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The potential impact of red fox *Vulpes vulpes* predation in agricultural landscapes in lowland Britain

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Recent legislative changes to red fox *Vulpes vulpes* control practices in Britain have focussed attention on the possible impact of fox predation on economically and ecologically important species in agricultural landscapes. We compared the estimated mass of prey consumed annually against the pre-breeding biomass of prey species on a farm in southern England. Medium-sized mammals (mainly rabbits *Oryctolagus cuniculus*) dominated fox diet in all seasons (74% of mass ingested); birds (mainly pheasants *Phasianus colchicus*), small mammals (mainly field voles *Microtus agrestis*) and large mammals comprised 11, 7 and 6% of the diet, respectively. The mass of rabbits, wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus* taken did not exceed the respective spring biomasses, indicating that fox predation was unlikely to be a significant limiting factor as all three species have a high rate of productivity. The impact on field voles was equivocal: the total mass consumed annually by foxes was equivalent to 2.7-5.7 times the estimated spring biomass, but this level of predation could be offset by recruitment. However, as field voles are a major dietary component of many predators and are likely to be confined to isolated habitat patches, the impact of predation on this species warrants further investigation. Predation on pheasants was equivalent to 34-81% of the estimated spring biomass: estimated levels of productivity derived from the literature would not have been sufficient to maintain pre-breeding population size. However, annual losses appeared to be fully compensated by immigration of reared birds from neighbouring farms. Predation on other avian taxa appeared insignificant.

Key words: diet, European rabbit, field vole, pheasant, predation, red fox, *Vulpes vulpes*

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Throughout its range, the red fox *Vulpes vulpes* is widely perceived as a major predator of game and livestock (e.g. Sargeant et al. 1984, Saunders et al. 1995, White et al. 2003). Although predation on pest species may be beneficial, large numbers of foxes are culled annually

in an attempt to increase the abundance of economically important species (Tapper 1992, Reynolds & Tapper 1996). Culling is also increasingly viewed as an effective management tool for the conservation of rare or endangered species (Côté & Sutherland 1997). However,

the evidence for the effectiveness of widespread culling is equivocal: whilst some studies have shown that reduced predator pressure from foxes, or foxes in combination with other predators, can increase prey abundance and/or productivity (e.g. Marcström et al. 1988, 1989, Pech et al. 1992, Tapper et al. 1996, Kinnear et al. 1998, Banks 2000), this is not always the case (e.g. Pech et al. 1992, Mayot et al. 1998, Kauhala et al. 1999). Furthermore, such studies have focussed on a relatively restricted number of species, mainly lagomorphs and tetraonids, with several prey populations being confined to islands with limited opportunity for immigration or emigration, or where the fox is an introduced species. Thus there are relatively few data on the impact of fox predation on a range of prey species in large-scale agricultural habitats.

For a given prey species, the impact of fox predation will, at the most basic level, be determined by the numbers of individuals killed by foxes and the relative importance of this rate of mortality in the overall dynamics of the prey. Consequently, a simple estimate of the effects of predation can be obtained from the simultaneous measurement of fox numbers, fox diet and prey dynamics. More complex assessments would include the impact of predation on different age and sex classes and the timing of predation relative to reproduction: however, such data are lacking for most prey species. Therefore, although such studies do not definitively indicate the effect of predation, they can be used to help identify species that may be adversely affected by a predator (Risbey et al. 1999) and serve as a useful precursor to more intensive and expensive investigations.

In Britain, the impact of predation by foxes is of fundamental importance in light of recent restrictions on the use of dogs to control fox numbers (Burns et al. 2000; www.hms.o.gov.uk). The diet of foxes in Britain has been investigated extensively (see review in Baker & Harris 2003). However, the data currently available are of limited use in identifying the possible impact of predation by foxes in rural Britain. First, previous studies span > 60 years, with most having been conducted between 1970 and 1980. In the last 50 years there have been significant changes in the abundance of several prey species in the UK, particularly rabbits *Oryctolagus cuniculus*, pheasants *Phasianus colchicus* and field voles *Microtus agrestis* (Tapper 1992, Harris et al. 1995, 2000). Second, the data collected in these studies have been analysed and presented in a number of different ways, thereby limiting their comparability. Lastly, only a single study has concurrently measured prey abundance and, therefore, been able to estimate the possible impact of fox predation on species of concern (Reynolds & Tapper 1995a).

Fox diet is known to vary substantially between sites (Reynolds & Tapper 1995a, Baker & Harris 2003), presumably in relation to prey availability. In agricultural landscapes, prey availability is likely to be influenced by patterns of agricultural production, but also by other land use interests. Consequently, to obtain a complete picture of the possible impact of foxes in Britain, it is necessary to obtain data from areas covering a wide range of agricultural and land use practices. For example, the study of Reynolds & Tapper (1995a) was conducted on an area dominated by cereal crop production and with game-rearing interests, including the control of predators (although fox control was suspended for part of that study). However, crops comprise only 25% of the total area of agricultural holdings in the United Kingdom (MAFF 2000), and the presence and degree of fox control varies among holdings; in two nation-wide surveys, 38–42% of farmers reported that they undertook no fox control (Vaughan et al. 2003, White et al. 2003).

The purpose of our study was to assess the possible impact of fox predation on a mixed organic farm in Wiltshire, UK, where no predator control was undertaken, by comparing the estimated mass of rabbits, pheasants, field voles, wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus* consumed annually by the resident fox population with the measured spring biomass of these prey species. The total mass of each prey species consumed annually was estimated from field data on fox diet composition and fox density in conjunction with the approximate annual food requirements for juvenile and adult foxes derived from a published study of captive foxes (Sargeant 1978) corrected for the larger body size of foxes in Britain. To enhance comparability, we have adopted the approaches outlined by Reynolds & Tapper (1995a).

