Effects of temporary captivity on ranging behaviour in urban red foxes (Vulpes vulpes)

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Abstract

Temporary removal of wild animals from a resident territory has the potential to markedly impact subsequent ranging behaviour, and may negatively affect post-release welfare and survival. Admission of sick or injured wildlife into temporary captivity (termed ‘rehabilitation’) is a common practice in the UK. However, post-release monitoring of rehabilitated animals is unusual or restricted to recording survival rates over limited time periods. As part of a wider study of urban fox behaviour, we employed an experimental approach to compare the ranging behaviour of seven rehabilitated and 13 wild-caught ‘control’ urban red foxes using GPS tracking. Foxes were tracked over a two-year period for an average of 48 nights, and seasonal and sex-related effects were controlled for via inclusion in statistical models. Three of the five movement parameters we investigated were irregular for the rehabilitated animals, relative to controls. These were: reduced likelihood of
establishing a stable home range (42.9/57.1% of rehabilitated foxes versus 84.6% of controls); larger home ranges (Kruskal Wallis test, $\chi^2 = 7.517$, df = 1, $p < 0.01$); and further distance travelled from release point, as measured by overlap between initial and final home ranges (Linear regression, $F_{1, 12} = 4.755$, df = 1, $P < 0.05$). Females moved greater distances than males overall, and foxes from both groups travelled further in spring, and delayed home range establishment in summer. However, these results were skewed by the movements of two apparently cooperatively breeding wild-caught vixens. Our data provide evidence of territorial displacement of rehabilitated foxes on release. We discuss the welfare implications of this finding.

Key words: red fox, ranging behaviour, captivity, rehabilitation, home range, ex situ
1. Introduction

Urban-dwelling simultaneously provides benefits and poses risks for wild mammals (Baker and Harris, 2007) particularly carnivores (Bateman and Fleming, 2012). The red fox (Vulpes vulpes) is widespread in UK conurbations (Scott et al., 2014), which in general are resource-rich, with low rates of anthropogenic persecution (Baker and Harris, 2007). However, high rates of injury from road traffic (Baker et al., 2007) and other form of misadventure, combined with enzootic disease (e.g. Soulsbury et al., 2007) and the visibility of foxes to the public, result in relatively high rates of admission of foxes to wildlife rehabilitation centres.

1.1 Wildlife rehabilitation

Wildlife rehabilitation is defined by the International Wildlife Rehabilitation Council (IWRC), as the ‘treatment and temporary care of injured, diseased, and displaced indigenous animals, and the subsequent release of healthy animals to appropriate habitats in the wild’ (Miller, 2012). Rehabilitation is common practice in the UK – an estimated 71,000 wild animals are annually admitted to rehabilitation centres, of which an estimated 28,000 are released (Grogan and Kelly, 2013). Despite this there is no universally agreed ‘successful outcome’ of rehabilitation (Mullineaux, 2014). Furthermore, the potentially negative ecological impacts of release following rehabilitation to receiving populations are often overlooked (Mullineaux, 2014) and impacts on the welfare of rehabilitated animals inadequately considered. Post-release monitoring is essential for evaluation of wildlife rehabilitation success (Mullineaux, 2014) yet is undertaken by few rehabilitation programmes (Guy et al, 2013). Instead, successful outcomes are usually evaluated in terms of release rates of admitted animals (Kelly et al., 2010).

Where post-release data are collected, it is often to determine survivorship rates over relatively short time periods. This is particularly evident in studies of raptors (e.g.
Leighton et al., 2008; Griffiths et. al, 2010), but is also true for mammals, e.g. hedgehogs (Erinaceus europaeus) (Molony et al., 2006) and polecats (Mustela putorius) (Kelly et al., 2010). Whilst assessing short-term survival is clearly an important objective, other measures of animal welfare are required to truly evaluate the rehabilitation process. This is especially true for carnivores because of their tendency to be socially complex (Gittleman, 1996) resulting in a greater potential for social stress and consequent negative effects. Techniques for determining survival such as radio and GPS tracking can be used to additionally monitor detailed movement patterns (i.e. ranging behaviour) at little extra effort and these data can be used as a proxy measure of disruption to social systems.

1.2 Behavioural ecology of red foxes

Red foxes are flexible in their social organisation and occupy contiguous and mutually exclusive group territories in several UK cities (e.g. Oxford: Doncaster and Macdonald, 1997; White et al, 1996; Bristol: Baker et al, 2000). In such resource-rich urban environments, foxes can occur at high densities (Harris and Rayner, 1986; Soulsbury et al., 2010). In accordance with the Resource Dispersion Hypothesis (RDH) urban foxes have small home ranges and large group sizes (Baker et al., 2000). Consequently, the creation of a vacant territory via death, removal or emigration of members of the resident social group, has the potential to markedly alter fox territory configuration, ownership and social group composition. This is particularly likely to be the case when vacating individuals are dominant (White et al., 1996) and overlap between adjoining groups is greatest; e.g. during the main dispersal period in late autumn (Robertson et al., 2000; Soulsbury et al., 2011) or when males make winter mating incursions into neighbouring territories (White and Harris, 1994).

