DRIFTING TERRITORIALITY IN THE RED FOX

VULPES VULPES

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SUMMARY

1. The spatial organization of a population of red foxes, Vulpes vulpes L., living in the city of Oxford was investigated and contrasted to that of a neighbouring population in the surrounding suburbs.

2. Both populations were organized in social groups, each of which occupied an exclusive territory. While territories in the suburbs were spatially stable, those in the city drifted in location continually, but they did so in such a way that the juxtaposition of neighbouring groups remained essentially unaltered across generations of occupants.

3. The hexagonal pattern of city ranges moved at a rate equivalent to the complete displacement of an average range (38.8 ha) every 13 months (3.01 ha month⁻¹), although drifting was more pronounced from November to April. City and suburban foxes had comparable diets and ranges of the same order of magnitude; the mobility of city foxes was associated with social instability due to a higher turnover of the population and a lower proportion of barren vixens.

4. As a response to constraints of the city environment not encountered in the suburbs, synchronous drifting of city ranges represents a rapid modification of behaviour since the urban niche first became occupied by foxes in the 1930s.

INTRODUCTION

Territoriality is arguably one of the most important behavioural traits affecting the spatial organization of animal populations (Lack 1954; Wynne-Edwards 1962) and, therefore, population dynamics (Lomnicki 1980). In a classic study, Kruuk (1972) showed that spotted hyenas, Crocuta crocuta (Erxleben), were territorial in one population but not in another, and that this difference was determined by the nature of their food supplies. The existence of territories, under one definition or another, is integral to many models relating availability of resources such as food, mates and shelter, to social behaviour and density-dependent regulation (Brown 1969, 1982; Emlen & Oring 1977; Macdonald 1983; Carr & Macdonald 1986; Lindström 1986). The phenomenon has been defined as the occupation of a defended (Noble 1939) or exclusive (Schoener 1968) area, or both (Wilson 1975). Davies (1978) recognizes territoriality where animals are spaced further apart than would be expected from a random occupation of suitable habitats. Territories are often considered as spatially stable (but cf. Davies & Green 1976) and this is explicit, for example, in Brown & Orians’ (1970) definition as a ‘fixed, exclusive area with the presence of defence that keeps out rivals.’

In many areas, resident red foxes (Vulpes vulpes) are distributed in just such a classically territorial pattern, although the sizes of their territories may vary over two
orders of magnitude between regions, from under 20 ha to more than 2000 ha (Ables 1969; Storm et al. 1976; Lindström 1989; Macdonald 1981; von Schantz 1981; Voigt & Macdonald 1985). Elsewhere, their home ranges overlap to such a varied extent as to fall outside most or all definitions of territoriality (Harris 1980). Although they usually forage separately, social groups of two to six adult foxes, generally composed of one male and several related females, may share each territory (Macdonald 1981). Reproductive parameters, such as vixens’ productivity, vary between populations, and between age-groups within populations (e.g. Englund 1970; Harris 1977; Lindström 1980) and this variation may be a corollary of the existence of social groups and the dominance hierarchies within them (Macdonald 1979, 1980).

Our understanding of the social behaviour of nocturnal mammals in general, and foxes in particular, has often depended on radio-tracking data to provide basic information on ranging patterns. Timed locations in space can also be used for analysing interactions between individuals (Macdonald, Ball & Hough 1980). Few studies have employed such data to full advantage, however, as the analyses often require sophisticated models (e.g. Dunn 1979), with underlying assumptions that may be unrealistic for the home range configurations or the protocol of data collection. This paper draws on recent developments in non-parametric techniques of analysis (Doncaster 1990) in order to quantify spatial mobility in the home ranges of red foxes living in the city of Oxford. Hitherto this has been a little studied aspect of territoriality and it was an unexpected outcome of an intensive study by radio-tracking. We distinguish group members from neighbours by the spatial distance between individuals and their relative utilization of shared space, as distinct from the geographical area occupied by each range. These results are interpreted by comparison with a neighbouring population occupying stable territories in the adjoining suburbs (Macdonald 1981). Lastly, we explore the characteristics of the city environment by which a territorial organization can be perpetuated even when the defended area is not identified by geographical points of reference.

