et al., 2019b). The model was also parameterised using available data collected within the region.

The simulations showed that there is a limit to which lamping alone could realistically reduce fox densities, suggesting that there would be diminishing returns by intensifying fox control effort beyond the ‘business-as-usual’ situation in terms of the number of hours spent lamping per week. Instead, reducing average rural habitat productivity across the region would be the most effective strategy in further reducing fox density. This has ethical benefits as culling remains highly controversial and risks causing animal suffering (Laidlaw et al., 2021). Although there is uncertainty about how much gamebirds contribute to regional fox population growth rate (chapter four), reducing the number of gamebirds released annually could play an important role in managing regional fox abundance and thus immigration pressure into population sinks (Madden, 2021).

'*All models are wrong, but some are useful*' (Box, 1976) is a foundational aphorism in statistics and ecological modelling. *In silico* simulations do not represent dynamic systems in all their intricate complexities; it is the role of the researcher to decide which aspects of fox behaviour are the most important to represent. This does not compromise their utility; on the contrary, they are some of the most advanced tools available to guide management (Railsback & Grimm, 2019). Nevertheless, some aspects of this model are likely to be oversimplifications. For instance, there is a rigid dispersal season in FoxNet, outside of which long-distance dispersal events do not occur. However, a fox-tagging study in the region recorded dispersal events just outside of this period in the spring (Porteus et al., 2024), hence the lack of dispersal outside of this season is demonstrably false. It is possible that this behaviour is the exception in the context of the wider region, and thus is of limited relevance from a management perspective. Moreover, seeking ever higher complexity is likely to result in a hopeless endeavour with diminishing value to the model outcome (Grimm et al., 2005). This notwithstanding, the accuracy of demographic modelling is determined by how closely the choice of parameter values align with reality, and how stationary these vital rates are in the future (Coulson et al., 2001). Circumstances that are difficult to forecast such as the spread of disease or major fluctuations in prey density might influence fox densities in the future. In general, this highlights that the FoxNet model should be used alongside direct field monitoring to ground truth the inferences.

FoxNet provides a tool to enable projections in the proportional reduction in fox density following management (‘Operational monitoring’; Francis et al., 2020). However, the outcome sought from seasonal fox culling in the NFNP is the short-term protection of waders during a phase of their life history whereby their susceptibility to fox predation is acute (i.e., the nesting period, March-July). As mentioned in chapter five, a predictive model linking nest predation risk to changes in fox and other predator population densities is currently lacking (‘Outcome monitoring’). Alternative, non-lethal forms of predator control (e.g., electrified fencing) also cannot be evaluated in the current FoxNet model, although they are widely implemented and can form an important component of a multifaceted predation management package (GWCT, 2020). Developing a model to facilitate this should be the focus of future work.

6.2. Closing remarks

Studies across Europe have identified nest predation as a major factor driving the decline of wading bird populations with generalist mesopredators such as the fox being implicated (McMahon et al., 2020). While it is increasingly accepted that the overabundance of mesopredators is an urgent issue for conservation in the UK (Roos et al., 2018), disagreements persist over how to solve the problem. Lethal control on restricted areas is widely practised as a conservation strategy (Reynolds & Tapper, 1996), although the ability of foxes to compensate for these losses through rapid recolonisation shows that it is not a long-term solution (Porteus et al., 2019a). Furthermore, coordinating fox control over much larger scales to prevent recolonisation is unlikely to be a feasible; besides, such intensive culling is likely to be ethically troublesome for many (Doherty & Ritchie, 2017).

In reality, restricted-area fox culling should be considered a temporary solution while other options are explored. Addressing the root causes of mesopredator overabundance is desirable for the sake of sustainability and animal welfare (Roos et al., 2018; Laidlaw et al., 2021), however, assessing the potential utility of alternative strategies requires robust, objective evidence. Baines (2025) suggested measures such as reconfiguring modified landscapes to make them less suitable for mesopredators, reintroducing top apex predators and reducing the amount of supplementary food available to mesopredators, should all be trialled to restore the native ecosystem. To this end, effective long-term management of foxes should be coordinated at a regional scale and needs to involve collaboration from various stakeholders including wildlife managers, estate gamekeepers, and the general public.

7. References

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8. Appendix

8.1. Chapter three supplementary materials

Figure S3.1. Examples of stomachs containing different types of anthropogenic foods and human-derived materials consumed by foxes. Clockwise from top left: i) peanuts, ii) cooked fish and potatoes, iii) pet food, cooked chicken, and an egg box label, iv) potato chips and remains of a rubbish bag.

i. Adequacy of sample size

Rarefaction curves can be used to test the adequacy of dietary sampling, whereby the total number of prey items or categories identified is plotted against the total number of samples (stomachs, scats etc.,) processed until an asymptote is reached. However, such analyses are not suitable for evaluating sample sizes for data on proportions. Nevertheless, the relative proportions of different categories should also stabilise after a certain number of samples (i.e., central limit theorem), beyond which additional samples do not provide any further insight (McQueen & Griffiths, 2004).