1.3 Territorial displacement
Temporary removal of an adult fox from a group territory might initiate displacement of that animal post-release, although the extent of this is likely to vary with age, sex and social status on removal. A returning fox might therefore be expected to make exploratory movements for establishing or joining a territory elsewhere. This process may mirror dispersal and is associated with high mortality due to animals traversing unfamiliar terrain and crossing more major roads (Baker et al., 2007). Robertson and Harris (1995) describe the ranging behaviour of two groups of captive-reared ‘juvenile’ foxes, classed as those under one year-old: one group released into a novel environment (‘hard-released’); and the other with site acclimation (‘soft-released’). An ‘erratic phase’ was observed for both groups immediately following release (although this was less marked in the latter group) characterised by episodic rapid movements, after which ranging behaviour became more constant and a smaller area was used, i.e. a home range. The duration of this erratic phase was longer than the period of unsettled movements reported for dispersing wild foxes and behaviour more disorientated.

1.4 Aims and objectives

Few studies describe the effects of captivity (and subsequent absence from a resident range) on adult carnivores. Previous research on post-release ranging behaviour and survival of red foxes focused on captive-reared juveniles in rural environments (Robertson and Harris 1995a and b) and did not have a control group as a baseline for comparisons. Our study fills a knowledge gap by investigating post-release movement of rehabilitated adult and sub-adult urban red foxes that were temporarily kept in captivity, as compared to a control group of ‘wild’ foxes over the same time period. Data were collected from the control group as part of a wider study aimed at characterising focal activity areas in urban foxes. We hypothesised that, if displaced, the rehabilitated foxes would behave differently to their counterparts in situ.
Specifically, we tested five predictions concerning rehabilitated relative to control group movements. These were that rehabilitated animals would: i) travel further from the point of release; ii) cover greater distances on a nightly basis; iii) move over a larger area; iv) be less likely to establish a stable home range; and v) take longer to establish a home range. Our findings will help to elucidate the potential impacts of ex-situ care of wild foxes on their post-release behaviour.

2. Methods

2.1 Study sites

The study was conducted between April 2012 and 2014 in eight urban areas in England and Wales, UK: Brighton and Hove, East Sussex; Woodingdean, East Sussex; Rustington, West Sussex; Teignmouth, Devon; Brixham, Devon; London; Manchester; and Newport, Gwent. A total of 20 foxes were tracked using GPS telemetry, of which 13 were wild-caught (7 males and 6 females) and seven were rehabilitated (5 males and 2 females) (see Table 1). Wild-caught foxes were released at the site of capture immediately, whereas rehabilitated foxes were released at the site of capture following an absence of between two and eight weeks. All wild-caught foxes were tracked in the city of Brighton and Hove (N 50.82253, E -0.137163; WGS84) whereas rehabilitated foxes were tracked in each of the towns or cities listed above (Table 1). Each fox was tracked for at least one season over a period of two years. Seasons were classified as: spring (March to May); summer (June to August); autumn (September to November); and winter (December to February).

2.2 Live-capture and attachment of GPS collars

Foxes were captured in galvanised steel humane cage traps (Pest-Go Limited, London, www.pestgo4u.com) measuring 5ft x 18’ with a mesh size of 2 inches x 2 inches. Up to 10 traps per capture session were deployed in private gardens or public
parks with restricted access. Traps were positioned along fox paths, gaps in fences or hedges, or other known access points, parallel to a wall, fence or tree where possible. The end of traps were placed against an obstruction or blocked with heavy objects to prevent foxes or non-target animals digging out the bait without entering the trap. Traps were baited with eggs, chicken or sausages and bait was also dragged along the ground in the area immediately surrounding the trap to create a scent trail. Traps were baited and set in the early evening and checked twice per night to minimise the length of time a fox was confined.

When a fox was captured, it was transferred to a galvanised steel 1 x 1 inch mesh holding cage, weighed, sexed and approximately aged (from size, time of year, and incisor-wear [Harris, 1978]) and assessed for suitability for anaesthesia. All cubs, pregnant vixens, and animals in poor body condition were immediately released. Combined anaesthesia was administered by intra-muscular injection in a graded syringe, with dosages determined by weight, and consisting of Medetomidine hydrochloride (0.02mg /kg body weight) (Domitor, 1mg/ml solution), Ketamine hydrochloride (4mg/kg) (Ketaset, 1ml solution) and Butorphanol tartrate (0.4mg/kg) (Torbugesic, 10 mg/ml solution). Anaesthesia was reversed prior to release of the fox using an intramuscular injection of Atipamezole hydrochloride (0.1mg/kg) (Antisedan, 5 mg/ml solution). Anaesthesia was carried out under Home Office licence, in accordance with the Animals (Scientific Procedures) Act (1986). The trapping procedure underwent ethical review under the Pharmacy and Biomedical Sciences School Ethics Committee at the University of Brighton.

