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ORIGINAL PAPER

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Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK?

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Abstract Forests within agricultural landscapes can act as safe harbourages for species that conflict with neighbouring landowners' interests, including mammalian predators. The agency responsible for the management of forests in upland Wales, UK, has permitted the killing of foxes (*Vulpes vulpes*) on their land as a "good neighbour policy" with the aim of reducing fox numbers. The principal method used was the use of dogs to drive foxes to a line of waiting shooters; a small number of foxes were also killed by shooting at night with a rifle. However, it has been postulated that recent restrictions on the use of dogs to kill foxes in Britain could lead to an increase in fox numbers in plantations. The aim of this study was to determine whether over-winter culling (i.e. driving foxes to guns using dogs and rifle shooting) in these forests acted to reduce fox density. Fox faecal density counts were conducted in commercial forests in Wales in autumn 2003 and spring 2004. Data were analysed from 29 sites (21 individual forests and 8 forest blocks, the latter consisting of pooled data from 20 individual forests). The over-winter change in faecal density was negatively related to the proportion of felled land and the proportion of land more than 400 m altitude, these associations probably reflecting reduced food availability. Over-winter change was positively associated with culling pressure (i.e. more foxes were killed where more foxes were present, or vice versa), but this was not significant. The number of foxes killed was large relative to the estimated resident population, but losses appeared to be negated (most likely) by immigration. Pre-breeding (spring) faecal density counts were significantly positively related to culling pressure, i.e. more foxes were killed with increased fox density or vice versa. Overall, there was no evidence to suggest that culling reduced fox numbers. Consequently, restrictions on the use of dogs to control foxes are unlikely to result in an increase in fox numbers in commercial forests.

Keywords Predator control · Human–wildlife conflict · Faecal counts · Hunting

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Introduction

Forests and woodlands increasingly exist as isolated patches within a mosaic of agricultural habitats, and this poses a range of management problems. For example, forests and woodlands may act as harbourages offering alternative food and breeding resources that may be scarce in the wider landscape, thereby promoting species abundance and spread. This is potentially a significant management issue where species such as mammalian predators (e.g. Polisar et al. 2003) might impact upon the interests of neighbouring landowners.

Throughout Europe, the red fox (*Vulpes vulpes*) poses a range of potential management problems, including the transmission of diseases, such as rabies (Flamand et al. 1992) and echinococcosis (Hofer et al. 2000), and predation on livestock, game and species of conservation concern (Marcström et al. 1988, 1989; Tapper et al. 1996; Mayot et al. 1998; Kauhala et al. 1999; Gortázar et al. 2000). Recent trends in fox abundance are equivocal, but numbers in some parts of Europe appear to have increased as a consequence of vaccination programmes following an outbreak of rabies (Chautan et al. 2000), and in upland regions of Britain, fox populations are believed to have benefited from the expansion of commercial forestry plantations, which offer shelter and sites for breeding (Chadwick et al. 1997). Frequently, such forests are viewed as source populations for the matrix of wider agricultural habitats in which they are located. This expansion in upland regions may have resulted in increased predation on livestock, although there are no quantified data to support this assertion, and upland-breeding bird populations (Baines et al. 2004; Summers et al. 2004).

The resolution of conflict between mammalian predators and humans is typically attempted by killing to reduce predator density (Tapper 1992; Reynolds and Tapper 1996; Conover 2002; Macdonald and Sillero-Zubiri 2004). Yet predator control is increasingly subject to public scrutiny, and there is the particular need to justify the benefits of killing animals vs the welfare implications associated with different practices (Fall and Jackson 2002). The primary consideration, however, is that lethal control is effective in achieving the objective(s) for which it is undertaken, i.e. reducing predator density, whilst other desirable traits include specificity, humaneness, cost-effectiveness and economy in the number of animals killed. Whilst some fox control practices have been studied in detail, there is a paucity of data for others. For example, in the discussions preceding the development of the Hunting Act 2004 (www.hmso.gov.uk), which restricts the use of dogs in the killing of red foxes in England and Wales (Burns et al. 2000), there were few data available on the effectiveness of the relevant practices in reducing fox density (but see Baker et al. 2002).