METHODS AND TECHNIQUES

We consider the home ranges of seventeen adult foxes resident in Oxford city, and radio-tracked for periods of 2–25 months between November 1980 and February 1983. These are compared with twenty-nine adults resident in the suburb of Boar’s Hill and radio-tracked for periods of 3–15 months between 1974 and 1980. The two populations were separated in places only by a busy motorway which was crossed frequently by itinerant and some territorial foxes (Macdonald & Newdick 1982). Details of the habitat preferences of urban foxes are given in Harris & Rayner (1986) and accounts of their diet in Harris (1981) and Doncaster, Dickman & Macdonald (1990).

Foxes were fitted with radio-collars conforming to a standard design (Macdonald & Amlaner 1980) and transmitting on 102 MHz. In both areas they were tracked from a car by one person (C.P.D. in the city) using a receiver (AVM Instruments Co., Champaign, Illinois, U.S.A.), and a three-element Yagi aerial fitted to the roof and rotated from the driver’s seat.

Foxes were tracked in the city for a total of 319 nights during 28 consecutive months. A nightly average of 92 ± 3 (S.E.) fixes was obtained in 177 nights of tracking from dusk to dawn. In so far as practical considerations allowed (foxes were
often difficult to catch for tagging and transmitters could only be expected to last 6–9 months), data were collected regularly on all concurrently equipped foxes by alternating nights of continuous tracking of one fox or a pair from the same group range (44% of nights), with discontinuous tracking of three to eight foxes. This protocol resulted in a total of 1491–1852 fixes in each hour of the night from 21.00 to 06.00 h with a further 3706 evening and morning fixes and 995 one-off daytime fixes. The protocol for tracking in the suburbs differed only in that the more open terrain facilitated more frequent observation of the tracked foxes through night-vision equipment.

The sizes and configurations of home ranges were reconstructed with a computer program (Voigt & Tinline 1980) to identify the 50 × 50 m grid-cells in which fixes on active and inactive foxes were located, including the eight ‘influence’ cells surrounding each non-peripheral cell in which a fix was located on an active fox. Cells that were visited only once by a fox on an excursion were removed from the analysis. Nevertheless, a simple plot of all the cells ever used regularly by an individual: its ‘total range’, was not asymptotic for ranges that were continuously moving, because it included the trail left behind the range as it shifted into new areas (cf. Harris et al. 1990).

The concept of a ‘prevailing range’ was therefore developed to provide a running estimate throughout the period an individual was tracked of the sizes and locations of areas it was currently frequenting (Doncaster 1990). An animal’s prevailing range was defined retrospectively for a given night to cover only those grid-cells visited on that night (if fixes had been collected), plus cells previously visited that would be returned to on any future night on which the fox was followed (and which were thus still in use). This procedure side-stepped the problem of non-asymptotic ranges by subtracting areas as they were abandoned definitively from the range, while still accounting for new acquisitions as they came into effect. The difference between total and prevailing ranges typical of city foxes is illustrated in Fig. 1 for a dog-fox monitored over 18 consecutive months. The prevailing range decreased in size during the last 9 months, despite a relatively constant rate of data collection (180 ± 36 radio-fixes month⁻¹), and it shifted in location, contributing to a continuously rising estimate of the total range.

