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# The impact of human attitudes on the social and spatial organization of urban foxes (*Vulpes vulpes*) before and after an outbreak of sarcoptic mange

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## Abstract

The red fox (*Vulpes vulpes*) population in the city of Bristol in southwest Britain has been studied continuously since 1977. From 1990, intensive behavioral data have been collected on the social organization and patterns of space utilization of 4-8 fox groups in northwest Bristol. The impact of a mange epizootic on the social organization and territorial behavior of urban foxes, and their inter-relationships with the resident human population has been studied.

From 1990-1994, mean social group size increased from 2.25 to 6.57 adults. This was associated with a high level of food provision; around 10% of households on each range fed foxes. Feeding of the foxes commenced following regular sightings, or in response to the presence of very tame individuals. The most fundamental change following the 1994 outbreak of mange was the marked increase in mortality rates, rapidly declining social group sizes and increasing range sizes. Ranges were expanded following the loss of all animals from a neighboring group. The underlying strategy appeared to be a process of enlarging range boundaries until competing conspecifics were encountered. Range expansion was not mediated by a decline in resource availability, and the new ranges encompassed successively greater levels of resources. Following range expansion, there was no change in the level of intra-group contacts, but the level of inter-group contacts declined.

Before the 1994 mange outbreak, despite the variation in territory size and hence number of households in each territory, the amount of food given to the foxes in each territory was similar both in terms of the median weekly amount of energy and in the minimum amount of food supplied. For 2 social groups, changes in the amount of food supplied by households closely mirrored changes in social group size, whereas for 2 other social groups changes in levels of food provisioning were not sufficient to match the increased energetic requirements as group size increased. The amount of food deliberately supplied for foxes by the residents appeared to have had a profound effect on the social organization of this fox population.

Following the worst of the mange epizootic, by early 1999 the fox population was <10% of the pre-mange density. Groups were markedly smaller, generally comprising a dominant pair. Subordinate animals were scarce, and exclusively females. Ranges were larger than those prior to the outbreak of mange and less stable, with large-scale movements of boundaries between seasons. Such changes were probably related to changes in the availability of scavenged foods: less than 1% of households were deliberately feeding the foxes in 1999. Consequently, the foxes appeared to be utilizing habitats such as woodlands and sports fields more frequently. It is unlikely that more people will start to feed the foxes again until they see the foxes regularly. Even then, public attitudes towards the foxes may be less favorable due to concerns about the transmission of mange to both pets and humans. It will be some years before the Bristol fox population attains pre-mange densities.

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## INTRODUCTION

The red fox (*Vulpes vulpes*) population in the city of Bristol in southwest Britain has been studied continuously since 1977, and is now probably the most intensively studied fox population anywhere in the world. The original focus was on population processes and the potential for the spread of rabies in British urban fox populations (Waterhouse 1971; Smith and Harris 1991). It was believed that the importation of a single rabid dog into Britain could lead to a rabies epizootic in an urban fox population (Waterhouse 1971).

More recent work has shown that the rabies virus is adapted to particular host species, and there are associated genetic changes in the virus (Smith et al. 1995). Although the problems of controlling an epizootic of fox rabies in an urban area would still be considerable (Harris and Smith 1990), the perceived risk of fox rabies being introduced to Britain by an infected dog is much lower than previously believed (Anon. 1998).

Since 1990, the focus of the work on Bristol's urban fox population has been on their behavior and inter-relationships with the resident human population. In particular, we wanted to identify:

1. The factors which determine territory size in urban foxes,
2. How group size and territory size and configuration are adjusted to changes in these determinants,
3. How perturbation affects group size and territory size, and
4. How changes in human behavior affected the dynamics of this fox population before, during and after an epizootic of sarcoptic mange.

We summarize these changes in this paper and briefly outline the present pattern of social organization in the Bristol fox population.

## METHODS

From 1990, intensive behavioral data have been collected on social organisation and patterns of space utilization of a small number of fox social groups in northwest Bristol (White and Harris 1994, White et al. 1996, Baker et al. 1998). The main habitat is semi-detached, inter-war housing with associated gardens; this is the preferred habitat for urban foxes in Britain (Harris and Rayner 1986). Other major habitat types include recreational playing fields, residential nursing homes and a cemetery. Fox population density was approximately 5 family groups km<sup>2</sup> (Harris 1981).

We initially studied 4-6 social groups each year, but 2 new groups were formed by the division of 2 existing groups. The key study techniques were capture-mark-recapture, radio tracking, DNA fingerprinting and questionnaire surveys. During the study period we

experienced an outbreak of sarcoptic mange. Previously, there had been no recorded cases of sarcoptic mange in Bristol from the onset of the study in 1977; the first case occurred in spring 1994.

Throughout this paper, the term cub refers to animals <6 months old, sub-adult to animals 6 to <12 months old, and adult to animals ≥12 months old. All animals are assumed to have been born on April 1st each year (Harris and Trehwella 1988). Seasons were defined as follows: spring as March-May; summer as June-August; autumn as September-November; winter as December-February.

### Capture and Handling Procedures

From autumn 1989, foxes were caught in cage traps set in private gardens. In addition, cubs were netted from under garden sheds, tagged and released back under the shed. Several of the animals born prior to 1990 had been marked as part of the long-term capture program undertaken in the city (Harris and Trehwella 1988). Capture, handling and marking techniques are described in Baker et al. (1998). Animals were aged by incisor wear (Harris 1978) and full-grown animals fitted with radio-collars transmitting at 173MHz.