Material and methods

Our study was conducted during 1995–1996 on an organic farm at Castle Combe, Wiltshire, UK (51°20'N, 2°13'W; altitude 92 m a.s.l.). Temperature range was approximately -7.3°C to 30.0°C with an annual rainfall of 506 mm (data for 1996 from Lyneham weather station 51°30'N, 1°59'W; UK Meteorological Office). The principal farming practices were the production of cereal and fodder crops and the maintenance of beef cattle; several fields were leased annually for sheep grazing. The farm covered an area of 352 ha; this consisted of 213 ha open fields (of which approximately 35% was cereal crops and 65% pasture/fodder crops annually), 110 ha woodland, 23 ha set-aside (i.e. rough grassland) and 6

ha marshland managed as a nature reserve. Neighbouring land, to which we did not have access, comprised farmland, a golf course, a motor racing circuit and a village. Predators were not culled on the study farm, but neighbouring landowners did control foxes. As fox territories overlapped these neighbouring farms, the resident fox population was subject to an unknown level of culling.

Pheasants were reared and released annually on two neighbouring farms but not on the study farm. At the commencement of the study there was only a limited amount of rabbit control, conducted principally by the farm manager. During winter 1995/96 and winter 1996/97 more intensive control was undertaken because of grazing damage to cereal crops. In all instances, rabbits were taken by ferreting during autumn and winter. Rabbits on neighbouring farms were culled all year round, primarily by shooting and ferreting.

Other vertebrate prey present included: domestic chickens, available from a nearby intensive poultry unit (where dead birds were often discarded) and from households in the vicinity where small numbers were kept for private use; and ducks and geese (Anseriformes) and rails (Ralliformes), available principally from the private nature reserve on the study farm. Passeriformes, Columbiformes, grey squirrels *Sciurus carolinensis*, common rats *Rattus norvegicus*, roe deer *Capreolus capreolus* and muntjac deer *Muntiacus reevesi* were present across the study site. Brown hares *Lepus europaeus* were present within 2 km of the study farm but were only observed on the study farm and immediate neighbouring farms on one occasion. Consequently, we have considered them absent as prey. Four other mammalian carnivores (badger *Meles meles*, stoat *Mustela erminea*, weasel *Mustela nivalis* and American mink *Mustela vison*) and four predatory bird species (kestrel *Falco tinnunculus*, sparrowhawk *Accipiter nisus*, buzzard *Buteo buteo*, and tawny owl *Strix aluco*) were also present.

Fox scats were collected during 1995 and 1996 from across the study farm during other routine activities, e.g. trap checking and prey abundance surveys. Scats were stored at -5°C prior to examination. Seasons were defined as spring = March-May, summer = June-August, autumn = September-November, and winter = December-February. Scats of cubs collected at breeding dens (April-June) were analysed separately (Lindström 1994).

Scats were analysed according to the procedures outlined by Reynolds & Aebischer (1991). Faeces were oven dried at 80°C to constant mass, weighed to the nearest 0.01 g, and then soaked for 24 hours in water before being physically separated and strained through a 0.5-mm sieve. The strained liquid was then left to settle for a further 24 hours before decanting off most of

the water, and air-dried. The remaining micro-fragment was then examined for earthworm chaetae. The total number of chaetae in the micro-fragment was converted to mass ingested as described by Reynolds & Aebischer (1991).

Each component of the macro-fragment was separated, dried and weighed. Fur types were identified to species using the keys of Day (1966) and Teerink (1991). Feather types were identified to order using Day (1966). Insect components were identified to order. All *Apodemus* fur was assumed to represent predation on wood mice; yellow-necked mice *Apodemus flavicollis* were present, but because of their more restricted distribution on the farm, we have assumed that wood mice were much more likely to be consumed. All lagomorph fur was assumed to represent predation on rabbits. The excreted mass of each macro-group was converted to ingested mass using conversion factors derived from captive feeding studies (Reynolds & Tapper 1995a).

For comparability with other studies, diet composition is presented as both the frequency of occurrence of each prey type in scats and percentage mass ingested. For the calculation of percentage mass ingested, only items considered to be of nutritive value were utilised. Mammalian prey was classified into three categories based on size: small mammals (<0.1 kg), medium-sized mammals (0.1-5.0 kg) and large mammals (> 5.0 kg). Unidentified remains of mammals and birds were assumed to be in direct proportion to the distribution of identified prey and were re-allocated accordingly. Limits for the contribution of each prey type to the diet were estimated using the bootstrapping procedure outlined by Reynolds & Aebischer (1991).

Fox abundance

To estimate the total mass of each prey group consumed by the resident fox population, it was necessary to estimate both the total number of foxes present and the total annual prey requirement of each adult and juvenile fox. It was not possible to census foxes using spotlight counts because of the restricted area of the study site and the large amount of wooded cover (Heydon et al. 2000). Furthermore, it was not possible to use radio telemetry to estimate fox density, as we could not set snares to catch the foxes because of the risk of catching badgers, which are legally protected in Britain; cage-trapping foxes proved unsuccessful. Therefore, the number of breeding groups on the study site was estimated by a complete count of the number of breeding dens on the study site, assuming each social group produced a single litter of cubs annually. Counts were conducted simultaneously by two or more researchers. Parallel transects

< 10 m apart were conducted throughout woodlands and areas of rough grass using a compass, and all hedgerows and other field boundaries were surveyed; no dens were observed in open fields. Surveys were conducted during May, when field signs (e.g. faeces and feeding remains) were most evident. The number of adult foxes and cubs in each social group was determined by observations at den sites. As we were not able to determine the exact spatial configuration of the resident foxes, maximum fox density was assumed to occur when all the foxes observed existed solely on the study farm; minimum fox density was estimated assuming each social group occupied a territory of 2.5 km² (Reynolds & Tapper 1995a).