The prevailing range is conceptually equivalent to an enumeration estimator (‘minimum numbers known alive’: Nichols & Pollock 1983) in capture–mark–recapture studies, equating the grid-cells making up a prevailing range on a night of tracking with a cohort of individuals. Subsequent reductions in the size of a cohort of grid-cells indicate areas that have been lost from the home range, in the same way that the enumeration estimator identifies death and emigration. The prevailing range, like an enumeration estimator, could not be calculated from the first and last periods of tracking a fox. The prevailing range estimate increased as a function of the cumulative fix total during the first nights of tracking, levelling off only when sufficient grid-cells had been utilized to represent the whole area in use at that time. For foxes in the city, the first range estimate after which an additional fifty ‘active’ fixes yielded <4 new grid-cells (1 ha) is henceforth referred to as the first true estimate. The size of the prevailing range being estimated influenced the number of fixes required to obtain a first true estimate (number of fixes = –21 + 5·46 × range size (ha), r = 0·74, F₁, 14 = 16·7, P = 0·001) with a mean requirement of 168 ± 16 fixes. Prevailing range estimates do not require that fixes were obtained each night,
but they do assume an absence of long-term trends in rates of collection. In particular, if fewer fixes were taken in the later stages of tracking an animal, some less frequently visited grid-cells may be incorrectly labelled as falling out of use. This source of error would be significant if the numbers of grid-cells being abandoned each month, from the group that had made up the first true estimate, was correlated negatively with the numbers of fixes obtained each month. No such correlation applied to any of the fox ranges used in the following analyses.

The extent of congruence in the utilization distributions of partially overlapping home ranges was quantified with an index of concordance (Doncaster 1990). This was calculated from Spearman's rank correlations between the numbers of independent radio-fixes (and influences, given 1/8 the value of fixes) obtained on each fox of a pair in each of the 50 × 50 m grid-cells used by one or both foxes. Values may lie between +1·0 (perfect overlap and identical utilization of shared areas), and −1·0 (areas heavily used by one fox are rarely or never used by the other, and vice versa).

RESULTS

The total home ranges of city foxes, though never asymptotic, averaged 93·4 ± 10·7 ha (range = 41·8–197·8 ha, n = 17) by the grid-cell method and excluding excursions (one-off visits to areas outside the usual range). As expected, total range estimates...
tended to be larger for foxes that were tracked over longer periods \( r = 0.48, P = 0.05 \). The city foxes showed considerable variation in the extent of overlap between neighbouring ranges, from which there emerged no clear pattern of territorial partitioning (Fig. 2a). In contrast, asymptotic total ranges of foxes resident in the suburbs averaged \( 54.3 \pm 5.3 \) ha (range = 14.7–107.3 ha, \( n = 29 \)). Plots of these ranges (Fig. 2b) demonstrated unambiguously a set of almost perfectly tessellated, long-term territories. Territorial boundaries in the suburbs frequently coincided with fixed geographical features such as roads and hedgerows, and some borders (notably, three stretches of minor road) remained stable across generations of foxes. Sightings of marked foxes indicated that some were visiting the same gardens for at least 6 years. Table 1 shows that the total ranges in the suburbs tended to overlap by less than one-quarter or by more than three-quarters, while those in the city showed no such polarization.

**Drifting ranges**

Instability in the size and location of city compared to suburban home ranges is illustrated with three examples in Fig. 3. Between the first and last dates that a fox was followed, shaded strata under each graph reveal new cohorts of grid-cells being

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**Fig. 2.** Plots of range configuration and overlap for the total home ranges of (a) ten city foxes (\( m = \) male, \( f = \) female) including a single representative from each group range; (b) twelve suburban foxes tracked over comparable periods. Shared areas of neighbouring home ranges are indicated by shading (• = 2, □ = 3, ■ = 4 foxes). While no exclusive territories could be identified in the city, the juxtaposition of three group ranges (arrowed) are shown for the suburbs, bordered, to the east, by the territories of two radio-collared vixens. Each of these group ranges contained only one adult male together with up to five adult females. The two circles represent average total ranges of 93.4 ha in the city and 54.3 ha in the suburbs.
TABLE 1. Contingency table for degrees of overlap between all pairs of intersecting total ranges in the city and suburbs

<table>
<thead>
<tr>
<th>Degree of overlap</th>
<th>1–25%</th>
<th>26–75%</th>
<th>76–100%</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>City ranges</td>
<td>86</td>
<td>41</td>
<td>30</td>
<td>157</td>
</tr>
<tr>
<td>Suburban ranges</td>
<td>58</td>
<td>3</td>
<td>24</td>
<td>85</td>
</tr>
<tr>
<td>Total</td>
<td>144</td>
<td>44</td>
<td>54</td>
<td>242</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 19.2, \ p < 0.0001 \]