Forest Enterprise Wales, the agency responsible for the management of national forests in Wales, operates a "good-neighbour policy" whereby it permitted fox control societies, mounted foxhunts and Forest Enterprise rangers to kill foxes on its land over the winter period. However, with the development of the Hunting Act 2004, some of these practices were going to be banned completely (e.g. mounted foxhunts that used hounds to chase and kill foxes above ground) or diminished in extent (e.g. fox control societies used a mixture of hounds and terriers to drive foxes from dense cover to a line of waiting shooters, typically consisting of local farmers or shooting enthusiasts—the Hunting Act 2004 prohibits the use of more than two dogs to drive foxes to guns, whereas previously, much larger numbers had been used), whereas others would be

Fig. 1 Distribution of forests surveyed. *Solid circles* denote individual forests included in the analyses; *open circles* denote forests grouped to form blocks in the analyses. *Solid triangles* denote forests excluded from the analyses because we either had no data on the number of foxes killed by fox control societies or no foxes were killed. The forest indicated by the *arrow* was excluded because of an extreme value (see Fig. 2). Figure created in DMAP

unaffected (e.g. forest rangers shot foxes at night with rifles with the aid of a spotlight). In this paper, we use the term "culling" to refer to the collective use of fox drives (battues), mounted hunts and shooting-to-kill foxes in the study forests. Such culling was not targeted at specific individuals within the population but consisted of the blanket killing of foxes of any age and sex. In addition to the culling pressure exerted directly in the forests, fox control was also undertaken by landowners on properties neighbouring Forest Enterprise land; this was predominantly done by shooting.

The principal objective, and the sole reason that culling was permitted on Forest Enterprise land by this agency, was to reduce fox density; any recreational component associated with these practices was considered of negligible importance relative to this primary purpose. An assumed secondary benefit was that a reduction in fox numbers in the forests would reduce impacts on neighbour-

Table 1 Summary of habitat and culling variables included in the statistical analyses (N=29)

Variable	Description	Mean (±SD)	Range	Normality test	
				Z	P
SCATA	Autumn faecal density (scats km^{-1} day^{-1})	0.0527±0.0452	0.0023–0.1719	1.075	0.198
SCATB	Spring faecal density (scats km^{-1} day^{-1})	0.0500±0.0313	0.0024–0.1316	0.572	0.899
DIFFER	Change in faecal density (scats km^{-1} day^{-1})	−0.0027±0.0396	−0.0933–0.0847	0.608	0.854
LOGAREA	Log(total forest area) (untransformed hectares)	3.190±0.352 (2,147±1,973)	2.465–3.960 (292–9,118)	0.558	0.915
RATIO	Ratio between forest area and perimeter	0.0319±0.0141	0.0135–0.0764	0.854	0.460
CLEARFELL	Area of felled land[a]	0.218±0.105	0.049–0.519	0.713	0.689
OPEN	Area of open land[a]	0.365±0.109	0.162–0.611	0.782	0.574
BROAD1–10	Area of broadleaved woodland aged 1–10 years[a]	0.100±0.042	0.000–0.179	0.775	0.586
BROAD11–30	Area of broadleaved woodland aged 11–30 years[a]	0.116±0.053	0.034–0.255	0.513	0.955
BROAD31–50	Area of broadleaved woodland aged 31–50 years[a]	0.053±0.043	0.000–0.146	0.707	0.700
BROAD51	Area of broadleaved woodland aged >50 years[a]	0.107±0.073	0.000–0.340	0.813	0.523
BROAD1–30	Area of broadleaved woodland aged 1–30 years[a]	0.160±0.049	0.062–0.255	0.649	0.793
BROAD1–50	Area of broadleaved woodland aged 1–50 years[a]	0.172±0.054	0.071–0.273	0.554	0.918
BROADALL	Total area of broadleaved woodland[a]	0.210±0.074	0.092–0.376	0.690	0.728
CONIFER 1–10	Area of coniferous woodland aged 1–10 years[a]	0.363±0.108	0.133–0.572	0.583	0.886
CONIFER 11–30	Area of coniferous woodland aged 11–30 years[a]	0.534±0.158	0.344–0.944	1.021	0.248
CONIFER 31–50	Area of coniferous woodland aged 30–50 years[a]	0.507±0.150	0.161–0.812	0.612	0.848
CONIFER51	Area of coniferous woodland aged >50 years[a]	0.304±0.142	0.000–0.533	0.492	0.969
CONIFER 1–30	Area of coniferous woodland aged 1–30 years[a]	0.683±0.152	0.454–0.997	0.746	0.634
CONIFER 1–50	Area of coniferous woodland aged 1–50 years[a]	0.942±0.135	0.668–1.212	0.491	0.970
CONIFERALL	Total area of coniferous woodland[a]	1.060±0.115	0.767–1.248	0.563	0.909
ALTITUDE1	Area of land at <300 m altitude[a]	0.507±0.398	0.000–1.223	0.948	0.330
ALTITUDE2	Area of land at 300–400 m altitude[a]	0.668±0.185	0.341–1.160	1.022	0.247
ALTITUDE3	Area of land at >400 m altitude[a]	0.500±0.307	0.000–0.968	0.774	0.586
SOIL1	Area of brown earth soils[a]	0.515±0.337	0.000–1.457	0.648	0.796
SOIL2	Area of iron pan soils[a]	0.445±0.243	0.000–1.021	0.341	1.000
SOIL3	Area of peaty gley soils[a]	0.415±0.228	0.000–0.927	0.796	0.551
SOIL4	Area of gley soils[a]	0.341±0.221	0.000–0.883	0.447	0.988
FOXKILL	Total number of foxes killed[b] (untransformed, number of foxes killed)	−1.6158±0.3907 (56±59)	−2.3657 to −0.7580 (8–273)	0.423	0.994
FCSKILL	Number of foxes killed by fox control societies[c] (untransformed, number of foxes killed)	−1.6564±0.3994 (53±58)	−2.3653 to −0.8316 (2–268)	0.424	0.994

