

Demography of rural foxes (*Vulpes vulpes*) in relation to cull intensity in three contrasting regions of Britain

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Abstract

The impact of deliberate culling of fox populations has been much debated. Although a local ($< 10 \text{ km}^2$) impact has been accepted, previous authors have denied that culling has any impact on a larger scale because local losses are compensated through immigration. Rather, it has been claimed that at this scale fox density is determined by resources, mediated through social behaviour and breeding suppression. We determined the impact of culling on a regional scale ($> 1000 \text{ km}^2$), using data on culling (Heydon & Reynolds, 2000), fox density (Heydon, Reynolds & Short, 2000) and productivity. The three U.K. study regions (size 1238–2322 km^2) were in mid-Wales (A), the east Midlands (B) and East Anglia (C). High productivity in regions A and C was associated with low density, high culling mortality and high overall mortality (all relative to region B), indicating that density was suppressed by culling. In region B (moderate) breeding suppression was associated with a higher density and lower cull than in regions A and C, implying that fox density was closer to the maximum sustainable by resources. We conclude that the impact of culling in different regions of Britain is variable, dependent on the regional prevalence, methods, and history of culling. However, it is clear that in a range of circumstances culling can substantially depress fox numbers, and that current fox densities reflect a history of culling. This conclusion is fundamental in considering the management of fox predation in farming and conservation contexts.

Key words: age-structure, Britain, mortality, productivity, *Vulpes vulpes*, culling

INTRODUCTION

It has been demonstrated experimentally (Tapper, Brockless & Potts, 1991; Reynolds, Goddard & Brockless, 1993) that local ($< 10 \text{ km}^2$), seasonal (March–September) culling of foxes (amongst other predator species) can substantially reduce predation by foxes even if its impact on fox numbers is likewise local and temporary. It remains unclear whether on a larger geographical scale ('regional', regions $> 1000 \text{ km}^2$) fox numbers are influenced by widespread culling effort.

The issue is important for two reasons. First, considerable sums of money are spent annually on fox culling in the belief that it suppresses fox numbers on a regional scale. In three regions of England and Wales, Heydon & Reynolds (2000) showed that foxes were culled on 88% of land properties. When asked the aim of culling, 72% of these farmers and landowners believed it contributed to suppression of fox numbers throughout the entire region in question. Pye-Smith (1997) estimated that collectively gamekeepers, fox hunts, farmers and others

kill 190 000 foxes annually in Britain, a figure that is unavoidably speculative and which Baker & Harris (1997) claim is a significant underestimate. During 1995–97, a sample of 544 gamekeepers culled 12 000 foxes annually (The Game Conservancy Trust National Game-Bag Census, unpubl. data). Tapper (1992) estimated that there are 2500 professional gamekeepers in Great Britain. Given a typical employment cost of £22 000 per gamekeeper, it is thus likely that 30% of the national fox cull costs private employers a total of £55 million annually. Second, if fox culling is effective on a regional scale, then it is important in determining the relative numbers of a key predator species and its prey across whole landscapes. Changes in fox culling practice are relevant not only for the farmer or game manager, but also for the conservationist and the ecological theoretician (Reynolds & Tapper, 1996; Reynolds, 1998). The potential relevance of deliberate predator management seems especially great when one considers the long history of fox culling in Britain and the rest of Europe (reviewed by Reynolds & Tapper, 1996).

Biological studies of fox populations and culling have given rise to mixed conclusions. Hewson (1986) concluded that culling in Scotland during the 1970s was

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unable to prevent regional population increases, and Macdonald & Johnson (1996) argued that culling by one widespread method (hunting with hounds) was not sufficient in itself to achieve regional suppression. Baker & Harris (1997) denied that present-day culling intensity was sufficient to suppress fox abundance, claiming that foxes 'regulate their numbers naturally' and that 'fox numbers are in balance with their food supply'. On the other hand, Harris & Smith (1987) concluded that fox culling in London (1580 km²) on behalf of Borough Councils reduced the adult breeding population by 20% and juvenile survival by 12%. An intensive campaign against foxes in southern Jutland, aimed to prevent the spread of rabies, was followed by fox kills reduced to 20% of previous levels; a corresponding increase in kills of small game species suggested that this reflected a substantial decrease in fox abundance (Jensen, 1966; Strandgaard & Asferg, 1980). Furthermore, many authors (Lloyd & Jensen, 1976; Lindström, 1982; Harris & Smith, 1987; Macdonald, 1987; Reynolds & Tapper, 1995) have concluded that anthropogenic mortality, whether deliberate or accidental, was the commonest cause of death in foxes.

To test whether culling does indeed determine fox numbers, the scientific ideal would be a designed experiment in which culling intensity was manipulated on a regional scale and the effects on fox abundance observed over several years. For obvious reasons, such an experimental approach is not practicable. Nevertheless, science can help to choose between competing models (Fig. 1) by rigorous examination of features that are diagnostic between them.

Before listing these features we first review the processes expected to determine population density. The instantaneous density of any population is the outcome of a history of two opposing processes: production and mortality. (In regions of sufficient size, immigration and emigration are assumed not to influence population dynamics appreciably. Later we review the validity of this assumption in our study; see Discussion.) Both regulatory and non-regulatory factors influence production and mortality, and hence instantaneous density. Regulatory factors must implicitly exist if the population is not to increase indefinitely or decline to extinction, but by definition their impact varies with population density. The concept of equilibrium densities (i.e. that a population will fluctuate around a level at which production and mortality are equal) is useful to understand the role of regulatory factors, but it must be remembered that the position of any equilibrium is determined by both regulatory and non-regulatory factors. Furthermore, in a continually perturbed system (such as a modern European agricultural landscape), equilibrium levels may be touched only as transitory states. Hence a particular regulatory factor may be inoperative or imperceptible over the range of actual historical densities, in which case it cannot be a determinant of the density observed.

