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The ecology of the red fox *Vulpes vulpes* in relation to small game in rural southern England

Jonathan C. Reynolds & Stephen C. Tapper

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Diet, population density, dispersion, and productivity of red foxes were investigated in an 11 km² area of mixed agriculture representative of much of lowland rural Britain, where medium-sized animals (adult weight 0.3-3.5 kg) were abundant. Four small game species within this size range - brown hare *Lepus europaeus*, pheasant *Phasianus colchicus*, grey partridge *Perdix perdix*, and redleg partridge *Alectoris rufa* - were also censused twice a year throughout the study. Fox diet was determined by analysis of faecal material, with diet of cubs at breeding dens analysed separately. Two-thirds of fox diet consisted of vertebrate prey in the range 0.3-3.0 kg. Prey types of overwhelming importance for foxes in other environments - such as small rodents, fruit and invertebrates - each contributed 10% or less to fox diet. Fox territory size was determined by radio-tracking eight adult foxes during a three-year period in spring, summer and autumn. Details of family group size, number of litters per group, and litter size were determined through field observation. Adjacent fox territories (mean size 2.7 km²) formed a contiguous mosaic with individual foxes spending less than 10% of their active time on ground shared with neighbouring groups. Typically each territorial group held an adult pair and had one litter of four cubs. Half of these groups had an additional, non-breeding vixen. Most known fox deaths were the result of deliberate control by man. Control on a central 4.75 km² farm reduced adult fox density and eliminated cub production there, and for the whole 11 km² study site deliberate control was almost sufficient in itself to negate annual numerical increase in fox numbers. The food requirements of foxes living at this density was estimated, and from this the biomass of lagomorphs and gamebirds consumed. Even assuming early dispersal of juvenile foxes, the biomass of these species consumed annually was substantial relative to that available at the onset of breeding. It is suggested that hare and rabbit populations were able to survive this heavy depredation because they have a long breeding season and foxes exploited annual production of young prior to maturity; by contrast, the pheasant population was supported artificially by release of hand-reared birds.

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The agricultural landscape of lowland Britain supports an assemblage of wild vertebrate species that derives partly from native fauna and partly from introductions. Several of these species are of interest to man as game species, and in many areas the system is deliberately managed to favour them as a secondary land-use alongside agriculture. Certain common predator species have been regarded as inimical to such game management, and limiting numbers of foxes *Vulpes vulpes* and other common predators has been a traditional part of such management for

200 years (Tapper 1992). In fact, little is known about the interdependence of such predators and their prey in this landscape. The ultimate purpose of the work reported here was to estimate the extent and significance of predation by foxes on medium-sized birds and mammals (adult weight 0.3-3.5 kg) that are of interest to man as 'small game' species. To do this, we needed to know the density and diet of foxes in relation to the density and productivity of their prey.

Fox social biology is very plastic in response to envi-

ronmental conditions (Niewold 1980, Lindström 1989, Macdonald 1983, Voigt & Macdonald 1984). Although this adaptability is of interest in itself, it also means that a study of fox density in one environment has limited relevance in another. In fact, most recent research on foxes in Britain has taken place in urban or suburban habitats (Harris 1977, 1981, Macdonald & Newdick 1982, Harris & Rayner 1986, Doncaster et al. 1990). Exceptions have been studies in 'rural suburbia' outside Oxford (Macdonald 1987), which has ribbon-development housing and includes significant fruit-growing areas, and in hill country with sheep farming in Cumbria (Macdonald *op. cit.*) and Wales (Lloyd 1980). Little intensive fox research employing modern techniques has taken place in the type of lowland agricultural landscape - dominated by arable crops and pasture - that makes up 64% of England and 47% of Britain as a whole (Anon 1989). Studies of foxes in agricultural areas elsewhere in Europe (Artois & Stahl 1989, 1991, von Schantz 1980, Berberich 1989, Artois et al. 1990, Carius et al. 1991), or in North America (Storm et al. 1976, Pils & Martin 1978), differed from British conditions in the species and density of prey available. Estimates of the extent of fox predation relative to prey abundance have been made in only a few situations (Piełowski 1976, von Schantz 1980, Erlinge et al. 1984a,b, Arthur & Stahl 1991).

In feeding habits too, a large body of literature (e.g. Englund 1965, Harris 1981, Macdonald 1987, Papageorgiou et al. 1988, Calisti et al. 1990, Reynolds & Aebischer 1991, Jedrzejewski & Jedrzejewska 1992) has shown the fox to be both generalist (using a broad range of food types in any one area) and eclectic (able to subsist on substantially different diets in different areas). From an ecological point of view, we can expect *a priori* three important consequences:

- Foxes (individuals and populations) are likely to be more resilient to changes in abundance of any single prey species than a specialist predator would be.
- Foxes are therefore more likely to limit production, abundance, or distribution of individual prey species than are specialist predators.
- The study of fox diet *per se* in one habitat or geographical region may shed little light on the ecological role of the fox in another.

For all these reasons, previous work on fox ecology was of uncertain relevance to the management of game or other wildlife in rural areas of lowland Britain. Game is exploited on 58% of land properties in Britain (Piddington 1981). This paper describes aspects of basic fox biology in an environment far more representative of this large fraction of Britain. Such basic details are also important

in contingency planning for rabies control through oral vaccination or poisoning, where the design of efficient baiting campaigns requires knowledge of both rural fox density and the extent to which rural foxes make use of scavenged food (Smith & Harris 1991).

Study area and game management

The study area (Fig. 1) was centred around West Wood Yates in the northeast corner of Dorset, England (50°55' N, 1°55' W). This area forms a southeast-facing part of the region known as Cranborne Chase, a chalk ridge lying southwest/northeast, at an altitude of 50 to 200 m above sea level, and overlain with calcareous, silty clay loam soils. Land use was dominated by cereal crops (Fig. 2). Roughly equal areas of grazing were given over to sheep and to beef or dairy cattle: about half of this was permanent pasture, half rotational leys. Mean field size varied between farms, ranging from 6 to 11 ha, with an overall mean of eight ha.

Work began in 1985 on one 4.75 km² farm (WW), but the study area was extended to 11 km² for the years 1986 and 1987 by including four adjoining farms (TF, CO, OA, UP) and a separately owned wood (GW). All farms held wild populations of grey partridge *Perdix perdix*, brown hare *Lepus europaeus*, and rabbit *Oryctolagus cuniculus*. Pheasant *Phasianus colchicus* and redleg partridge *Alectoris rufa* also bred in the wild, but these populations derived substantially from birds recently released to boost hunting stocks and could not be considered evolutionarily attuned to local conditions. Neighbouring farms differed in farming practices, game shooting pressure, releasing of reared gamebirds, and in fox control.

