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ECOLOGY AND RANGING BEHAVIOUR OF RED FOXES IN THE CITY OF OXFORD

ECOLOGIA E COMPORTAMENTO DELLA VOLPE (*VULPES VULPES*) NELLA CITTÀ DI OXFORD

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ABSTRACT

Red foxes (*Vulpes vulpes*) living in the city of Oxford, like those in its neighbouring suburbs, are organized into social groups which each defend a territory. While territories in the suburbs are spatially stable, those in the city continually drift in location. They move in synchrony with their neighbours and the prevailing pattern is a honeycomb of group ranges of relatively small but constant size. The city environment is characterized by a high level of disturbance, which may favour range mobility, and by a patchy and highly divided mosaic of habitats. A quantification of patch density leads us to propose an explanation for the small size of territories and the existence of more adults than a single pair, in terms of the dispersion of habitat patches and competition for food resources contained therein.

Key words: Urban environment, Ecology, Territorial behaviour, Vulpes *vulpes*, England.

RIASSUNTO

Le popolazioni di Volpe (*Vulpes vulpes*) insediate nella città di Oxford e nelle aree suburbane limitrofe sono organizzate in gruppi sociali che difendono un proprio territorio. Mentre i territori nelle aree suburbane sono spazialmente stabili, quelli presenti in città cambiano continuamente posizione. Questi ultimi si muovono sincronicamente con quelli limitrofi e la disposizione prevalente è simile al favo delle api con territori relativamente piccoli, ma di dimensioni costanti. L' ambiente cittadino è caratterizzato da elevato disturbo, che pub favorire la mobilità dei territori, e da un mosaico molto vario di ambienti. La presenza di territori di ridotte dimensioni occupati da più adulti e non da una singola coppia di volpi sembra dipendere dall'alternanza e variabilità degli ambienti e dalla competizione per le risorse alimentari.

Parole chiave: Ambiente urbano, Ecologia, Comportamento territoriale, *Vulpes vulpes*, Inghilterra.

INTRODUCTION

The observations by Macdonald (1977, 1981) that red foxes in the suburbs of Oxford live in territorial groups of more adults than a monogamous pair, and Harris' (1981) record of very small and apparently non-exclusive home ranges in the city of Bristol (**3.6** pairs/km^2 in home ranges of 27 ha), prompt questions about the nature of the urban environment which gives rise to these living conditions. The home ranges of red foxes in rural areas tend to be considerably larger than those in towns, averaging 960 ha in Minnesota (Storm et al., 1976) and over 2000 ha in Ontario (Voigt and Macdonald, 1985). Moreover, these rural foxes are thought more commonly to live in pairs than in social groups (Macdonald, 1981).

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An intensive programme of radio-tracking red foxes in the city of Oxford, U.K. (Doncaster, 1985) has revealed an organization of social groups defending territories, which is similar to that of **foxes** in **a** suburban study area *6* km from the city centre (Macdonald, 1981). The territories of city foxes, however, shifted in location continually while those outside the city remained stable (Doncaster and Macdonald, in press). In this paper we summarize the characteristics of the spatial organization of these city foxes, as revealed by radio-tracking, and show how they can be influenced by the dispersion of habitat patches in the city.

DEFINITIONS

1. STATIC INTERACTION

The spatial overlap of two home ranges and the congruence of at least part of their utilization distributions (UDs) is termed "static interaction" (c.f. dynamic interaction as defined by Macdonald et al., 1980). It was estimated from radio-tracking data by correlating the two UDs, which were obtained from the grid-cell method of range analysis (Siniff and Tester, 1965) by scoring each independent radio-fix into cells of 50 x 50 m and counting the eight influence cells surrounding each non-peripheral cell in which an active **fix** was located (Voigt and Tinline, 1980). The index of static interaction was given by a Spearman's rank correlation of the numbers of fixes and influences (given **one** eighth the value of true fixes) in each grid-cell that was frequented by one or both animals. This gave a value approaching + 1.0 for complete range overlap and perfect concordance of the two UDs, or -1.0 for little range overlap and/or discordance in the UDs. The method is robust to varying degrees of range overlap, ranges of unequal size, and different sampling intensities (Doncaster, **1990).**