In fox populations, competing models (Fig. 1) may be distinguished by comparing several quantifiable factors between populations:

(i) *Reproductive performance*. Previous workers (e.g. Chirkova, 1953; Englund, 1970; Lindström, 1982; Harris & Smith, 1987) have commonly found that productivity is reduced in fox populations at higher densities or in poor food years (i.e. when near the environmental carrying capacity), through lower reproductive performance at every stage from conception to weaning. Bakken (1993) found similar effects in captive foxes, while Hartley *et al.* (1994) identified a stress-related physiological mechanism for the effect. These reproductive properties are believed to be density-dependent, regulatory influences on population dynamics. Under this accepted paradigm, low reproductive performance may be regarded as diagnostic between a population experiencing the regulatory effects of finite resources and internal competition (i.e. close to a 'resource ceiling'), and one that is suppressed below that level by other factors.

(ii) *Size of cull*. If culling were plausibly a factor governing fox numbers, then the total cull must be large relative to the annual production of young foxes. An obvious way to establish this is simply to compare the two for a given area.

(iii) *Survival/mortality*. If culling did suppress fox numbers, then culling mortality would, to a considerable degree, be additive to other mortality, and overall mortality rates would be higher where culling was more intense. The additional component of culling mortality might also be expected to have a differential impact on the various age-classes. Hewson (1986) in Scotland, and Lloyd (1980) in Wales, both reported that there were fewer old foxes (> 3 years) in areas with intensive fox management, though Englund (1970) found that culling created disproportionate mortality on juveniles. Whatever the details, survival for at least some age-classes is expected to differ under heavy and light culling regimes, and might be reflected in age-structures given random samples.

The expected characteristics of fox populations under the different models are indicated in Fig. 1. Note that these are relative measures: in reality there will be a continuum of population states between the model categories, and categorization of a population can be made only through comparison with others. The null hypotheses actually tested are that parameters do not differ between populations. Also, because current density is the result of historical levels of reproduction and mortality, present-day measures of productivity, culling and other mortality may provide only a suggestion of culling levels in the recent past.

To investigate the impact of culling on fox numbers we examined human-fox relations in three rural areas of Britain between 1995 and 1998. Sample regions of 1238–2322 km² were selected to provide a cross-section of agricultural land-use and fox management traditions, and in each area fox abundance (Heydon *et al.*, 2000) and culling practices (Heydon & Reynolds, 2000) were investigated. In this paper, we use these and further demographic data collected from the same areas to examine the probable impact of culling on fox numbers at a regional scale.

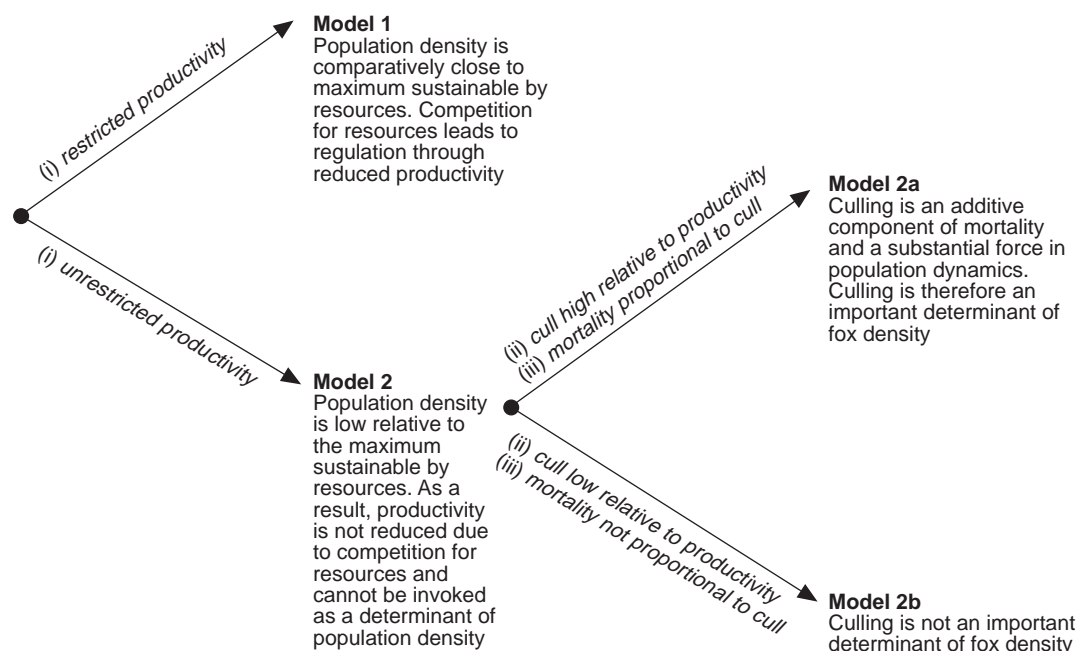


Fig. 1. Competing models to explain observed fox density.

MATERIALS AND METHODS

Study regions

Study regions were based on the area used by a single fox hunt (known as a hunt 'country'). Although hunts are diverse in form and activity, the essence of a fox hunt is a pack of specially bred dogs which are used to seek out and kill foxes (see Carr, 1986; Macdonald & Johnson, 1996). Hunt countries represent the largest areas over which any single form of fox culling is co-ordinated. Although intended to be exclusive hunting domains, other independent fox culling efforts take place within any hunt country. In this study the focal hunts were the David Davis Hunt in mid-Wales (region A), the Cottesmore Hunt in the east Midlands (region B), and the West Norfolk Hunt in East Anglia (region C, see Heydon & Reynolds, 2000: fig.1). The geographical regions to which the study relates were refined *post-hoc* to include all 5 × 5 km Ordnance Survey National Grid squares from which questionnaires describing fox control by landowners and tenant farmers were returned (Heydon & Reynolds, 2000). Regions were of similar latitude (range 52°32'N to 52°45'N).