To determine the number of stomachs required to accurately quantify the proportional contribution of anthropogenic food to stomach contents for each season, the mean volume of anthropogenic food to overall stomach content volume was calculated (i.e., FO*V/100) at each sample size class (starting from 10 and increasing in increments of 5 samples to a maximum number of samples). The difference in the mean volume (mV) of anthropogenic food between consecutive 5-sample size classes was calculated as:

$$D_{(n)} = P_{(n+5)} - P_{(n)} \tag{2}$$

where D is the difference between consecutive 5-sample sizes, P is the mV of anthropogenic food in the overall stomach contents for the specified 5-sample size class, and n is the 5-sample size class. The value of D at a given sample size will depend to some extent on the order in which the stomachs were sampled. Therefore, this was repeated after randomly shuffling the order of the stomachs in the dataset, 1000 times. The median D at each sample size class was calculated based on these 1000 permutations. When the median D reached ≤ 0.01, the sample size was considered to be adequate. This analysis was carried out using a custom R script.

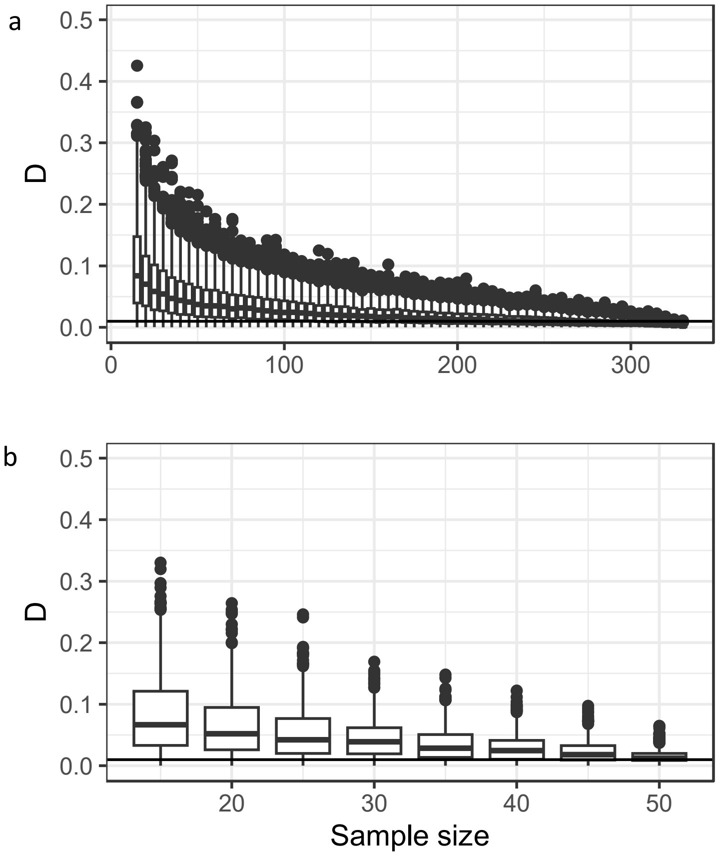

Figure S3.2. Mean percentage difference in proportion of each food category between 5-stomach sample size classes for the a) reproductive period and b) dispersal period. Boxplots denote median, interquartile range and range for each sample size class from 1000 permutations

ii. Number of foxes subsidised by anthropogenic food

The number of adult males (N_{sm}), adult females (N_{sf}) subsidised by anthropogenic food, is given by the total amount of anthropogenic food consumed annually by adult males (A_{cm}) and adult females (A_{cf}), divided by the annual prey requirement of an individual adult male (P_m) or adult female (P_f). The number of cubs (N_{sc}) theoretically subsidised by anthropogenic food is given by the total amount of anthropogenic food consumed annually by cubs (A_{cc}) divided by the sum of the food requirements for individual cubs for each week of the year (F_i):

$$N_{sm} = A_{cm}/P_{m},$$

[S1]

$$N_{sf} = A_{cf}/P_{f},$$

[S2]

$$N_{sc} = A_{cc}/\sum_{i=1}^{52} F_{i}.$$

[S3]

The annual consumption of anthropogenic food by adult males (A_{cm}) and adult females (A_{cf}) is given by the number of individual adult males (N_{m}) and adult females (N_{f}), multiplied by the annual prey requirements of each of an individual adult male (P_{m}), or adult female (P_{f}), and the proportion of diet that is anthropogenic food (A). The annual prey requirements of adult males (P_{m}) and adult females (P_{f}) is given by their weekly prey requirements, multiplied by 52. The weekly prey requirements are given by the weekly consumption rate of adult foxes from North Dakota (0.48 kg/kg adult/week; Sargeant, 1978), scaled and raised to the power of 0.75 to account for differences in metabolic rate due to the larger average body mass of British foxes (Kleiber, 1932). The proportional contribution (mean volume) of fox diet by anthropogenic food was estimated by stomach content analysis, as described in the methods section of the main paper. For samples whereby the sex was recorded (N = 350), no difference was detected between the sexes in the consumption of anthropogenic food, therefore, the same value of A was used for both sexes (A = 0.14):

$$A_{cm} = N_{m}P_{m}A,$$

[S4]

$$A_{cf} = N_{f}P_{f}A.$$

[S5]

The annual consumption of anthropogenic food by cubs (A_{cc}) is given by the sum of the weekly consumption of anthropogenic food by cubs over the course of a year. The weekly consumption of anthropogenic food by cubs is based on the number of cubs produced (N_{c}), multiplied by the proportion of cubs remaining in a given week of the year (C_{i}), multiplied by the prey requirements of cubs during a given week of the year (F_i), and the proportion of diet that is anthropogenic food (A):

$$\mathrm{A}_{cc} = \sum_{\mathrm{i}=1}^{52} \mathrm{N}_c \mathrm{C}_\mathrm{i} \mathrm{F}_\mathrm{i} \mathrm{A}$$