During the study, captive-bred pheasants were released in autumn on two (WW and UP) of the five farms (Table 1). On WW, pheasants were trapped every spring, and hens retained to produce eggs for captive rearing. This resulted in very low hen pheasant densities at WW during

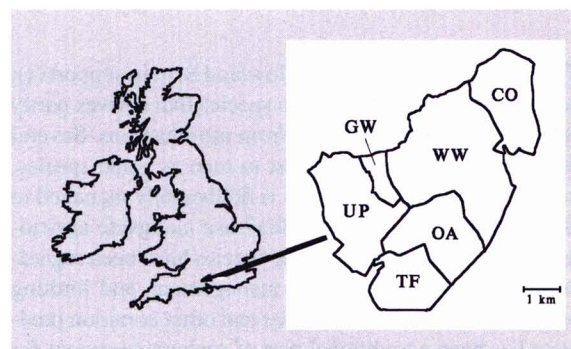


Figure 1. Location of the study area in Dorset, England, and (enlarged map) the constituent farms referred to in the text.

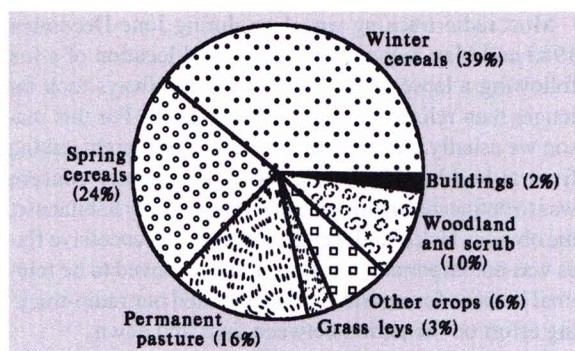


Figure 2. Land use in the study area for 1985. The proportion of different crops differed only marginally from this pattern in 1986 and 1987.

spring and summer. The number of captive-bred pheasants released on WW increased in each year of the study.

Pheasants were released in three ways. A small proportion were hatched and reared under bantam hens: these were released at six weeks of age with their foster mothers, and were untagged. The remainder were reared intensively in indoor pens until eight weeks of age (July), when they were wing-tagged and transported either to a large fox-proof release pen, or else for immediate release in woods or patches of cover around the estate. Birds were effectively captive in the release pen until able to fly over the 2.4-metre fence, usually by about 10 weeks of age. However, many birds remained in the release pen or roosted there long after the release.

About 100 pheasants were released annually from a release-pen at UP. These could not always be tagged, and neither were we able to recover tags on all shoot days, so these birds are not detailed in Table 1. On OA, 50 redleg partridges were released during summer 1986.

Potential predators of small game common in the area included fox, stoat *Mustela erminea*, domestic cat *Felis catus*, badger *Meles meles*, sparrowhawk *Accipiter nisus*, and buzzard *Buteo buteo*. The last three species are fully protected by law. Additional gamebird egg predators included carrion crow *Corvus corone*, magpie *Pica pica*, jackdaw *Corvus monedula*, jay *Garrulus glandarius*, and

rook *Corvus frugilegus*. Predator control was sporadic except on WW, where a part-time gamekeeper was employed. Here foxes were taken using snares, and by night-shooting; litters of cubs were also destroyed in 1985-1986 using cyanide gas. Fox control effort on WW was greater in 1986 than in 1985, and was suspended completely at our request during January to August 1987. The local impact and effectiveness of deliberate fox control in the area are discussed in Reynolds et al. (1993).

Methods

Counts of game species

Gamebirds (pheasant, grey partridge and redleg partridge) were counted using binoculars from a four-wheel-drive vehicle in spring and early autumn, following established census techniques (Potts 1980, Hill & Robertson 1988, Stoate & Tapper 1993). Spring counts had to be completed before arable crops grew tall enough to obscure birds, somewhat before the main nesting period. Because dispersal probably continued after the spring counts, autumn partridge counts (after crop harvest) showed slightly higher adult numbers than spring counts. For this reason, we used autumn adult numbers to infer both spring breeding density and hen loss, following Potts (*op. cit.*). Male pheasants are behaviourally very conspicuous in spring, but spring counts tend to underestimate female pheasants due to their more cryptic behaviour (Hill & Robertson *op. cit.*). Autumn pheasant counts probably underestimate all pheasants due to cryptic behaviour.

Hares were counted at night using a spotlamp and binoculars from a stationary vehicle (Barnes & Tapper 1985). On each night, counts were made from a succession of positions giving maximum coverage of the total area. The area of land visible at each counting position was determined in daylight, and the number of hares seen was adjusted to allow for hidden ground. It took 4-5 favourable nights to census the entire area. As far as possible, adjacent farms were censused on consecutive nights, but nights with imperfect viewing conditions were avoided. The figures used here are the maximum for each

Table 1. Captive-bred pheasants released at West Woodyates, and wing-tag recoveries before and after shooting, 1985-1987.

Year	No of birds released/year	Wing-tags recovered					
		1985		1986		1987	
		Known predated	Shot	Known predated	Shot	Known predated	Shot
1985	136	0	16 (12%)	6	11 (10%)	1	0
1986	361	-	-	16	168 (49%)	8	9 (2%)
1987	780	-	-	-	-	92	127 (18%)

part of the study area in each group of counts. Groups of counts were repeated - using the same counting positions - in February-April while winter crops were still sufficiently short, and again after harvest in October-December. The precise dates depended on other scheduled work and on favourable weather conditions.

Rabbits tend to run to cover when illuminated at night, and were therefore counted from a moving vehicle driven past the warren. Behavioural studies in the Netherlands (Wallage-Drees 1989) have shown that in general only 15-30% of the rabbit population is active above ground. Thus in contrast to our counts of other species, which estimate total numbers, the rabbit counts are merely an index of abundance, and spring and autumn numbers may have been three to seven times those counted. Where we wished to estimate rabbit biomass, we have assumed that rabbit populations were five times our field counts.

In biomass estimates, we have assumed average weights for rabbits of 1.5 kg, hares 2.8 kg, grey partridge 0.38 kg, redleg partridge 0.5 kg, male pheasant 1.45 kg, and female pheasant 1.1 kg.

Capture and radio-tracking of foxes

Foxes were captured using wire snares, with stops preventing closure beyond a 19-centimetre circumference. Snares were checked at six-hour intervals, which probably limited capture success, but ensured that foxes were handled soon after capture. Since handling times could be as short as 10 minutes, immobilising drugs were not used. Adult foxes were equipped with collar-mounted two-stage radio-transmitters on 173.25 MHz (Televilt, Storå, Sweden, or Bio-Track, Wareham, England). Both adult and juvenile foxes were fitted with three-centimetre reflective ear-tags in various colour combinations, allowing individual recognition in daylight or with a spotlight at night.