Sources of material

Uteri and lower jaws from foxes culled as part of normal control activities were collected from gamekeepers, professional fox controllers and fox hunts operating in the 3 study regions and adjacent areas between 1995 and 1998 (Table 1). Additional uteri ($n = 138$) and jaws ($n = 348$) collected from other parts of the U.K. during the same period (as part of ongoing

monitoring work) were used to develop the ageing and reproductive techniques described below. All samples were stored at -20°C .

Age structure of culled foxes

Tooth sectioning procedures

The age of foxes at death was determined from the number of annual growth lines (annuli) visible in the tooth cementum. Canine teeth were preferred for ageing because of their large size and symmetrical shape. Premolar teeth were used where canines were unavailable or damaged. Teeth were extracted from the lower jaw after boiling in water.

Occlusion of the central pulp cavity was used to distinguish young-of-the-year from older animals (Grue

Table 1. Number of foxes of both sexes from which jaw samples were collected for age-determination, by region and source of material. Material collected 1995–98. The number of vixens from which uterus samples were obtained during March–July (inclusive) are also given: this subset were used to estimate productivity

Sources of material	Region					
	A		B		C	
	Jaws	Uteri	Jaws	Uteri	Jaws	Uteri
Gamekeepers	86	17	191	66	128	45
Fox hunts	11	1	91	0	0	0
Gunpacks	5	3	0	0	0	0
Other	3	0	6	1	2	0
Total	105	21	288	67	130	45

& Jensen, 1979). As Goddard & Reynolds (1993) recorded no cementum annuli in *V. vulpes* canine teeth < 58% occluded, it was assumed that all canines < 50% occluded (to allow for sampling error and variation) had yet to develop cementum annuli. These teeth were not analysed further. The degree of occlusion was determined by measuring the maximum diameters of both the tooth and the pulp cavity of a transverse section of tooth cut from the base of the enamel.

Teeth were sectioned following a modified version of the Isomet saw technique outlined by Johnston *et al.* (1987), using an Isomet low speed saw fitted with a single 10.2 cm × 0.3 mm diamond wafering blade (series 15 HC, No. 11-4244, Buehler, Lake Bluff, IL 60044, U.S.A.) rather than a pair. Root ends of teeth were mounted on glass slides with epoxy resin (Araldite Rapid, Ciba Evode Ltd, Stafford, U.K.) orientating the tooth so that a sagittal section (*c.* 20–40 µm thick) could be removed by making 2 parallel cuts with the saw. Sections were hand-ground to 15–20 µm thick using abrasive paper, and decalcified in 5 % nitric acid. Mayer's haematoxylin, warmed to *c.* 40 °C, was used to stain sections, which were subsequently washed in water and mounted on slides using a 5 mg gelatine/100ml distilled water solution (modified from Grue & Jensen, 1973). Sections were dehydrated by passage through an alcohol series, cleared in toluene and permanently mounted in DPX. Tooth sections were examined by optical microscopy at 35 × and 100 × magnification.

Ageing foxes from tooth sections

Foxes with a pulp cavity occlusion of < 50% were assumed to be < 1 year old. Where occlusion exceeded this value, age was determined from the number of cementum annuli. Owing to the well-documented difficulties of interpretation (e.g. Grue & Jensen, 1973; Johnston *et al.*, 1987), each tooth section was assessed independently by 2 people. This was undertaken, without reference to either the date of death or percentage occlusion of the tooth. Where both observers agreed on the number of cementum annuli, that value was accepted. Where there was disagreement, both observers re-assessed the tooth section and used percentage occlusion and date-of-death information to make a revised assessment. (Where agreement could still not be reached a second tooth was sectioned.)

Cementum annuli were first detectable as a distinct line separate from the tooth outer edge between July and September (based on examining 874 teeth). Assuming a birth date averaging 1 April (Hewson, 1986), the first cementum annulus is therefore evident at 15–17 months of age, the second at 27–29 months, etc. This is later than the January–March period reported by Goddard & Reynolds (1993) but is similar to other studies (see review by Grue & Jensen, 1979). Using this knowledge foxes were aged from the number of cementum annuli present and their date of death. For samples from July to September with a visible line, the

proximity of the line to the tooth outer edge of the cementum (indicating a newly formed line) was considered. Adult foxes yet to form their first cementum line were distinguished from early born cubs on the basis of percentage occlusion (in cubs at this time occlusion was < 40% whereas in adults it was > 60%).

Foxes were assigned to age-classes based on their recruitment into the adult population on 1 January of the year following birth (i.e. at age 9 months). Foxes progressed to the next age-class at the same time each subsequent year they survived. Animals < 9 months of age were classified as age-class 0, those between 10 and 21 months as age-class 1, and so on.

Life history

Comparison of age-structure between regions and sexes was carried out on age-class data. Because not all cubs killed were represented in samples, comparisons of age-structures and calculations of mortality/survival rates were possible only for adult age-classes.

Comparison of adult age-structure between regions and sexes was examined using logistic regression of the proportion of males against region and age-class. Further understanding of the age-class data was obtained by transforming them into life-history tables, following established methods (Caughley, 1977). The age-structure of culled samples was treated as if it was a representative sample of the dying (rather than a sample of the living). This seemed a reasonable assumption, given that culling mortality was clearly substantial, and that previous studies elsewhere have found culling to be a major – if not the major – cause of death (Lindström, 1982). We discuss this and other assumptions later.

Annual and seasonal (winter and summer) mortality rates were also calculated from the changes observed in fox density between autumn and spring line-transect surveys (Heydon *et al.*, 2000). Post-production fox densities were estimated from spring fox density, adult sex ratio (based on culled foxes), and estimates of regional litter size (from placental scar counts, including non-breeding vixens). These figures were then compared with autumn density to estimate summer mortality. Winter mortality was estimated simply by comparing densities between autumn and the following spring. Variance and standard errors for derived values were calculated using Taylor series linearization (Seber, 1982: ch. 1). Mortality rates were compared using a generalised χ^2 statistic (Sauer & Williams, 1989). Where variation between samples was significant, *a posteriori* multiple comparisons of 2 samples were carried out using the Z-test.