Normality was tested using a one-sample Kolmogorov–Smirnov goodness of fitness test. P>0.05 indicates sample is normally distributed. Mean values are of transformed variables where appropriate.
[a]All areas are arcsine square-root-transformed proportions of total forest area
[b]Transformed as Log[(total foxes killed + 0.01)/area]
[c]Transformed as Log[(total foxes killed by fox control societies + 0.01)/area]

ing landowners' interests. As fox drives were used because other methods of control were not effective in terms of killing large numbers of animals in this habitat, in the lead-up to the introduction of the Hunting Act 2004, it was argued that a ban would result in a significant increase in fox numbers. Central to the logic of this argument was that fox drives (and, to a lesser degree, mounted hunts; see "Results" for the relative importance of these practices in terms of the number of foxes killed) were effective in reducing fox density prior to the implementation of the legislation. However, if, prior to the Act coming into force, fox drives (and mounted hunts) did not actually result in any change in fox density, then any amendments to permissible codes of practice are unlikely to result in an increase in fox numbers in the forests; under these circumstances, fox population size would appear to be primarily affected by factors other than anthropogenic culling such as resource availability.

Therefore, the aims of this study were to (1) determine whether the culling pressure exerted by fox control societies and Forest Enterprise rangers was related to over-winter changes in fox numbers in commercial forests in Wales and (2) to investigate those factors associated with pre-breeding (spring) fox abundance. We use these results to assess whether culling by fox control societies was or was not effective in reducing fox density in commercial forests. At the time of the study, approximately 100 organisations throughout Wales operated fox drives assisted by dogs, killing approximately 10,000–15,000 foxes annually (R. Cook, personal communication). Sixty-three fox control societies and 11 mounted hunts operated in Forest Enterprise woodlands, although not all hunts operated in these forests each year.

Methods

Faecal transect surveys (Baker et al. 2002; Webbon et al. 2004) were undertaken in 44 Forest Enterprise forests (Fig. 1) between 1 October–12 November 2003 (autumn) and 3 March–13 April 2004 (spring); these periods correlate with the onset of the dispersal period and the period prior to/when the cubs are born. Faeces (scats) do not appear to be used in social communication in this species (Macdonald 1980), such that underlying patterns of scat deposition are unlikely to vary with density and social disruption, but that scat numbers will vary with density per se. Faecal counts have been shown to be a reliable index of abundance in fox species in terms of comparisons between spatial locations (Cavallini 1994) and to reflect changes in fox numbers between seasons (Sharp et al. 2001). In addition, estimates of absolute abundance derived from faecal counts have been shown to correlate well with estimates derived from other methods in the UK (see Webbon et al. 2004).