Radio-tagged foxes were tracked using a modified four-wheel-drive vehicle, fitted with a telescopic mast extending to four metres, twin Yagi antenna switchable between null and peak systems (Mariner Radar, Lowestoft, England), and solid-state compass sensor with remote display (Marinex, Poole, England). Access by roads, tracks and field margins allowed reception of signals from any part of the study area, and transmitter-receiver distance was usually 0.5-1 km. Triangulation from a succession of bearings made within 10 minutes allowed fixes to be made at 30-minute intervals. Error triangles resulting from three intersecting bearings were typically in the range 0-1 ha, depending mainly on how fast the fox was travelling. Where successive locations were identical, variability of signal strength was taken to indicate continued activity; direct observation on several occasions confirmed that this was a reliable indicator.

Most radio-tracking was done during June-December 1985 and May-September 1987. Initial location of a fox following a lapse of more than an hour always took far longer than relocating after a shorter lapse. For this reason we usually tracked one fox for an entire night, taking fixes at half-hour intervals. Since our primary concern was to delineate territories rather than to study habitat use, the obvious lack of independence between successive fixes was not important. Daytime activity proved to be minimal in these foxes, and we concentrated our radio-tracking effort on the period between dusk and dawn.

Harmonic mean contours (Dixon & Chapman 1980) were calculated for each fox from locational data spanning each three-month period, using a 20-metre grid. Beyond 40 locations, or 5-6 nights' continuous tracking, addition of further data from within a three-month period altered estimates of territory size by less than 5%.

Untagged foxes

An estimate of fox density requires knowledge of social group composition as well as territory size. Untagged foxes were sometimes observed during radio-tracking sessions, during hare counting, and at other times. Foxes were also deliberately sought by spotlamping at night, when tagged foxes could be distinguished by the reflective tape on radio-collars and ear-tags. It was often possible to tell the sex of a fox (by size, head-shape and behaviour) when seen in daylight and sometimes when spotlamping. Many individuals also had distinctive coat markings or other features. During March-July young-of-the-year were distinguishable from adults by size and coat characteristics. In some cases, the presence of an untagged fox was confirmed only when it was recovered dead (see below).

These observations were compiled to build up knowledge of territorial group composition, using the following assumptions, based on Macdonald's (1987) conception of fox social organisation:

- All adult vixens observed were assumed to be resident.
- All adult dog-foxes observed between March and October were assumed to be resident.
- Young-of-the-year were assumed to be resident until October.

In several territories, untagged but individually recognisable foxes were seen more than once; all such observations were consistent with the assumptions given.

Cubbing earths were discovered by field searches during the spring of each year, and cubs were counted by watching at the earth. Placental scar counts were also obtained from four vixens killed in the area. Because some cub mortality takes place between birth and weaning, ob-

servation at earths must underestimate the number of cubs born, while placental scar counts overestimate the number of cubs weaned (Lindström 1981, Allen 1983). In calculating the food requirements of cubs we have used cub counts at earths for a conservative estimate of cub food requirements.

Additional information

Foxes killed by road traffic or by gamekeepers, or found dead through natural causes, were collected and examined. All freshly dead foxes were subjected to a basic postmortem examination to establish cause of death where this was not obvious. Young-of-the-year were distinguished from adults by the size of the canine pulp cavity, while age of adults in years was determined using tooth cementum lines (Goddard & Reynolds 1993, Reynolds et al. 1993). Placental scars were counted in undamaged uteri of adult females.

Collection and analysis of faecal material

We analysed 633 fox scats collected throughout the study area during 1985-1987, plus a further 192 cubs scats collected at four earths during May-June. The latter derive solely from food brought to cubs by adults. Scats found elsewhere come from the free-ranging population of foxes, whose age-structure varies seasonally. We aimed to ensure constant sample sizes throughout the spring, summer and autumn to correspond with our radio-tracking effort. In seasonal comparisons below, scats judged to be older than 14 days were excluded from analysis.

In laboratory procedures, particular attention was paid to the accurate quantification of invertebrates in fox diet, reliable distinction between hare fur and rabbit fur, and the disproportionate breakdown of different food remains into microscopic fragments. The basic methodology is described in Reynolds & Aebischer (1991), but modifications were necessary to cope with material analysed early in the study where the volume of microscopic remains was not recorded (see Appendix).

From the resulting estimate of diet composition, we extrapolated to estimate the biomass of each prey species ingested by foxes for the whole study area and for separate territories. This required estimates of total daily food requirements for adults and growing cubs, which we derived from Sargeant (1978), scaling to allow for the larger body size of British foxes compared with those in North America.

Subsamples of scats were compared using chi-squared tests on proportions of scats containing each food type. Spatial and temporal trends were analysed by log-linear modelling using the GENSTAT V statistical package.

Results

In total, 11 adult foxes and three juveniles were captured (Table 2). Although the number of foxes caught was modest, the recapture of four adults (three times in one case) suggests that capture efficiency was good in relation to adult density. Of the 11 adults fitted with radio-transmitters, eight (five in 1985, three in 1987) gave useful results.

All foxes were caught without injury, with the excep-

Table 2. Foxes caught and tagged during the study period, 1985-1987. (m: male, f: female; ad: adult, juv: juvenile).

Year caught	Code	Sex	Age class at capture	Age at death (yrs)	Month first caught	No of times caught	Last month known alive	Fate
1985	OXF	f	ad		March	3	April 1986	Unknown
1985	PEA	f	ad	5	March	1	August 1985	Died 13 August, pneumonia
1985	RUD	m	ad	5	March	1	September 1985	Shot 22 September
1985	CAM	m	ad	4	March	2	December 1985	Found dead June 1986, cause unknown
1985	CUS	m	ad	2	March	1	December 1985	Snared January 1987, 4.5 km from 1985 territory
1986	-	m	ad	3	January	1	January 1986	Shock death
1986	-	m	ad		February	2	February 1986	Unknown, assumed transient
1986	-	f	juv		June	1	June 1986	Unknown
1986	-	m	juv	3	June	1	July 1986	Found dead March 1990, 6 km from point of capture
1986	SAM	f	ad		November	2	September 1987	Unknown
1987	-	f	ad		February	1	February 1987	Shot November 1991, 1.5 km from point of capture
1987	CRU	m	ad	1	February	1	September 1987	Shot September 1987
1987	SNO	f	ad		February	1	September 1987	Unknown
1987	-	f	juv	<1	June	1	November 1987	Shot November 1987