Annual prey requirements

Sargeant (1978) recorded a prey consumption rate of 0.48 kg prey/kg/week for male and female foxes weighing 4.75 kg and 4.68 kg, respectively. Male and female foxes in Britain weigh approximately 6.50 kg and 5.50 kg (Harris & Lloyd 1991), indicating mass-specific consumption rates of 0.44 i.e. $0.48 \times (4.75/6.50) \times (6.50/4.75)^{0.75}$ (J. Rayner, pers. comm.) and 0.46 kg prey/kg/week, respectively, and a total weekly requirement of 2.86 kg prey for males and 2.53 kg prey for females. Therefore, over the course of one year, an adult male and female would consume approximately 149 and 132 kg of prey, respectively.

During lactation, females increased their consumption rate by 0.57 kg prey/cub/week (Sargeant 1978), which relates to an additional prey consumption rate of 0.12 kg prey/kg/week (i.e. $0.57/4.68$). This would imply an increased prey requirement of 2.54 kg prey for each cub over the four-week denning period in Britain (i.e. $[0.12 \times (4.68/5.50) \times (5.50/4.68)^{0.75}] \times 5.50 \times 4$).

Cubs were assumed to consume no prey in the first four weeks of life. Individual cub food requirements were assumed to peak at 28 weeks after birth at 1.3 times the adult requirement, and then decline to the adult rate at 52 weeks (Reynolds & Tapper 1995b) when they attained a final mass of 6.00 kg. Under this scenario, each juvenile fox would consume 144 kg of prey over the course of one year. However, there was a marked drop in the number of scats found in the autumn season, which is consistent with the onset of the dispersal period. Therefore, we have assumed that all cubs dispersed on 1 October; given the magnitude of culling undertaken on neighbouring farms it is almost certain that the study site was a source of dispersing individuals. This would potentially underestimate the mass of prey consumed by the cubs if they did not all disperse, but would be partly offset by undetected deaths after the cubs left

the dens and before 1 October. Under this scenario, each juvenile fox would consume 60 kg of prey over the course of one year.

Rabbit abundance

We could not conduct transect counts (e.g. Parer & Price 1987, Moller et al. 1996) of rabbits on the study site, as many warrens were located in woodlands. Although trapping was undertaken to mark individuals, this is an unreliable method of estimating rabbit population size (Cowan 1984). Consequently, we estimated rabbit numbers by quantifying the relationship between the number of active entrance holes and the number of rabbits killed for those warrens ferretted as part of the rabbit control programme; the number of active entrances has been found to correlate with rabbit numbers (Cowan 1991a). We then surveyed the whole study site to determine the number of active entrances for each warren. The relationship between the number of active holes and the number of rabbits was then used to estimate the total number of rabbits present.

A maximum separation distance of 50 m between successive sets of holes was taken to indicate separate sampling units. This reflected the practices of the persons undertaking rabbit control; commonly they would ferret a set of holes before moving to another set close by. However, it is unlikely to reflect the true distribution of warrens on the farm, as warrens are often < 50 m apart (Cowan 1983). Therefore, we use the phrase 'warren units' to describe the unit areas controlled. For analyses, we used only the number of adult rabbits killed; adult animals were defined as > 1.0 kg.

Not all the rabbits in a warren will be captured during ferreting. In a population of marked animals, Cowan (1984) calculated that approximately 31% of males and 45% of females known to be resident were captured using this technique. Therefore, to estimate the total number of rabbits present in our study population we have multiplied the number of adult animals ferretted and killed by a factor of 2.63 (i.e. $1/0.38$) to calculate the total number of adult rabbits present.

Wood mouse, bank vole and field vole abundance

We utilised 10 live-capture trapping grids to measure the abundance of wood mice and field voles in two habitats: woodland (N = 4) and grassland (N = 6). Each grid comprised 7 × 7 grid points spaced 10 m apart with one Longworth trap (Penlon Ltd, Oxfordshire, UK) at each grid point, giving an effective trapping area of 0.49 ha. Each grid was run for four consecutive nights at approximately 12-week intervals between July 1995 and Jan-

uary 1997 inclusive. Traps contained bedding material, were baited with oats and fly pupae, and set each evening and checked each morning during the trapping period. Animals were identified to species, sexed, weighed and marked using fur clips (Gurnell & Flowerdew 1994). Abundance was estimated using the minimum number alive per trapping session (Otis et al. 1978); this provided a minimum estimate of rodent density. Estimates of densities in habitats not trapped were obtained from the literature.

The abundance of bank voles was estimated from the data obtained for wood mice. Previous live-trapping studies and the examination of animal carcasses found

in discarded bottles indicate that wood mice are approximately 1.75 times as abundant as bank voles (Harris et al. 1995). Therefore, bank vole abundance was estimated by multiplying wood mice pre-breeding density by 0.57. Abundance estimates were not undertaken for other small mammal species (e.g. house mouse *Mus musculus* and common rat), as foxes consumed these species infrequently.