Fig. 3. Three examples of changes in size and location of prevailing ranges, represented graphically and with plots of the changing configurations for the two mobile ranges. Shaded strata under each graph distinguish groups of 50 × 50 m grid-cells which at one time constituted new additions to the prevailing range and show how they subsequently diminish in size as the range shifts more or less quickly into new areas. Vertical arrows indicate the first date at which the estimate of range size was no longer dependent on fix total. (a) Yearling city vixen f5, who dispersed from her natal range in March into a continually shifting range 1 km away, where she was shot in April at a stage of late gestation; (b) city dog-fox, ml, tracked from 8 months to 2 years old when killed in road traffic, whose range retained an area with a regular feeding site for 12 months from March 1981 (dense stippling); (c) suburban dog-fox showing a range that remained largely stable over 1 year.

recruited into the prevailing range for the first time, and simultaneous decreases in the size of old cohorts which earlier had constituted the entire prevailing range. These changes represent definitive shifts in location of the entire prevailing range, as distinct from periodic use of parts of some larger home range. In contrast, one-off exploratory trips which did not result in a longer-term movement are shown graphically in Fig. 3 by sharp peaks in range size of very short duration (e.g. Fig. 3b, 30 March 1981). The number of these short-term peaks was probably underestimated because each animal could not be tracked every night.
City ranges were not spatially stable over months or even weeks. They moved in step-wise extensions to encompass new areas whilst at the same time contracting other parts of the range to expel old areas. Drifting could be continuous over months at a time, or interspersed with more stable periods. An approximate quantification of the rate of range drift is given by the shrinking sizes of areas that at one time constituted the entire prevailing range. With the animal’s focus of activity gradually drifting to new districts the diminishing size of the first true estimate of the prevailing range gives a minimum estimate of drift for the whole period over which a fox was tracked, as indicated by the lightly stippled base-parts of the graphs in Fig. 3a–c. Table 2 summarizes the spatio-temporal analysis, including this estimate of range drift, for the ten most extensively tracked city foxes (≥600 fixes covering periods of ≥100 days).

Prevailing ranges remained rather constant in size throughout the transmitter life of each fox, with 95% confidence limits 0.4–3.7% of their means, but they also showed little variation between foxes, with a mean of means = 38.8 ± 4.4 ha. No difference was apparent between dog-foxes and vixens (permutation test on means, \( P = 0.78 \)). Mean prevailing ranges were 0.37 ± 0.04 times the size of their corresponding total ranges. Conversely, not all the prevailing range was used on each night. Nightly ranges were calculated for fifty-three fox-nights in which individuals had been followed closely from first to last activity (mean interval between ‘active’ fixes = 6 min); the areas covered on these nights, summed from the numbers of grid-cells crossed by lines joining consecutive fixes (Doncaster 1985), were 0.42 ± 0.02 times the size of their corresponding prevailing ranges.

Average range drift in the city calculated from the mean drift for each fox was 3.36 ± 0.67 ha month\(^{-1}\), considerably more than the average drift of 0.31 ± 0.11 ha month\(^{-1}\) for the eight most intensively tracked suburban foxes (approximate \( t_{9,7} = 4.5, P < 0.002 \)). Mean rates of drift for each fox were not dependent on prevailing range size (\( r = 0.21, P = 0.55 \)). They were independent also of the number of radio-fixes (\( r = 0.02, P = 0.96 \)); a weak negative correlation was obtained, however, with transmitter life (\( r = -0.36, P = 0.30 \)) indicating a small effect on drift estimates due to the foxes that were tracked for only a portion of the year, which might be expected over a longer period to revisit some of the areas identified as having been abandoned definitively.