Forests consisted predominantly of commercial stands of conifers of various ages (mainly Sitka spruce *Picea sitchensis* and, to a lesser extent, hybrid larch *Larix × eurolepsis* Henry and Scots pine *Pinus sylvestris*) and areas of broadleaved woodland (e.g. ash *Fraxinus excelsior*, oak *Quercus petraea* and silver birch *Betula pendula*) and scrub. Forest Enterprise Wales manages 1,260 km^2 of woodland, constituting 44% of Welsh woodlands and 6% of the land area of Wales. Surveys were timed to coincide with the period immediately prior to and following the main period of activity of fox control societies. Average fox home range size in commercial forests in Scotland was approximately 520 ha (O'Mahoney et al. 1999), and Lloyd (1980) estimated range size in agricultural landscapes in upland Wales as approximately 650 ha. These are equivalent to circular ranges of 2.6 and 2.9 km in diameter, respectively. Therefore, forests were a minimum of 5 km apart to ensure statistical independence.

Transects followed linear features (e.g. footpaths, rides and vehicular access roads) through each forest and were walked twice in each of the two survey periods. This "repeated-measures" approach did not necessitate random placement of transects, but it did implicitly assume that the pattern of use of habitat features was consistent in the two sampling periods. There was very little vegetation or fallen foliage at ground level on transect routes and no apparent difference in the height or extent of ground cover between survey periods. Consequently, temporal differences in cover were deemed unlikely to have affected the comparability of faecal counts in autumn and spring.

On the first walk in each survey period, all fox faeces less than 3 m from one edge of each footpath or road were removed; on the second walk, all fresh faeces were recorded and collected. Walks were conducted 17–22 days apart. Between one and three transects were undertaken in each forest depending on forest size: approximately one, two and three transects were undertaken for forests less than 16, 16–32 and more than 32 km^2 in area, respectively. Faecal density (S) in each season was calculated as $S=F/(DT)$, where F was the number of fresh fox faeces found on the second walk, D was the distance surveyed (km) and T was the number of days between the two walks. Where more than one transect was walked in a forest, S was calculated as the average faecal density across all transects.

The relationship between habitat and culling variables and (1) the autumn–spring change in faecal density ($C=S_{\mathrm{SPRING}}-S_{\mathrm{AUTUMN}}$) and (2) spring faecal density was examined using general linear models. C will be positive where the faecal density in spring was higher than in autumn (i.e. an increase in faecal density over the winter period), zero where spring and autumn faecal density was the same (no change in faecal density over winter) and negative where faecal density in spring was lower than in autumn (a decline in faecal density over winter). Values of C greater than or equal to zero indicate that culling was not effective in reducing faecal density.

For statistical analyses, two measures of culling effort were utilised: (1) the total number of foxes killed per hectare by fox control societies, mounted foxhunts and Forest Enterprise staff, and (2) the number of foxes killed only by fox control societies per hectare. Habitat variables extracted from the Forest Enterprise geographic informa-

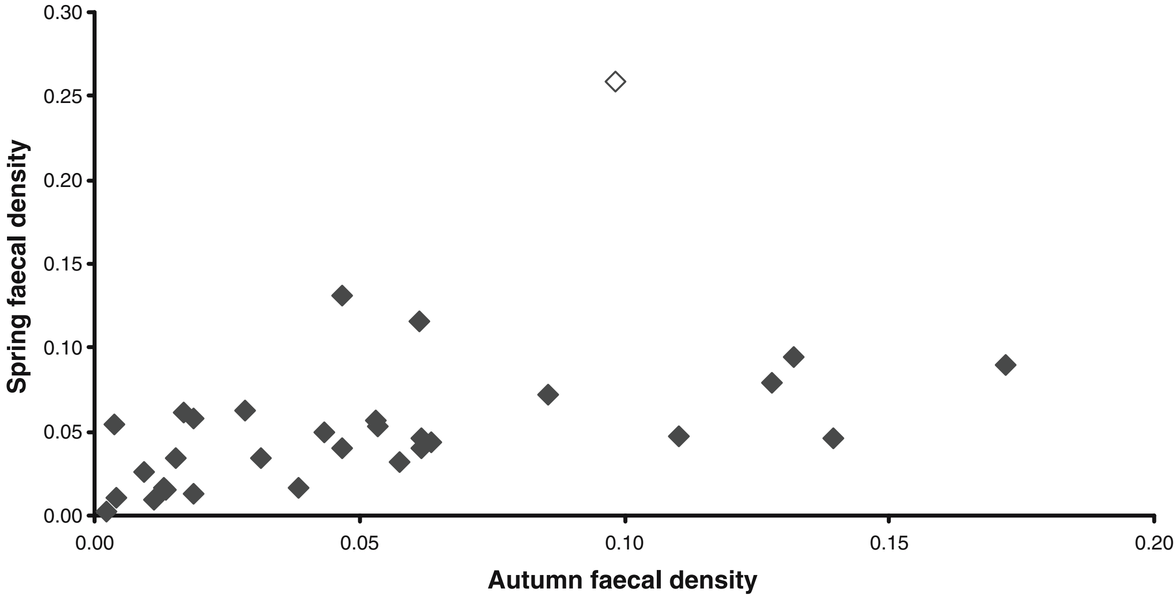

Fig. 2 Relationship between autumn and spring faecal density counts. *Open symbol* indicates outlying data point excluded from subsequent data analyses