2. PREVAILING RANGE

Territories are generally described in terms of a fixed and exclusive area defended against rivals (Brown and Orians. 1970, Wilson, 1975, but cf. Davies and Green, 1976). Numerous observations in Oxford city of resident foxes attacking intruders led us to conclude that their home ranges were defended against neighbours and itinerant foxes (Doncaster, 1985; Newdick, 1983). However, the notion of a fixed area was inappropriate for city home ranges because their geographical locations changed from month to month. For ten city foxes intensively tracked over 2-25 months (620-3427 radio-fixes), home-range ***sizes*** remained dependent on the cumulative fix scores throughout their tracking histories. It was clear that the home range being used at any given time did not correspond with the total range observed over the whole period. We therefore developed the concept of a prevailing range (Doncaster, 1990). For each night on which tracking data were collected, the prevailing range of a fox was defined retrospectively to cover only those parts of its total home range visited on that night, plus areas previously visited that would be returned to on any future night on which the fox was followed. The number of 50 x 50 m grid-cells (and adjoining influence cells: Voigt and Tinline, 1980) constituting a prevailing range is conceptually equivalent to Minimum Numbers Alive in capture-mark-recapture studies, equating grid-cells with numbers of individuals. The group of grid-cells (or cohort) that had copstituted the first estimate of a fods prevailing range size (the first night for which size was no longer dependent on cumulative fix total) could thus be monitored throughout the animal's subsequent tracking history. The rate at which it diminished in size **as** the animal's focus of activity gradually drifted to new districts provided an estimate of the rate of range drift. Under this definition of prevailing range, these changes in position were definitive for the **known** history of the fox.

SPATIAL ORGANIZATION

The average prevailing range size of four dog-foxes and *six* vixens (average of 1523 fixes over 304 **days** per animal) was 38.8 ha, or close to one-third the mean total range area of 93.4 ha, with little variation between foxes (SE = 4.4 ha, range = **21.6-62.8).**

Prevailing ranges drifted in the order of 30-40 ha a year, with an average rate of 3.4 hdmonth (SD = 2.12), significantly faster than the rate of 0.3 ha/month for suburban foxes (Doncaster and Macdonald, in press).

SOCIAL ORGANIZATION

Because city home ranges were continually drifting across the town, a simple plot of their configurations gave a blurred picture of the static interaction between them, and it was not possible by this method to distinguish members of the same group from members of neighbouring groups. However, analysis of static interaction between pairs of foxes that were tracked at similar times, together with the instantaneous separations between foxes tracked on the same nights, revealed a hexagonal packing of group ranges in the **city, as** shown in **Fig. 1.** At least one group contained simultaneously an adult dog-fox and *two* breeding vixens.

Ranges drifted in synchrony so that the juxtaposition of neighbouring groups remained essentially unaltered across generations of occupants (Doncaster and Macdonald, in press). The ranges occupied by foxes at any one time were thus clearly organized in a territorial system, in the sense that territorial animals should be spaced further apart than would be expected from a random occupation of suitable habitats in the study area (Davies, 1978). However, this fixed grid of territory boundaries moved at a rate equivalent to covering the width of an average prevailing range in one year.

We believe that the ultimate explanation for drifting is that the city environment is inherently disturbed, by pedestrian and road traffic, habitat management, and construction and demolition work. Such interference causes rapid and unpredictable perturbations in the pattern of food availability within the mosaic of urban habitats (Dickman and Doncaster, 1987, 1989). It also reduces the average life-span of city foxes to 12 months, giving vixens barely sufficient opportunity to produce a first litter (Doncaster and Macdonald, in press). The poor life expectancy of city vixens may destabilize the matrilineal dominance hierarchy of social groups, thereby disrupting the mechanisms of social suppression of reproduction (Macdonald, 1979). ***As*** the identity of neighbouring foxes is often changing, so is the status of each and the relationships between individuals, and their individual contributions to the group’s territory. City ranges then drift as resident foxes compete with their neighbours, and with the continual influx of itinerants, in a labile social structure for access to food in patches that may remain viable for only a short period. The prevailing dispersion of these resources in space will in turn influence the juxtaposition of territories as they drift in synchrony.