Prior to the outbreak of mange, group composition was assessed annually on April 1st. Following the outbreak, data on group size are given for each season, data on group size and composition consider adults only. Animals that died or dispersed during the year or season were included in the group total for that year/season. Animals that changed groups were assigned to their "new" group from the start of the year/season following their movement. Criteria for assessing group composition are described by Baker et al. (1998).

### Radio-tracking Procedures

Radio tracking was conducted on foot (Harris 1980). A single person followed individual animals continuously for an 8-hour period between 19:00 and 03:00 hrs or 20:00 and 04:00 hrs. Following the outbreak of mange, additional shorter periods of radio tracking were also conducted. Up to 4 animals were followed each night, but with a maximum of 2 animals from the same social group to minimize disturbance. Locational fixes were recorded every 5 minutes on a dictaphone. At each fix, animals were assigned to a 25 m grid cell and classified as active or inactive based upon fluctuations in the signal received.

Minimum convex polygons (MCPs) were used to identify individual seasonal home ranges because these accurately reflect the pattern of space use within the urban environment (Saunders et al. 1993). Pre-mange home ranges were based on a minimum of 200 active fixes, this being the mini-

imum number needed to obtain asymptotic range estimates (Harris et al. 1990). Larger numbers of fixes were required post-mange to obtain asymptotic home range estimates.

Intra- and inter-group encounters were monitored during radio-tracking sessions by scanning the radio-frequencies of all collared individuals both in the group to which the focal animal belonged and in adjacent groups. An encounter was defined as an inter-individual separation distance <25 m (White and Harris 1994). Encounter rates were considered on a pair-wise (dyad) basis; only dyads consisting of the focal animal and another collared individual were utilized for analyses, and only where at least 3 collective nights' data had been obtained.

### Questionnaire Surveys on Food Availability

Before the mange epizootic, food of human origin (termed scavenge for convenience) formed approximately 60% by volume of the diet of Bristol foxes; most other food types individually formed <10% each of the diet (Saunders et al. 1993). The availability of scavenged food was quantified by a series of questionnaire surveys. During autumn 1992, all 499 households on the Barley Croft range were asked to complete a questionnaire detailing: the number of years they had been resident; whether they owned any dogs or cats; and whether they had or were still supplying food for: (i) foxes; (ii) other nocturnal mammals such as badgers (*Meles meles*) or hedgehogs (*Erinaceus europaeus*); (iii) garden birds on a bird table; (iv) garden birds on the ground; (v) pets, such that some food could be left in the garden and available to foxes. This survey was repeated in autumn 1993; 1100 households (including the original 499) on the Barley Croft, Briarwood, Lower Abbey Road, Sandyleaze and West Dene ranges were asked to complete a questionnaire similar to that in 1992.

The 84 households (out of 899) on the Barley Croft, Briarwood, Lower Abbey Road and West Dene ranges that supplied food for the foxes were then asked to keep a more detailed account of the nights that they supplied food and the weight given on each occasion in each of 5 food categories: bones and carcasses; meat; pet food; bread; and miscellaneous. During the autumn of 1993, data were collected from the Lower Abbey Road and West Dene groups for 1 week and from the Barley Croft and Briarwood groups for 2 weeks. During the spring of 1994, data were collected from all 4 groups for 3 consecutive weeks. These data were then converted to energy values (Saunders et al. 1993). To allow for variations in recording accuracy among households, energy data were expressed as blocks of 0.2MJ, which is approximately 10% of the average daily energy expenditure of an adult fox in this area (Saunders et al. 1993). In all calculations we "rounded down", so values are minimum figures.

After the onset of mange, territory size expanded considerably, and so the 1,626 households on the expanded Briarwood range were surveyed in autumn 1995 and asked the same questions as in the 1992 survey. In addition, they were asked: how long they had supplied food to the foxes; whether they had recently stopped putting food out and, if so, when and why; and whether food was given on an irregular basis to "test" whether foxes were still in the area with the intention of resuming regular feeding if the food was consumed.

To determine the temporal stability of scavenged food sources, all households on the Barley Croft, Briarwood, Lower Abbey Road and West Dene ranges which had fed or were feeding the foxes when surveyed in 1992, 1993 or 1995 were contacted again during 1997 and asked when and why they started and stopped feeding the foxes. Of these, 110 completed questionnaires.

## RESULTS

### Changes in Group Size

Sixty-nine tagged and 16 untagged animals were resident in the study groups as adults (40 males, 39 females, 6 animals of unknown sex). The overall sex ratio was equal ( $n=79$ ,  $X^2=0.01$ ,  $df=1$ ,  $P>0.05$ ); this was the case both before and throughout the mange outbreak. Subordinate males ( $n=28$ ) were as common as subordinate females ( $n=31$ ) ( $X^2=0.15$ ,  $df=1$ ,  $P>0.05$ ), with up to 4 males present in a single group. Subordinates were typically philopatric offspring from previous years (Baker et al. 1998).

Changes in group size before and after mange are shown in Figure 1. In the period before the appearance of mange, mean ( $\pm$ SD) group size rose from  $2.25\pm 0.25$  adults in 1990 ( $n=4$  groups) to  $6.57\pm 0.92$  in 1994 ( $n=8$  groups). The majority, but not all, groups increased in size; the largest individual social group contained 10 adults in 1994. Following the appearance of mange, there was a steady decline in mean group size to winter 1995, when the last animals in the study area died.

### Pattern of Mortality

The pattern of mortality before and after mange is illustrated in Figure 2. Before mange, the annual rate of death of adults was low: 10% per annum, range 0-19% ( $n=4$  years and spring 1994). The main cause of death was road traffic accidents (38%). The first case of mange was detected in spring 1994; this was a subordinate male which moved away during the winter, returned in March and was recovered dead on the last day of May (spring) 1994.