[S6]

The weekly prey requirements of cubs were determined following Porteus (2015). Data on weekly mean cub weight during the first six months postpartum from Sargeant (1978) were fitted to a Richards' growth function using least squares (Johnson et al., 1975), with the cubs reaching a mean adult weight of 4.72 kg after 12 months. Scaling this growth curve to the mean adult weight of British foxes (6.09 kg) allowed calculation of the weekly weight of cubs during their juvenile year. Weekly food consumption rates of cubs during their first six months (Sargeant, 1978) were fitted using a Hassell (1975) function under the assumption that food consumption per cub peaked at 1.3 times mean adult levels at 28 weeks postpartum, declining to mean adult levels by 12 months of age when they reached mean adult weight (Reynolds & Tapper, 1995). Finally, the fitted consumption/time curve was used to calculate the weekly cub food requirements. The female lactation per cub over the first four weeks was also added to the weekly cub food requirement and removed from the weekly adult food requirement. To specify the number of cubs across each week of the year, all cubs produced were assumed to survive for the first 22 weeks from the mean birth date (4th April) until the first week of autumn (5th September), before declining linearly by 5% each week for 20 weeks until there were no more cubs. This assumes that the population is at equilibrium, with all cubs either dispersing, dying, or replacing lost adults during the autumn and winter.

The total number of adult males (N_m) and adult females (N_f) in the New Forest is given by the adult (i.e., > 1 year old) population density (D; individuals km^{-2}), multiplied by the proportion of adults that are female (R), (or 1 minus R for adult males), and the total area of the New Forest managed by Forestry England where culling takes place (henceforth: 'New Forest'; 255.06

km^2). Logbooks of culling records could be used to estimate the sex ratio of the population, if it can be assumed that the proportion of adult females and adult males culled reflects that of the overall population. However, data suggests there is a tendency for more male than female samples to be collected, especially during the dispersal period (September-January), possibly because more males disperse as itinerants from their natal territories than females (Porteus, 2015). This may, in turn, bias the estimated balance of resident females to males. Indeed, the proportion of foxes culled in the New Forest between April 2021 and July 2022 that were female was 0.45. More than twice as many male foxes were culled during the dispersal period than female foxes (September 2021 – January 2022; 41 and 19, respectively). Therefore, in the absence of evidence to the contrary, an adult sex ratio of 0.5 was assumed:

$$N_m = D(1 - R)255.06, \tag{S7}$$

$$N_f = (DR)255.06. \tag{S8}$$

The total number of cubs produced in the New Forest per year (N_c), is given by the total number of adult females (N_f), multiplied by the proportion of adult females that successfully breed (B), and the average litter size of adult females (L):

$$N_c = N_f BL. \tag{S9}$$

Monte Carlo simulations were used to investigate the impact of uncertainty in the input variables on the output variables. One million simulations were employed, where a random value was drawn from each input variable's range of plausible values. The justification for the distribution and bounds for each input variable is described below. All statistical analyses were carried out in R v4.2.2 (R Core Team, 2022).

The mean and standard error of adult body masses was taken for individuals sampled (N = 25) close to the study area (Hampshire, Dorset, Wiltshire) recorded during the Fox Monitoring Survey (FMS; GWCT unpublished data). These values were used to define a normal distribution of adult male (M_m) and adult female body (M_f) masses, from which a random value was drawn during each simulation:

$$M_m \sim N(6.72, 0.28), \tag{S10}$$

$$M_f \sim N(5.46, 0.15). \tag{S11}$$

iii. Landscape-based estimates

An estimate of adult fox density in the New Forest was derived based on national average pre-breeding adult fox population densities calculated for different habitat categories (Webbon et al., 2004). A shapefile representing the land classes across Great Britain from the Countryside Survey 2007 (Bunce et al., 2007) was rasterized and clipped to the extent of the New Forest area in QGIS v3.28 (QGIS Development Team, 2023). The extent (km^2) of each different land class within the New Forest was calculated. These land classes were grouped into broader landscape categories according to Walsh & Harris (1996). The broader landscape categories found within the New Forest were arable a, arable b, and pastural a. Plausible ranges in average adult fox density for each landscape category were estimated by simulating normal distributions with means and standard errors specific to each landscape category from Webbon et al. (2004):

$$D_{\text{Arable a}} \sim N(0.99, 0.26), \tag{S12}$$

$$D_{\text{Arable b}} \sim N(0.79, 0.17), \tag{S13}$$

$$D_{\text{Pastural a}} \sim N(1.88, 0.44).$$

[S14]

These distributions were multiplied by the extent of the corresponding landscape category in the New Forest to provide a plausible range of total number of adult foxes in each landscape class:

$$N_{\text{Arable a}} = D_{\text{Arable a}} * 99.56,$$

[S15]

$$N_{\text{Arable b}} = D_{\text{Arable b}} * 104.56,$$

[S16]

$$N_{\text{Pastural a}} = D_{\text{Pastural a}} * 50.94.$$

[S17]

These were summed and divided by the total areal extent of the New Forest to provide the plausible range for the overall adult fox density:

$$D_{\text{New Forest}} = (N_{\text{Arable a}} + N_{\text{Arable b}} + N_{\text{Pastural a}}) / 255.06$$

[S18]

iv. Local-based estimates

Although direct estimates of adult fox density in the New Forest are not currently available, data on adult fox density is available for other areas in the region. GPS-tagging of foxes was carried out between 2016-2017 on Britford estate and between 2018-2019 on Somerley estate, two areas of the Avon Valley located to the west of the New Forest area (for more details, see GWCT, 2020; Porteus et al., 2024). Given the contemporary nature of these data and the close geographic proximity to the New Forest, these may serve as useful proxies for the current adult fox density in the latter.