Anaesthetised animals were fitted with GPS Tellus collars bearing VHF and GSM modules (manufactured by FollowIt, Lindesberg AB, Bandygatan 2, SE 711 34, Lindesberg, Sweden) and remotely-programmable drop-off units for collar retrieval at
the end of the study. Collars weighed a maximum of 240g, within the 3% of minimum body weight guideline for welfare of tagged animals (Kenward, 2001).

2.3 Data analysis

GPS collars were programmed to record location data in the form of WGS84 X and Y coordinates from satellites every 10-15 minutes, which were downloaded automatically onto digitised maps of the study areas (www.followit.se). These locations formed the basis of all subsequent analyses. The inter-location interval was chosen to maximise the resolution of the data whilst reducing the probability of temporal autocorrelation, on the basis that within this period a fox would be able to comfortably cross an average home range (Doncaster and Macdonald, 1997).

All spatial and statistical analyses were computed in Ranges (Version 8, Anatrack Ltd, 52 Furzebrook Road, Wareham, BH20 5AX, Dorset, United Kingdom) and R (Version 3.2.0: R Foundation for Statistical Computing, Vienna, Austria).

2.3.1 Estimation of error

An experiment was conducted to estimate the error associated with location data derived from the Tellus GPS collars within an urban environment. A fixed route was followed within an area of central Brighton and Hove within which wild foxes were tracked. One observer carrying a GPS collar paused at 15-minute intervals (corresponding to the study inter-location interval) at 9 predefined and mapped road intersections. Satellite locations were later downloaded and deviation from true locations recorded as straight-line distances using the measuring tool in ArcMap Version 10.3.1, 2015 (Environmental Systems Research Institute [ESRI], Redlands, California, USA). The mean difference in metres (± SE) between true locations and those downloaded from GPS satellites was 19.411 (± 5.433). This was deemed acceptable to robustly meet the study objectives given that inferences were derived
from comparisons between capture status groups (i.e. wild-caught versus rehabilitated foxes) with similar error.

2.3.2 Incremental area analysis

Quantification of animal movement is commonly described by the Utilisation Distribution (UD) - a relative frequency distribution for animal locations in space and time (e.g. Van Winkle, 1975). Kernel density estimators (KDE) are widely reported in the literature as robust statistical tools for quantitatively describing the UD (e.g. Worton, 1989; Cuming and Cornélis, 2012). We used KDE (‘kernels’) as the basis of the movement analysis conducted in our study. Movements of all foxes were initially characterised using Incremental Area Analysis (IAA) generated by 99% kernel isopleths, which plot the area used by each individual as successive locations are added (Kenward et al, 2008). In this process the number of locations that characterise a stable home range for a defined period is determined as the point at which the curve plateaus and the area traversed remains the same with successive locations – also known as an asymptote (Springer, 2003). Inflection points were identified by eye from IAA plots and used as a measure of: i) whether or not individual foxes reached stable home ranges (asymptotes) and; ii) if asymptotes were reached how long this process took in terms of number of locations and number of nights. In addition, we determined the number of locations/nights to reach 100% of the total area used; hereafter termed ‘maximum area’ and contrasted this with time to reach asymptote for each animal. This was to identify and characterise any accelerated periods of movement over large areas, analogous to the erratic phase documented by Robertson and Harris (1995a) and occurring prior to habitual use of a smaller area, i.e. a home range. Thus, we would expect resident animals to reach maximum area and asymptote more-or-less simultaneously, whereas displaced animals would be expected either to reach asymptote at a later stage than maximum area, or not at all. Datasets were
truncated accordingly and all subsequent analyses were conducted on truncated data. Any individual foxes exhibiting unusual behaviour that was considered to be anomalous were subsequently removed and all analyses re-computed.

2.3.3. Time to asymptote and maximum area

Potential effects of capture status on the number of nights to reach: i) asymptote; and ii) maximum area were investigated using Poisson regression within a Generalised Linear Model (GLM). To investigate potentially confounding effects of sex and season, both of these variables were included as model terms. A three-way interaction term was also included between capture status (hereafter ‘CS’), sex and season. A backwards stepwise procedure of model selection was followed where non-significant terms were sequentially removed in order of lowest $F$ values.