Productivity

Female productivity was investigated by examining uteri for evidence of postpartum placental scars

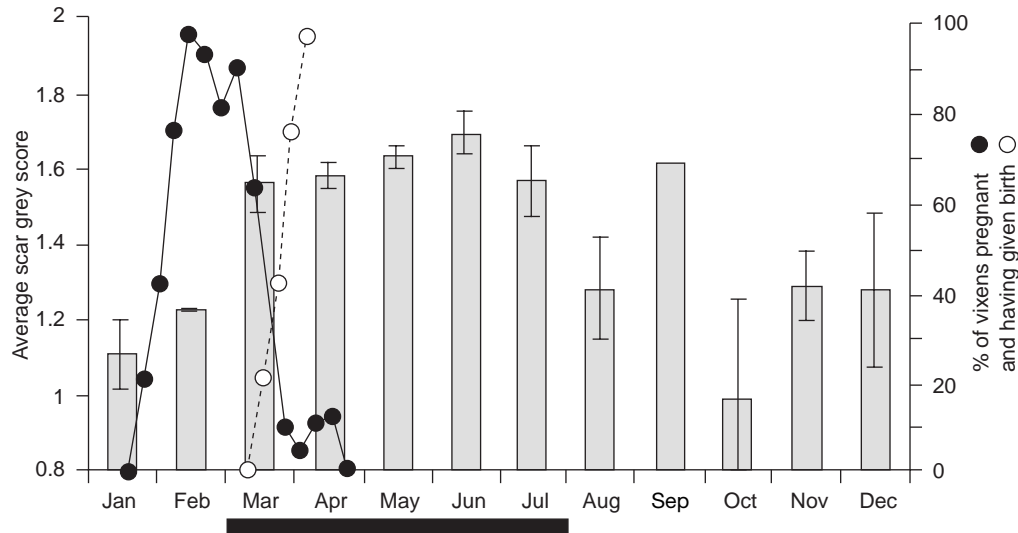


Fig. 2. Average grey score of scars (\pm SE) from uteri collected each month. Dark horizontal bar, months from which uteri were used in litter size estimation (September value based on a single uterus). Also shown are the percentage of vixens pregnant and predicted to have given birth each month (after Lloyd, 1980).

(Englund, 1970; Lindström, 1981). Four measures of productivity were considered: (1) percentage of non-breeders in the population; (2) total number of embryos; (3) intra-uterine losses; (4) estimated litter size.

Procedure for determining the number of placental scars

Uteri were washed in water to remove blood and cut open from the cervix to the ovaries. Any fluid within the uterus obscuring scars was cleared before examination. Scars were assessed using light sources above and below the uterus placed on a white laminated sheet. The location and degree of swelling of individual scars was recorded, as was the degree of scar definition. Differences between scars within the same uterus were especially noted. Individual scars were then graded using a Kodak Reflection Density Guide (Kodak publication number Q-16, Eastman Kodak Company, Rochester, New York) with a range of 22 shades of grey between white and black on a scale of 0.0–2.0 (light source above only). The grey scale was not used for uteri collected immediately after parturition, as scars had not yet developed the characteristic dark pigmentation. To provide a permanent record, each uterus was photographed alongside the grey scale (Ilford 100 Delta Professional film DX 135).

The use of a grey scale (with 6 shades) to assess placental scars was first proposed by Englund (1970) and has since been widely adopted. However, to date every study has used its own unique scale, the details of which are not published. The Kodak Reflection Density Guide used here provides a standard, which will allow comparisons between future studies.

Interpreting placental scars

Placental scars were classified as either dark or pale

scars. In general, a scar was classified as dark if pigmentation formed a distinct band across the uterus and rated ≥ 1.4 on the grey-scale or the scar site was swollen with substantial fluid matrix (the typical state of a scar soon after birth). A scar was defined as pale if pigmentation formed an indistinct pigmented band < 1.4 on the grey-scale. In assigning scar status particular attention was paid to variation in pigmentation and swelling between scars within the same uterus. The purpose of classification was to distinguish between scars left by foetuses believed to have successfully completed gestation (dark scars), and scars either left by foetuses that had been re-absorbed or carried over from earlier pregnancies (pale scars).

Productivity was assessed using uteri from females killed between March and July, inclusive. Outside this period progressive fading of scars made it difficult to detect all scars, and to distinguish confidently between dark and pale scars (Fig. 2). Uteri collected in January and February were also used if it was evident that parturition had occurred recently. The number of scars per uterus classified as dark using these procedures did not vary significantly between the months for which uteri were used (ANOVA, $F_{6,231} = 1.07$, $P = 0.382$).

Definitions of productivity measures

(1) *Non-breeder.* Vixens whose uteri showed either no evidence of placental scars, or total embryo loss during pregnancy were defined as non-breeders.

(2) *Total embryo number.* This was the sum of all dark and pale type scars. Any scars carried over from one breeding season to the next (evident in some non-breeding vixens) could not be reliably distinguished and excluded. The possibility of such carry-over means that the total scar count can give a reliable tally of embryos conceived in the current year only for first-time breeders.

We discuss below evidence that carry-over is actually insignificant. For comparison of regional populations the total scar count of all females clearly does provide a meaningful longer-term index of conception rate.

(3) *Intra-uterine losses*. The proportion of pale scars among all placental scars. This is a relative rather than absolute measure of losses, as some embryos may be re-absorbed before they attain a developmental stage capable of leaving a scar. As above, potential carry-over of scars from earlier breeding attempts means that only first-time breeders give a reliable measure of actual losses. Females with no scars were excluded from analysis.