INFLUENCE OF RESOURCE DISPERSION ON RANGE **PACKING**

The honeycomb pattern of similar-sized territories that has been observed conforms with a model of competitive segregation in two key respects: it

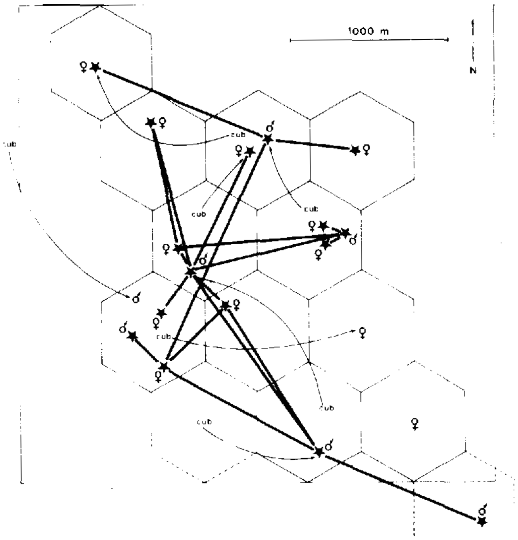

Fig. 1 – The dispersion of prevailing ranges (hexagons) in the city study area. Adult dog-foxes (m) and breeding vixens (f) are marked by stars, and the lines joining concurrently tracked foxes are proportional in length to the mean instantaneous separations between them (obtained from 4180 pairs of locations taken in 30-min. time-blocks). Spearman's coefficients for between-group estimates of static interaction were < -0.6 for 11 congruent boundaries, < -0.4 for seven, and unknown for one; within group estimates were all $> +0.2$. The total area covered by these prevailing ranges is 47% of the 917 ha (surrounding box) known to have been used by the 18 foxes during the three year period of study. Dispersals are marked by curved arrows.

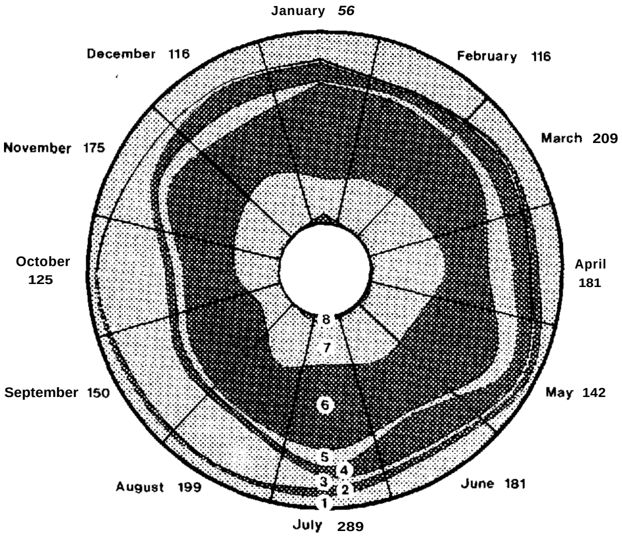

Fig. 2 – The proportions by dry weight of major categories of food in faeces collected in each month of the year (with sample sizes). 1: small mammals, 2 insects, 3: fruit, 4: birds, 5: lagomorphs, 6: scavenge, 7: soil, 8: domestic food. (Adapted from Doncaster et al., 1990).

constitutes the highest density at which exclusive areas can be packed together, and it has a high ratio of territory area to length of defended perimeter. What are the factors that favour a size in the order of 40 ha for most territories? In particular, why are they so small compared to other estimates in the literature; or conversely, why are they not even smaller when at 40 ha they support more adults than a single breeding pair? The dispersion of food resources seems likely to be implicated in any explanation, in so far as territories may exist as a consequence of competition for exclusive access to these resources (Macdonald, **1983; Carr** and Macdonald, **1986).**

Figure 2 shows that city foxes had a broad diet throughout the year, of which the major components were scavenge **(37%** overall), earthworms **(27%)** and wild vertebrates (25%), with proportions similar to those in the diet of suburban foxes (Doncaster and Macdonald, in press). Food is generally abundant in Oxford city (Doncaster et al., 1990) but, for the category of small mammals at least, availability varies in relation to habitat type and management (Dickman & Doncaster, 1987, 1989). In so far as each of the habitats encountered in the town (gardens, woodland copses, orchards, playing fields, roads etc.) contains a characteristic combination of food resources, their dispersion may be a factor in some way determining the honeycomb pattern of group territories.