2.3.4 Home range size

Fixed kernels were used to generate 95% home range isopleths (i.e. all locations, excluding outliers) defining an area in hectares (ha), for the foxes in each of the CS groups that reached asymptote. Although Least Squares Cross Validation (LSCV) for estimating the smoothing parameter ($h$) in KDE is recommended by a number of authors (e.g. Seaman et al, 1999; Horne and Garton, 2006) it is sensitive to sample size and can under-smooth kernel isopleths, resulting in artificially fragmented home ranges, particularly when using data derived from GPS tracking (Kie et al., 2010). In the current study fox locations were individually assessed by eye and compared to both LSCV-inflected and fixed KDE, with the latter better representing actual movement patterns overall. Testing for normality and equal variance was performed prior to analysis by generating histograms and using Bartlett’s test for homogeneity. Home range size was non-normally distributed with unequal variance (Bartlett’s test,
\( K^2 = 28.281, \text{ df } = 1, P < 0.001 \) hence comparisons between CS groups were computed using the Kruskal Wallis non-parametric test.

### 2.3.5 Distance travelled

Inter-location analysis, which generates distances between all locations for each animal, was computed for the: i) asymptote and ii) maximum area datasets. Each dataset was cleaned before use as follows: all ‘daytime’ fixes – defined as the period between 08:00 h and 16:00 h were removed (this period was based on the earliest evening activity and the latest morning activity observed by foxes during the study, used throughout the year for consistency); distances were totalled for each night and divided by the number of hours over which data were recorded to derive a distance per hour (DPH) per night. The effects of CS, sex and season, and a three-way interaction term on DPH were subsequently investigated for each dataset using linear regression. Exploration of normality and heterogeneity was performed via generation of histograms on both observed data and residuals, and Bartlett’s test for homogeneity. Both response variables (and residuals) were non-normally distributed, with unequal variance (Bartlett’s test, asymptote: \( K^2 = 51.553, P < 0.001 \); maximum area: \( K^2 = 58.768, P < 0.001 \)) and were subsequently log-transformed for analysis.

### 2.3.6 Home range overlap

To investigate home range shifts in rehabilitated foxes as a potential consequence of displacement, fox locations for each CS category were pooled over 3-day periods and 95\% home range polygons were generated using fixed kernel density estimators (KDE). We considered three days to be long enough to generate a sufficient number of locations to robustly describe the UD, and short enough to be sensitive to changes over time. Percentage overlap between initial (first 3 days) and last (last 3 days) home ranges were computed using overlap analysis, and converted into proportions.
Proportional overlap was approximately normally distributed and variances were equal (Bartlett’s test, $K^2 = 1.382$, $P > 0.05$) hence comparisons between CS groups were computed using simple linear regression.

3. Results

Of the 20 foxes, 19 (95%) survived the tracking period, with one rehabilitated male (RH7) dying of a suspected brain tumour five days post-release. In addition, one wild-caught male (WC8) dispersed from its putative home range in Brighton and Hove 73 days following release, and 65 days after asymptote was reached. The fox travelled approximately 70 km in a straight-line distance from the point of origin (315 km in total) traversing surrounding rural areas and towns before the GPS collar battery failed and tracking ceased. Furthermore, two wild-caught females (WC12 and WC13) tracked simultaneously and lactating when captured in spring were observed to be provisioning the same litter of cubs, although it is unknown which vixen gave birth to the litter.

3.1 Proportion reaching asymptote

Of the 13 wild-caught (WC) foxes, 11 (84.6%) reached asymptote during the tracking period. Of the 7 rehabilitated (RH) foxes only 4 reached asymptote (57.1%) and this was reduced to 3/7 (42.9%) when RH7 was removed.

3.2 Time to asymptote and maximum area

Rehabilitated foxes were more variable than wild-caught ones in the time taken to a) traverse 100% of the total area covered (i.e. time to reach maximum area) (Figure 1; Table 2) and; b) time to reach asymptote, where this occurred (Figure 2; Table 2). Capture status (CS) influenced time to maximum area (GLM, Likelihood ratio $\chi^2 = 4.251$, $df = 1$, $P < 0.05$) with RH foxes taking longer to reach maximum area than WC
There was an effect of season (GLM, Likelihood ratio $\chi^2 = 23.427$, $df = 3$, $p < 0.001$) where foxes took longer in summer than any other season (winter, $MLPE = -1.389$, $z = -3.939$, $p < 0.001$; autumn, $MLPE = -0.999$, $z = -3.225$, $p < 0.01$; spring, $MLPE = -1.418$, $z = -4.958$, $p < 0.001$). A significant interaction between season and CS ($\chi^2 = 22.570$, $df = 2$, $p < 0.001$) was also detected. A greater proportion of wild-caught foxes reached asymptote and maximum area simultaneously, i.e. home ranges encompassed the full extent of the area used (Table 2). CS had no effect on time to asymptote (GLM, Likelihood ratio $\chi^2 = 1.337$, $df = 1$, $P > 0.05$) but there were seasonal differences (GLM, Likelihood ratio $\chi^2 = 14.262$, $df = 2$, $P < 0.001$) where foxes reached asymptote more quickly in winter than in autumn ($MLPE = -1.012$, $z = -2.570$, $p < 0.05$) or spring ($MLPE = -1.155$, $z = -2.570$, $p < 0.05$).