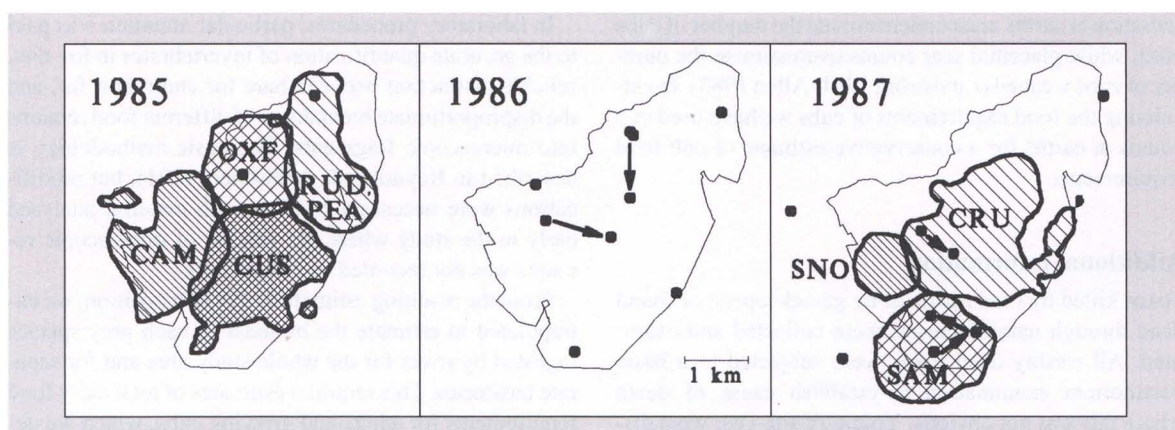


Figure 3. Territory boundaries (90% harmonic mean contours) for the 3-5 radio-collared foxes and location of known litters of cubs (solid dots) for each of the three years 1985, 1986 and 1987. The basic study area is indicated by the faint outline. Arrows indicate movements of cubs between earths. Where known, litters outside the study area are also indicated.

tion of an adult male in 1986 which suffered a foot injury as an (indirect) result of snaring; although the injury was small, was treated at capture, and did not become infected, the fox died within 48 hours of release, apparently from shock. More than half of captures were made at or beyond the edge of what later proved to be that individual's territory, suggesting that foxes may be more vulnerable to snares on unfamiliar ground.

Neither of the other two foxes radio-tagged in 1986 gave any useful data. Signals from one vixen were received only intermittently for two days after capture. This vixen was shot in 1991 just 1.5 km north of the study area, amongst deep valleys where radio-tracking was impossible, and was assumed to have been resident there. Furthermore, the fate of an adult male is unknown; because it was neither seen nor received by radio after tagging, this animal was assumed to have been transient.

Fox density and cub production

Because no territory boundaries were determined in 1986, estimates of fox density and cub production per unit area are based exclusively on data for 1985 and 1987.

Dispersion of territories

Home-range areas, and the behaviour of foxes within them conformed precisely with Niewold's (1980) and Macdonald's (1987) conception of fox territoriality. Harmonic-mean contours enclosing 90% of locations for each radio-tracked fox when active gave nearly contiguous contours for adjacent home-ranges (Fig. 3), and were adopted as an objective means to delineate territories even without a complete knowledge of all surrounding territories. By this definition, 90% of movements by each fox were confined within its territory while 10% represented

excursions beyond territory boundaries. Territory boundaries and locations of known litters of cubs are shown in Figure 3 for each of the three years. Further details of these territories are given in Table 3. One territory, that of the vixen SNO in 1987, was substantially smaller than other territories, and was also exceptional in that it was occupied solely by one non-breeding vixen.

Four territories were defined in 1985, three in 1987. Territory boundaries occurred in quite different places in these years. No territory boundaries were defined in 1986. Mean territory size for six fox territories occupied by breeding fox groups (i.e. excluding SNO in 1987 - see Discussion) was $2.72 \pm 0.66 \text{ km}^2$ (mean \pm 95% confidence limits).

Social group composition

The composition of social groups, where known, is shown in Table 3. As in other studies (e.g. Macdonald 1987, Lindström 1989, Niewold 1980, Mulder 1985), both sim-

Table 3. Territory sizes of eight foxes radio-tracked in 1985-1987 and composition of territorial and breeding groups (m: male, f: female).

Fox code	Year	Sex	Territory area (km ²)	Breeding group
OXF	1985	f	1.8	m + f + >3 cubs
RUD, PEA	1985	m,f	2.6	m + f + 4 cubs
CAM	1985	m	2.9	m + f + ? cubs
CUS	1985	m	3.2	m + f + ? (presence of cubs uncertain)
OXF	1986	f	unknown	m + 2f + >10 cubs
SAM	1987	f	2.2	m + 2f + 4 cubs
CRU	1987	m	3.6	m + f + 4 cubs
SNO	1987	m	0.7	f only, no cubs

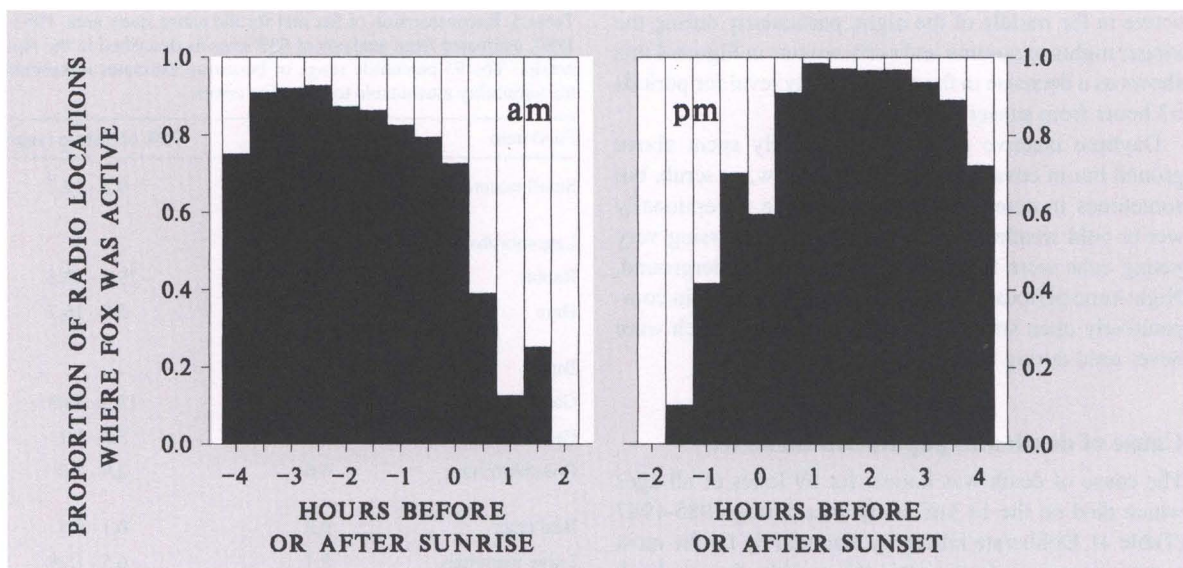


Figure 4. Activity patterns of foxes based on combined radio-tracking data for seven individuals during May-December, 1985 and 1987. Degree of activity is plotted against the number of hours from sunrise (am, left) and sunset (pm, right).

ple pairs (dog-fox + vixen) and extended pairs (dog-fox + two or more vixens) were observed. Here, three out of seven groups had two vixens, i.e. on average there were 1.43 ± 0.48 vixens per dog-fox. A further territory was occupied during April-September solely by a single vixen, who did not breed; before April and after September other foxes, including the neighbouring vixen SAM, were observed on this same territory.