The overall mean range drift for the ten city foxes in Table 2 was 3.01 ± 0.43 ha month\(^{-1}\) over 67 fox-months (141 ± 12 m month\(^{-1}\), square-root transformation), equivalent to the complete displacement of an average prevailing range every 13 months. Rates of range drift in the city did not differ significantly between dog-foxes and vixens (respectively 2.53 ± 0.59 ha month\(^{-1}\), \( n = 34 \) and 3.50 ± 0.61 ha month\(^{-1}\), \( n = 33, t_{65} = 1.14, P = 0.26 \)). Drifting ranges were occupied by both young and old individuals. The estimates of drift were obtained for the ten city foxes at ages of 7–29 months, with above-average range drift being recorded during 58% of months in which they were still yearlings (\( n = 12 \)) and during 33% of months in which they were ≥1 year old (\( n = 55 \), Fisher’s exact test, \( P = 0.11 \)).

The prevailing ranges of the ten city foxes in Table 2 differed little in size from month to month, with a standard error of 1.09 around the overall mean of 38.8 ha (\( F_{11,55} = 0.25, P = 0.99 \)). Rates of range drift, however, differed significantly between months (square-root transformation, \( F_{11,55} = 2.76, P = 0.006 \)). Duncan’s multiple range test and a non-parametric test (Table 3 and Appendix 1) indicated
Table 2. Home range characteristics of the ten most intensively tracked city foxes (average per fox of 1523 fixes over 305 days). Total range was summed from the total of all $50 \times 50$ m cells known to have been visited (except on excursions); mean prevailing range was calculated from the estimated prevailing range on each night following the first true estimate; range drift was estimated from the reduction in size of the first true estimate of prevailing range for each month in which the fox was subsequently tracked.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Fox Number</th>
<th>Number of fixes</th>
<th>Transmitter life (days)</th>
<th>Total range (ha)</th>
<th>Prevailing range (ha)</th>
<th>Range drift (ha month$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>S.E.</td>
</tr>
<tr>
<td>m</td>
<td>1</td>
<td>3427</td>
<td>562</td>
<td>112·5</td>
<td>44·9</td>
<td>0·52</td>
</tr>
<tr>
<td>m</td>
<td>2</td>
<td>1767</td>
<td>747</td>
<td>163·8</td>
<td>55·0</td>
<td>0·26</td>
</tr>
<tr>
<td>m</td>
<td>3</td>
<td>1187</td>
<td>153</td>
<td>54·3</td>
<td>32·8</td>
<td>0·30</td>
</tr>
<tr>
<td>m</td>
<td>4</td>
<td>750</td>
<td>207</td>
<td>122·3</td>
<td>28·5</td>
<td>0·37</td>
</tr>
<tr>
<td>f</td>
<td>1</td>
<td>2151</td>
<td>100</td>
<td>93·3</td>
<td>38·9</td>
<td>0·59</td>
</tr>
<tr>
<td>f</td>
<td>2</td>
<td>1912</td>
<td>294</td>
<td>105·3</td>
<td>49·8</td>
<td>0·55</td>
</tr>
<tr>
<td>f</td>
<td>3</td>
<td>1466</td>
<td>297</td>
<td>73·8</td>
<td>21·6</td>
<td>0·05</td>
</tr>
<tr>
<td>f</td>
<td>4</td>
<td>1205</td>
<td>269</td>
<td>139·5</td>
<td>62·8</td>
<td>1·15</td>
</tr>
<tr>
<td>f</td>
<td>5</td>
<td>742</td>
<td>203</td>
<td>197·8</td>
<td>26·1</td>
<td>0·46</td>
</tr>
<tr>
<td>f</td>
<td>6</td>
<td>620</td>
<td>211</td>
<td>91·8</td>
<td>27·3</td>
<td>0·51</td>
</tr>
</tbody>
</table>
higher rates of drift in winter months (November–April) than summer months. Although fewer foxes had been tracked in the summer, the ranges of two dog-foxes and two vixens that were tracked in both periods drifted faster during the winter than during the summer (paired-sample permutation test on period means, $P = 0.06$). No systematic differences were detected between the sexes in monthly range drift (paired-sample permutation test on mean drift by sex each month except May when only males were tracked, $P = 0.37$). The months in which male ranges drifted faster on average than female ranges were, however, grouped from August to December plus February, female ranges drifting faster in other months.