Table 2 Correlation between individual independent variables and (1) over-winter change in faecal density (SCATB-SCATA) and (2) spring faecal density (*N*=29)

Variable		Over-winter change in faecal density		Spring faecal density	
		R	*P*	*R*	*P*
Forest size variables	LOGAREA	0.314	0.097	0.046	0.814
	RATIO	−0.180	0.351	0.268	0.160
Habitat variables	CLEARFELL	−0.409	0.027	−0.128	0.507
	OPEN	−0.029	0.883	−0.203	0.291
	BROAD1–10	0.150	0.439	0.246	0.199
	BROAD11–30	0.116	0.549	−0.192	0.318
	BROAD31–50	0.383	0.040	−0.034	0.861
	BROAD51	0.541	0.002	0.062	0.751
	BROAD1–30	0.224	0.244	−0.015	0.938
	BROAD1–50	0.286	0.133	−0.022	0.912
	BROADALL	0.470	0.010	0.032	0.871
	CONIFER1–10	0.014	0.943	0.134	0.489
	CONIFER11–30	−0.048	0.804	0.296	0.119
	CONIFER31–50	0.032	0.870	−0.151	0.433
	CONIFER51	0.126	0.515	−0.210	0.274
	CONIFER1–30	−0.036	0.854	0.361	0.054
	CONIFER1–50	−0.003	0.987	0.264	0.166
	CONIFERALL	0.081	0.675	0.172	0.372
Altitude variables	ALTITUDE1	0.544	0.002	−0.127	0.513
	ALTITUDE2	−0.096	0.619	0.150	0.438
	ALTITUDE3	−0.637	<0.001	−0.046	0.814
Soil variables	SOIL1	0.117	0.546	−0.195	0.310
	SOIL2	−0.044	0.823	0.212	0.269
	SOIL3	−0.244	0.202	0.278	0.144
	SOIL4	0.163	0.398	0.111	0.565
Culling variables	FOXKILL	0.156	0.420	0.383	0.040
	FCSKILL	0.298	0.116	0.253	0.185

Variables as defined in Table 1

tion database were total forest area (ha); perimeter–area ratio; and the area of (1) clearfell land; (2) open land; (3) broadleaved and coniferous woodland (each subdivided into classes ≤10, 11–30, 31–50 and >50 years old), (4) land at less than 300, 300–400 and more than 400 m altitude; and (5) land on major soil types (brown earth, iron pan, peaty gley and gley).

Habitat areas were analysed as arcsine, square-root-transformed proportions of total forest area. Independent variables were preliminarily selected if they were significantly correlated with the dependent variable (α<0.05); variables were transformed to meet the assumption of normality where appropriate (Table 1). All preliminarily selected variables were then tested for cross-correlation; where independent variables were correlated, the variable most significantly correlated with the dependent variable was selected for inclusion in the model. Variables were initially entered into a full-factorial model, with non-significant interaction terms and individual variables removed sequentially. Model residuals were checked for normality. All analyses were conducted using SPSS (Kinnear and Gray 2000).

Results

In 20 cases we were only able to obtain information on the number of foxes killed or the habitat composition for blocks of forests rather than the individual forests. Therefore, these were pooled into eight forest blocks: in