Cub production

Through unfamiliarity with the area we located only two litters of cubs in 1985, but five in each of 1986 and 1987 (Fig. 3). However, the spacing of territories in 1985 and 1987, and of known litters in 1986 and 1987, suggest a similar density of breeding earths in all three years.

Typically, only one litter of cubs was produced per social group (Table 3), and all litters counted at earths consisted of four cubs, except in one case where two litters were apparently merged at a single earth and attend-

ed by both mothers. For comparison, placental scars averaged 5.75 ± 1.89 per vixen.

Between birth and weaning, cubs were housed in a variety of underground burrows. Typically, cubs were born in small burrows - often an enlarged rabbit burrow - but were moved to a bigger structure once the cubs were weaned and active above ground, or else in response to disturbance. Of 15 litters of cubs found within the study area during 1985-1987, 10 at some stage occupied setts that had been created or previously used by badgers. Since the end of our study, several of these setts have again been used by badgers.

Activity patterns

Foxes were consistently nocturnal, with activity usually beginning within one hour after sunset and ending within one hour after sunrise (Fig. 4). There was also a tendency for individuals to spend periods of 0.5-3 hours in-

Table 4. Causes of death for the 59 foxes examined in Dorset during the study period, 1985-1987.

Age group	Gassed	Shot	Snared	Assumed dead (vixen killed)	Road casualty	Other (also caused by man)	Poison	Natural mortality
Adults	0	6	5	0	1	1	1	2
Weaned juveniles	0	3	0	0	1	0	0	0
Cubs	12	5	0	17	1	0	0	0
Unknown	0	2	0	1	0	0	0	1
Total	12	16	5	18	3	1	1	3

active in the middle of the night, particularly during the longer nights of autumn and early winter: in Figure 4 this shows as a decrease in the mean activity level for periods >3 hours from sunset and sunrise.

Daytime inactive periods were usually spent above ground but in cover (woodland, hedgerow, or scrub, but sometimes in cereal crops). Only during exceptionally wet or cold weather, or when vixens were nursing very young cubs were full-grown foxes found underground. Night-time periods of inactivity were often spent in comparatively open sites, such as open pasture, which were never used during the day.

Cause of death and population turnover

The cause of death was known for 59 foxes of all ages which died on the 11 km² study area during 1985-1987 (Table 4). Deliberate killing by man was by far the most common cause of death within this sample, though death by this means was also the most likely to be known. Of 11 adult foxes radio-tagged and included in Table 2, four died while radios still functioned to allow recovery and postmortem examination: two (PEA and CAM) of these died through natural causes (disease, old age), two (RUD and CRU) were killed by man.

Diet

Fox diet based on the 633 scats collected away from cubbing earths is indicated in Table 5. Vertebrate prey predominated in the diet, ranging from small rodents to scavenged large mammals like deer *Capreolus capreolus* L. or *Cervus dama* L. and domestic sheep. The bulk of the diet (70% of fresh biomass) consisted of medium-sized mammal and bird species of adult weight 0.3-3.0 kg.

Fur of other vertebrate predators occurred occasionally, including stoat, badger, and domestic cat. In a few scats - from both adults and cubs - we found fox fur attached to pieces of skin, implying actual consumption of

Table 5. Reconstruction of fox diet for the entire study area, 1985-1987, estimated from analysis of 633 scats as described in the Appendix. The 95-percentile range of bootstrap estimates represents the variability attributable to sampling errors.

Food item	% of diet	95% bootstrap range
Small mammals	11.2	9.5 - 12.7
Lagomorphs:		
Rabbit	37.0	29.9 - 43.3
Hare	11.1	5.7 - 16.7
Birds:		
Galliformes	16.3	13.9 - 18.9
Passeriformes	4.5	3.3 - 5.7
Columbiformes	4.0	2.9 - 5.0
Bird eggs	0.2	0.1 - 0.2
Large mammals	9.4	6.5 - 13.9
Fruit	2.1	1.6 - 2.6
Invertebrates:		
Beetles	2.2	1.8 - 2.6
Earthworms	2.0	-

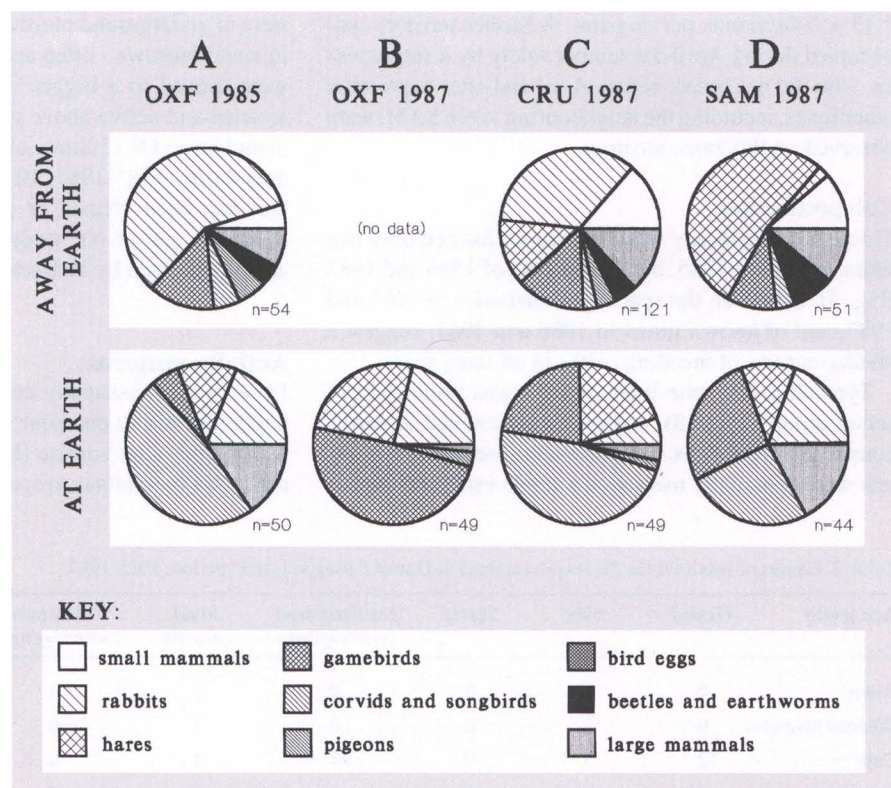


Figure 5. Composition of fox diet on four territories (A-D) at cubbing earths (below) and elsewhere (above).