**Are city foxes territorial?**

Figure 4 compares the index of concordance between pairs of total and prevailing ranges of city foxes, and pairs of total ranges of suburban foxes. Prevailing city and total suburban ranges clearly have a bimodal distribution of concordance scores. From pairs of total to pairs of prevailing city ranges (Fig. 4a and b) all index values
increase in magnitude except one (arrowed), in which a vixen (f4) and her 6-month-old son (m6) partitioned their range. Some pairs of foxes show high concordance in the area occupied and its utilization (these are members of the same group), while other pairs have little concordance in either the area occupied or its utilization, or both (members of neighbouring groups).

Although city foxes occupied continuously shifting ground, the non-random spacing of their prevailing ranges suggests that territorial borders could be identified in terms of the relative juxtapositions maintained by different groups during the study. As a first step towards reconstructing the dispersion of prevailing ranges, the space that individuals maintained between each other was estimated from instantaneous separations between all concurrently tracked pairs. A total of 4180 separations obtained in 30-min time-blocks was used to calculate mean separations between sixteen foxes in twenty paired comparisons. These relative distances were then mapped over the geographical locations of the foxes' total ranges (illustrated in Fig. 2a). Finally, the index of concordance differentiated neighbours (values $<-0.4$, Fig. 4) from group members ($>+0.2$), resulting in the topological arrangement shown in Fig. 5 of territorial borders encompassing twelve prevailing ranges of average size.

Prevailing ranges at the centre of the study were surrounded by five or six neighbours each, giving a honeycomb arrangement of groups (Fig. 5). At least one range was occupied simultaneously by two breeding vixens and a dog-fox. That this arrangement was being actively sustained was also indicated by numerous observations of radio-tracked resident foxes in agonistic encounters with other foxes (Hough 1980; Newdick 1983; Doncaster 1985). With each group maintaining its borders to neighbouring groups, the whole pattern shown in Fig. 5 shifted during the study.
FIG. 5. The dispersion of prevailing ranges in the city study area. Adult dog-foxes (m) and breeding vixens (f) are marked by filled circles. The lines joining concurrently tracked foxes are proportional in length to the mean instantaneous separations between them. Bars outlining group ranges indicate the magnitude of Spearman’s coefficient for the static interaction between neighbouring foxes (II $< -0.4$; III $< -0.6$; III $< -0.8$). The coefficient for static interaction within groups was $> +0.4$ for five of six comparisons. Twelve group ranges are identified for a sample of eighteen radio-tagged foxes; with an average prevailing range area of 38.8 ha, these cover 426.5 ha, or 47% of the total area of 916.9 ha (surrounding box) known to have been used by them during the 3-year study.

An example is given in Fig. 6 of two abutting group ranges that shifted in synchrony over an 18-month period. They thereby maintained the social juxtaposition of their occupants, despite changes in the identity of group members. The yearling m6 was killed by a car in November 1981; ml was likewise killed in June 1982, after which the range of his mate f2 expanded in size until her death in June 1983. M5 was tagged as a cub in 1979, 3.5 km from the adult range where he was tracked from April to August 1981, and was last seen in October 1983. Vixen f4, of which m6 was an offspring, occupied the same group as m5 at least to November 1982.
Factors contributing to range drift

Drifting ranges fall outside the concept of territories as defended areas because the occupied ground is continually changing. Rather, a drifting territory may be defined by the distance its members maintain from neighbouring groups. This difference is one of degree, as even stable ranges might drift between years. What then encourages more rapid drift in the city?