### 3.3 Home range size and overlap

For the 15 foxes that reached asymptote, mean 95% home range size (± SE) was 118.5 (± 67.23) hectares for RH foxes and 14.2 (± 3.26) hectares for WC ones, and this difference was statistically significantly (Kruskal Wallis test, $\chi^2 = 7.517$, $df = 1$, $p < 0.01$). In addition, proportional overlap between the first and last 95% 3-day home ranges differed between CS groups (Linear regression, $F_{1,12} = 4.755$, $df = 1$, $P < 0.05$) and was smaller in RH foxes ($MLPE = -0.498$, $t = 2.181$, $P < 0.05$). Two of the four RH foxes (50%) and one of the 11 WC foxes (9%) showed zero proportional overlap between the ranges (see Figure 3 for examples).

### 3.4 Distance travelled

Mean DPH per night (± SE) for the period until maximum area was reached was 290m (±24.9) for RH foxes and 361.3m (±41.9) for WC ones. There was no difference between the two groups (Linear regression, $F_{1, 179} = 0.4554$, $P > 0.05$).
However there were seasonal differences, with greater distances travelled in spring than in summer (Table 3). Following removal of RH7 the results changed little; again there was a seasonal effect and distances were greater in spring (Table 3). Mean DPH per night (± SE) for the period until asymptote was reached was 204.6 m (±26.1) for RH foxes and 374.6 m (± 46.5) for WC ones. Wild-caught foxes travelled further than rehabilitated ones (Table 3) and females travelled further than males. Again, DPH varied between seasons but in this case foxes travelled further in spring than in winter. A significant interaction was detected between CS and sex (Table 3).

Following removal of WC12 and WC13, sex became non-significant (Linear regression, $F_{1, 139} = 2.0771, P > 0.05$) but the effect of CS and season remained (Table 3). Again the results did not change markedly following removal of RH7.

### 4. Discussion

#### 4.1 Evidence of territorial displacement

Our findings showed that several aspects of urban fox ranging behaviour were different in animals that had been subject to temporary captivity, and we interpret these irregular movements as evidence of displacement of rehabilitated foxes from a resident area. We present evidence to support prediction one - that rehabilitated foxes would travel further from the point of release – in the form of reduced overlap between initial and final home ranges in rehabilitated animals. Our data are also consistent with prediction three – that of rehabilitated foxes moving over a larger area, as evidenced by larger home ranges in this group; and four – of proportionally fewer rehabilitated foxes establishing a stable home range.

However, for other movement measures we either did not detect a difference between capture status groups, or found the reverse relationship. Wild-caught foxes travelled
further on a nightly basis during the period until a stable home range was reached, which contrasts with prediction two – that rehabilitated foxes would travel greater distances. We explain this apparently anomalous finding in section 4.2. There was also no difference between capture status groups in the time taken to reach a stable home range (which conflicts with prediction five), although rehabilitated foxes did take longer to traverse the maximum area used. We argue that the lack of a delay in home range establishment by rehabilitated foxes may actually reflect a dichotomous relationship between captivity and movement patterns where either rehabilitated animals were completely displaced (and home range establishment simply did not occur) or they were not displaced at all. As non-displaced foxes comprised the asymptote cohort, a comparison with wild-caught animals would reveal little difference between the two groups.

Data were less precise for rehabilitated than control animals, notwithstanding the subsequent unusual behaviour of WC8. This may simply reflect both smaller sample sizes, and unbalanced datasets for the former group, particularly for the asymptote subset, which was by nature restricted to data from fewer individuals. However it may also suggest that there are individual-based factors that cause foxes to respond unpredictably following release from temporary captivity, which were not explicitly modelled in this study.

4.2 Seasonal and sex-related patterns

Seasonal patterns in time to establish a stable home range, and nightly distance travelled, did not vary between capture status groups in our study. For both groups greater distances were travelled in spring, and the establishment of stable home ranges was delayed in the summer and accelerated in the winter. This is broadly consistent with the stages of the fox reproductive cycle, and associated shifts in both energetic requirements and territorial activity, which themselves reflect changing
weather conditions. However, the extent to which seasonal changes in food availability drive these patterns is unclear. Although food availability is widely considered to be a limiting factor driving territory size and ranging behaviour in carnivores (Macdonald, 1983) anthropogenic food sources are significant components of urban fox diet (e.g. scavenged food comprised 64% of fox diet by weight in Bristol [Saunders et al., 1993]) and tend to be more consistently available throughout the year than natural food items (White et al., 1996).