(4) *Estimated litter size*. This was taken to be equivalent to the total number of dark placental scars. Carry-over does not affect this value. It is, however, a maximum estimate of litter size, as perinatal deaths would mean that not all dark scars represent viable cubs.

Analysis of productivity data

A tendency among females breeding for the first time to produce smaller litters than older animals has been noted in several studies (Kolb & Hewson, 1980; Allen, 1983; Cavallini & Santini, 1996). Such differences, if they exist, would bias regional comparisons if samples differed in age composition. There was, however, no significant within-region variation in litter size, either when first-time breeders (age-class 1) were compared to all older age-classes ($\chi^2_{[2]} = 3.02$, $P = 0.221$) or when age-classes 1, 2, and > 2 were compared ($\chi^2_{[4]} = 6.06$, $P = 0.195$). To further ensure that possible age effects did not result in misleading interpretation of data, female age-class (1 or > 1) was considered as a factor during subsequent analysis.

Regional variation in total embryo numbers and estimated litter sizes (residuals of which were normally distributed) were compared by analysis of variance with *post hoc* comparisons of the differences between means by the method of least significant difference. Analysis was carried out using the statistical package GENSTAT 5 (Release 3.2, 2nd edn, Copyright 1991, Lowes Agricultural Trust, IACR, Rothamstead, U.K.).

Intra-uterine losses were analysed by logistic regression (in GENSTAT 5, using a binomial error distribution and logit link function), modelling the number of embryos surviving to parturition relative to the number conceived.

Cub production vs annual fox cull

Cub production was estimated and comparisons made between regions as described above. The annual fox cull was determined from a survey of fox control by land-owners, farmers, gamekeepers, fox hunts and gun packs in each region (Heydon & Reynolds, 2000). Two estimates of the cull were obtained for each region. In one ('implied cull'), regional culls were estimated by extra-

polarization from a regression model of reported culls against land-use variables. The other ('minimum likely cull') also incorporated a generous correction for reporting error (Heydon & Reynolds, 2000). Productivity and cull estimates for each region were compared using a generalized χ^2 statistic (Sauer & Williams, 1989).

RESULTS

Sex ratio and age-structure of culled foxes

Age-structures for culled foxes in the three regions are given in Table 2. For adults, there was no significant effect of region on sex-ratio ($\chi^2_{[2]} = 0.23$, $P > 0.05$), nor any interaction between region and age-class ($\chi^2_{[6]} = 8.14$, $P > 0.05$): hence adult age-structure among culled foxes was unaffected by region. Across all regions sex-ratio varied significantly and in a linear fashion with adult age-class ($\chi^2_{[1]}$ for linear components = 6.01, $P < 0.05$; $\chi^2_{[2]}$ for non-linear components = 2.01, $P > 0.05$) such that the proportion of males among culled adult foxes declined steadily from 0.55 in age-class 1 to 0.30 in age-class 4+. This implies that adult mortality rates were constant for each adult age-class but different for male and females. Weighted mean annual mortality rates estimated for adult foxes from culled samples were 0.54 ± 0.22 for females, 0.62 ± 0.22 for males, and 0.58 ± 0.22 for both sexes combined.

As a result of age-structure, the overall proportion of males among culled foxes from all three regions was 0.52 ± 0.22 . This did not differ significantly from a 1 : 1 sex ratio ($Z = 0.70$, $P = 0.24$), hence in subsequent calculations we have assumed that half of the adult fox population was male.

Population mortality

Mortality in the whole fox population was estimated from field surveys of fox density pre- and post-production (Table 3). Annual mortality rates (all age-classes) varied such that region C $>$ region A $>$ region B, but differences were not significant. Winter mortality rates were significantly higher than summer mortality rates in region B ($Z = 2.06$, $P = 0.040$) and region C ($Z = 1.99$, $P = 0.046$), but not region A ($Z = 0.88$, $P = 0.376$), where substantial mortality also occurred during summer.

Productivity

Non-breeders

All adult females for which uteri were collected in regions A and C showed evidence of having successfully produced litters, whereas in region B 19% of females failed to produce cubs (Table 4). The 13 non-breeders in this region belonged to age-classes 1, 2, 3 and 4 ($n = 7, 4, 1$ and 1, respectively). The age distribution of these non-

Table 2. Age-structure of culled foxes collected, with calculated survival and mortality for adult foxes in each region, during 1995–98

Age-class ^a	Region					
	A		B		C	
	No.	% (adults)	No.	% (adults)	No.	% (adults)
0	24	–	41	–	19	–
1	43	53.1	141	57.3	60	55.0
2	19	23.5	68	27.6	25	22.9
3	14	17.3	23	9.3	18	16.5
4	2	2.5	8	3.3	4	3.7
5	2	2.5	2	0.8	0	0.0
6	1	1.2	2	0.8	1	0.9
7	0	0.0	1	0.4	1	0.9
8	0	0.0	1	0.4	0	0.0
	1 ^b	q ^c	1	q	1	q
1	1.00	0.53	1.00	0.57	1.00	0.55
2	0.47	0.50	0.43	0.65	0.45	0.51
3	0.23	0.74	0.15	0.62	0.22	0.75
4	0.06	0.40	0.06	0.57	0.06	0.67
> 4	0.04	1.00	0.02	1.00	0.02	1.00

^a Age-class 0 = birth year, 1 = first adult year, etc. (see Methods).^b 1 = proportion of first-adult-year cohort surviving at start of age-class.^c q = proportion of first-adult-year cohort dying within each age-class.**Table 3.** Calculation of seasonal mortality estimates for foxes in each region, from observed changes in fox density between spring (pre-breeding) and autumn (post-breeding, pre-dispersal) line-transect surveys (Heydon *et al.*, 2000)