After the appearance of mange, the mortality rate increased dramatically in autumn 1994 and was

approximately 35% per season, range 24-58% (n=6 seasons). This was an annual mortality rate of approximately 82%. Three entire social groups were lost during summer 1995, one further group disappeared in autumn 1995 and the remaining groups were lost during winter 1995. While mange was the main cause of death until the end of summer 1995, and there were no recorded road deaths. Thereafter, road traffic accidents accounted for half of the last 4 recorded deaths. In total, mange accounted for 91% of deaths from spring 1994 to winter 1995 inclusive (n=44). There was no sex bias in the number of males (n=21) versus the number of females (n=20) recovered dead from mange ( $X^2=0.02$ ,  $df=1$ ,  $P>0.05$ ).

### Changes in Territory Size

Prior to the onset of mange, territories were very stable (White et al. 1996), but with a trend towards decreasing mean ( $\pm$ SD) range size from  $29.5\pm 12.1$  ha in 1990 (n=4) to  $18.2\pm 5.2$  ha in 1994 (n=8). This was in part due to the formation of 2 new groups (West Dene in 1992 and Briarwood in 1993) from the division of 2 existing ranges (Lower Abbey Road and Barley Croft respectively). In both cases, the existing range was divided between a mother and her daughter.

Following the onset of mange, ranges tended to remain stable until the disappearance of a neighboring group. The first groups were lost in summer 1995 and it was only after then that there was a significant change in range size. After a range was lost, surviving neighbors expanded their range to include this vacant space. As mange mortality continued and more groups were lost, ranges continually expanded. By summer 1995 average range size was still only  $26.9\pm 14.0$  ha (n=5). In autumn 1995 average range size had increased to  $82.8\pm 28.6$  ha (n=3), and in winter 1995  $209.6\pm 127.5$  ha (n=3), when average range size had increased approximately eleven-fold since 1994.

### Effects of Changing Population Density on Encounter Rates

White and Harris (1994) give data on the rates of intra-group encounters before the onset of mange. Since intra-group encounters showed neither seasonal nor sex-specific differences, mean daily encounter rates of males and females were pooled and compared between seasons. Throughout the mange outbreak, we could detect no statistically significant difference in intra-group encounter rates between summer 1992, winter 1994, and summer, autumn and winter 1995 combined (Kruskal Wallis test:  $X^2=5.24$ ,  $df=2$ ,  $P>0.05$ ), although with a rapidly declining population sample sizes were small, and in autumn and winter 1995 there was only 1 dyad each. Increasing range size did not, therefore, appear to affect intra-group encounter rates.

White and Harris (1994) also gave dyadic inter-

group encounter rates before mange. While these did not show sex-specific differences, mean daily inter-group encounter rate in winter was 4.4 times higher than in summer and autumn (White and Harris 1994). Therefore, to compare between seasons, the observed inter-group encounter rates in winter were divided by 4.4. After mange, there was a statistically significant decrease in inter-group encounter rates between winter 1994 and summer 1995/autumn 1995 combined (Mann Whitney test:  $U=49.5$ ,  $n_1=18$ ,  $n_2=11$ ,  $P<0.05$ ). Thus, increasing range size reduced inter-group encounter rates.

### Availability of Scavenged Foods to Urban Foxes

We then looked at changes in food availability to see if these could account for:

1. The increases in mean group size before mange,
2. The division of two social groups, and
3. The increase in range size after the mange epizootic.

There were 6 potential sources of scavenged food: food deliberately supplied for foxes, badgers, hedgehogs etc.; compost heaps; bird food; pet food; dustbins; and general rubbish. On the study site, the last 2 sources were negligible because new "wheelie" bins excluded foxes and rubbish bags were rarely used, and there were very few public rubbish bins. The number of houses per fox territory ranged from 119-499. Regardless of the number of houses, the percentage deliberately feeding foxes was consistent at approximately 10% (range 7-12%), i.e., on each territory there were 14-49 households known to be feeding foxes (Figure 3). A further 18% also fed garden birds on the ground (range 8-30%) and 23% fed birds on a bird table (range 17-26%). Left over pet food was a rare source of scavenge, only available from around 1% of households. We do not have comparable data on the availability of compost heaps, but a survey in 1999 indicated that approximately 34% of households possess one (n=163).

### Reasons for Feeding Foxes

Of the households that supplied information on why they started to feed the foxes, the most common reason (63%) was simply that foxes were seen regularly and feeding was started as a means to get better and longer views of the animals (Figure 4). Another major factor stimulating people to start feeding the foxes was the presence of tame animals, i.e. animals which tolerated close human presence and would even take food from the hand. On the Barley Croft and Briarwood groups one very tame female frequently went into peoples' homes and would take food from anyone. A similar female, but not quite as tame, was also present on the Lower Abbey Road and West Dene ranges. In both instances, these females

were present in the year preceding the division of their parents' ranges; hence each one influenced the feeding responses of households on 2 ranges.

Following the outbreak of mange, the main reason people stopped feeding the foxes was because no foxes were seen or the food put out was left (combined 65% of cases) (Figure 5). Thus, food was only withdrawn after the foxes themselves had died from mange.

### **The Amount of Food Supplied**

The energy requirement of a breeding pair of foxes is 4MJ/day or 28MJ/week (Saunders et al. 1993). Of the households that recorded how much food they provided for the foxes, the maximum energy was 9.2MJ/week; this was a person who regularly brought home a bucketful of scraps from a nursing home where he worked. The average amount of food supplied was approximately 2.4MJ/week, the median 1.8MJ/week. The most common source of food was household scraps, but many people bought commercial pet food specifically for foxes. One regular can of dog food would supply over half the total daily energy requirement of 1 fox.