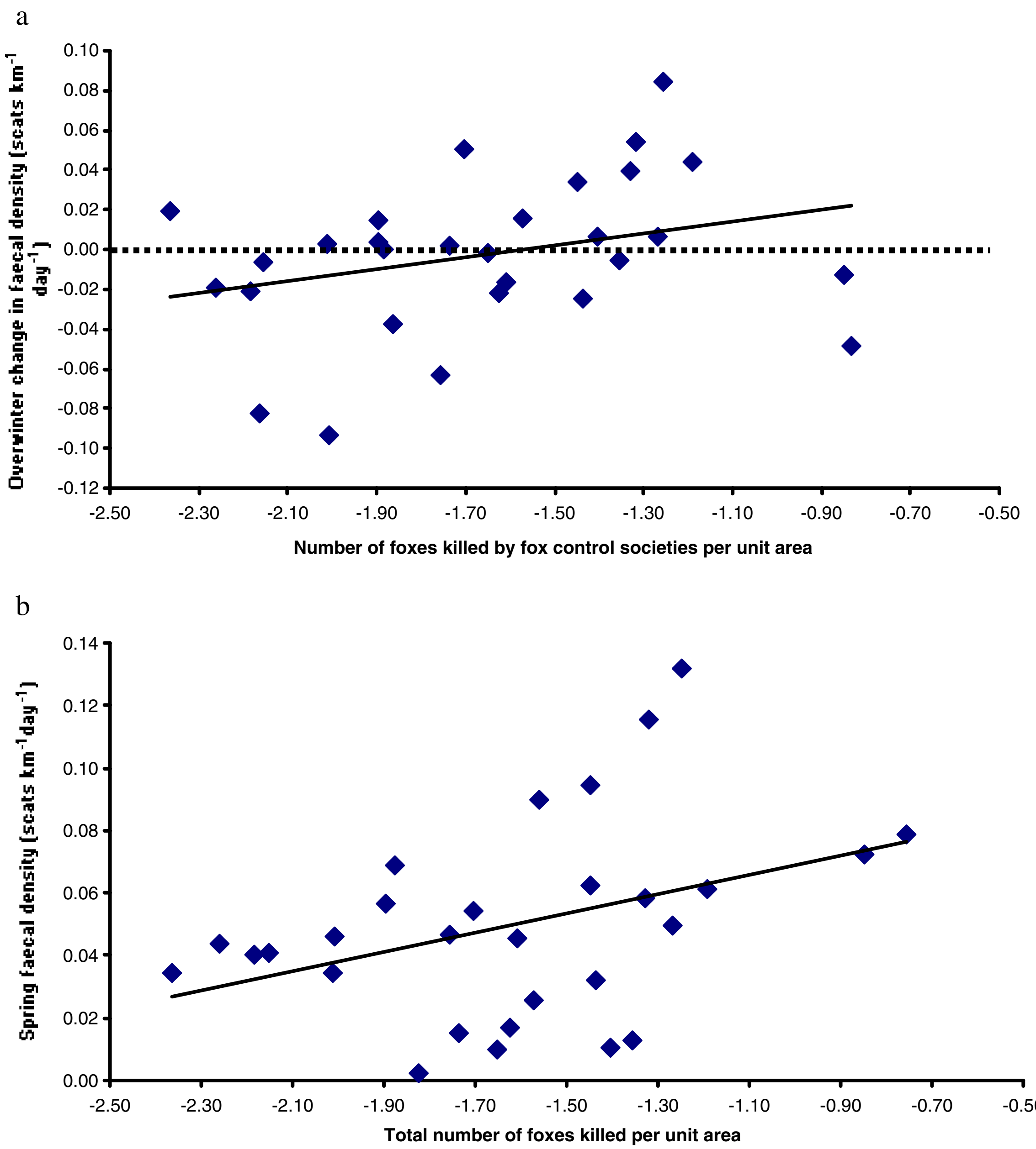

Fig. 3 Relationship between culling pressure and the over-winter change in faecal density (**a**) and spring faecal density (**b**)

Table 3 Correlation between preliminarily selected variables correlated with the over-winter change in faecal density (N=29)

	ALTITUDE3	ALTITUDE1	BROADALL
ALTITUDE1	R=−0.865, P<0.001	–	
BROADALL	R=−0.743, P<0.001	R=0.647, P<0.001	–
CLEARFELL	R=0.013, P=0.945	R=0.050, P=0.797	R=−0.235, P=0.220

these instances, S was taken as the mean faecal density across forests merged in each block. Two further forests were excluded from all subsequent analyses: in one forest, we had no data on the number of foxes killed by fox control societies; in the other forest, no foxes were killed. Lastly, one forest was also excluded as an outlying data point following the procedures outlined by Hair et al. (1998) (Fig. 2). In this instance, faecal density in spring was substantially higher than in the remaining forests (0.2589 scats km^{-1} day^{-1} compared to 0.0024–0.1316 scats km^{-1} day^{-1}). Therefore, for statistical analyses, we utilised data from 29 forests/forest blocks.