Region		Estimated density ^a (foxes/km ² ± SE)				Mean mortality rate ^b (% ± SE)		
		Autumn 1995	Spring 1996	Autumn 1996	Spring 1997	Winter	Summer	Annual
A	Fox density	0.74 ± 0.15	0.32 ± 0.07	1.05 ± 0.14	0.49 ± 0.13			
	Predicted density if no mortality ^a		0.74 ± 0.15	1.37 ± 0.28	1.05 ± 0.14			
	Estimated mortality		0.42 ± 0.17	0.32 ± 0.31	0.56 ± 0.19	55 ± 27	23 ± 23	66 ± 24
B	Fox density	2.76 ± 0.25	0.79 ± 0.25 ^c	2.48 ± 0.24	1.17 ± 0.16			
	Predicted density if no mortality ^a		2.76 ± 0.25	2.44 ± 0.61	2.48 ± 0.24			
	Estimated mortality		1.97 ± 0.35	−0.04 ± 0.65	1.31 ± 0.29	62 ± 16	−2 ± 27	61 ± 19
C	Fox density	0.57 ± 0.11	0.14 ± 0.03	0.60 ± 0.11	0.18 ± 0.04			
	Predicted density if no mortality ^a		0.57 ± 0.11	0.58 ± 0.11	0.60 ± 0.11			
	Estimated mortality		0.43 ± 0.11	−0.02 ± 0.16	0.42 ± 0.12	73 ± 27	−4 ± 27	72 ± 30

^a Spring estimates were calculated using the mean litter sizes from Table 2 and the sex ratio of culled adult foxes.^b For foxes of all ages negative values indicate a higher than expected autumn population.^c Based on only one transect.

breeders was not significantly different from that of breeders in region B (Fisher's test statistic = 1.42, $P = 0.96$). Of the seven first-time breeders, two had no scars (i.e. no evidence that they were ever pregnant) and five showed complete embryo loss (2 to 7 pale scars).

Classification of vixens as non-productive on the basis of placental scars is supported by the following observations:

(1) All 13 vixens classified as non-productive were killed during April–May, yet placental scars were faded (mean score = 1.1) or absent. Lindström (1981) indicates that

appreciable fading of scars occurs over *c.* 30 weeks post-partum. The onset of reproduction is strongly related to latitude (Lloyd, 1980). At the latitude of this study, pregnancies can commence in early January, gestation lasts 52 days, and births before early March are very exceptional. It therefore seems unlikely that 20% of vixens in the region B had given birth to viable cubs as early as December or January.

(2) Among eight vixens classified as having lost their entire pregnancy *in utero*, five were examined as intact carcasses for signs of sucking cubs. Of these, four showed no sign of lactation. The fifth was classified as

Table 4. Female productivity in the three study regions. Estimates are based on examination of uteri for placental scars. Material collected during March–July (inclusive), 1995–98

	No. of females examined	No. of females without placental scars	Total embryos (mean \pm SE) ^a	% intra-uterine losses (mean \pm SE) ^a	Estimated litter size at birth (mean \pm SE) ^a	No. of breeding females with total embryo loss ^a	Total % non-productive females (\pm SE) ^b	Net productivity across all females (mean cubs/female/year) (\pm SE)
Regions								
A	21	0	7.24 \pm 0.46	10.6 \pm 2.8	6.38 \pm 0.41	0	0	6.38 \pm 0.41
B	67	5	6.95 \pm 0.25	32.1 \pm 4.1	4.85 \pm 0.32	8	19.4 \pm 4.8	4.49 \pm 0.32
C	45	0	7.56 \pm 0.32	17.6 \pm 2.4	6.24 \pm 0.35	0	0	6.24 \pm 0.35
Age-class								
Age class 1	72	2	7.18 \pm 0.27	23.7 \pm 3.2	5.63 \pm 0.32	5	9.7 \pm 3.5	5.49 \pm 0.34
Older age classes	61	3	7.00 \pm 0.29	23.7 \pm 3.4	5.53 \pm 0.29	3	9.8 \pm 3.8	5.26 \pm 0.31

^a These columns refer only to females with placental scars.^b The sum of data columns 2 and 6, expressed as a percentage of data column 1.

lactating. Lactation, of course, does not imply that a vixen is suckling her own cubs, because subordinates may suckle the cubs of dominant vixens.

(3) Of five vixens with no scars, only one was examined intact, and showed no sign of lactation.

For the remaining three reproductive parameters examined, there were neither significant ($P > 0.05$) differences between females breeding for the first time and older animals (see Table 4) nor any interaction between age-class and region. Carry-over of scars from one pregnancy to the next is therefore not considered to have had a detectable effect on reproductive measures.

Total embryo number

Considering only females with placental scars, there was a small but significant effect of region on total scar number (ANOVA, $F_{1,129} = 3.29$, $P = 0.04$), with fewer scars found in uteri from females in region B than elsewhere (Table 4). Variation between regions was not however significant among females believed to have successfully produced cubs ($F_{2,113} = 0.48$, $P = 0.620$).

Intra-uterine losses

Again considering only females with placental scars, intra-uterine embryo loss varied significantly ($\chi^2_{[2]} = 30.4$, $P < 0.001$) with the greatest losses observed in region B and the lowest in region A (Table 4). Differences between region B and the other areas were significant ($t_{81} = 4.33$ and $t_{107} = 4.07$ for regions A and C, respectively, $P < 0.001$). Variation between regions A and C was not ($t_{64} = 1.56$, $P > 0.05$).

Estimated litter size

Litter sizes differed significantly between regions (ANOVA, $F_{2,130} = 8.50$, $P < 0.001$, Table 4). The average birth litter size for all females showing placental scars was nearly two cubs less in region B than in either

of the other regions (both $P < 0.01$). Considering only females which successfully produced cubs, average litter size was again smaller in region B (5.57 ± 0.25) than in the other regions, though the difference was not significant ($F_{2,114} = 1.82$, $P = 0.166$).