On each of the 4 ranges, for 10 of the 18 weeks when scavenge availability was recorded, the known minimum recorded energy supplied by households was above the 28MJ/week needed by a single pair of foxes. However, this did not include those households who fed the foxes but did not supply any data. To estimate the total amount of food supplied for the foxes on each range, we assumed that the "missing" households supplied the median amount of food (i.e. 1.8MJ/week): from conversations with the householders, we knew that they had been feeding the foxes, but had not completed their record form. Including these estimates for missing data, the median energy value supplied by households on each range was approximately 40MJ/week, i.e. well in excess of the energy requirements of the breeding pair. This was consistent across all 4 groups. Furthermore, this was only 1 source of scavenged food.

The relationship between group size and the amount of food supplied by households on the Barley Croft and Briarwood groups is shown in Figure 6. For the period before the mange outbreak, the amount of scavenged food deliberately supplied for the foxes appeared to be sufficient on its own to drive both changes in group size, and also to promote the splitting of this group in 1993. The figures for the other 2 groups surveyed (Lower Abbey Road and West Dene) indicate that the amount of food supplied by households was not sufficient to drive the observed changes in group size, but may have promoted the division of the territory as each new territory provided very similar weekly amounts of energy.

The situation changed during the mange epidemic, although quantifying this proved problematic after

range boundaries started to undergo major shifts. For the Briarwood group, the amount of food available from the households known to be feeding the foxes ranged from 67.0-88.2MJ/week from spring 1994 through to summer 1995, mean ( $\pm$ SD) 78.3 $\pm$ 7.2MJ/week, n=6 seasons. Despite this excess of food, the range was expanded in autumn 1995, and the amount of scavenged food available increased to around 130MJ/week. This range was further enlarged in winter 1995. This implies, therefore, that ranges did not increase in size in response to a decline in food availability, but simply to the disappearance of neighboring social groups. This conclusion was reinforced by the reasons given by people for stopping feeding the foxes: they only changed their feeding patterns after the fox population had declined following mange.

## **DISCUSSION**

The mange epizootic in Bristol provided a unique opportunity to test a number of behavioral theories and to examine the relationship between humans and urban foxes. In addition, it also allowed us to examine how changes in population density affect fox behavior and the potential for the spread of diseases such as rabies (White et al. 1995). This was facilitated by the considerable amount of data collected prior to the onset of mange.

We were aided because the epizootic was widespread, first appearing in the rural area to the south of the city and then spreading through the city and into the rural fox population to the north. This prevented rapid recolonization, a problem with manipulation experiments. In fact, in spring 1999, 5 years after the appearance of mange, the fox population on the study area was still <10% of that present at the onset of the mange outbreak, with average range size approximately 60 ha. Because all the foxes in our study groups died, the foxes that recolonized the study area appeared to originate from survivors in social groups neighboring those detailed in this paper. Furthermore, the prevailing pattern of social organization in the new population showed some marked differences to that prior to and during the outbreak of mange.

### **The Effects of Changing Density on Population Processes**

The most fundamental change following the outbreak of mange was the marked increase in mortality rates and the increase in the size of the ranges of the surviving individuals. However, ranges were only expanded following the loss of all animals from a neighboring group. The underlying strategy appeared to be a process of enlarging range boundaries until competing conspecifics were

encountered. This range expansion was not mediated by a decline in resource availability, and the new ranges encompassed successively greater levels of resources.

Prior to the outbreak of mange, the mortality risk imposed by conspecific competitive interactions was high (Harris and Smith 1987). Active range expansion, i.e. encroaching onto and securing space already held by an existing group would, therefore, have been costly in terms of the risk of serious injury. However, expanding into an adjacent area only after the previous group had disappeared would significantly diminish these costs. The establishment of new borders in these circumstances may, therefore, occur with little overt aggression. But why should foxes expand their ranges in the absence of a decline in food availability?

One possible advantage of maintaining congruent ranges is the elimination of interstices between groups. Recent work on the dispersal behavior of foxes has shown that itinerant behavior is not, as previously thought, a significant feature of dispersal. Instead, dispersers move for limited periods of time, making exploratory movements from their natal or small temporary ranges (Hough 1980, Woollard and Harris 1990, Robertson and Harris 1995, Macdonald and Courtenay 1996). These temporary ranges may serve as secure bases that, over time, may be expanded to form the final range. So interstices between territories may be occupied by dispersing or itinerant individuals, which then seek to expand these small areas and establish their own territory at the expense of the resident territory holders (e.g. Macdonald and Courtenay 1996). This in turn could render existing territories untenable. By removing these interstitial areas, territory holders may pre-empt such losses with only a minimum increase in defense costs, since their "new" neighbors are also likely to be territory holders who have little or nothing to gain by escalating inter-group conflicts. Certainly, with increasing range size, inter-group contact rates declined.

The maintenance of large ranges may also be beneficial in that it would be possible to sub-divide the territory at some later date, thereby promoting the fitness of descendant offspring without them having to compete directly with conspecifics (Lindström 1986). Range division occurred on the study site twice before the mange outbreak, with ranges divided between parents and daughters. By this means, the offspring of existing dominant animals attained breeding status without any detrimental effect upon the reproductive output of the dominant animals. The number of grand-offspring produced through this strategy increased dramatically (Baker 1995). However, there are also a number of costs associated with maintaining larger ranges. One was the increased risk of road mortality following range expansion.

