



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

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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, we identified the major food resources that are being exploited by foxes in the New Forest area and examined temporal and spatial patterns in the presence of specific food categories, 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. We also estimated 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. 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. Our 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.

Keywords *Vulpes vulpes* · The new forest · Diet · Human waste · Breeding waders

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 (Reynolds and Tapper 1995; Diaz-Ruiz et al.

2013; Soe et al. 2017; Fleming et al. 2021; Castañeda et al. 2022). 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 (Leckie et al. 1998; Balestrieri et al. 2011).

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 (Ghosal et al., 2016; Reshamwala et al. 2018), leftover viscera and carrion from hunting (Tobajas et al. 2022; Schwegmann. et al. 2023), livestock, free-roaming game animals, and cultivated crops (Dell’Arte and Leonardi 2005; Jacquier et al. 2020; Reshamwala et al. 2021), and food left out for pets and wildlife (Harris 1981). Diversionary feeding might also subsidise populations (Kubasiewicz

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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. 2015). 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 (Bateman and Fleming 2012; Scott et al., 2018) 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 (Newsome et al. 2015; Plaza and Lambertucci 2017).

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') (Maroo and Yalden 2000; Prugh et al. 2009; Ritchie and Johnson 2009), and high food supplementation (Harris 1981; Pringle et al. 2019). 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 UK's 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 km², 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 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 and 2022, trail cameras were used to monitor the fate of 140 wader nests of high conservation concern (mainly curlew and lapwing nests), and out of 62 recorded nest predation events, 56% 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 (Harris 1981; Reynolds and Aebischer 1991; Reynolds and Tapper 1995; Peterson et al. 2021). We 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, we modelled the occurrence of broad food categories 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. We then used these data alongside supplementary data 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.

Materials and methods

New forest stomach samples

We collected 447 fox stomachs from individuals culled by professional wildlife managers within the area of the New Forest managed by Forestry England, 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 (Fig. 1). Many of the foxes culled by wildlife managers were baited to safe shooting locations with dog biscuits following initial detection by trail cameras. Hence, we would expect dog biscuits to be present in the stomachs of foxes shot over bait sites. The location