Pheasant abundance

The size of the pre-breeding pheasant population was estimated from counts conducted during spring 1995 and 1996 in the two hours after dawn and before dusk

Table 1. Frequency of occurrence of prey types in fox faecal samples. Figures give the percentage of faeces containing each prey group. Because of multiple occurrences of prey groupings in the same scats, subtotals and totals are not the sum of the individual components. Figures in parentheses give the number of scats analysed. T denotes that the prey occurred in <0.5% of scats.

Prey type	Spring		Summer	Autumn	Winter	Mean
	Adults (N = 200)	Cubs (N = 100)	Adults (N = 350)	Adults (N = 150)	Adults (N = 185)	Adults
Mammals	90	93	84	79	90	86
Small mammals	22	13	12	10	17	16
<i>Apodemus</i> spp	2	2	2	1	3	2
<i>Clethrionomys glareolus</i>	2	1	4	3	2	3
<i>Microtus agrestis</i>	13	6	6	5	10	9
<i>Mus musculus</i>	2	2	0	1	0	1
<i>Rattus norvegicus</i>	2	0	0	1	1	1
Unidentified	2	2	1	0	1	1
Medium-sized mammals	69	71	69	66	74	70
<i>Sciurus carolinensis</i>	2	0	T	0	2	1
<i>Oryctolagus cuniculus</i>	68	71	69	66	74	70
Large mammals	5	6	2	3	4	4
<i>Meles meles</i>	0	4	1	1	2	1
<i>Vulpes vulpes</i>	1	2	1	1	1	1
<i>Capreolus capreolus</i>	4	0	1	1	2	2
<i>Ovis</i> spp.	1	0	0	0	0	T
Unidentified mammals	10	9	7	3	6	7
Birds	29	35	22	15	32	25
Passeriformes	13	15	5	5	9	8
Wild Galliformes	6	12	6	4	7	6
Domestic Galliformes	2	2	2	1	3	2
Columbiformes	3	2	1	1	1	2
Anseriformes	1	2	2	3	1	4
Falconiformes	0	0	0	0	1	T
Ralliformes	1	0	1	0	0	1
Unidentified birds	5	2	5	2	12	6
Bird eggs	2	2	7	1	1	3
Insects	10	52	51	47	14	31
Coleoptera	10	52	50	47	14	30
Orthoptera	0	0	1	0	0	T
Diptera	0	0	1	1	0	1
Lepidoptera	0	0	0	0	1	T
Unidentified	0	0	T	0	0	T
Seeds & berries	3	0	7	14	10	9
Earthworms	28	19	31	38	30	32
Non-edible vegetation	51	75	48	29	50	45
Soil & stones	6	2	10	6	3	6
Other non-food items	0	4	2	3	1	2

Table 2. Percentage mass of prey ingested. Figures in parentheses give 95 percentile ranges obtained from bootstrapping (Reynolds & Aebischer 1991). Bootstrapping limits for mean adult diet was calculated from random samples of 150 scats from each season to avoid overdependence on any single season. T denotes that the prey accounted for < 0.5% of prey ingested.

Prey type	Spring		Summer	Autumn	Winter	Mean
	Adults (N = 200)	Cubs (N = 100)	Adults (N = 350)	Adults (N = 150)	Adults (N = 185)	Adults (N = 600)
Small mammals	7 (4-10)	T (T)	5 (3-8)	8 (3-14)	6 (3-9)	7 (5-8)
<i>Apodemus sylvaticus</i>	1 (0-2)	T (T)	1 (0-2)	1 (0-3)	1 (0-2)	1 (0-3)
<i>Clethrionomys glareolus</i>	T (T)	T (T)	1 (0-2)	2 (0-3)	T (T)	1 (0-2)
<i>Microtus agrestis</i>	4 (1-6)	T (T)	3 (1-4)	3 (1-7)	5 (2-6)	4 (2-7)
Medium-sized mammals	74 (65-80)	58 (45-75)	79 (74-84)	72 (62-81)	73 (66-79)	74 (68-77)
<i>Oryctolagus cuniculus</i>	73 (65-79)	58 (45-75)	79 (74-84)	72 (62-81)	73 (66-79)	74 (68-77)
Large mammals	7 (2-14)	10 (0-24)	2 (0-4)	8 (0-16)	6 (2-10)	6 (2-9)
Birds						
Passeriformes	6 (3-9)	14 (3-15)	2 (1-4)	1 (0-3)	5 (2-7)	3 (2-5)
Wild galliformes	5 (2-8)	17 (3-31)	6 (2-9)	4 (0-8)	6 (3-11)	5 (4-9)
Domestic galliformes	1 (0-3)	1 (0-3)	1 (0-2)	1 (0-2)	2 (0-5)	1 (1-3)
Columbiformes	1 (0-3)	T (T)	1 (0-2)	1 (0-1)	T (0-1)	1 (0-1)
Other birds	T (T)	1 (0-2)	2 (1-4)	2 (0-6)	T (0-1)	1 (0-2)
Bird eggs	T (T)	T (T)	T (T)	T (T)	T (T)	T (T)
Insects	T (T)	T (T)	1 (1-2)	2 (1-3)	T (T)	T (T)
Seeds & berries	T (T)	T (T)	1 (0-2)	2 (1-4)	1 (0-2)	1 (1-2)
Earthworms	T (T)	T (T)	T (T)	T (T)	T (T)	T (T)