Our findings showed interactions between: i) season and capture status in terms of time to traverse maximum area used; and ii) sex and capture status in terms of nightly distance travelled for the period until a stable range was reached. There are two well-documented processes by which male and female movement patterns might be expected to differ from random over the annual cycle in resident foxes. These are: increased female activity in spring and summer due initially to lactation and subsequently to provisioning of semi-dependent cubs (e.g. Saunders et. al, 1993); and winter expansion of male ranges due to forays in search of extra-group mating opportunities (e.g. White and Harris, 1994; White et al., 1996; Soulsbury et al., 2011).

In our study the behaviour of the wild-caught female cohort was skewed by breeding and putative alloparenting exhibited by the two vixens WC12 and WC13. Removal of these two animals from the main dataset both eliminated the effect of sex on nightly distance travelled, and lessened the effect of season (presumably by reducing the breeding spike in activity in spring) resulting in a more uniform effect of capture status for non-breeding animals. However the greater nightly distances travelled by wild-caught foxes persisted.

Although this at first appears unexpected in the context of prediction two (that rehabilitated foxes would travel greater distances) the prediction is only logical where distances represent cumulative trajectories in one direction rather than repetitive
movements within a smaller area. The latter are consistent with: i) patrolling of
resident territories; ii) exploiting reliable resources such as food supplied by
householders; and iii) denning, and rearing cubs. Supplementary feeding of foxes by
householders in Brighton and Hove is common whilst fox densities and
corresponding territorial defence are high (Scott and Tolhurst unpublished
observations). Furthermore, home-ranges were small for wild-caught foxes in the
current study and at least two animals were provisioning cubs, supporting the
assertion that greater distance travelled was indicative of resident territorial
behaviour.

4.3 Patterns of space use

Three distinct patterns of space use emerged in our study: one where a stable home
range was never established; a second where home range extent was equal to the
maximum area covered; and a third where maximum area peaked at an early stage,
and home range was established later. Under the classification system presented by
Dekker et al (2001), the first pattern is similar to the early stages of dispersal or of
itinerant animals that are non-territorial and range over large areas. The second
pattern suggests that the fox is resident and, either solely or jointly, defends an
existing territory. The third indicates an initial exploratory period where the fox
ranges widely over a large area before ‘settling’ on a smaller section of that area for
habitual use (i.e. a home range) and is analogous to the two-stage process reported by
Robertson and Harris (1995) for captive-bred juveniles. Based on this classification,
in the current study the relative proportion of dispersing or itinerant foxes was higher
for the rehabilitated group, indicating that for these animals temporary captivity led to
territorial displacement. However this pattern was not universal – for example two of
the wild-caught foxes in the study could also be categorised as dispersing or transient.
As both of these animals were non-breeding vixens of approximately 4-5 years of
age, it is possible that they were transient as a consequence of social exclusion from a
group territory. Patterns of space use are however inevitably dynamic where foxes
occur at high-densities in urban areas with high rates of population turnover.

4.4 Welfare implications of displacement

Dispersal is linked to an increase in mortality (e.g. Robertson and Harris, 1995; Baker
et al. 2007) and we demonstrate here the similarities between dispersal and the ranging
behaviour of displaced rehabilitated animals. It therefore follows that foxes subject to
rehabilitation might subsequently be at greater risk of death. The single fatality
recorded during our study was a rehabilitated animal but this was believed to have
occurred due to existing disease and was therefore a probable cause rather than
consequence of captivity. Thus we did not find evidence of greater mortality in the
rehabilitated cohort during the study period. However, there are a number of social
and nutritional stressors that dispersing and itinerant foxes are vulnerable to,
including: i) the threat of aggressive extra-group encounters (White and Harris,
1994); the absence of enriching social contact between members of the same social
group (e.g. Hovland et al., 2011); and iii) the higher energetic costs associated with
erratic movements, lack of knowledge of the location of food patches, and the
opportunity costs of foraging time lost (Robertson and Harris, 1995b). The displaced
rehabilitated foxes in our sample are likely to have suffered at least some of these
negative yet sub-lethal effects, with potential long-term implications for survival.
Further research into these effects is necessary to determine the full consequences of
displacement.

4.5 Limitations of the study

Limitations of the study include: i) lack of replication of both capture status groups
across different urban areas and associated potential for bias arising from city-specific
factors; and ii) small and unbalanced datasets, particularly when comparing ranging
parameters for foxes that reached home range asymptote. Further work with a larger
sample of rehabilitated animals is advised to determine whether the variability of this
group is an inherent characteristic or an artefact of small sample size.

4.6. Management implications and conclusions

We present evidence of perturbed ranging behaviour in foxes subjected to temporary
captivity. Further work is needed to confirm these findings, however in accordance
with the precautionary principle we recommend that where possible, time in captivity
is limited, and alternatives to ex situ care are considered in the decision-making
process.