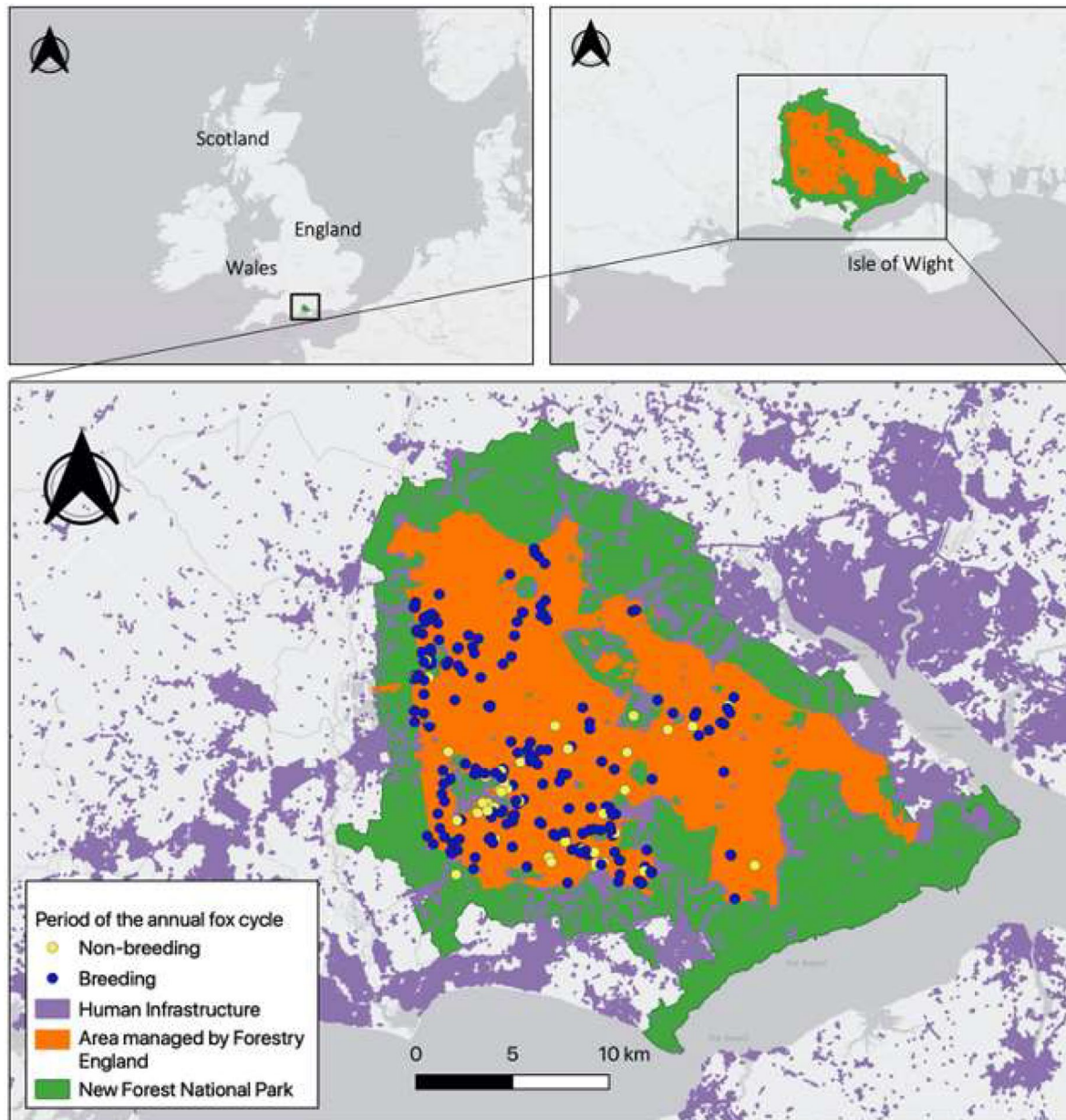


Fig. 1 Distribution of non-empty fox stomachs sampled across the New Forest Forestry England-managed area for which date of collection and sample location was recorded ($N=363$)

(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 $-20\text{ }^{\circ}\text{C}$ in laboratory freezers and defrosted prior to dissection.

Laboratory methods

We removed the contents of each stomach and grouped them 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; Online Resource 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. We took the mass (g) of each category using electronic weighing scales. All analyses were based on non-empty stomachs.

Stomach content composition of foxes

We calculated the absolute frequency of occurrence (FO=number of samples containing a specific category/total number of samples x 100) of each category and the relative volume (V =total estimated volume of each category as ingested/number of samples containing that category) of each category whenever it was ingested. We compared these values 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 and Parish 1985). We treated categories occurring in negligible proportions within a given stomach (<1% overall volume) as not being present. To examine whether there were differences in stomach content during distinct periods of the annual fox cycle, we separately analysed stomachs collected during two distinct periods: (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). We assessed changes in niche breadth by calculating Levin's standardised index for each period (Krebs 1999):

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

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).

We evaluated the adequacy of our sample size using a rarefaction curve analysis to determine how the difference in proportion of each food category changes with increasing sample size (McQueen and Griffiths 2004). In brief, we calculated the difference in mV of anthropogenic food (D) between consecutive sample size classes, increasing in increments of 5, and repeated using 1000 permutations. When the median D reached ≤ 0.01 we considered the sample size to be adequate. A more detailed description is provided in the supplementary material (Online Resource 1) and the R script is also provided (Online Resource 2).

Factors influencing stomach contents

We used binomial logistic regression 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, we extracted urban and suburban land parcels 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. We calculated the distance (m) from the location where each fox stomach was collected to the nearest human infrastructure boundary 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, we constructed models with the presence in fox stomachs as the binary response variable (present/absent), and three 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, we averaged the top models (cumulative sum of AIC weights ≤ 0.95) and took the coefficients of this averaged model (Burnham and Anderson 2002) using the R package 'MuMIn' (Bartoń 2022).