(Robertson et al. 1993). Counts were made on foot using a telescope. Males were classified as territorial and non-territorial based on plumage and behavioural characteristics (Hill & Robertson 1988). Every area on the farm was surveyed five times in both years to ensure that all territorial males were identified (Robertson et al. 1993), although not all areas on the farm could be surveyed within each two-hour period. Harem size was calculated as the maximum number of females observed < 25 m from a territorial male during any of the five counts. This method has been shown to reliably indicate the number of territorial males, but to underestimate the numbers of females and non-territorial males (Robertson et al. 1993). To account for the cryptic behaviour of females, minimum female density in spring was estimated as the sum of maximum observed harem sizes divided by 0.85 (Robertson et al. 1993). Minimum non-territorial male density was estimated from the maximum number seen in an area on any of the five counts. The

census was repeated in autumn to estimate the change in population size, and to record the number of females associated with young. However, autumn counts are likely to underestimate the size of all three classes of individuals due to cryptic behaviour (Robertson et al. 1993). Furthermore, comparisons with spring census data may be complicated by the immigration of pen-reared birds from neighbouring areas. Figures are expressed as the average for the two years.

Results

Fox diet

Medium-sized mammals were the most frequently recorded prey in the faeces of adult foxes, followed by non-edible vegetation (e.g. grass, small twigs and pine needles), earthworms, insects, birds and small mammals, respectively (Table 1). Other prey types were typically

found in < 10% of scats in each season. There were only minor seasonal variations in the frequency of occurrence of the different prey groups. The most frequently occurring items in the diet of dependent cubs were non-edible vegetation and medium-sized mammals, with a greater occurrence of insects and birds and less reliance on earthworms (see Table 1).

The single most important prey in terms of mass ingested was rabbit, which accounted for 74% of the diet of adult foxes (range: 72-79% across seasons; Table 2). Three other prey groups each comprised $\geq 5\%$ of the prey intake of adult foxes; small mammals (mean 7%, range: 5-8% seasonally), large mammals (mean 6%, range: 2-8%), and wild galliformes (mean 5%, range: 4-6%). Dependent cubs were less reliant on rabbits (58%) and consumed larger amounts of wild galliformes (17%), passeriformes (14%) and large mammals (10%).

Fox abundance and prey requirements

Three breeding dens were located on the study site during each of the two years, and 31 observations at these dens indicated that mean (\pm SD) group size was 2.50 ± 0.55 adults ($N = 6$). Mean (\pm SD) emergent litter size was 4.17 ± 0.75 cubs ($N = 6$). Fox scats were found throughout every season indicating that foxes were present throughout the study period. However, there was a decline in the number of scats found during autumn that was coincident with the onset of the dispersal period (Harris & Trehwella 1988). This is consistent with a decline in the number of foxes present at that time.

Maximum fox density was assumed to occur when all the foxes observed existed solely on the study farm. Corresponding group density would be 0.85 groups/km², with a pre-breeding and post-breeding density of 2.13 adults/km² and 5.68 foxes/km², respectively. Minimum fox density was estimated assuming each social group occupied a territory of 2.5 km² (Reynolds & Tapper 1995a). This would indicate a group density of 0.40 groups/km², and pre- and post-breeding densities of 1.00 adults/km² and 2.67 foxes/km², respectively.

The total annual prey requirement for a group of 2.50 adults and 4.17 cubs was approximately 608 kg. Assuming juvenile foxes are resident at the den during April-June and disperse on 1 October, the seasonal pattern of consumption for each fox group is as follows: spring = 130 kg (adults 97 kg, juveniles at den 33 kg); summer = 243 kg (adults 88 kg, juveniles at den 43 kg, juveniles away from den 112 kg); autumn = 149 kg (adults 87 kg, juveniles away from dens 62 kg); winter = 86 kg (adults only). At minimum and maximum pre-breeding densities of 0.40-0.85 groups/km², respectively, the annual prey demand was approximately 243-517 kg prey/km².

Rabbit abundance

Approximately 940 adult rabbits were killed during the rabbit control programme; of these, 827 rabbits from 24 warren units provided usable data for quantifying the relationship with warren size. For three warrens ferreted in both years, we have used an average value to calculate the relationship between adult numbers and warren size. The number of active holes recorded was significantly correlated with the number of adult individuals ferreted and killed: $y = 0.33x + 13.2$, where y is the number of adult rabbits killed and x is the number of active entrance holes (Pearson correlation coefficient: $r = 0.81$, $N = 24$, $P < 0.001$). We identified 79 warren units across the study site, with a total of 2,895 active entrance holes. This would equate to a ferretable population of approximately 969 adult rabbits and a standing crop of 2,548 adult rabbits. Assuming an average weight of 1.5 kg (Reynolds & Tapper 1995a), the pre-breeding biomass on the study site was 3,822 kg ($\sim 1,086$ kg/km²).

Combining the seasonal pattern of consumption for adults, juveniles at the breeding den and juveniles away from the breeding den, and the seasonal diet composition of adults and cubs (i.e. juveniles at the breeding den; see Table 2), each fox group would consume approximately 443 kg of rabbit over the course of one year. At minimum and maximum fox densities of 0.40-0.85 groups/km², this is equivalent to the consumption of 624-1,329 kg of rabbit on the study site as a whole (~ 177 -378 kg/km²; Fig. 1A).

Wood mouse, bank vole and field vole abundance

Multiplying the spring densities of each species (Table 3) by the amount of available habitat (110 ha of woodland and 23 ha of grassland), the small mammal population in spring comprised approximately 5,832 wood mice and 483 field voles. In addition to these two habitat types, there was an additional 75 ha of cereal crops that would also have supported wood mice; field voles are rarely found in this habitat. Assuming a density of 1/ha for wood mice in cereal crops (Harris et al. 1995), this would indicate a total population of 5,907 wood mice and 483 field voles. Assuming a standard weight of 20 g

Table 3. Seasonal small mammal density in woodland ($N = 4$ trapping grids) and grassland ($N = 6$ trapping grids) habitats. Figures give number per hectare (mean \pm SD) and are based on the minimum number trapped in each trapping session.