One corollary of such "territorial budding" is that related animals will remain in close proximity to each other, possibly leading to the formation of enduring familial bonds (Macdonald and Courtenay 1996). Short distance dispersal to neighboring groups will also lead to the formation of clusters of related individuals. In the Bristol fox population as a whole, the average dispersal movement pre-mange was 3.4 social groups for males and 1.2 groups for females (Trehwella et al. 1988). The close relatedness of adjacent groups pre-mange has been confirmed by recent genetic analyses (P. Baker, S. Funk, M. Bruford and S. Harris, unpublished data), which showed that several of the neighboring dominant animals are themselves related. In the long-term, these bonds may serve to further reduce the potential conflict between neighboring territory holders (the "good neighbor" strategy of Macdonald and Courtenay 1996).

### **Lessons for Rabies Control**

The mange epizootic also provided an ideal opportunity to test a number of assumptions of rabies control models. These generally assume that contact rates remain the same despite changes in population density as a result of a control program or the disease itself. Changes in either intra-group or, especially, inter-group contact probabilities can have profound implications for the rate of disease spread (White et al. 1995). In this paper, we have shown that reductions in fox population density affected inter-group but not intra-group contact rates. We are currently examining how this may affect the rate of spread of rabies in a British urban fox population.

When planning to use baits (poison or vaccine) to control a rabies epizootic, Trehwella et al. (1991) showed that the very low rate of bait uptake by urban foxes was problematic. This may be due to the large amounts of scavenged food available to the foxes. It is possible that rates of bait uptake could be increased either by: (i) distributing these in gardens where the foxes are already being fed; or (ii) restricting people from feeding the foxes during a rabies epizootic. Both of these ideas need to be tested.

### **The Impact of Human Feeding Behavior on Fox Population Processes**

The area used for this study had a low rate of human population turnover; approximately 80% had been resident for >5 years, and 62% for >10 years (P. Baker, unpublished data). Whether this influenced the level of provisioning of the foxes is unclear, since there are no comparable data from other urban areas. Despite the variation in territory size and hence the number of households on each territory, the amount of food given to the foxes each week was similar both in terms of the median weekly amount of energy and in the minimum amount of food supplied. For both

measures, energy availability was far in excess of the 28MJ/week required solely by a breeding pair of foxes. However, food provided for the foxes is just 1 source: there are other sources of scavenged food, and other food sources (insects, earthworms, birds, mammals, etc.). For 2 social groups, changes in the amount of food supplied by households very closely mirrored the changes in the number of animals observed on the ranges. However, the magnitude of the changes in scavenge availability was not sufficient to match the energetic requirements of the observed increase in the number of animals for 2 other social groups, suggesting a switch to a greater reliance on some other food source. What is clear, however, is that the amount of food deliberately supplied for foxes by the residents was such that it could have had a profound effect on the social organization of this population, although it must be stressed that controlled manipulative experiments are required before we can be certain that the increase in scavenge availability caused the observed population changes.

### The Present Situation and Future Prognosis

By early 1999, the fox population was <10% of the pre-mange density. Groups were markedly smaller, generally comprising a dominant pair: subordinate animals were scarce, and exclusively females. Ranges were larger than those prior to the outbreak of mange and less stable, with large scale movements of boundaries between seasons. Such changes were probably related to changes in the availability of scavenged foods: <1% of households were deliberately feeding the foxes in 1999. Consequently, the foxes appeared to be utilizing habitats such as woodlands and sports fields more frequently.

Mange was still prevalent in 1999, and half of the breeding females showed signs of infection. All the females not showing any signs of infection were >5 years old, suggesting that they may have lived through the entire mange outbreak: it is unclear whether these individuals have a greater resistance to infection. Furthermore, mortality amongst offspring was high, with 73% dying before they were one year old. Of these, 75% died from mange. Pre-mange, the mortality rate of animals in their first year was 56% (Harris and Smith 1987). The continued presence of mange and the high level of cub and sub-adult mortality will prevent rapid population recovery.

One further factor to consider is the future pattern of scavenge availability. The questionnaire surveys suggest that it is unlikely that people will start to feed the foxes again until they see the foxes regularly. Even then, public attitudes towards the foxes may be less favorable due to concerns about the transmission of mange to both pets and humans. Such attitudes are unlikely to change so long as mange is common in the fox population. We conclude, therefore, that it will be

some years before the Bristol fox population attains the densities observed pre-mange.