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, we modelled the annual number of foxes being subsidised by this resource. To do this, we estimated the total number of adult males, adult females, and cubs in the New Forest 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. We used Monte Carlo simulations to represent the plausible range of our input parameters, thus accounting for uncertainty (Fig. 2a, b). Full details of how we derived our estimates are provided in the supplementary material (Online Resource 1) and distributions of input parameters are provided in Table 1. All analyses were carried out in R v4.2.2 (R Core Team 2022) using a custom script (Online Resource 3).

Pre-breeding adult population density was a key input parameter for our 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, we considered several potential population densities based on (i) landscape-based estimates of fox densities recorded across

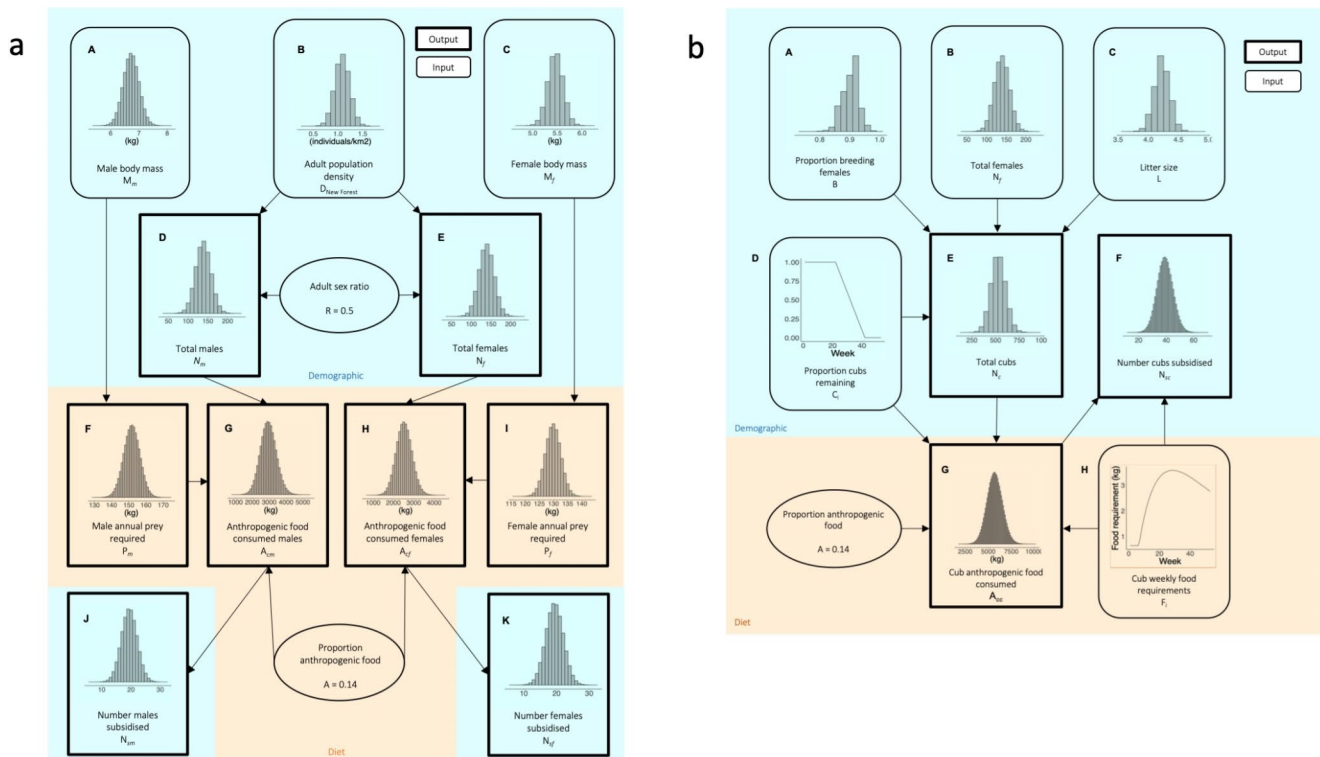


Fig. 2 a) Schematic representation of the data used to estimate the number of adult foxes supported by anthropogenic food. The landscape-based scenario of adult population density is depicted for illustration. (A) Male body mass distribution. (B) Adult population density distribution. (C) Female body 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 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	-	-

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 (GWCT 2020; Porteus et al. 2024). At Somerley, some tagged-fox territories encompassed parts of the New Forest, immediately adjacent to important curlew breeding sites.