Habitat	Species	Spring	Summer	Autumn	Winter
Woodland	Wood mouse	48 \pm 9	39 \pm 15	37 \pm 1	24 \pm 10
	Field vole	-	-	-	-
Grassland	Wood mouse	24 \pm 23	29 \pm 31	49 \pm 47	30 \pm 33
	Field vole	21 \pm 31	43 \pm 58	28 \pm 24	20 \pm 21

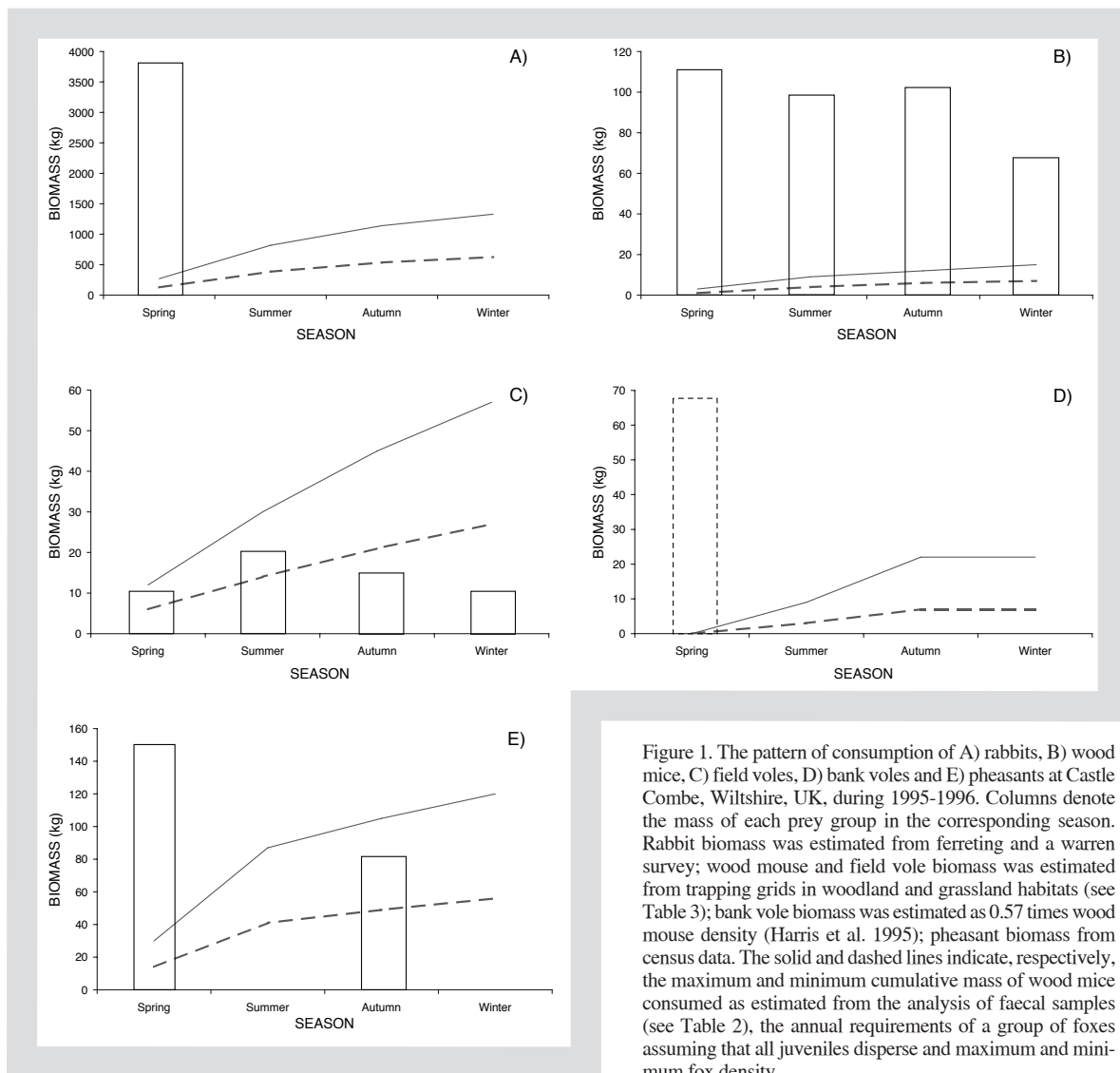


Figure 1. The pattern of consumption of A) rabbits, B) wood mice, C) field voles, D) bank voles and E) pheasants at Castle Combe, Wiltshire, UK, during 1995-1996. Columns denote the mass of each prey group in the corresponding season. Rabbit biomass was estimated from ferreting and a warren survey; wood mouse and field vole biomass was estimated from trapping grids in woodland and grassland habitats (see Table 3); bank vole biomass was estimated as 0.57 times wood mouse density (Harris et al. 1995); pheasant biomass from census data. The solid and dashed lines indicate, respectively, the maximum and minimum cumulative mass of wood mice consumed as estimated from the analysis of faecal samples (see Table 2), the annual requirements of a group of foxes assuming that all juveniles disperse and maximum and minimum fox density.

for an adult of each species (Yalden & Morris 1990), the standing crop of wood mice and field voles was 118 kg (~34 kg/km²) and 10 kg (~3 kg/km²), respectively. The corresponding standing crop for bank voles, based on the abundance of wood mice, was 3,367 individuals, with a total biomass of 67 kg (~19 kg/km²).