How are habitat patches distributed through the town? In a preliminary analysis, the dispersion of discrete patches of all habitat types was estimated in a sample plot covering 400 ha of the study area (see Dickman and Doncaster, 1987 for a validation of the method of classifying patches). This plot was divided into 4 ha quadrats and the number of patches (as defined by dividing walls, hedgerows, roads etc.) was counted in each quadrat. The frequency distribution of patch density in all 100 quadrats (Fig. **3)** did not differ significantly from random. The distribution of patches can equally be described by an index of dispersion (modified from David and Moore, **1954):**

$$I_d = 1 - (\text{variance}/\text{mean})$$

which gives a negative value for a clumped dispersion of patches, zero for a random dispersion and a value approaching $+1$ for a regular (even) dispersion in the number of patches per quadrat. For this sample, I_d was close to zero at $+0.172$.

This result may not be surprising considering that the initial, arbitrary, choice of **4** ha quadrats provides a rather fine scale of resolution for the dispersion of habitat patches in the town. Moreover, there is no a priori reason for supposing that it corresponds with the scale at which foxes perceive their environment. In this respect we know at least that foxes occupy territories of roughly equal size, in the region of 40 ha, or ten times larger than the 4 ha quadrats. The number of habitat patches in 40 ha quadrats should therefore be a closer approximation to the scale at which foxes resolve the city environment, in terms of the resources available to them within the territory. If 40 ha is an optimum size for territories in Oxford city, we should look at how the distribution of habitat patches will change when sampled from quadrats up to and beyond this size.

A computer model was developed to analyse the nature of the relationship between patch dispersion and quadrat size. The frequency distribution in Fig. **3**

was assumed to be representative of the whole town and was duplicated 100 times across a simulated area of 40,000 ha (varying at random the location of patch clumps in each 400 ha plot). One hundred sets of 8 ha quadrats were then sampled from within this area and the dispersion index (I_d) was calculated as above. The procedure was repeated for quadrats of increasing size, up to 400 ha where all 100 quadrats necessarily contained the same number of patches and therefore $I_d = 1$. The results are graphed in Fig. 4, after performing 100 replicates to account for the random location of patch clumps within the 400 ha units. A statistically significant increase in the dispersion index towards regularity occurs in direct relation to quadrat size only for quadrats ≥20 ha.

If the quadrats are thought of as fox territories, the relationship in Fig. 4 demonstrates that symmetry in the numbers of patches per territory is directly related to territory size for territories of 20 ha and more, becoming increasingly balanced between larger territories. Although the perfectly regular distribution of patches between 400 ha territories was pre-determined by assuming that all the contagion in the environment was contained within the original 400 ha plot, the general nature of the relationship is valid: around the observed size of territories in Oxford (40 ha), patches are more regularly distributed between territories as average territory size increases. This result has interesting biological implications if patch dispersion in some measure reflects resource availability. If this assumption is justified (see below), we can go on to predict that competitive segregation of available food resources between residents should manifest itself in an approximately even distribution of patches between the territories. Figure 4 then shows that the larger the size of an average territory, between 20 and 40 ha and upwards, the closer it approaches a condition of competitive equilibrium given by a regular distribution. By inference, therefore, an increase in competitive pressure for access to resources by residents in territories ≥20 ha should favour larger average territories, and this continues to be the case even beyond the minimum size necessary to support a monogamous pair. Social groups of foxes thus may persist in the city simply because the competitive segregation of patchily distributed resources tends to favour larger territories for all resident individuals, and without any functional advantage necessary to the presence of extra adults in these large territories (see Carr and Macdonald, 1986 and Macdonald and Carr, 1989 for a theoretical approach to the same problem).