fox flesh rather than self-grooming. This probably represents both cannibalism amongst litter-mates, and infanticide and scavenging by adults (cf. Macpherson 1969, Scott 1943, Pulliainen 1963, Kuyt 1972, Macdonald 1977). Examination of stomach contents from dead foxes revealed no food items that would not have been adequately quantified by faecal analysis, with the possible exception of livestock afterbirths (one occurrence).

Scats collected at the earth differed significantly from scats collected elsewhere in the same territory during the spring and summer (Fig. 5). For Territory A (OXF 1985) where cubs were destroyed in April food requirements are reduced accordingly.

Adults fed cubs almost exclusively on vertebrate prey in the 0.3-3.5 kg range, though the relative frequency of hares, rabbits, gamebirds and rooks varied markedly between different earths. Small mammals and invertebrates scarcely featured in cub diet at any earth. Remains of large mammals, mainly sheep, were found in cub scats, and portions of young lambs were found at two cubbing earths.

Apart from these differences, seasonal trends in diet were difficult to quantify. Log-linear analysis of scat composition by site and season revealed significant site*season interactions for small mammals, for birds in general, and specifically for Columbiform birds (Table 6). Some of the seasonal patterns and site*season interactions are readily understood: e.g. wood pigeons *Columba palumbus* L. were quite commonly consumed in late winter/early spring, but only on farms where pigeon shooting took place (TF, WW). Rook nesting colonies were present on every fox territory, but rooks were mostly consumed during May when young fledglings were vulnerable. Geotrupid beetle remains were found seasonally in scats on all sites, with peak consumption in June-September, but only reached appreciable levels in diet on one farm (TF: see Figure 6, territory D). This may reflect differences between farms in anthelmintic treatment of cattle: e.g. Ivermectin is known to create an inhospitable breeding environment for invertebrates in the dung of treated cattle (Madsen et al. 1990).

The discovery of site*season interactions severely constrains analysis, because dividing data by both factors results in unacceptably small ($n < 5$) sample sizes. For this reason, we are unable to build any seasonal trends into subsequent modelling. Also, because estimates of different dietary components are not independent, it is not legitimate to examine interrelationships between them without manipulative experiment. However, for those dietary components that do not exhibit site*season interactions, one may reasonably correlate the occurrence of any one item in the diet with abundance of that item on the ground. For 1986 data, we used rank correlation by farm and game species of spring game counts either with

Table 6. Variation of fox diet with site (farm) and season (3-month period). Log-linear analysis, F-test. Probability levels: * < 0.05 ; ** < 0.01 ; *** < 0.001 ; ns = not significant. Probability levels are given in brackets where significant site*season interactions occur.

Food Item	Site	Season	Site*season
Small mammals	(*)	(ns)	***
Rabbits	***	ns	ns
Hares	**	*	ns
Birds (all):	(***)	(**)	**
Galliformes	*	ns	ns
Passeriformes	ns	*	ns
Columbiformes	(*)	(***)	*
Bird eggs	ns	*	*
Beetles	***	***	ns

the proportion of scats found on that farm containing each game species, or with the estimated proportion of that game species in fox diet. No significant correlation was found for rabbit or hare, but the proportion of gamebird in fox diet was positively correlated with the spring pheasant density (Spearman statistic, $P < 0.05$).

Survival and production of wild partridges

Over the whole 11 km², annual nesting density of grey partridges was 2.1-2.6 pairs per km². The proportion of grey partridge females lost during each nesting season - calculated from autumn counts (number of single males/total number of males) and assumed to represent loss of incubating females through predation - varied between 0 and 21%, representing a lost biomass of 0-0.2 kg/km². Redleg partridges had spring densities of 1.1-2.8/km², and hen loss calculated in the same way amounted to 19-30%, or 0.1-0.4 kg/km². The mean chick production per surviving hen partridge was 2.8-4.4 for grey partridge, 1.7-2.7 for redlegs.

Survival of released pheasants

The shooting return rate (proportion of released birds shot in the following shooting season) was 12% in the season 1985-1986, 47% in 1986-1987, and 16% in 1987-1988 (see Table 1).

Foxes undoubtedly capitalised on pheasants that were vulnerable. Although the release pen on WW was fox-proof, hurricane-force winds in October 1987 brought down a tree onto the fence, allowing access by foxes. During that single night, 75 reared pheasants were killed by foxes and their bodies or remains recovered by us: 58 of these came from the release pen.

Consumption of small game species in relation to prey density

The cumulative consumption of small game species by foxes was estimated for three territories in 1987 for which we had good data on both diet and prey density (Fig. 6), illustrating a range of conditions. After 31 July, adult and cub diet were assumed to be identical.

For different reasons the food requirements per unit area on territories A and C were relatively low: A was contained within the game-keepered estate WW, where the cubs were destroyed by gassing at about five weeks of age. Territory C, which also included parts of WW, was relatively large but held by only a pair of foxes with cubs. By contrast, the fox breeding group on D included a supernumerary non-breeding female, and was a relatively small territory, resulting in high food requirements per unit area.

Spring biomass of small game species on these territories ranged from 100 to 300 kg/km². Because territory size, social group size, and fox diet composition varied between territories, consumption of small game species per km² by foxes also varied twofold. The simple models shown in Figure 6 describe a 12-month period from 1 March, assume that cubs were born on 1 April, and that measurable preparturition costs of pregnancy began on 1 March. Although we do not know when cubs dispersed, the earliest likely date is 1 September, and it is clear that by this date consumption of small game species was already large relative to their spring biomass.

Gamebirds eaten before 1 July (typical hatching date) must have been wild-breeding adult birds. The highest estimated breeding season consumption of gamebirds (25.48 kg/km², 1 March to 31 July) occurred on territory D with no access to a release pen and with a low spring gamebird density (19.34 kg/km²). The lowest gamebird consumption occurred on territory A where the fox social group was depleted by control measures: here 24% of available spring gamebird biomass was estimated eaten by 31 July.