For each estate, the home range area of resident foxes tagged in each year were estimated using 95% isopleths obtained from local convex hulls. These areas were used to estimate the minimum resident density and minimum total density given the number of tagged foxes, with the latter also including transient foxes (i.e., those that died or dispersed) (Porteus et al., 2024). Only adult foxes were tagged during the study. These figures thus represent minimum pre-breeding adult fox densities, as they do not account for adults that were not tagged during the tagging period (March-June). Uniform distributions bounded by the smaller and larger adult fox population density recorded over the two years in which the GPS-tagging work was conducted within each estate, were specified. These distributions were applied to the Monte Carlo simulation separately, to examine the output according to whether the situation in the New Forest closely resembled that of each individual estate:

$$D_{\mathrm{Britford}} \sim U(8.74,\ 12.25), \qquad [S19]$$

$$D_{\mathrm{Somerley}} \sim U(1.84,\ 2.90). \qquad [S20]$$

Alongside stomach samples, uteri samples were also taken from culled vixens (N = 150). The site of a developing foetus is indicated by the presence of pigmented scars, with dark (primary) scars indicating a cub taken to full term, and light (diffuse) scars indicating foetuses that were reabsorbed prior to whelping. Upon dissection of each uterus, and the number of dark and light scars was counted following the exact procedure outlined by Heydon & Reynolds (2000). Females showing primary scars were considered as ‘breeders’, whereas those showing only diffuse or no scars as ‘non-breeders’. Productivity was considered only for vixens killed between March and July, inclusive, as outside this period distinguishing between primary and diffuse scars can be made difficult by progressive fading (Heydon & Reynolds, 2000). From this sample of breeders and non-breeders, bootstrapping was employed with one million replicates to generate a plausible distribution for the proportion of breeding females, from which a random sample was drawn during each simulation.

The number of primary scars or foetuses for vixens killed between March and July, inclusive, was used to provide an estimate of litter size for each breeding female. Bootstrapping was employed with one million replicates to generate a plausible distribution for the litter size of breeding females in the New Forest, from which a random sample was drawn during each simulation.

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8.2. Chapter four supplementary materials

Table S4.1.

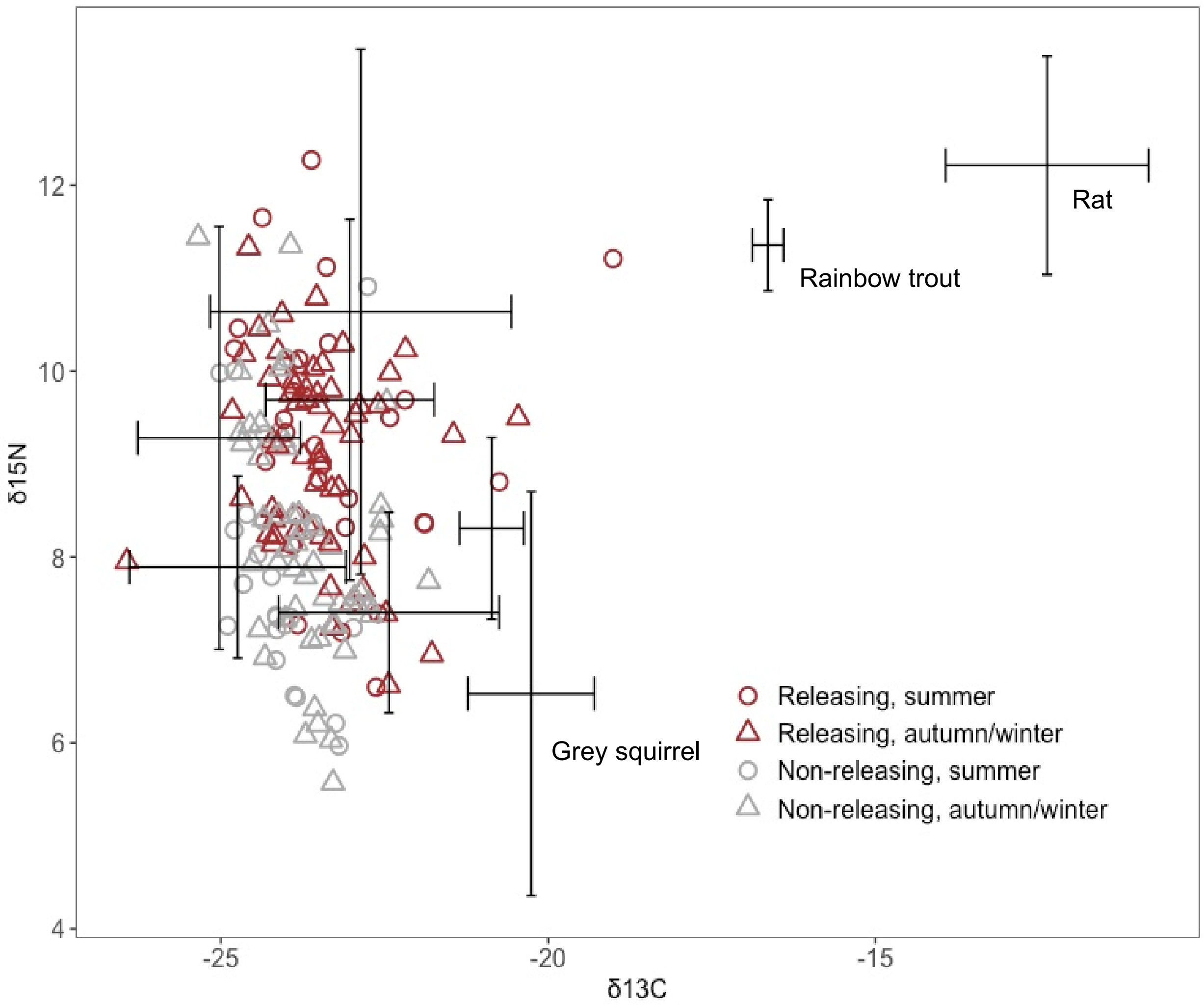
Protocol performed for vibrissae and soft tissue samples delipidation prior to isotopic measurement.