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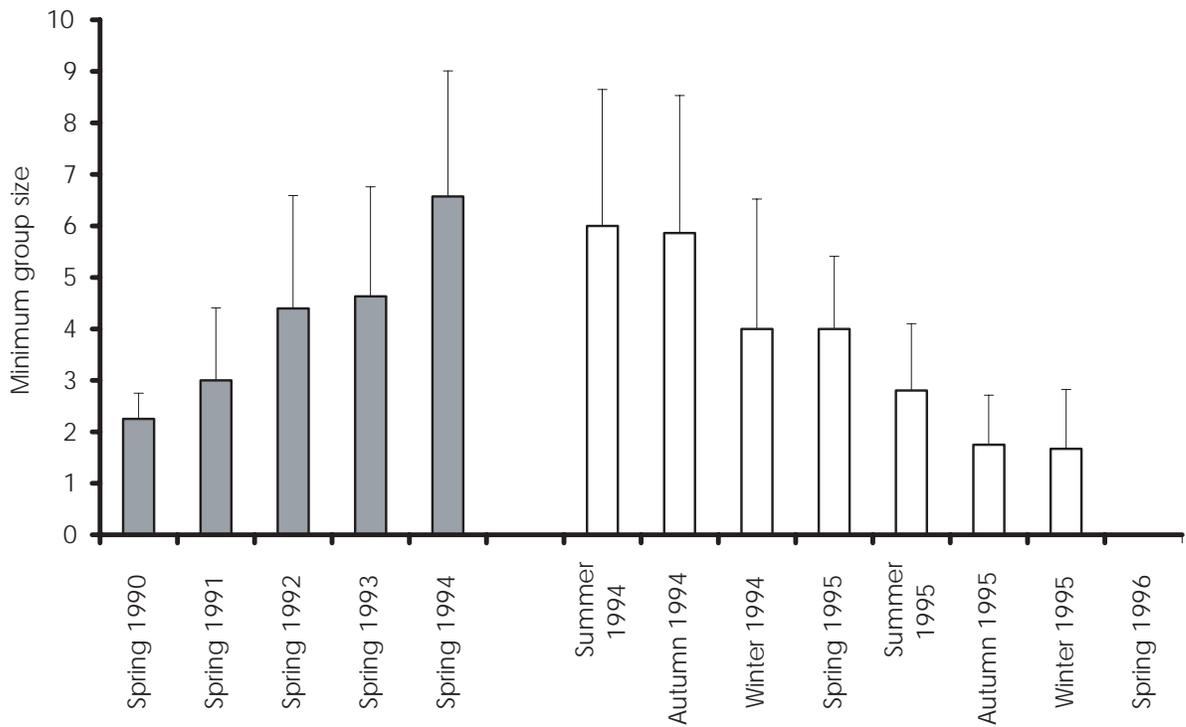


Figure 1. Changes in mean ( $\pm$ SD) adult group size in the period before and after mange. The dashed line marks the onset of the mange epizootic.

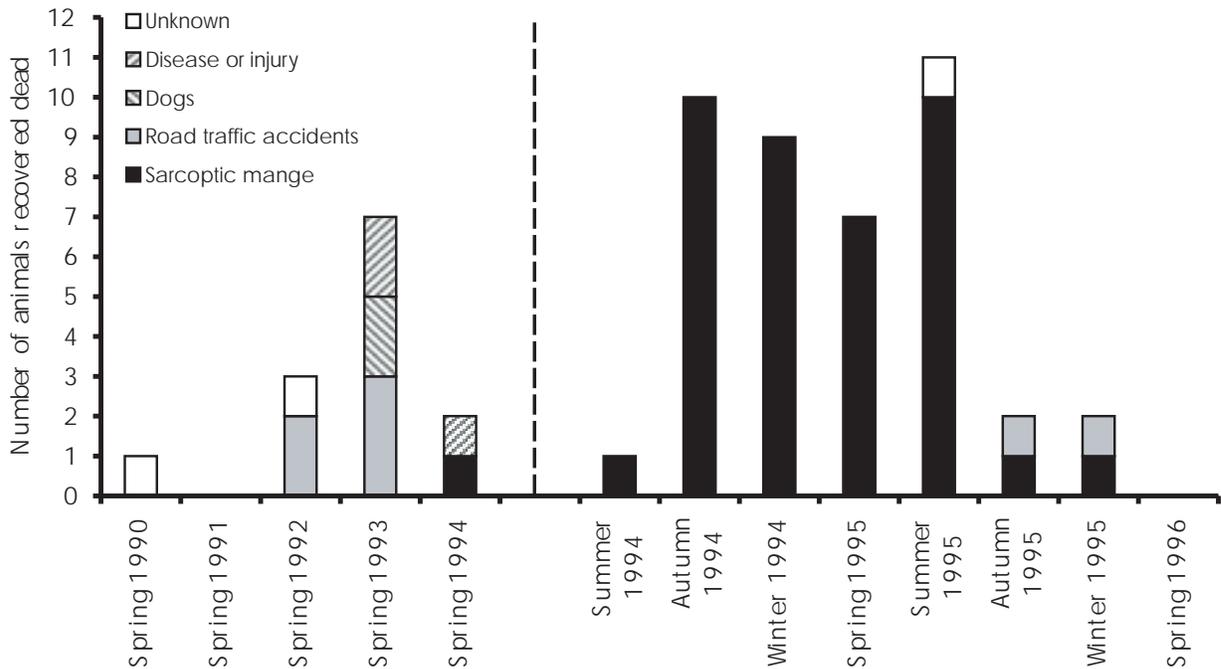


Figure 2. Changes in causes of mortality of adult foxes before and after mange. The dashed line marks the onset of the mange epizootic.