Results

Out of the 447 fox stomachs collected, 33 were empty. We found dog biscuits 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 $2.43 (\pm 1.25 \text{ SD})$. Only 72 (18.4%) stomachs contained four or more categories. For the breeding period, the mean number of food categories per stomach was $2.46 (\pm 1.26 \text{ SD})$, with 64 (19.2%) stomachs containing four or more categories. For the non-breeding period, the mean number of categories per stomach was $2.29 (\pm 1.14 \text{ SD})$, with eight (15.4%) stomachs containing four or more categories.

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 (Fig. 3). Specifically, anthropogenic food comprised 13.9% of mV (Table 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; Fig. 3). Herptiles, gamebirds, fish, and indigestible material were relatively uncommon items ($\leq 2\%$ mV; Fig. 3). Additionally, 22.6% of the mV could not be unequivocally assigned to any specific category (Fig. 3).

The mV for several food categories was similar ($\leq 5\%$ 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 2). In general, the niche breadth was similar during the breeding ($B=0.55$) and non-breeding ($B=0.52$) periods (Table 2).

The median D for anthropogenic food for the breeding period fell below 0.01 after ~265 samples, indicating that our sample size ($N=333$) for this portion of the year was adequate (Online Resource 1). Given the smaller sample size for the non-breeding period, the median D marginally did not fall below 0.01 (Online Resource 1), although the median D after 50 samples (0.015) was close to the threshold value, indicating that additional samples would not greatly change our inferences on the amount of anthropogenic subsidisation during this part of the year.

Factors influencing occurrence of food items

Overall, 363 stomach samples were obtained with both date of collection and precise geographic coordinates. We detected a significant negative relationship between the occurrence of anthropogenic food in fox stomachs and