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References

organisation of red foxes (Vulpes vulpes) before and during an outbreak of sarcoptic


Figure 1 Incremental Area Analysis (IAA) plot of number of locations to reach maximum area (i.e. 100% of Home Range Area) for rehabilitated (n = 7) versus wild-caught (n = 13) foxes, expressed as mean % area used (± SE).
Figure 2 Incremental Area Analysis (IAA) plots of number of locations to reach home range asymptote for rehabilitated (n = 4) versus wild-caught (n = 11) foxes, expressed as mean area used (± SE). Dotted lines represent data for a single animal (rehabilitated female RH5).
Figure 3 Examples of variation in percentage overlap between initial (first 3 days) and final (last 3 days) 95% home range kernel isopleths for rehabilitated and wild-caught foxes; showing a) rehabilitated female RH5; and b) wild-caught male WC9, tracked in Autumn 2013
<table>
<thead>
<tr>
<th>Code</th>
<th>Sex</th>
<th>Approx. age</th>
<th>Capture status</th>
<th>Season tracked</th>
<th>Year tracked</th>
<th>Area Tracked</th>
<th>Total locations</th>
<th>Total nights</th>
</tr>
</thead>
<tbody>
<tr>
<td>WC1</td>
<td>Male</td>
<td>2 years</td>
<td>WC</td>
<td>Spring</td>
<td>2012</td>
<td>Brighton</td>
<td>4181</td>
<td>17</td>
</tr>
<tr>
<td>WC2</td>
<td>Male</td>
<td>2 years</td>
<td>WC</td>
<td>Spring</td>
<td>2012</td>
<td>Brighton</td>
<td>1620</td>
<td>65</td>
</tr>
<tr>
<td>WC3</td>
<td>Female</td>
<td>4 years</td>
<td>WC</td>
<td>Spring</td>
<td>2012</td>
<td>Brighton</td>
<td>1558</td>
<td>19</td>
</tr>
<tr>
<td>WC4</td>
<td>Female</td>
<td>1 year</td>
<td>WC</td>
<td>Spring</td>
<td>2012</td>
<td>Brighton</td>
<td>1515</td>
<td>30</td>
</tr>
<tr>
<td>WC5</td>
<td>Male</td>
<td>2 years</td>
<td>WC</td>
<td>Spring</td>
<td>2013</td>
<td>Brighton</td>
<td>1341</td>
<td>22</td>
</tr>
<tr>
<td>WC6</td>
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<td>1 year</td>
<td>WC</td>
<td>Spring</td>
<td>2013</td>
<td>Brighton</td>
<td>2637</td>
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<td>WC7</td>
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<td>2 years</td>
<td>WC</td>
<td>Spring</td>
<td>2013</td>
<td>Hove</td>
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<td>WC8</td>
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<td>2 years</td>
<td>WC</td>
<td>Autumn</td>
<td>2013</td>
<td>Hove</td>
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<td>133</td>
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<tr>
<td>WC9</td>
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<td>10 months</td>
<td>WC</td>
<td>Autumn</td>
<td>2013</td>
<td>Brighton</td>
<td>681</td>
<td>147</td>
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<tr>
<td>WC10</td>
<td>Female</td>
<td>5 years</td>
<td>WC</td>
<td>Winter</td>
<td>2013</td>
<td>Brighton</td>
<td>968</td>
<td>87</td>
</tr>
<tr>
<td>WC11</td>
<td>Female</td>
<td>8 months</td>
<td>WC</td>
<td>Winter</td>
<td>2014</td>
<td>Brighton</td>
<td>784</td>
<td>86</td>
</tr>
<tr>
<td>WC12</td>
<td>Female</td>
<td>2 years</td>
<td>WC</td>
<td>Spring</td>
<td>2014</td>
<td>Brighton</td>
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<tr>
<td>WC13</td>
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<td>4 years</td>
<td>WC</td>
<td>Spring</td>
<td>2014</td>
<td>Brighton</td>
<td>245</td>
<td>16</td>
</tr>
<tr>
<td>RH1</td>
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<td>1 year</td>
<td>RH</td>
<td>Spring</td>
<td>2012</td>
<td>Newport</td>
<td>1718</td>
<td>32</td>
</tr>
<tr>
<td>RH2</td>
<td>Male</td>
<td>2 years</td>
<td>RH</td>
<td>Spring</td>
<td>2012</td>
<td>Brixham</td>
<td>2327</td>
<td>31</td>
</tr>
<tr>
<td>RH3</td>
<td>Male</td>
<td>1 year</td>
<td>RH</td>
<td>Spring</td>
<td>2012</td>
<td>Manchester</td>
<td>1047</td>
<td>19</td>
</tr>
<tr>
<td>RH4</td>
<td>Female</td>
<td>18 months</td>
<td>RH</td>
<td>Spring</td>
<td>2012</td>
<td>London</td>
<td>1141</td>
<td>16</td>
</tr>
<tr>
<td>RH5</td>
<td>Male</td>
<td>3 years</td>
<td>RH</td>
<td>Summer</td>
<td>2013</td>
<td>Rustington</td>
<td>2220</td>
<td>36</td>
</tr>
<tr>
<td>RH6</td>
<td>Female</td>
<td>8 months</td>
<td>RH</td>
<td>Autumn</td>
<td>2013</td>
<td>Teignmouth</td>
<td>1629</td>
<td>110</td>
</tr>
<tr>
<td>RH7</td>
<td>Male</td>
<td>11 months</td>
<td>RH</td>
<td>Winter</td>
<td>2014</td>
<td>Woodingdean</td>
<td>102</td>
<td>9</td>
</tr>
</tbody>
</table>