Each fox group would consume approximately 5 kg of wood mice, 5 kg of bank voles and 19 kg of field voles annually. At minimum and maximum fox densities, these figures are equivalent to the consumption of 7-15 kg of wood mice (~2-4 kg/km²), 27-57 kg of field voles (~8-16 kg/km²) and 7-15 kg of bank voles (~2-4 kg/km²) on the study site as a whole (Fig. 1B-1D).

Pheasant abundance and mortality

On average, 42 territorial males, nine non-territorial males and 57 females were counted during the spring censuses. Applying the conversion factor of Robertson et al. (1993) to account for hidden females, these figures indicate a pre-breeding density of 33.5 birds/km² (territorial males, 11.9/km²; non-territorial males, 2.6/km²; females, 19.0/km²). Assuming male pheasants weighed 1.45 kg and females 1.10 kg (Reynolds & Tapper 1995a), the spring standing crop of pheasants was 148 kg (42.0 kg/km²). Autumn counts identified 37 males and 24 females, giving a density of 18.5 birds/km² (males, 10.5/km²; females, 8.0/km²); the equivalent biomass was 85 kg (~24.1 kg/

km²). Only three females were observed with young, with an average brood size of three young.

Annually each fox group consumed approximately 40 kg of pheasants. At minimum and maximum fox densities of 0.40-0.85 groups/km², this is equivalent to the consumption of 56-120 kg on the study site as a whole (~16-34 kg/km²; Fig. 1E). Consumption rates were particularly high during spring and summer while pheasants were breeding: overall 73% (41-87 kg) of the total mass consumed annually was taken during 1 March - 31 August.

Discussion

In our study, adult foxes were most reliant on rabbits throughout the year; on average, rabbits comprised 74% of the diet (see Table 2). Other prey groups consumed, in decreasing order of importance, were small mammals, large mammals and wild Galliformes. The occurrence of large mammals probably reflected scavenging on road casualties (e.g. badgers and deer) or illegally poached individuals (deer), although foxes will predate deer fawns. The diet of juveniles at breeding dens was markedly different, with a greater reliance on birds, in particular wild Galliformes (see also Lindström 1994). This probably reflects the optimum allocation of food resources by adults during central place foraging (Lovari & Parigi 1995).

To assess the potential impact of fox predation on a given prey species it is necessary to consider the mass of prey consumed in the context of the likely recruitment of a comparable biomass over the course of one year. The maximum estimated mass of rabbits consumed on the study site was 1,329 kg per annum, which is equivalent to the consumption of 886 adult individuals (1.5 kg each). In comparison, assuming an equal adult sex ratio, the estimated biomass of the pre-breeding population (3,822 kg) is equivalent to a reproductive population of approximately 1,274 females. Maximum adult mortality for a high-density population in the UK is likely to be in the order of 65% (Cowan 1991b), indicating a loss of 1,656 adult individuals (2,484 kg) in the course of one year. Assuming that fox predation was wholly additive to this mortality, the total biomass lost (1,329 + 2,484 = 3,813 kg = 2,542 adult individuals) would be fully compensated by the recruitment of just 2.0 adult offspring for each female within the pre-breeding population. In reality, predation by foxes was likely to be the major form of mortality in this population, such that the assumed mortality rate is likely to wholly incorporate any estimate of predation; this would have been fully compensated by the recruitment of 1.3 adult offspring

per female (i.e. 1,656/1,274). These recruitment rates are entirely plausible given that productivity (at birth) in agricultural landscapes in England averages 14-22 young per female per year (Trout & Smith 1995), although there are few specific data on the rate at which young are recruited into breeding populations at different densities. Therefore, despite the heavy reliance on rabbits, it is unlikely that fox predation would have regulated the size of the rabbit population (see Pech et al. 1992, Banks 2000).

This is also likely to be the case considering predation in addition to the mortality exerted by the rabbit control programme. During the control programme undertaken in two winter seasons approximately 940 rabbits were killed. As this mortality was exerted at around the time of the onset of breeding in the rabbit population, it would have had the effect of reducing the size of the pre-breeding rabbit population. With approximately equal numbers taken each year and an equal sex ratio, the pre-breeding population would have been reduced to approximately 1,039 females. To recover to pre-control levels (2,548 adults) with an additive 65% adult mortality rate would necessitate a recruitment rate of 2.6 adult offspring per female in the reduced population, which is in the likely range for rabbits in agricultural landscapes (Trout & Smith 1995). At this density, therefore, the level of control exerted is unlikely to have exerted any economic benefit in reducing crop damage.

Foxes are generally unlikely to exert a limiting effect on generalist small mammal species in lowland agricultural landscapes, as these typically constitute only a minor component of the diet (Baker & Harris 2003), and foxes occur at substantially lower densities. In this study, maximum consumption rates by foxes accounted for 13% of the spring biomass of wood mice (see Fig. 1B) and 22% of the spring biomass of bank voles (see Fig. 1D). In conjunction with a high intrinsic rate of increase (wood mice, $r = 12.43$; bank vole, $r = 6.22$; Bright 1993), it is improbable that foxes exerted any influence on the wood mouse or bank vole populations.