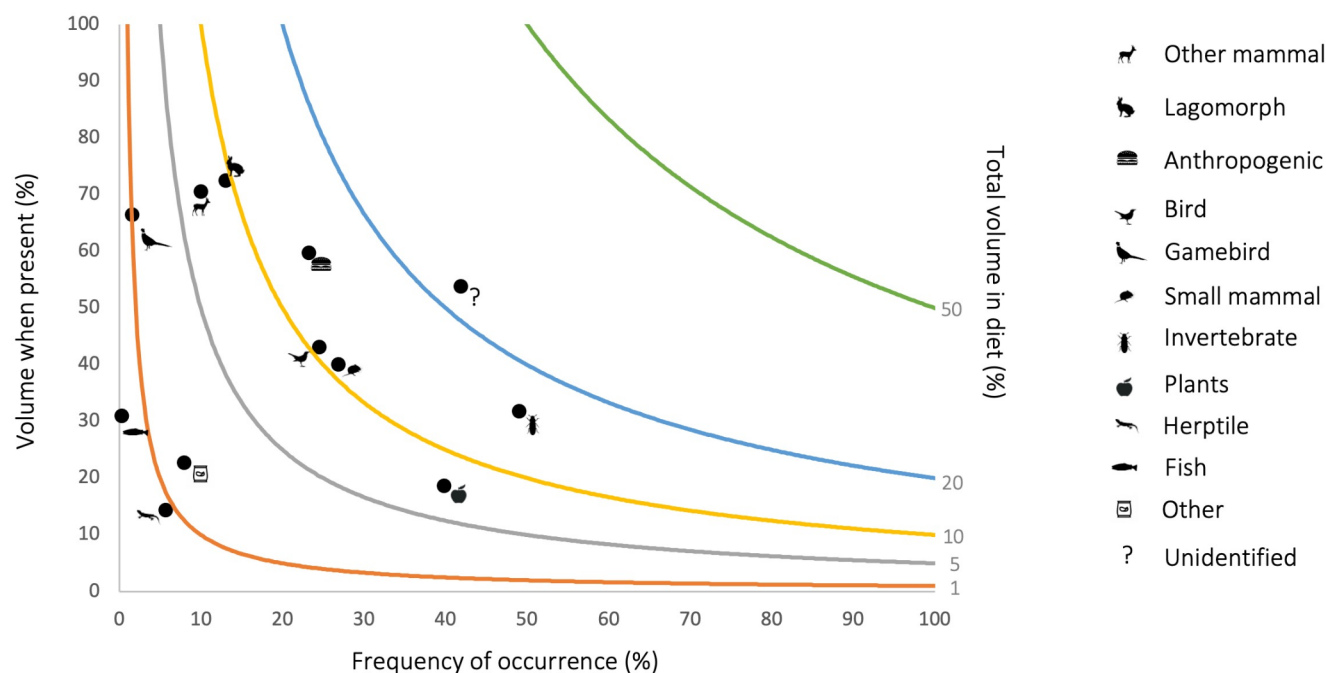


Fig. 3 Diet habits of foxes in terms of volume of a given food category when present (V) against its frequency of occurrence (FO). Isopleths connect points with equal relative volume (mV)

Table 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

Category	Sub-category	Period								
		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
	<i>Sciurus carolinensis</i>	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	-	-	-
	<i>Anguis fragilis</i>	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		

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

distance to the nearest human infrastructure boundary (-0.0013 ± 0.00039 SE; $p < 0.001$; Table 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), whereas the occurrence of lagomorphs was greater during the non-breeding period (-1.09 ± 0.36 ; $p < 0.01$; Table 3).

Number of foxes subsidised by anthropogenic food

The output of our Monte Carlo simulations used to estimate the annual number of foxes subsidised by anthropogenic food is provided in Table 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.

Discussion

We used stomach content analysis to examine the diet of foxes in the New Forest and analysed spatial variation in stomach contents with respect to human infrastructure. We also estimated the theoretical number of foxes supported by anthropogenic food within the managed area of the New Forest. We found that 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

Table 3 Coefficient values (\pm 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

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

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

other key food categories such as invertebrates, small mammals, lagomorphs, and non-game birds (Table 2). Notably, our findings suggest that foxes were readily exploiting anthropogenic food subsidies associated with human settlements and other infrastructure throughout the year. The output from our 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., Harris 1981; Ghoshal et al. 2016), 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 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 population numbers, resulting in increased nest and chick predation in the surrounding area (Esque et al. 2010; Selva et al. 2014; Harju et al. 2021) - so-called 'hyper-predation' (Taylor 1979; Shapira et al. 2008; Maeda et al. 2019). 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 and Jackson 2002).

Aside from suburban areas (Harris 1981; Doncaster et al. 1990; Saunders et al. 1993), anthropogenic food has not normally featured in previous analyses of rural fox diet in the UK (Reynolds and Tapper 1995; Leckie et al. 1998; Webbon et al. 2006), although the use of scat to analyse diet in these studies could have prevented its detection (Peterson et al. 2021). Our 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 (Rodewald et al. 2011; Reshamwala et al. 2018).

Although the output from our Monte Carlo simulations is subject to a great deal of uncertainty, our 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 and Reynolds 2000). Evidence of extreme population densities in Britford – among the highest ever recorded in mainland Britain outside of urban areas – maybe 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 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).

We found evidence that fox diet in the New Forest changed slightly during different periods of the annual fox

Table 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	

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 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 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 and 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 we cannot determine 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).

We note that 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 and 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 our 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. 2019; Porteus et al. 2019). Immigration rates in the region are particularly high (Porteus et al. 2019), 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 (Contesse et al. 2004; Handler et al. 2020). Furthermore, although gamebird shooting is not an important land-use within our study area, gamebirds are typically released on shooting estates (Madden and Sage 2020) of which there are several around the boundaries. However, we found scant evidence of gamebirds in our 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).

Conclusion

We have 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, our results 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.

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Declarations

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