Keratinaceous tissue samples

1- Remove a clump of the sample using lab scissors
2- Delipidation (under extraction hood)
    a. Put sample in a 2 mL microcentrifuge tube using tweezer
    b. Cover sample with chloroform:methanol solution (2:1)
    c. Agitate for 4h
    d. Drain chloroform:methanol solution from the tube with a pipette and discard
3- Rinsing and drying
    a. Cover sample with distilled water
    b. Agitate for 30 seconds
    c. Drain most of the water with a pipette and discard
    d. Dry in oven at 60°C for 24h with the lids open
4- Tin capsule preparation
    a. Weigh 0.7 mg (± 0.5) of the sample after tare in tin capsules
    b. Fold tin capsules into a tight cube
    c. Store in ELISA well plate

Soft tissue samples

1- Defrost samples and place in a 2 mL microcentrifuge tube
2- Refreeze (-20°C) for 24h
3- Lyophilize (-80°C) for 48h
4- Powder reduction
    a. Use a pestle to grind the sample into a fine powder in the tube
5- Delipidation (under extraction hood)
    a. Cover sample with chloroform:methanol solution (2:1)
    b. Agitate for 4h
    c. Centrifuge for 5 min at 4000 rpm
    d. Drain chloroform:methanol solution from the tube with a pipette and discard
    e. Repeat steps a-d twice
6- Rinsing and drying
    a. Dry in oven at 50°C for 48h with the lids open
7- Tin capsule preparation
    a. Weigh 500 ug of animal powder, or 10 mg of plant powder in tin capsules
    b. Fold tin capsules into a tight cube
    c. Store in ELISA well plate



e sources excluded from the main analysis (grey squirrel, rainbow trout & rat). Diet sources were adjusted to convert sampled tissue isotope ratios to the actual tissue of consumption, and by the trophic discrimination of fox hair. Bars indicate mean ±1 SD

Table S4.2. Mean isotopic ratios and digestible elemental concentrations for sampled fox sources used for Bayesian stable isotope mixing models.

	δ13C (‰)		δ15N (‰)		Digestible elemental concentration		
Source	Mean	SD	Mean	SD	[C]	[N]	Sample size
Other bird	-25.5	2.3	7.2	2.8	51.5	14.1	51
Mammal	-27.6	1.2	5.9	2.3	51.5	14.1	79
Invertebrate	-25.6	1.3	6.3	1.9	51.5	14.1	17
Human diet	-23.5	0.5	4.9	1.0	52.8	6.9	29
Fruit	-27.3	1.7	4.5	1.0	45	1.5	16
Galliformes	-25.0	1.7	4.0	1.1	51.5	14.1	24

Table S4.3. Breakdown of the fox hair samples collected for use in the present study.

Year	Moult period	Releasing			Non-releasing			
		M	F	U	M	F	U	
2018	Summer							
	Autumn/Winter	3	1					4
2019	Summer	5	7		3	4		19
	Autumn/Winter	4	4		1	2		11
2020	Summer	4	1					5
	Autumn/Winter	9	5	1	13	10		38
2021	Summer	7	4		11	6		28
	Autumn/Winter	13	14		5	7	1	40
2022	Summer							
	Autumn/Winter	2			2	1		5
2023	Summer							
	Autumn/Winter				5	4	3	12
TOTAL		47	36	1	40	34	4	162