Discussion

Fox territory size, social structure, productivity, and population turnover

The very small territory occupied by SNO in 1987 may have been an example of a non-breeding subordinate individual confined to an inferior annex of a group range (von Schantz 1981), since the neighbouring breeding vixen SAM was observed within SNO's territory both before April and after September 1987. SNO's territory contained a high proportion of pasture compared with surrounding breeding territories, and this vixen was observed foraging for invertebrates in this habitat far more frequently than other radio-tagged foxes.

Excluding SNO, the mean fox breeding territory size (270 ha) lay well within the extremes for other British habitats: 40 ha in suburban Oxford and 1,000 ha in the hill country of northern England (Macdonald 1987). The mean litter size of four at weaning was close to the mean birth litter size for Britain of 4.5 (Lloyd 1980). With one exception, each territory produced a single litter of four cubs, even where an additional vixen occurred, as in 50% of cases.

The population immediately post-breeding would thus have comprised 37.7% adults and 62.3% cubs. Following Lloyd et al. (1976), 62.3% of this population must be removed *per annum* to produce a stable breeding population.

Known mortality on the entire area accounted

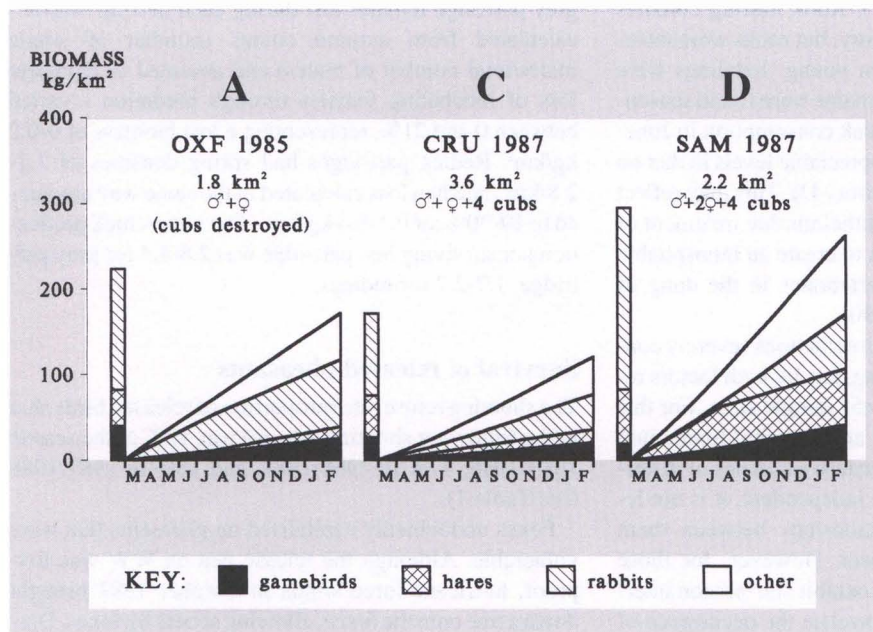


Figure 6. Estimates of cumulative consumption of small game species by foxes on three separate territories during March to February, compared with the spring biomass of small game. The spring biomass of small game available on each territory is plotted on the left of each figure.

for 57.3% of the fox population immediately post-breeding (24% of the adult population, 70% of weaned cubs), with deliberate fox control effort accounting for 50.2% overall. Accidental anthropogenic mortality accounted for a further 4%. Fox control at WW was unexceptional compared with other known situations, but the gamekeeper certainly prevented fox production locally, and created a 'sink' area (Reynolds et al. 1993). For the study area as a whole, deliberate control negated most of the annual growth in fox numbers. On a wider scale, given that 58% of land properties in Britain are managed for game (Piddington 1981) and that not all fox control is related to game management, it seems likely that deliberate control is a major force in rural fox population dynamics.

The estimated rate of population turnover is within the range found in other rural European populations (50–70%, Lloyd et al. 1976). It is also comparable with that found in urban British fox populations (56–66%, Macdonald & Newdick 1982, Harris & Smith 1987) where anthropogenic mortality (especially on roads) is equally important. By contrast, a rural population in Pembrokeshire, Wales, at high density and with low productivity had a turnover rate of only 40% (Lloyd 1980).

Fox diet and relation to numbers of small game

The utilisation of many food types places the fox in a position of ecological security at the top of a widely based resource pyramid. As noted above, the consequent numerical relationships could allow the fox population to limit productivity, recruitment or abundance within individual prey species, especially those which were already uncommon and/or unproductive.

Fox diet depended heavily on medium-sized birds and mammals (adult weight 0.3–3.5 kg), particularly during April–June when adults fed cubs at the earth. Several authors have noted a higher frequency of prey animals in this size range at cubbing earths than in adult diet, though the evidence has usually been the uningested remains of larger animals (Lindström 1994). Lindström himself compared cub and adult diet through scat analysis, and our study supports his conclusion that the difference is real. Although adults may include small prey (e.g. small rodents, invertebrates) in their own diet during the denning season, they preferentially carry larger prey to their cubs.

Requirements for prey of this size during the denning period could be met by harvesting adult prey that had not yet successfully reproduced, and by harvesting part-grown young prey. Of the prey species exploited in this way, the two lagomorph species have an extended breeding season, and production of young would have begun prior to our spring counts, counteracting predation losses. Both species can be highly productive and may be re-

garded as staple foods in this environment. The consequences of fox predation for the hare population are to be considered elsewhere (Reynolds & Tapper, unpubl.).

Other small game species were less common and less productive. For example, the breeding season loss of roughly one quarter of female grey and redleg partridges was similar to other areas with no predator control (Tapper et al. 1991, Reynolds et al. 1992). Hen loss of this magnitude severely limits productivity of the partridge population (Tapper et al., *op. cit.*). In a radio-tracking study of grey partridges at a similar density about 30 km away (Reynolds et al. *op. cit.* and unpubl.) we found foxes to be the most frequent predator on adult female partridges. In the present study we could not quantify fox predation on partridges as distinct from other gamebirds; but even if foxes had been exclusively responsible for loss of hen partridges in the present study, the biomass these might have contributed (less than 0.6 kg/km²) towards the total annual food requirements of the fox population (81 kg/km²) would have been very small (<1%). It is therefore clear that partridge populations at this density could not have been a significant determinant of fox density.

In contrast, we might expect pheasants to be one determinant of fox density in the study area. Pheasant numbers were supported locally by autumn release of captive-bred poults which greatly outnumbered the wild breeding population, ensuring an attractive food resource of up to 170 kg/km² that was certainly exploited by foxes. We might expect this to result variously in a denser breeding population, increased litter sizes, improved cub survival, and/or delayed cub dispersal. The present study offers only a small sample by which to examine these possibilities, and we have no data on dispersal dates. However, fox territories which did include pheasant release pens (OXF in 1985, CRU and SNO in 1987) were not consistently larger or smaller than other territories, and there was no consistent difference in fox group size. There was therefore no evidence from this study that increasing the autumn density of pheasants by releasing reared birds increased predation pressure by foxes on the wild-breeding population of pheasants or on other game species. Further, release pens did not act as a 'magnet' inciting extraterritorial movements or territory breakdown.