Productivity

Expressed as cubs born amongst all females in the population (i.e. taking into account females with no evidence of having conceived), productivity differed still more markedly between regions, ranging from 4.49 cubs born/female in region B to 6.38 cubs/female in region A (Table 4).

Cub production vs annual fox cull

Estimated cub production varied four-fold regionally ($\chi^2_{[2]} = 13.6$, $P = 0.001$, Table 5). Production in region C was significantly lower than in both region A ($Z = 2.10$, $P = 0.036$) and region B ($Z = 3.13$, $P = 0.002$). Although production was higher in region B than region A, this difference was not significant ($Z = 1.15$, $P = 0.249$).

The predicted annual cull (implied cull) exceeded productivity in region A ($Z = 1.30$, $P = 0.192$) and region C ($Z = 4.45$, $P < 0.001$), although only in the latter case was the difference significant (Table 5). In region B, the implied cull was lower, but not significantly, than productivity ($Z = 0.36$, $P = 0.723$). Minimum likely cull estimates, which incorporated a correction for potential over-reporting, were lower than productivity in all three regions. However, the difference was only significant in region B ($Z = 3.36$, $P = 0.001$).

DISCUSSION

Are the study populations regulated by resources?

Productivity differed significantly between regions and only in region B was there evidence of lowered produc-

tivity normally associated with competition for resources. Although cub production per square kilometre was higher in region B in line with adult breeding density, individual vixens produced on average 2.0–2.5 fewer cubs than their counterparts in regions A and C. This difference arose primarily through increased mortality of embryos *in utero* rather than differences in conception rate. Vixens who had apparently lost their entire pregnancy before parturition were observed only in region B.

We conclude that in region B fox density was high relative to resource availability, while in the other two regions density was well below the level at which competition for resources influences reproduction. We emphasize that these assessments are relative: fox reproduction can be more suppressed than any of these populations illustrate. While productivity in region B was 4.5 cubs per vixen, productivity of 4.0 and 3.8 cubs per vixen has been measured in London and Bristol, respectively (Harris & Smith, 1987, excluding effect of neo-natal losses), while an extreme 3.0 cubs/vixen was recorded in Sweden by Englund (1970).

Is it plausible that suppression is caused by culling?

Total mortality in relation to estimated cull

Because of their complex derivation from field surveys and productivity data, it is not surprising that mortality rates showed no significant differences between regions. Although not significantly different, estimates suggested that total mortality increased with increasing cull, consistent with culling being additive to other mortality. Furthermore, seasonal patterns of mortality matched knowledge about culling practices in the three regions. Thus in regions B and C, winter mortality rates were significantly higher than summer mortality. In these areas, the bulk of fox culling took place in autumn/winter (Heydon & Reynolds, 2000). In region A, winter and summer mortality were not significantly different. Here, hunting with hounds and terriers continued through spring in response to requests from sheep-farmers.

Size of the cull relative to productivity

In all three regions the size of the total cull of foxes was consistent with it being a major force in fox population dynamics. This is true whether the data were accepted at face value (the implied cull), or whether they were adjusted to allow for the worst conceivable reporting error (minimum likely cull). Relative to annual production, culls were highest in region C and lowest in region B.

In both region A and region C, the implied cull exceeded annual cub production. We cannot distinguish whether this is because of reporting bias (double reporting, exaggeration, etc.) or population processes (immigration, population decline) or a combination of

these, although we can rule out the possibility of sampling bias. Comparison with other studies (Tapper, 1992; Macdonald & Johnson, 1996) suggests that implied culls are at least in line with those previously reported.

If the cull was accurately reported, then clearly in regions A and C it was sustainable only if there was substantial immigration from outside each of the regions. Replacement of culled foxes from outside the culling area is a recognized feature where local, isolated culling effort creates a 'sink' effect (Harris & Saunders, 1993; Reynolds, Goddard & Brockless, 1993; Reynolds, 1995). Dispersing foxes have an especially high risk of mortality (Marcström, 1968), and as a result observed dispersal distances are often quite modest (e.g. Trehwella & Harris, 1988). The fox's physical capacity for dispersal is much greater, and distances up to 245 miles (394 km) have been recorded (Ables, 1965). Thus the potential 'source' area to supply replacement foxes to a culling 'sink' may be enormous. Data collection in the present study was not designed to explore spatial effects within study regions, but examination of fox culls within region C suggested that in coastal 25-km² grid-squares, culls were appreciably lower than in inland squares. This was certainly not the result of a lack of culling effort, as some of the largest shooting estates were concentrated here, so it was presumably because at the coast, culled foxes could be replaced only from inland areas. Taking region C as a 'sink', the difference between the implied cull and estimated production would require the existence of a 'source' area with the size and productivity of region B. In fact, region B was separated from region C by only 40 km and could be a source area for immigration to region C.

Population age-structures in relation to culling

Adult age-structure amongst culled animals did not differ significantly between regions. Thus, if differences in mortality rates are real, they probably most affect juveniles. We estimated juvenile mortality rates indirectly, by combining reproductive and adult age data. These estimates support the notion that culling caused increased juvenile mortality.

There are several hazards in attempting to estimate age-specific mortality rates by applying life-history table techniques to data of this kind (Caughley, 1977). In particular, the necessary assumption of a stable age-distribution may be invalid. Also, the samples (Table 1) may not be unbiased with respect to age. But whether we use mortality rate estimates or the cull as our measure of mortality, it is clear that higher mortality in regions A and C is not matched by the unrepressed reproductive performance in these regions (Table 5).