M: Male; F: Female; U: Unknown

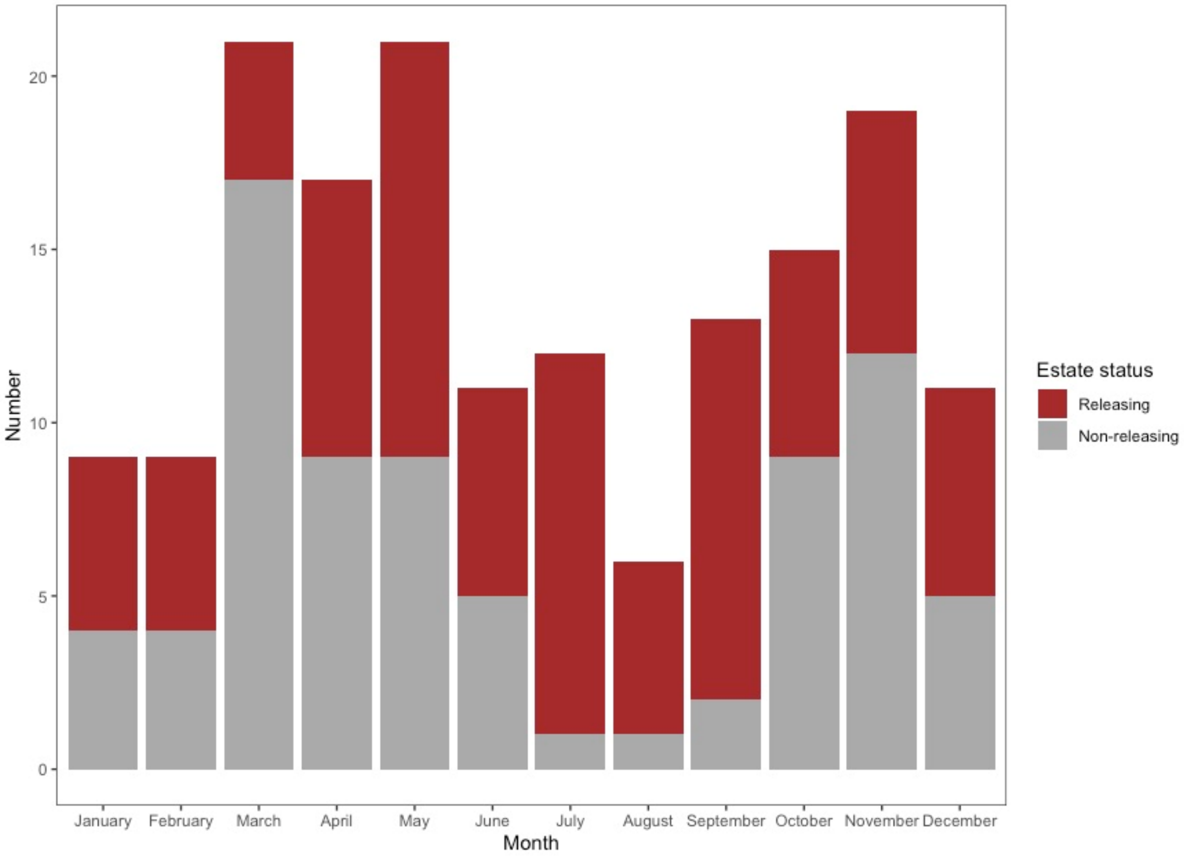


Figure S4.2. Number of samples obtained in each month on releasing and non-releasing sites

Table S4.4. Posterior mean, standard deviation, and quantiles of source percent contribution estimates for each model (%).