Table 1: List of foxes that were GPS-tracked during the 2-year study, showing capture status (WC = wild-caught; RH = rehabilitated), approximate age and sex, season, location and length of time tracked in terms of both nights and number of locations.
<table>
<thead>
<tr>
<th>Capture Status (CS)</th>
<th>Mean nights to maximum area (±SE)</th>
<th>Mean nights to asymptote (±SE)</th>
<th>Proportion asymptote equals max. area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rehabilitated</td>
<td>8.43 (±3.44)</td>
<td>15.00 (±2.66)</td>
<td>2/4* = 50%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1/4** = 33%</td>
</tr>
<tr>
<td>Wild-caught</td>
<td>9.54 (±2.64)</td>
<td>11.73 (±1.03)</td>
<td>7/11 = 64%</td>
</tr>
</tbody>
</table>

**Table 2** Summary of movement parameters by capture status group, showing: mean number of nights to reach: i) maximum area (100% of area used) and ii) home range asymptote; and proportion of animals for which maximum area and asymptote were reached simultaneously (* including and ** excluding RH7).
### Table 3

Significant variables predicting distance travelled by foxes in metres per hour per night for the time period until: i) asymptote was reached; and ii) maximum area was reached, using linear fixed effects models. ANOVA = Analysis of Variance; CS = capture status; x operator indicates interaction term. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. 

<table>
<thead>
<tr>
<th>Variable</th>
<th>ANOVA</th>
<th>$P$</th>
<th>Variable</th>
<th>ANOVA</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time period until maximum area reached</td>
<td></td>
<td></td>
<td>Time period until asymptote reached</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>$F_{3, 181} = 2.799$</td>
<td>*</td>
<td>CS</td>
<td>$F_{1, 168} = 28.56$</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sex</td>
<td>$F_{1, 168} = 13.95$</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Season</td>
<td>$F_{2, 168} = 5.71$</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>CS x Sex</td>
<td>$F_{1, 167} = 7.10$</td>
<td>**</td>
</tr>
<tr>
<td>Results after fox RH7 removed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>$F_{3, 179} = 2.980$</td>
<td>*</td>
<td>CS</td>
<td>$F_{1, 166} = 28.86$</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sex</td>
<td>$F_{1, 165} = 14.47$</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Season</td>
<td>$F_{2, 168} = 3.24$</td>
<td>*</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>CS x Sex</td>
<td>$F_{1, 165} = 7.33$</td>
<td>**</td>
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<tr>
<td>Results after foxes WC12 and WC13 removed</td>
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<td></td>
</tr>
<tr>
<td>CS</td>
<td>$F_{1, 141} = 22.76$</td>
<td>***</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>$F_{2, 141} = 4.38$</td>
<td>*</td>
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<td></td>
</tr>
</tbody>
</table>
### Table 4

Post-hoc tests for significant variables predicting distance travelled by foxes in metres per hour per night for the time period until: i) asymptote was reached; and ii) maximum area was reached, using linear fixed effects models. MLPE = Maximum Likelihood Parameter Estimate; WC = wild-caught, RH = rehabilitated; v. = versus; direction of difference indicated by positive or negative operator. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

<table>
<thead>
<tr>
<th></th>
<th>Time period until maximum area reached</th>
<th></th>
<th>Time period until asymptote reached</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>MLPE</strong></td>
<td><strong>$t$</strong></td>
<td><strong>$P$</strong></td>
<td><strong>MLPE</strong></td>
</tr>
<tr>
<td>Spring v. Summer</td>
<td>0.167</td>
<td>2.43</td>
<td>*</td>
<td>WC v. RH</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Spring v. Winter</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>♀ v. ♂</td>
</tr>
<tr>
<td><strong>Results after fox RH7 removed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring v. Summer</td>
<td>0.167</td>
<td>2.45</td>
<td>*</td>
<td>WC v. RH</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Spring v. Winter</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>♀ v. ♂</td>
</tr>
<tr>
<td><strong>Results after foxes WC12 and WC13 removed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WC v. RH</td>
<td>0.27</td>
<td>4.52</td>
<td>***</td>
<td></td>
</tr>
<tr>
<td>Summer v. Spring</td>
<td>0.16</td>
<td>2.40</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Summer v. Winter</td>
<td>0.28</td>
<td>2.43</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>