Mean (±SD) forest/forest block size and transect length was 21.47±19.73 km^2 and 24.29±15.78 km, respectively. The mean number of foxes killed by all control methods and the number killed by gunpacks alone was 56±59 (range 8–273) and 53±58 (range 2–268), respectively. These figures corresponded to a total culling pressure of 3.59±3.80 foxes killed per square kilometer (range 0.43–17.46) and a culling pressure from gunpacks alone of 3.34±3.52 killed per square kilometer (range 0.43–14.73).

Autumn–spring change in faecal density

The over-winter change in faecal density (C) was negatively correlated with the area of clearfelled land (Table 2). There was a positive association with the area of broadleaved woodland aged 31–50 and more than 50 years. Therefore, the total area of broadleaved woodland was selected for the preliminary model. The area of land at less than 300 and more than 400 m altitude was positively and negatively associated with over-winter change in faecal density, respectively. There was a positive association between C and culling pressure, indicating a tendency for faecal density to increase over the winter period in areas of high culling pressure (Fig. 3a).

However, several of these preliminarily selected variables were correlated with one another (Table 3). ALTITUDE3 and CLEARFELL were selected for inclusion in the final model. Individually, both the area of land at an altitude more than 400 m and the area of clearfell were significantly negatively associated with the over-winter change in faecal density in the final model, but the interaction term was not (Table 4).

Table 4 Results of the general linear model for factors associated with the over-winter change in faecal density

Variable	Df	Mean square	F	Significance (P)
ALTITUDE3	1	1.748×10^{-2}	23.929	<0.001
CLEARFELL	1	7.028×10^{-3}	9.618	0.005
Error	26	7.307×10^{-4}		
Total	28			

Spring faecal density

Spring faecal density was significantly positively related to the total number of foxes killed (but not the number killed by fox control societies) (Fig. 3b). The correlation with the area of coniferous woodland aged 1–30 years was also nearly significant (P=0.054; Table 2), so both variables were included in the preliminary model. In the final model only the total number of foxes killed was significant ($F_{1,27}$=5.057, P<0.05).

Discussion

Spring faecal density was positively related to the area of coniferous woodland aged 1–30 years, although the correlation was not quite statistically significant. This relationship is likely to be related to changes in stand structure affecting the increased availability of prey groups such as small rodents and rabbits *Oryctolagus cuniculus* (Fernandez et al. 1994; Petty 1999). The over-winter change in faecal counts was negatively correlated with ALTITUDE3 and CLEARFELL, i.e. a high proportion of forest at altitudes more than 400 m or an increase in the proportion of felled land in the forest tended to result in a decline in faecal density over the winter period ($S_{SPRING}<S_{AUTUMN}$), whereas a decrease in the proportion of these habitat types tended to result in an increase in faecal density over the winter period ($S_{SPRING}>S_{AUTUMN}$). This is consistent with known patterns of food availability. For example, recently cleared land is likely to hold lower densities of small mammals because of the lack of cover (Fernandez et al. 1994; Ecke et al. 2002), and rabbit and field vole (*Microtus agrestis*) abundance tend to decrease with increasing altitude (Adamczewska-Andrzejewska 1999; Trout et al. 2000). Therefore, an increase in the proportion of these two habitats, and, by implication, a decrease in the proportion of other more favourable habitats may result in the decreased availability of food during winter, thereby leading to a reduction in fox numbers over the winter period.

The over-winter change in faecal density was not significantly associated with culling pressure. In fact, faecal density declined from autumn to spring (C-negative, $S_{SPRING}<S_{AUTUMN}$) at low levels of culling and increased (C-positive, $S_{SPRING}>S_{AUTUMN}$) with increased culling pressure. Similarly, although spring faecal density was significantly correlated with the combined culling pressure exerted by fox control societies, mounted hunts and Forest

Enterprise rangers, the relationship was positive, implying that more foxes were killed where more foxes were present or vice versa. Therefore, there is little evidence to suggest that culling in these forests exerted a significant negative effect on fox numbers. Over-winter culling of foxes to reduce spring numbers in Scotland has also been shown to be ineffective with, as in the current study, a trend towards higher fox numbers in spring when culling pressure is high (Hewson 1986).