An analysis of the frequency of occurrence of undigested prey remains in 1939 city and 2799 suburban faeces collected throughout the year showed that their diets were largely comparable (see Doncaster, Dickman & Macdonald 1990, for analytic methods). City foxes took scavenged items more frequently than suburban foxes (50% versus 38%, paired-sample permutation test on monthly differences, \( P < 0.001 \)), and earthworms less frequently (37% versus 49%, \( P = 0.003 \)); while no significant differences (\( P > 0.05 \)) were apparent in the monthly frequencies of occurrence of small mammals (23% versus 17%), rabbits (9% versus 9%), birds (19% versus 14%), fruit (17% versus 20%) and invertebrates (22% versus 20%), other foods occurring at <3% frequency. These diets were more similar to each other than either was to most other published studies (Macdonald 1981; Doncaster, Dickman & Macdonald 1990).

Both populations, moreover, foraged within prevailing ranges with sizes of the same order of magnitude, in comparison to the spectrum of 20 to >1000 ha for fox ranges throughout the U.K. (Macdonald 1981). Prevailing ranges in the city, however,
were significantly smaller than the stable suburban ranges (approximate \( t_{9,28} = 2.24, P < 0.05 \)), indicating a higher population density in the city than in the suburbs assuming equivalent sized groups. The stability of fox populations in the suburbs facilitated estimation of adult group size at an average of 4.4 (Macdonald 1981). In contrast, although we had evidence that urban groups generally had at least three members (Newdick 1983; Doncaster 1985), their instability prevented us obtaining comparable estimates of group size.

The average lifespan of forty-one foxes recovered dead in the city was 12 months (calculated from dental cementum annuli, Jensen & Nielson 1968) and for 62% of these, death was attributable to road traffic. Only one fox had reached its fifth year, while 63% were yearlings. Despite comparable effort, corpses were retrieved from the suburbs much less frequently, but eleven postmortems gave an average age of 5 years, with seven (60%) aged 5 years or older (a significant difference between the populations, \( t_{50} = 3.99, P < 0.001 \)). We cannot know how closely these samples of foxes dying reflect the age structure of the survivors in the two areas, but the prevalence of old foxes in the suburban sample is so marked that it could not readily be explained as a sample bias. Furthermore, two of seventeen resident vixens in the city and twelve of twenty-four in the suburbs were barren, showing no evidence of pregnancy or of bearing cubs (\( \chi^2_1 = 6.47, P = 0.011 \)).

**DISCUSSION**

Rates of range drift, as opposed to dispersal or excursions into another range, were in the order of 30–40 ha year\(^{-1} \) in the city, equivalent to the size of an average prevailing range, and ten times the rate of drift in the suburbs. City ranges moved in synchrony so that, over the 3 years of the study, the illusion of randomly overlapping total ranges (Fig. 2a) was replaced by the clearly territorial system (*sensu* Davies 1978) of a honeycomb pattern of congruent ranges (Fig. 5). Areas that were abandoned from one group range subsequently became part of a neighbour’s range (Fig. 6), hence the varied degrees to which total home ranges overlapped one another (Table 1). The high rates of drift from November to April (Table 3) are likely to reflect (i) a reshuffling of the social hierarchy as yearling foxes (particularly males) disperse in autumn and early winter, followed by (ii) intense activity during mating in January and February (the relatively low rate of drift in January perhaps reflecting a staking out of territories, particularly by males, preparatory to mating), and (iii) subsequent changes to the range structure of cubbing vixens.

Both urban and suburban populations had comparable diets and ranges of the same order of magnitude. Although our mortality samples are small, they indicate a possible key difference between the two populations given by an absence of long-established residents in the city. The city environment is inherently disturbed by busy road traffic, but also by pedestrians, habitat management, construction and demolition, etc. These factors may act in combination, reducing the average lifespan so that vixens have barely sufficient time to produce a first litter, but also causing rapid and unpredictable perturbations in the pattern of food availability (Dickman & Doncaster 1987, 1989; Doncaster, Dickman & Macdonald 1990). Although Oxford’s city foxes have shorter life spans than their suburban counterparts, published figures indicate that some rural fox populations are subject to higher mortality than are city foxes (e.g. Harris 1977). However, data are unavailable to
separate conclusively the influences of patterns of mortality and food availability on the spatial organization of different populations.