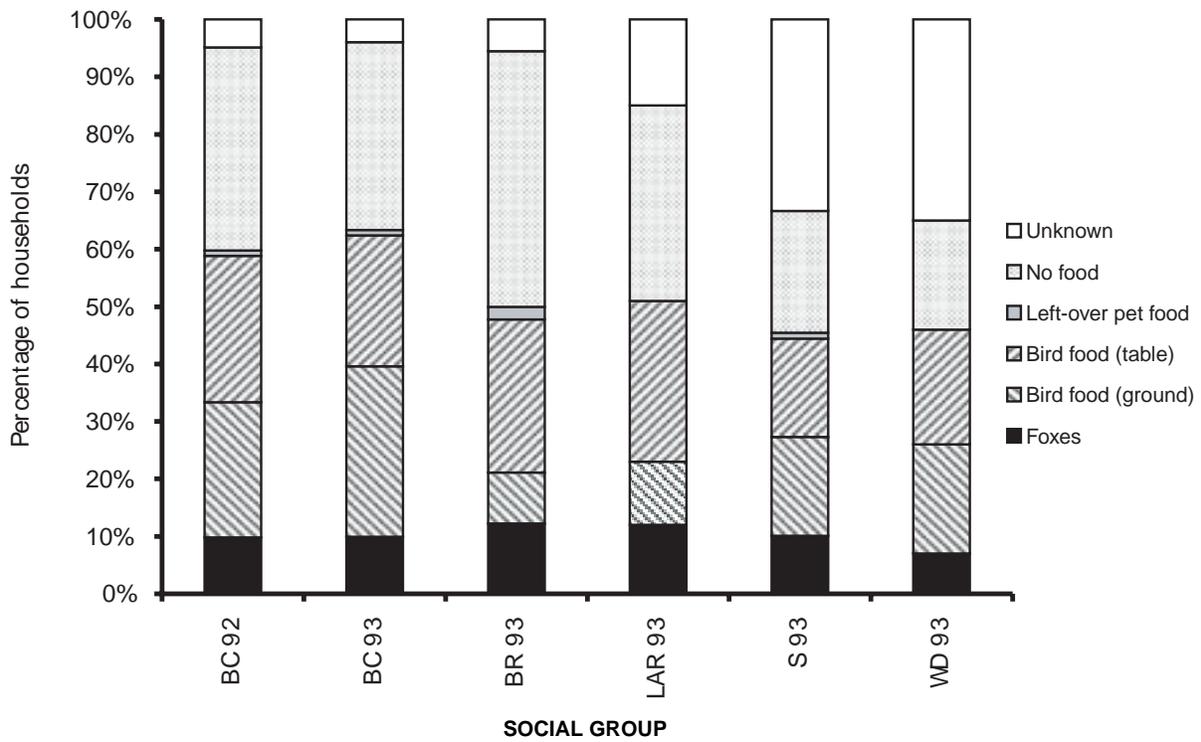


Figure 3. The percent of households supplying different sorts of scavenged food on one fox range in 1992 and five ranges in 1993, before the onset of the mange epizootic.

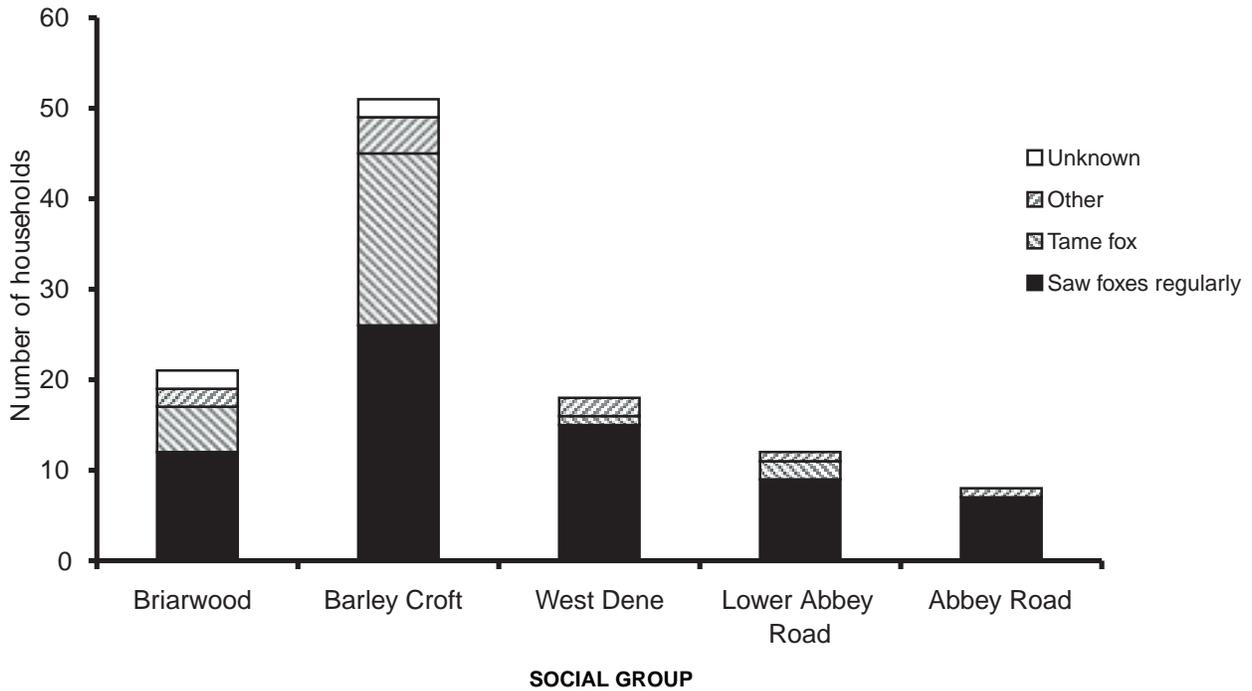


Figure 4. Reasons why 110 households on five ranges started to feed foxes, before the onset of the mange epizootic.