		Mean	SD	2.5%	5%	25%	50%	75%	95%	97.5%
Estate	p.Estate.Fruit	0.37	0.15	0.03	0.07	0.29	0.40	0.48	0.57	0.60
	p.Non estate.Fruit	0.19	0.11	0.02	0.03	0.11	0.18	0.25	0.38	0.44
	p.Estate.Galliformes	0.13	0.07	0.03	0.04	0.07	0.11	0.16	0.26	0.30
	p.Non estate.Galliformes	0.29	0.09	0.10	0.13	0.23	0.29	0.35	0.43	0.45
	p.Estate.Human diet	0.10	0.06	0.01	0.01	0.05	0.09	0.14	0.21	0.24
	p.Non estate.Human diet	0.07	0.06	0.00	0.00	0.02	0.06	0.10	0.18	0.20
	p.Estate.Invertebrate	0.13	0.12	0.00	0.01	0.04	0.08	0.18	0.41	0.47
	p.Non estate.Invertebrate	0.05	0.06	0.00	0.00	0.02	0.04	0.07	0.15	0.19
	p.Estate.Mammal	0.13	0.07	0.03	0.04	0.08	0.11	0.16	0.25	0.29
	p.Non estate.Mammal	0.37	0.09	0.14	0.20	0.31	0.37	0.43	0.50	0.52
	p.Estate.Other bird	0.16	0.09	0.01	0.01	0.09	0.15	0.22	0.32	0.35
	p.Non estate.Other bird	0.04	0.03	0.00	0.01	0.02	0.03	0.05	0.10	0.11
Moult	p.Summer.Fruit	0.28	0.20	0.02	0.03	0.09	0.26	0.45	0.60	0.64
	p.Winter.Fruit	0.24	0.13	0.02	0.04	0.15	0.23	0.33	0.46	0.50
	p.Summer.Galliformes	0.19	0.11	0.02	0.03	0.10	0.18	0.27	0.39	0.43
	p.Winter.Galliformes	0.18	0.09	0.02	0.03	0.11	0.17	0.24	0.33	0.36
	p.Summer.Human diet	0.09	0.07	0.01	0.01	0.04	0.08	0.14	0.23	0.26
	p.Winter.Human diet	0.13	0.08	0.01	0.01	0.07	0.13	0.19	0.26	0.28
	p.Summer.Invertebrate	0.12	0.12	0.01	0.01	0.04	0.09	0.17	0.37	0.45
	p.Winter.Invertebrate	0.12	0.09	0.00	0.01	0.05	0.11	0.18	0.29	0.33
	p.Summer.Mammal	0.23	0.15	0.02	0.04	0.10	0.20	0.34	0.50	0.53
	p.Winter.Mammal	0.27	0.11	0.05	0.09	0.20	0.27	0.34	0.44	0.47
	p.Summer.Other bird	0.09	0.07	0.00	0.01	0.03	0.06	0.13	0.24	0.27
	p.Winter.Other bird	0.06	0.05	0.00	0.00	0.02	0.05	0.09	0.16	0.19
Estate + Moult	p.Estate.Summer.Fruit	0.25	0.17	0.02	0.03	0.11	0.21	0.37	0.57	0.62
	p.Estate.Summer.Galliformes	0.13	0.08	0.02	0.03	0.07	0.12	0.17	0.27	0.31
	p.Estate.Summer.Human diet	0.07	0.05	0.00	0.01	0.03	0.06	0.10	0.17	0.20
	p.Estate.Summer.Invertebrate	0.14	0.17	0.00	0.00	0.03	0.07	0.17	0.54	0.59
	p.Estate.Summer.Mammal	0.15	0.08	0.04	0.05	0.10	0.14	0.20	0.29	0.32
	p.Estate.Summer.Other bird	0.26	0.15	0.01	0.02	0.13	0.29	0.37	0.46	0.49
	p.Estate.Winter.Fruit	0.32	0.15	0.02	0.04	0.22	0.34	0.42	0.54	0.57
	p.Estate.Winter.Galliformes	0.15	0.08	0.03	0.04	0.09	0.14	0.20	0.29	0.33
	p.Estate.Winter.Human diet	0.08	0.06	0.00	0.00	0.03	0.07	0.13	0.20	0.23
	p.Estate.Winter.Invertebrate	0.14	0.13	0.00	0.00	0.03	0.10	0.21	0.39	0.45
	p.Estate.Winter.Mammal	0.14	0.09	0.03	0.04	0.08	0.12	0.19	0.31	0.35
	p.Estate.Winter.Other bird	0.17	0.09	0.01	0.01	0.10	0.18	0.23	0.31	0.34
	p.Non estate.Summer.Fruit	0.14	0.13	0.01	0.01	0.05	0.11	0.20	0.40	0.48
	p.Non estate.Summer.Galliformes	0.26	0.10	0.07	0.10	0.19	0.26	0.32	0.41	0.44
	p.Non estate.Summer.Human diet	0.06	0.05	0.00	0.00	0.02	0.04	0.08	0.15	0.18
	p.Non estate.Summer.Invertebrate	0.06	0.07	0.00	0.00	0.01	0.03	0.07	0.18	0.22
	p.Non estate.Summer.Mammal	0.44	0.12	0.12	0.20	0.38	0.46	0.52	0.60	0.63
	p.Non estate.Summer.Other bird	0.05	0.04	0.00	0.01	0.03	0.05	0.07	0.13	0.15
	p.Non estate.Winter.Fruit	0.16	0.11	0.01	0.01	0.08	0.15	0.22	0.37	0.45
	p.Non estate.Winter.Galliformes	0.31	0.11	0.06	0.10	0.24	0.32	0.39	0.47	0.50
	p.Non estate.Winter.Human diet	0.07	0.07	0.00	0.00	0.01	0.05	0.11	0.22	0.26
	p.Non estate.Winter.Invertebrate	0.06	0.07	0.00	0.00	0.01	0.04	0.08	0.20	0.25
	p.Non estate.Winter.Mammal	0.36	0.11	0.11	0.17	0.31	0.37	0.44	0.52	0.54
	p.Non estate.Winter.Other bird	0.04	0.03	0.00	0.00	0.02	0.03	0.05	0.09	0.11
Grid	p.global.Fruit	0.23	0.13	0.03	0.05	0.13	0.21	0.30	0.46	0.52
	p.global.Galliformes	0.28	0.09	0.10	0.13	0.21	0.27	0.34	0.42	0.46
	p.global.Human diet	0.02	0.02	0.00	0.00	0.01	0.02	0.03	0.06	0.08
	p.global.Invertebrate	0.13	0.11	0.00	0.01	0.04	0.10	0.18	0.35	0.39
	p.global.Mammal	0.19	0.09	0.03	0.05	0.12	0.19	0.26	0.36	0.38
	p.global.Other bird	0.16	0.08	0.02	0.03	0.10	0.16	0.21	0.30	0.33
Estate + Grid	p.Estate.Fruit	0.21	0.12	0.02	0.04	0.11	0.19	0.28	0.42	0.46
	p.Non estate.Fruit	0.25	0.21	0.01	0.02	0.09	0.20	0.37	0.67	0.76
	p.Estate.Galliformes	0.16	0.07	0.05	0.06	0.11	0.16	0.21	0.28	0.31
	p.Non estate.Galliformes	0.35	0.12	0.12	0.15	0.28	0.36	0.43	0.55	0.58
	p.Estate.Human diet	0.04	0.04	0.00	0.00	0.01	0.03	0.05	0.11	0.13
	p.Non estate.Human diet	0.02	0.02	0.00	0.00	0.00	0.01	0.02	0.06	0.08
	p.Estate.Invertebrate	0.14	0.14	0.00	0.01	0.04	0.10	0.19	0.44	0.50
	p.Non estate.Invertebrate	0.05	0.06	0.00	0.00	0.01	0.03	0.06	0.15	0.19