We suggest that drifting territoriality in Oxford city is largely a consequence of the social instability entailed by such abrupt changes to population structure and food availability. In both city and suburban populations, territories were shared by a social group of vixens (Fig. 5; Macdonald 1981; Doncaster 1985). However, the high population turnover in the city may have de-stabilized the matrilineal dominance hierarchy and reduced the age difference amongst survivors. A likely outcome would be disruption of social mechanisms which in the suburban population prevent subordinate vixens from breeding (Macdonald 1979), hence the small proportion of city vixens found to be barren. As the identity of group members was frequently changing, so were their status and individual relationships, and their individual contributions to the group’s territory. City ranges would then drift as resident foxes compete with their neighbours and the continual flux of itinerants from surrounding ranges, for access to currently available mates and food resources that often remain viable only for a short period. Increased birth rates may have been sufficient to counterbalance the high mortality, as we have no evidence of itinerant foxes moving into the city from outside, but four examples of emigration from the city to the suburbs (Hough 1980; Newdick 1983; Doncaster 1985). Many post mortem studies have shown variation in the incidence of barren females between populations (e.g. Englund 1970), and our observations, like those for other cities (Harris 1979), fall within the recorded variation.

Whether the synchronous drifting of city ranges is an adaptation to, or a consequence of, the urban environment, it represents a significant modification of behaviour which is comparable to the adaptations of many bird species to city habitats (Diamond 1986). The persistance of a territorial organization despite the high mobility of ranges is the more remarkable for the rapidity with which foxes have occupied the urban niche since the 1930s (Teagle 1967; Macdonald & Newdick 1982) and the high densities of resident foxes that are supported there (1.4 times the suburban density on the basis of home range size, this study).

We know of no other record of drifting ranges in the literature on foxes, although Sargeant (1972) described a rural fox pair expanding their range on the death of a neighbouring male. His observation did not continue long enough to see a definitive change in the location of the range, but it suggests that the accumulation of many such (frequent) events may result in continual drifting. Mobility on the scale demonstrated for city foxes could be an aspect of the territorial behaviour of more species than is currently recognized, because few studies of home ranges have been sufficiently detailed to reveal small but frequent range shifts over time. A likely consequence of ignoring these movements would be to underestimate the actual extent of territorial behaviour, as in our analysis of total ranges which failed entirely to identify a territorial organization. Computer programs for quantifying range drift from radio-tracking data are available from the authors on request. The conceptual similarity between population survival as measured in capture-mark-recapture studies, and the ‘survival’ of grid-cells making up a home range, suggests that existing survival estimators (such as Surge, see Clobert, Lebreton & Allainé 1987) could also be exploited to standardize measures of range drift.
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REFERENCES


Drifting territoriality


(Revision received 6 August 1990)
APPENDIX 1

Against a null hypothesis that mean values of home-range drift in each month are independent, we wish to test for relatedness in mean drifts of successive months. By assigning a binary flag to each month, either high (to the highest 6 months) or low (to the lowest 6 months), we can record the number of times the flag changes sign in going through a complete 12-month cycle. This will be an even number, between two (if all high months are grouped together, followed by all low months) and twelve (if successive months alternate).

The number of ways of arranging six ‘high’ and six ‘low’ labels over the 12 months is \( \binom{12}{6} = \frac{12!}{(6!)^2} = 924 \). If the distribution of ‘high’ and ‘low’ months is random, the number of flag changes during a 12-month cycle will be given by the random variable \( X \) with the following distribution:

\[
\begin{align*}
P(X = 2) &= \frac{12}{924} = 0.013 \\
P(X = 4) &= \frac{150}{924} = 0.162 \\
P(X = 6) &= \frac{400}{924} = 0.433 \\
P(X = 8) &= \frac{252}{924} = 0.273 \\
P(X = 10) &= \frac{108}{924} = 0.117 \\
P(X = 12) &= \frac{2}{924} = 0.002
\end{align*}
\]

On a one-tailed test, the two flag changes observed (Table 3) are significantly fewer than expected from a random distribution, at \( P = 0.013 \).