In the absence of a measurable correlate of resource availability, the number of patches per territory represents a simplified but plausible index for the city environment. For example, a critical minimum of patches may be required per territory in order to ensure a sufficient variety of habitat types to buffer the frequent perturbations in food availability as patches cycle irregularly between depletion and enrichment. However, certain patches are preferentially utilized by foxes, particularly those containing woodland (for lying up by day) and large gardens (for foraging by night). The analysis is currently being extended to account for each habitat separately. First results indicate that some habitats have an increasingly even dispersion only when sampled from quadrats above 40 ha, while others (the hypothesis would suggest that these are subject to the most intense

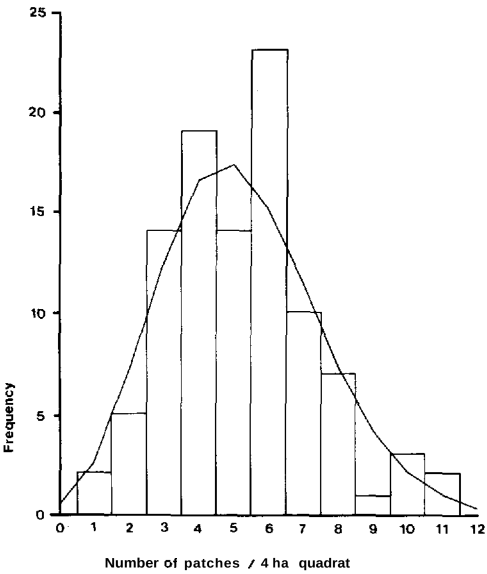

Fig. 3 — The frequency distribution of discrete habitat patches in 100 lots of **4** ha quadrats within a 400 ha plot in the city study area (mean = 5.250, variance = 4.348). The distribution does **not** differ significantly **from** the Poisson (also shown) with a G-test ($G_8 = 9.92$, P = 0.27).

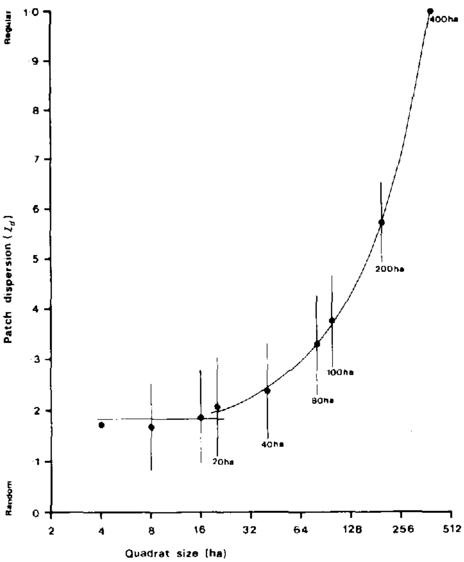

Fig. 4 — The relationship between the dispersion of patches (given by: I_d = 1 - variance/mean) and the **size** of quadrat **from** which the dispersion **is** sampled, **for** the **frequency** distribution of habitat patches shown in Fig. **3** (means +/- 1SD for 100 replicates). I_d does not **change** significantly **for** quadrats **up** to 16 ha (**$F_{2,297} = 1.94$**, P = 0.15). For quadrats ≥20 ha, the regression equation is: $I_d = 0.161 + 0.00209 \times$ SIZE, **with** a coefficient of correlation: r **= 0.953.**

competition) have an increasingly even dispersion between quadrats of 20 to 40 ha in size (Doncaster, in prep.),

The conclusion drawn from Fig. 4, that the number of foxes supported in a territory is related to patch distribution, is based on the observation that all territories have approximately the same size (SE of 4.4 ha around a mean size of 38.8 ha). That territories should be of similar size can also be predicted in terms of defence costs. Although the irregular dispersion of patches does not preclude the existence of territories containing only the minimum resources for a monogamous pair, in a patchy world such areas would have complicated boundary configurations and concomitantly high defence costs. Some such territories would inevitably extend over large areas of low resource density while others would cover clumps of many resources in a small area. The net result of border disputes between foxes in small and large territories might well be that larger ones are poached from all sides by neighbouring foxes living in smaller and more easily defended territories, until the areas defended and the resources they contain are approximately equal between groups.