	p.Estate.Mammal	0.18	0.08	0.04	0.05	0.11	0.17	0.23	0.32	0.36
	p.Non estate.Mammal	0.27	0.14	0.02	0.04	0.17	0.27	0.37	0.49	0.52
	p.Estate.Other bird	0.28	0.12	0.02	0.04	0.22	0.29	0.36	0.46	0.51
	p.Non estate.Other bird	0.06	0.04	0.01	0.01	0.03	0.05	0.08	0.13	0.16
Moult + Grid	p.Summer.Fruit	0.21	0.14	0.02	0.04	0.10	0.19	0.30	0.48	0.54
	p.Winter.Fruit	0.22	0.16	0.01	0.02	0.09	0.20	0.31	0.54	0.62
	p.Summer.Galliformes	0.28	0.11	0.08	0.11	0.20	0.28	0.35	0.48	0.51
	p.Winter.Galliformes	0.25	0.11	0.05	0.07	0.17	0.25	0.32	0.43	0.46
	p.Summer.Human diet	0.02	0.02	0.00	0.00	0.00	0.01	0.02	0.06	0.07
	p.Winter.Human diet	0.02	0.03	0.00	0.00	0.00	0.01	0.02	0.08	0.10
	p.Summer.Invertebrate	0.13	0.12	0.01	0.01	0.04	0.09	0.19	0.38	0.43
	p.Winter.Invertebrate	0.24	0.21	0.00	0.01	0.08	0.19	0.35	0.69	0.77
	p.Summer.Mammal	0.18	0.11	0.02	0.03	0.10	0.17	0.25	0.37	0.42
	p.Winter.Mammal	0.15	0.11	0.01	0.01	0.06	0.13	0.22	0.35	0.38
	p.Summer.Other bird	0.17	0.09	0.02	0.03	0.10	0.17	0.23	0.34	0.36
Individual	p.global.Fruit	0.12	0.09	0.01	0.01	0.05	0.10	0.17	0.30	0.35
	p.global.Galliformes	0.11	0.07	0.01	0.01	0.06	0.10	0.15	0.24	0.27
	p.global.Human diet	0.14	0.08	0.02	0.03	0.08	0.13	0.19	0.28	0.30
	p.global.Invertebrate	0.04	0.03	0.00	0.00	0.02	0.03	0.06	0.10	0.12
	p.global.Mammal	0.43	0.10	0.20	0.28	0.39	0.44	0.50	0.57	0.60
	p.global.Other bird	0.23	0.08	0.07	0.10	0.17	0.23	0.28	0.36	0.38
Estate + Individual	p.Estate.Fruit	0.05	0.06	0.00	0.00	0.01	0.03	0.07	0.17	0.22
	p.Non estate.Fruit	0.13	0.08	0.01	0.02	0.07	0.12	0.17	0.28	0.32
	p.Estate.Galliformes	0.13	0.12	0.00	0.01	0.04	0.10	0.18	0.38	0.46
	p.Non estate.Galliformes	0.14	0.07	0.02	0.04	0.09	0.13	0.18	0.25	0.27
	p.Estate.Human diet	0.22	0.12	0.02	0.04	0.14	0.21	0.30	0.43	0.47
	p.Non estate.Human diet	0.06	0.04	0.00	0.01	0.03	0.05	0.09	0.14	0.17
	p.Estate.Invertebrate	0.03	0.03	0.00	0.00	0.01	0.02	0.05	0.10	0.12
	p.Non estate.Invertebrate	0.21	0.10	0.02	0.04	0.14	0.21	0.27	0.39	0.44
	p.Estate.Mammal	0.30	0.17	0.01	0.01	0.13	0.34	0.43	0.54	0.57
	p.Non estate.Mammal	0.20	0.08	0.05	0.07	0.14	0.19	0.25	0.34	0.37
	p.Estate.Other bird	0.28	0.14	0.04	0.07	0.18	0.26	0.37	0.53	0.56
	p.Non estate.Other bird	0.27	0.07	0.07	0.15	0.24	0.28	0.31	0.36	0.38
Moult + Individual	p.Summer.Fruit	0.04	0.03	0.01	0.01	0.02	0.04	0.05	0.09	0.11
	p.Winter.Fruit	0.10	0.08	0.01	0.01	0.04	0.08	0.14	0.26	0.31
	p.Summer.Galliformes	0.11	0.08	0.00	0.01	0.04	0.09	0.15	0.25	0.29
	p.Winter.Galliformes	0.11	0.08	0.01	0.02	0.06	0.10	0.15	0.26	0.30
	p.Summer.Human diet	0.14	0.08	0.01	0.02	0.08	0.14	0.19	0.27	0.30
	p.Winter.Human diet	0.04	0.03	0.00	0.00	0.01	0.03	0.05	0.09	0.11
	p.Summer.Invertebrate	0.05	0.05	0.00	0.00	0.01	0.04	0.08	0.14	0.16
	p.Winter.Invertebrate	0.49	0.13	0.13	0.24	0.44	0.51	0.57	0.66	0.69
	p.Summer.Mammal	0.41	0.09	0.21	0.26	0.36	0.41	0.47	0.55	0.58
	p.Winter.Mammal	0.20	0.09	0.05	0.06	0.14	0.20	0.27	0.36	0.38
	p.Summer.Other bird	0.25	0.09	0.07	0.10	0.19	0.25	0.31	0.39	0.41
	p.Winter.Other bird	0.06	0.07	0.00	0.00	0.01	0.03	0.06	0.23	0.30