At the most basic level, approximately 60–80% of a fox population would need to be removed annually to achieve effective limitation of population growth (Hone 1999; Harding et al. 2001), these figures equating approximately to the level of annual productivity. In this study, forest size averaged 21 km^2. Assuming an average territory size of 5.2 km^2 (O'Mahoney et al. 1999), an average group size of two adults (Lloyd 1980) and a litter size of six cubs (Heydon and Reynolds 2000), each forest would contain a maximum of approximately 32 foxes in autumn, i.e. excluding any juvenile or adult mortality. In comparison, an average of 56 foxes were killed in each forest. Consequently, the culling programme was removing roughly double the size of the maximum pre-culling population, yet this resulted in a negligible change in fox density. In this context, the culling undertaken by fox control societies, mounted hunts and rangers appeared to have no utilitarian value with respect to reducing fox numbers.

The most likely explanation for this failure to reduce the size of the predator population is immigration from neighbouring areas. In Britain and elsewhere, the level of culling is dictated by individual landowners so that any landscape consists of a mosaic of different culling intensities, e.g. in Britain, foxes were not controlled on 38–42% of farms surveyed (Vaughan et al. 2003; White et al. 2003), and there has also been a substantial decline in the number of gamekeepers (Tapper 1992). Such heterogeneous patterns of culling will tend to create a "source-sink" dynamic at the landscape level, with areas of limited or no culling acting as sources of recolonizing individuals for heavily culled areas. These systems tend to be typified by two properties: (1) the number of animals culled on individual properties can dramatically exceed the carrying capacity for that property, and (2) even where large numbers are killed, this can still result in no or only a temporary reduction in fox numbers (e.g. Kinnear et al. 1998; Reynolds et al. 1993; Thomson et al. 2000; Burrows et al. 2003; Summers et al. 2004). Consequently, the effective reduction of populations at individual sites (such as forests) will be dependent on the intensity, duration and timing of culling at that site, and the size of the potential immigrant base. The latter will be determined by the level and spatial distribution of culling across sites within the landscape, the propensity for individuals to disperse into vacant areas (Frank and Woodroffe 2001) and how effectively these combine to form a buffer against immigration. Over-winter culling of foxes is likely to be particularly ineffective, as this is coincident with the main period of dispersal, and dispersing foxes can move considerable distances (Trewhella et al. 1988), so recolonization is likely to be rapid and occur over a large spatial scale. In such a scenario, the study forests were acting as sinks for foxes from neighbouring areas rather than as a source for populations in the wider agricultural landscape.

From a management perspective, this potentially poses a significant challenge. Given the emotive attitudes typically associated with predator-culling programmes, managers are increasingly likely to be called upon to balance the needs of separate groups of stakeholders with conflicting viewpoints, e.g. farmers, sport hunters, recreational users (e.g. Knowlton et al. 1999). At the most basic level, there is the need to be able to make informed decisions about the likely benefits of culling predators. Yet the results of this study indicate that the ability to predict the effectiveness of culling programmes is dependent on a thorough understanding of landscape-level processes, the data for which are unlikely to be readily available.

Conclusion

Habitat-related characteristics and not culling pressure were the best indicators of change in fox faecal density and spring faecal counts in the study forests. Those habitat characteristics associated with these variables were consistent with known patterns of food availability. However, the correlations observed in this study do not necessarily imply a causal relationship with fox density. Consequently, further data collected both across years and within different landscapes would be beneficial: experimental manipulations, although potentially desirable, are unlikely to be achievable given the emotiveness associated with this issue and the need for the cooperation of large numbers of landowners and other persons. In addition to the effects on fox density, these studies should also consider quantified measures of the impact of fox predation on, e.g. livestock and game, and whether this is related linearly with predator density and/or predator reduction (see Moberly et al. 2003). Further consideration should also be given to the possible effects of culling in exacerbating levels of damage. For example, the perturbation of populations and amplifying patterns of movement is known to exacerbate the transmission of diseases (e.g. Donnelly et al. 2003; M. Vervaeke, unpublished data), and immigrating individuals may also exert higher levels of predation relative to resident individuals (Althoff and Gipson 1981; Frank and Woodroffe 2001). Consequently, current forms of fox management in forests could be detrimental to neighbouring landowners' interests.

However, the results of this study do indicate that levels of culling prior to the enactment of the Hunting Act 2004 were not sufficient to reduce fox density within the commercial forests studied. Furthermore, given that the majority of foxes killed in the surrounding agricultural habitats was taken by shooting, which is unaffected by the legislative changes and which is unlikely to change in prevalence following the ban (White et al. 2003), we conclude that the restrictions on the use of dogs to control foxes is unlikely to result in increased fox density in these commercial forests.

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