Competing models

We assume, on the basis of considerable agreement among earlier authors (see Introduction), that breeding

Table 5. Cub production vs annual fox cull. Adult female density in spring was determined from line-transect surveys (Heydon *et al.*, 2000; average for 1996 and 1997) and the sex ratio of culled adult foxes. Litter size was determined from placental scar counts (values include non-breeding females). Cull estimates are based on questionnaire surveys of all groups culling foxes in each region (from Heydon & Reynolds, 2000). All figures are means \pm SE

	Region		
	A	B	C
Productivity			
Adult fox density (km ⁻²)	0.41 \pm 0.10	0.98 \pm 0.21	0.16 \pm 0.03
Female density (km ⁻²)	0.21 \pm 0.06	0.46 \pm 0.10	0.08 \pm 0.02
Litter size	6.38 \pm 0.41	4.49 \pm 0.34	6.20 \pm 0.35
Cub production (km ⁻²)	1.33 \pm 0.39	2.05 \pm 0.49	0.49 \pm 0.10
Cull estimates (km⁻²)			
Implied cull	1.91 \pm 0.21	1.85 \pm 0.29	2.66 \pm 0.48
Minimum likely cull	0.71 \pm 0.06	0.37 \pm 0.11	0.41 \pm 0.18
% of cub production accounted for			
Implied cull	143	90	539
Minimum likely cull	53	18	83

suppression indicates crowding relative to resources, and that this is a relative feature, i.e. less suppression indicates more scope for population growth. If universally true, model 1 would predict all three regions to be similar for the measures of breeding suppression. Consistent, significant differences in the four measures of productivity between the three regions favour model 2 over model 1 for two out of the three regions. Model 2a predicts these regions to be ranked in the same order as mortality and culling pressure. Independent estimates of mortality and of culling pressure seem to confirm this.

This study was not a manipulative experiment, hence could not unequivocally falsify any of the competing models. Differences in productivity between populations could be intrinsic (the result of selection) rather than reflecting crowding relative to resources. However, this interpretation would run counter to mainstream interpretation (see Introduction) which holds crowding-induced differences in productivity to be large relative to intrinsic differences. The mechanisms by which lowered productivity arise support this interpretation. The correspondence in rank order of the three regions for productivity, population density, overall mortality and culling pressure could also be coincidental, especially considering the sizeable errors of some of these estimates. However, since all the evidence in this study points in the same direction, the likelihood of coincidence seems remote.

We suggest culling as the probable cause of low fox density and high productivity. Because experimentation at this geographical scale is not feasible, we cannot unequivocally discount confounding factors that could also give rise to suppressed fox numbers and/or suppressed productivity. On the other hand, the most plausible confounding factors (road traffic and disease) are not supported by ancillary information. Road traffic can be a major cause of fox mortality (Harris & Smith,

1987), but the volume of traffic on all classes of road was greater in region B than in regions A and C (Department of the Environment, Transport and the Regions, National Road Traffic Survey, unpubl. statistics), and hence could not have caused the pattern of density and productivity observed. Sarcoptic mange is the only epidemic disease of foxes in Britain likely to suppress either density (Lindström, 1992) or productivity (Pence & Windberg, 1994). Preliminary analysis of questionnaire returns from independent samples of vets, gamekeepers and fox hunts all indicate that the incidence of infection in foxes was similar in the three regions and low compared with other parts of Britain (J. C. Reynolds & C. E. Bennett, pers. obs.).

The present study gathered data over a short period (2 years), and it might be argued that differences between regions in fox reproductive performance represented short-term states for each population – perhaps related to changeable food resources (e.g. Chirkova, 1953; Englund, 1970) – rather than demonstrating long-term differences related to regional culling pressure. We believe this interpretation to be implausible because it leaves unexplained the substantial differences in fox density between the three regions, which do not fit perceptions of food resources, and which remained consistent during the 2 survey years (Heydon, Reynolds & Short, 2000). Additionally, the magnitude of the reported cull implies that culling must be a major force in fox population dynamics. Thus the combination of density, productivity, mortality and cull size strongly favour a longer-term explanation.

Conclusion and implications

From among the competing models (Fig. 1), we conclude that fox populations in regions A and C are close to model 2a (population density reduced by culling), while in region B the population is closer to model 1 (population density determined by resources). This interpretation accords with the popular understanding of the three areas among farming and field-sports communities. In region A (mid-Wales) and region C (East Anglia), community motivation and effort to govern fox numbers is high (for sheep farming in region A and game management in region C). In region B (east Midlands), sport hunting has claimed priority for at least 200 years: here regular hunting consistent with a moderate fox density has been the objective, and much of the cull must be compensatory with other mortality. Even in region B, culling is a large component of total mortality, and reduction of culling would lead to some increase in the fox population. As noted, this population is below a density at which suppression of breeding is extreme, and our evidence suggests that culling is indeed at least partly additive to other forms of mortality.

We refute empirically the assertion of Baker & Harris (1997) that fox populations regulate their own numbers. The fox populations in regions A and C were demon-

strably not self-regulating through suppression of breeding and were unlikely to be at an equilibrium determined by resources. Culling is currently a substantial additive component of overall mortality in all three regions and is therefore an important determinant of fox density. So the fox densities observed reflect a history of fox culling by man. In other words, culling has been effective at a regional scale.

The fox is a managed species in Britain, but its management is highly controversial. Predation by foxes can conflict with the interests of animal or poultry husbandry, or with the conservation of wild prey species (Reynolds & Tapper, 1996). The controversy primarily concerns the importance of that predation for different interest groups, the effectiveness of culling and other remedial measures, and the humaneness of culling methods. In this study we have shown that culling as a whole can effectively depress fox numbers on a regional scale as well as locally, even though much of the culling effort is locally applied and not regionally co-ordinated. Consequently, the level of conflict experienced must be viewed in the light of not only local conditions and management but also the prevalence, methods and history of culling in the surrounding region.

We believe it is a crucial conceptual step to appreciate the importance of human interference in determining the predator–prey relationships found in modern environments. Both the importance of foxes as predators and the consequences of regulating fox management practices must now be reconsidered.

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