Between parts of the study area, the proportion of gamebird in fox diet was correlated with spring gamebird density. The biomass of gamebirds consumed by foxes amounted to 9.8 kg/km² between 1 January and the start of the shooting season (1 November). On territories encompassing parts of the shooting estate WW (i.e. OXF in 1985, CRU in 1987), this consumption amounted to 16 kg/km² and 13 kg/km², respectively. In comparison with the 50–100 kg/km² shot on WW during each winter period, these may seem moderate predation losses. However, these two 'harvests' by fox and man derive chiefly

from two different sources of production, the small wild-breeding population and the captive-bred population, respectively. On all three fox territories modelled, gamebird consumption by foxes was substantial relative to the wild-breeding gamebird population, and one territory (SAM in 1987) was certainly a gamebird 'sink' as a result of fox predation alone.

The shooting return rate of released pheasants broadly mirrored the pattern of anthropogenic fox mortality, which was most effective in 1986. The return rate for 1987 releases was extremely poor even when allowance is made for the birds killed within the release pen. These data are therefore consistent with the suggestion that foxes were a major predator of released pheasants.

Remains of larger mammals (roe deer, badger, cat, domestic sheep) were a consistent feature of fox diet in this study, and these species formed an estimated 9% of fox diet. We assume this intake resulted largely from scavenging at already dead carcasses, although Lindström et al. (1994) present experimental evidence that foxes can in fact be a significant predator on roe deer fawns.

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Appendix

For comparative purposes, the exact procedure followed in deriving fox diet from scat composition is important. We detail below modifications of the methodology described in Reynolds & Aebischer (1991) which (a) allowed us to make use of scats analysed early in the study when the volume of microscopic material in scats was not measured; (b) corrected for known identification bias and failure to identify; and (c) gave the most likely interpretation of results. The actual figures used are given in Appendix Table I.

- The numbers of scats containing remains identified as rabbit and hare fur were adjusted to correct for known biases in identification (as *per* Reynolds & Aebischer *op. cit.*). Scats containing unidentified lagomorph remains were assigned *pro rata* into 'rabbit' or 'hare' categories.
- Unidentified bird remains were assumed to include Galliform, Passeriform or Columbiform bird remains in the same proportions as identified bird remains, and were 'reallocated' to those categories.

Appendix Table I. Constants used in reconstruction of diet from scat analysis in this study and according to Stahl (1990). A: Adult/subadult scats collected away from cubbing earths; B: Cub scats collected at cubbing earths.

A: Food Category	Percentage broken down to microscopic remains ^a	Density in scats ^a undigested	Percentage ingested ^b	Ratio of fresh weight of intake to dry weight of remains ^b	Net conversion factor (Volume of remains to biomass of food)
Small mammals	0.0	0.312	100.0	23.1	7.21 ^c
Lagomorphs ^d					
Rabbit	0.0	0.349	100.0	38.9	13.58 ^c
Hare	0.0	0.349	100.0	38.9	13.58 ^c
Birds:					
Galliformes ^e	0.167	0.369	91.7	28.3	13.67 ^c
Passerines ^f	0.167	0.369	91.7	28.3	13.67 ^c
Columbiformes	0.167	0.369	91.7	28.3	13.26 ^c
Bird eggs	0.0	0.356	100.0	9.1	3.24 ^c
Beetles	0.0	0.371	100.0	12.4	4.60 ^c
Large mammals	0.0	0.356	-	50.0	17.80 ^g
Fruit	0.0	0.356	100.0	15.0	5.34 ^c
<hr/>					
B:					
Food category					
Small mammals	0.0	0.366	100.0	23.1	8.45
Lagomorphs ^d					
Rabbit	0.0	0.281	54.0	69.1	35.96
Hare	0.0	0.281	42.0	69.1	46.23
Birds:					
Galliformes ^e	0.0	0.270	67.0	106.5	42.92
Passerines ^f	0.0	0.270	67.0	106.5	42.92
Columbiformes	0.0	0.270	92.0	17.9	5.25
Bird eggs	-	-	-	-	-
Miscellaneous	0.0	0.635	100.0	50.0	31.75
Beetles	-	-	-	-	-
Earthworms	-	-	-	-	-

Data sources: ^aThis study; ^bStahl (1990).

Notes: ^dAssumes lagomorphs were juveniles; ^eAssumes all Galliform birds were pheasants; ^fAssumes all Passeriform birds were rooks; ^gBiomass killed or taken; ^hBiomass ingested.

- From the 393 fully-analysed scats (Table 2 in Reynolds & Aebischer *op. cit.*), we calculated the average volume of each food category in scats where that food type occurred. Remains of vegetation and fox fur were assumed to represent an intake of material with no nutritional value, and were excluded at this stage. Similar figures were calculated separately from the 192 cub scats. Multiplying these average volumes by the number of scats containing each category of remains gave the accumulated volume of macroscopic remains for all scats, including those where microscopic remains had not been measured.
- For scats collected away from cubbing earths, the accumulated volume of all categories of bird remains were multiplied by 6/5 to correct for the disproportionate breakdown of feathers into unidentifiable microscopic fragments (Reynolds & Aebischer *op. cit.*). This correction was not applied to cub scats since regression analysis showed no relationship between the microscopic fraction of cub scats and other contents of the same scats.
- For each food category, the accumulated volume of macroscopic remains was multiplied by density (estimated as *per* Reynolds & Aebischer *op. cit.*, for the 393 adult scats and 192 cub scats separately) and by the conversion factors shown in Appendix Table I based on Stahl (1990), to give estimates of the ingested biomass in each food category. These were divided by the proportion of each prey type ingested in Stahl's study to estimate biomass of entire prey animals, and thence percentage dietary composition.
- According to Stahl (*op. cit.*), young fox cubs are less efficient in consuming and digesting adult lagomorphs than young ones. We have assumed that all lagomorphs eaten were juveniles, leading to a conservative estimate of the biomass eaten.
- As described in Reynolds & Aebischer (*op. cit.*), detailed analysis of 49 randomly selected scats from this study suggested that earthworms formed only 1.2% of the diet. Since this was so small, we assumed that each fox scat represented a constant intake of 1.57 g fresh weight of earthworms. As earthworm chaetae were extremely rare in cub scats (despite large amounts of soil) we assumed that earthworms did not form part of cub diet.