A simplified case of the city environment is shown in Fig. 5, with three hypothetical patterns of resource dispersion (for a general account, see Pielou, 1977). The sample areas illustrated are scaled to cover 300 ha and they each contain 100 arbitrary resource units (RU) of equal richness. The sample area in Fig. 5a shows a regular distribution of RU. It is divided into 11.1 fox territories so that each covers 27 ha, which is similar to the size of home-ranges for monogamous pairs in the city of Bristol (Harris, 1981). As each territory then contains 9 RU (100/11.1) it can be assumed for the purposes of the model that a breeding fox requires access to 4.5 RU; these territories thus support sufficient RU for the minimum group size of one breeding pair. In the environment with a somewhat more clumped dispersion of resources given in Fig. 5b, competitive segregation results in an equal division of RU only between territories of larger size, specifically 39 ha for this degree of resource clumping. They then surround 13 RU each (100 x 39 ha/300 ha), sufficient for one breeding pair with 4 RU left over, which might support a non-breeding helper (Macdonald, 1983)[1]. This mirrors the situation observed in Oxford city; if each RU has a short life-span then territories would drift to accommodate the moving pattern. The resources in Fig. 5c have a still more heterogeneous dispersion and they are equally divided between territories of 63 ha, each containing 21 RU (100 x 63 ha/300 ha) or sufficient for one pair and three helpers. Social pressures might not permit such large groupings, in which case the territories break down into smaller units of varying size (averaging 27 ha) and containing one pair each. This irregular pattern of smaller units is unstable, however, in so far as territories with more widely dispersed resources have longer boundaries and therefore require a greater defence effort than those that surround clumps of many resources.

In conclusion, our observation of a honeycomb pattern of similar-sized territories in Oxford (40 ha), suggests that the available resources in the city are

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[1] Carr and Macdonald (1986) make the point that secondary (possibly non-reproductive) occupants of a territory may require, or at least tolerate, lower food security than that required by the primary occupants.

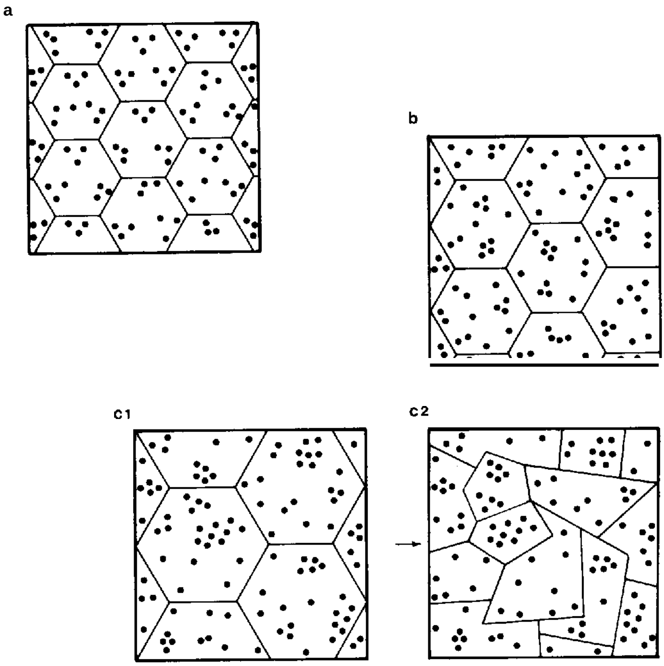

Fig. 5 – Three hypothetical dispersion patterns for 100 resource units (RU: filled circles) within an area of 300 ha, and the sizes of hexagonal territories when resources are evenly distributed between them. From (a) to (c) the resources have an increasingly heterogeneous dispersion, and they are evenly distributed between territories of 27, 39 and 63 ha respectively. Territories in environment (c1) contain more than twice the number of RU than in environment (a), and they may break down into smaller units of irregular size, as shown in (c2).

competitively segregated into defended territories. We have shown how the perceived distribution of habitat patches in Oxford city is dependent on the sampling scale, becoming increasingly regular when sampled from quadrats of 20 ha and larger. By analogy, the distribution of habitat patches (and the resources they contain) between territories also will be more regular for larger territories. As an approximately regular distribution of resources between territories is an expected outcome of competitive equilibrium, the average range size should be larger in the presence of competition between neighbouring residents for access to resources than in the absence of competition. Competitive pressure may favour larger territories even than are required by a monogamous pair, with the result that social groups are supported in each territory without there necessarily being a functional advantage to the presence of extra adults. This is presumably the case in Oxford city, where 40 ha territories can be occupied by at least three breeding adults.

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