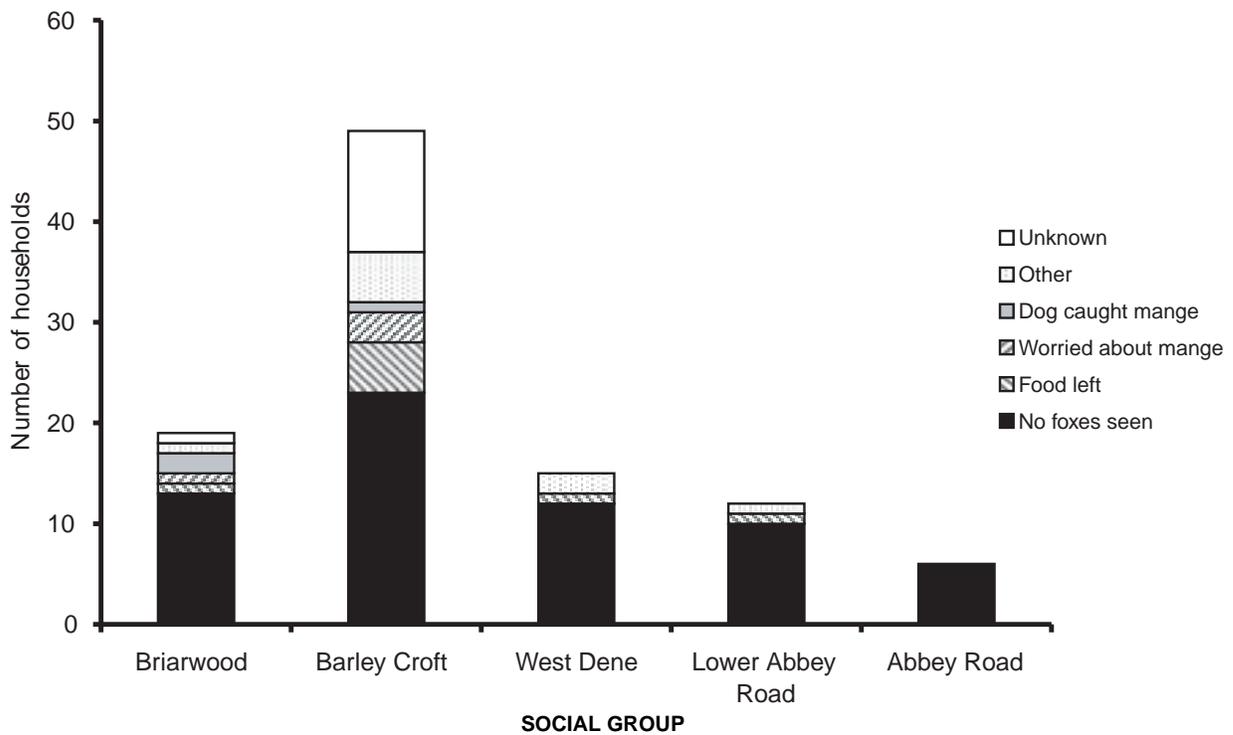


Figure 5. Reasons why 110 households on five ranges stopped feeding the foxes during the mange epizootic.

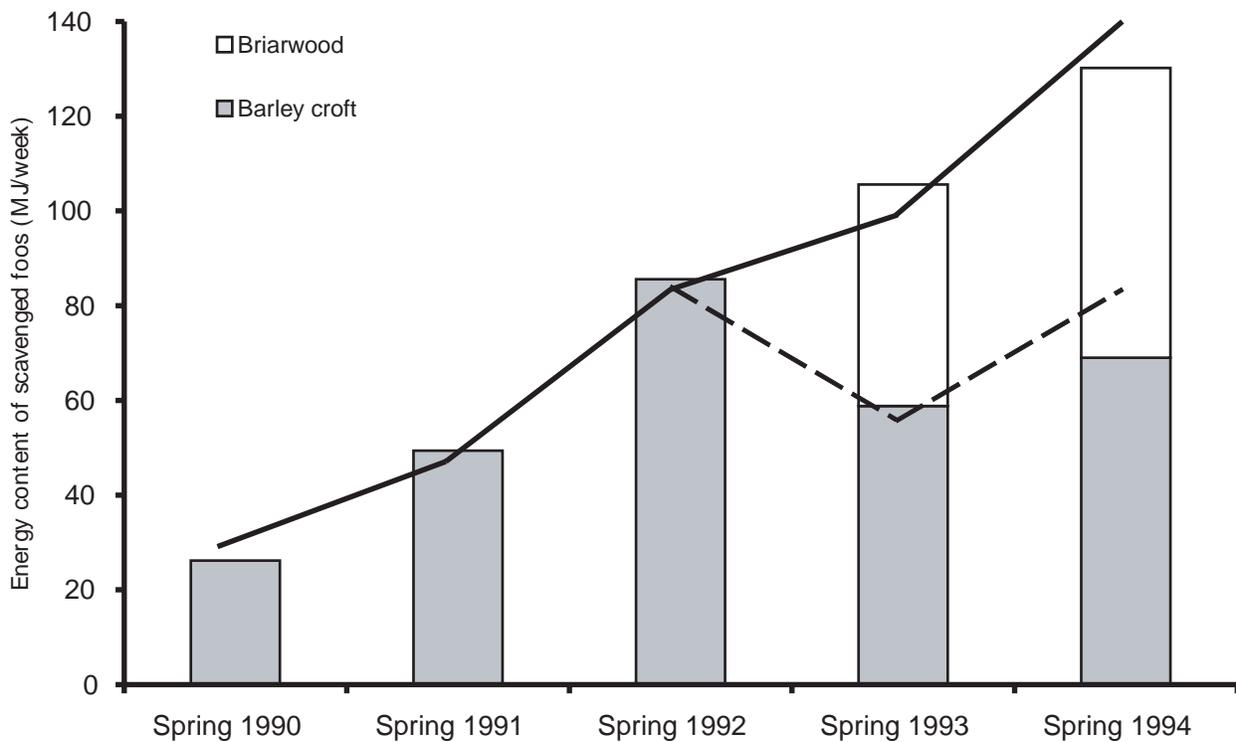


Figure 6. The relationship between amount of food supplied by household and fox group size. The original group split into two (Barley Croft and Briarwood) in early 1993. The bars show the amount of food supplied by households and the lines the amount of food required to support all the adult animals known to be resident in the group(s), assuming an energy requirement of 14MJ/week for each animal. The dashed line indicates the amount of food required to support the adult animals on the Briarwood range only.