In contrast, minor prey species with specialised requirements may be more vulnerable to the effects of fox predation. For example, field voles have been shown to be susceptible to the effects of habitat fragmentation (Crone et al. 2001) and, in this study, they were confined to small, isolated areas of rough grassland. Despite this limited distribution, they comprised the major portion of the small mammal component in the diet of foxes. As a result, the mass consumed by foxes exceeded the spring biomass of voles by a factor of 2.7-5.7 times (see Fig. 1C) and this species is also likely to have been consumed by a range of other predators (Dyczkowski & Yalden

1998). However, field voles have a high intrinsic rate of increase ($r = 8.21$; Bright 1993), such that even substantial losses to predators may be offset by reproduction. In addition, the trapping regime utilised may have underestimated field vole density, e.g., Gurnell & Flowerdeew (1994) recommend using a small inter-trap interval and pre-baiting traps to maximise capture rates. As a result, the impact of predation on field voles is equivocal.

Fox predation did appear to exert an effect on the pheasant population. The mass of pheasant consumed annually (56–120 kg) was equivalent to 38–81% of the spring standing crop (see Fig. 1E). The majority of the mass consumed was taken during spring and summer (41–87 kg), when pheasants were breeding, and prior to the likely immigration of released birds from neighbouring farms. Consequently this provides an indication of the potential impact on the breeding population. Most predation during these seasons was likely to have involved females, as they are particularly vulnerable during nesting and incubation (Hill & Robertson 1988). Assuming (probably conservatively) that 60% of the mass of prey consumed during spring and summer related to predation on females, the consumed mass of 41–87 kg would be equivalent to the loss of 22–47 females from a minimum estimated pre-breeding population of 67 (i.e. $57/0.85$), indicating that a minimum of 20–45 females survived the breeding season. These data would indicate a survival rate of approximately 0.30–0.67 for the period 1 March – 31 August; these are at the low end of the scale for rates calculated in other studies (Robertson 1991, Riley & Schulz 2001).

We do not have figures for the productivity of the females in this population, as autumn counts would exclude females that had successfully reared broods to independence. However, data from the British Trust for Ornithology's nest recording scheme suggest that approximately 29% of females surviving the breeding season would have successfully produced a brood (Robertson 1991); we have elected to use this figure rather than the 66% for the Pheasant Nest Recording Scheme run by the Game Conservancy Trust (Robertson 1991), as this latter scheme is focussed only on shooting estates where predator control is typically undertaken. Assuming an average brood size of 3.2 young (Robertson 1991), these figures indicate the production of 19–42 fledged young, approximately half of which would be females. This is below the level of productivity required to sustain the population and excludes losses of breeding females to other causes during the breeding season (e.g. agricultural machinery, road traffic accidents) and subsequent autumn and winter mortality of both juvenile and adult pheasants. Consequently, predation by foxes would have

been sufficient to eradicate the pheasant population within a few years. Additional factors that may also have reduced productivity in our study include reduced availability of optimal habitats for mating and reproduction (Robertson et al. 1993) and low chick survival as a consequence of poor invertebrate availability (Hill 1985), although pesticides had not been used for a number of years.

Yet despite this level of predation, there was little difference in pheasant population size between the two years surveyed, indicating that the population appeared to be maintained by the immigration of captive-reared birds from neighbouring farms. Therefore, the results of this study and others (Robertson 1988, Reynolds & Tapper 1995a, Mayot et al. 1998, Riley & Schulz 2001) suggest that in Britain the current abundance of this introduced species is heavily dependent on the release of millions of birds annually (Tapper 1992), and that maintaining populations at current levels is reliant on practices such as habitat management and predator control (Mayot et al. 1998). Such practices are likely to have beneficial (e.g. Clarke & Robertson 1993) and detrimental (e.g. Tompkins et al. 2002) effects on other species in agricultural communities. Therefore, this system represents an unusual example of the repeated facilitated introduction of an alien species. However, it has been proposed that released birds may have a detrimental effect on the productivity of wild-reared (individuals reared in the wild by females that were themselves hand-reared; Game Conservancy Trust 1997) or wild birds (birds reared in the wild by females that were themselves reared in the wild; Game Conservancy Trust 1997), such that free-living populations that do not consist of large numbers of hand-reared birds may be more robust to the impacts of fox predation.

Summary

In summary, two species may have been limited by the observed pattern of fox predation on the study site; pheasants and field voles. However, in the case of pheasants, this was wholly offset by immigration from neighbouring farms. The detrimental effect on field voles is less clear, and is also dependent upon predation by other species. Nationally this species is fundamentally important. As a consequence of isolation from continental Europe, mammalian communities in Britain are skewed in favour of predatory species (0.95 predator species per prey species versus 0.60 predator species per prey species in continental Europe), such that the available prey base may be limiting the abundance of mammalian predators (Harris et al. 2000). Of the 19 prey species present in Britain, the rabbit and field vole predominate in the

diet of a range of predators (e.g. Dyczkowski & Yalden 1998), with other prey species never (e.g. mole *Talpa europaea*, shrews *Sorex* spp.) or rarely (e.g. bank vole, house mouse) taken (Harris et al. 2000). Furthermore, field vole numbers in Britain appear to have declined significantly since the early 1900s, when vole 'plagues' were common (Elton 1942); this decline is probably attributable to loss and fragmentation of preferred habitats. Consequently, we would recommend further research into the potential effects of predation on field vole populations, and vice versa.

The effects of fox predation on rabbits and pheasants observed in our study are similar to those observed by Reynolds & Tapper (1995a), despite differences in absolute and relative prey density, tentatively suggesting that the trends observed in our study may be common to ecologically similar species. However, both studies were conducted in lowland habitats in the south of England. Therefore, further similar studies are required in a range of habitats and across a range of prey densities to fully estimate the potential impact of foxes across Britain.

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