

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

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11 [adam.grogan@rspca.org.uk](mailto:adam.grogan@rspca.org.uk)12 **Abstract**

13 Temporary removal of wild animals from a resident territory has the potential to  
14 markedly impact subsequent ranging behaviour, and may negatively affect post-  
15 release welfare and survival. Admission of sick or injured wildlife into temporary  
16 captivity (termed ‘rehabilitation’) is a common practice in the UK. However, post-  
17 release monitoring of rehabilitated animals is unusual or restricted to recording  
18 survival rates over limited time periods. As part of a wider study of urban fox  
19 behaviour, we employed an experimental approach to compare the ranging behaviour  
20 of seven rehabilitated and 13 wild-caught ‘control’ urban red foxes using GPS  
21 tracking. Foxes were tracked over a two-year period for an average of 48 nights, and  
22 seasonal and sex-related effects were controlled for via inclusion in statistical models.  
23 Three of the five movement parameters we investigated were irregular for the  
24 rehabilitated animals, relative to controls. These were: reduced likelihood of

25 establishing a stable home range (42.9/57.1% of rehabilitated foxes versus 84.6% of  
26 controls); larger home ranges (Kruskal Wallis test,  $\chi^2 = 7.517$ ,  $df = 1$ ,  $p < 0.01$ ); and  
27 further distance travelled from release point, as measured by overlap between initial  
28 and final home ranges (Linear regression,  $F_{1, 12} = 4.755$ ,  $df = 1$ ,  $P < 0.05$ ). Females  
29 moved greater distances than males overall, and foxes from both groups travelled  
30 further in spring, and delayed home range establishment in summer. However, these  
31 results were skewed by the movements of two apparently cooperatively breeding  
32 wild-caught vixens. Our data provide evidence of territorial displacement of  
33 rehabilitated foxes on release. We discuss the welfare implications of this finding.

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44 **Key words:** red fox, ranging behaviour, captivity, rehabilitation, home range, ex situ

## 45 **1. Introduction**

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

### 53 **1.1 Wildlife rehabilitation**

54 Wildlife rehabilitation is defined by the International Wildlife Rehabilitation Council  
55 (IWRRC), as the ‘treatment and temporary care of injured, diseased, and displaced  
56 indigenous animals, and the subsequent release of healthy animals to appropriate  
57 habitats in the wild’ (Miller, 2012). Rehabilitation is common practice in the UK – an  
58 estimated 71,000 wild animals are annually admitted to rehabilitation centres, of  
59 which an estimated 28,000 are released (Grogan and Kelly, 2013). Despite this there  
60 is no universally agreed ‘successful outcome’ of rehabilitation (Mullineaux, 2014).  
61 Furthermore, the potentially negative ecological impacts of release following  
62 rehabilitation to receiving populations are often overlooked (Mullineaux, 2014) and  
63 impacts on the welfare of rehabilitated animals inadequately considered. Post-release  
64 monitoring is essential for evaluation of wildlife rehabilitation success (Mullineaux,  
65 2014) yet is undertaken by few rehabilitation programmes (Guy et al 2013). Instead,  
66 successful outcomes are usually evaluated in terms of release rates of admitted  
67 animals (Kelly et al., 2010).

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69 Where post-release data are collected, it is often to determine survivorship rates over  
70 relatively short time periods. This is particularly evident in studies of raptors (e.g.

71 Leighton et al., 2008; Griffiths et. al, 2010), but is also true for mammals, e.g.  
72 hedgehogs (*Erinaceus europaeus*) (Molony et al., 2006) and polecats (*Mustela*  
73 *putorius*) (Kelly et al., 2010). Whilst assessing short-term survival is clearly an  
74 important objective, other measures of animal welfare are required to truly evaluate  
75 the rehabilitation process. This is especially true for carnivores because of their  
76 tendency to be socially complex (Gittleman, 1996) resulting in a greater potential for  
77 social stress and consequent negative effects. Techniques for determining survival  
78 such as radio and GPS tracking can be used to additionally monitor detailed  
79 movement patterns (i.e. ranging behaviour) at little extra effort and these data can be  
80 used as a proxy measure of disruption to social systems.

## 81 **1.2 Behavioural ecology of red foxes**

82 Red foxes are flexible in their social organisation and occupy contiguous and  
83 mutually exclusive group territories in several UK cities (e.g. Oxford: Doncaster and  
84 Macdonald, 1997; White et al, 1996; Bristol: Baker et al, 2000). In such resource-rich  
85 urban environments, foxes can occur at high densities (Harris and Rayner, 1986;  
86 Soulsbury et al., 2010). In accordance with the Resource Dispersion Hypothesis  
87 (RDH) urban foxes have small home ranges and large group sizes (Baker et al.,  
88 2000). Consequently, the creation of a vacant territory via death, removal or  
89 emigration of members of the resident social group, has the potential to markedly  
90 alter fox territory configuration, ownership and social group composition. This is  
91 particularly likely to be the case when vacating individuals are dominant (White et al.,  
92 1996) and overlap between adjoining groups is greatest; e.g. during the main dispersal  
93 period in late autumn (Robertson et al., 2000; Soulsbury et al., 2011 ) or when males  
94 make winter mating incursions into neighbouring territories (White and Harris, 1994).

## 95 **1.3 Territorial displacement**

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

#### 111 **1.4 Aims and objectives**

112 Few studies describe the effects of captivity (and subsequent absence from a resident  
113 range) on adult carnivores. Previous research on post-release ranging behaviour and  
114 survival of red foxes focused on captive-reared juveniles in rural environments  
115 (Robertson and Harris 1995a and b) and did not have a control group as a baseline for  
116 comparisons. Our study fills a knowledge gap by investigating post-release movement  
117 of rehabilitated adult and sub-adult urban red foxes that were temporarily kept in  
118 captivity, as compared to a control group of ‘wild’ foxes over the same time period.  
119 Data were collected from the control group as part of a wider study aimed at  
120 characterising focal activity areas in urban foxes. We hypothesised that, if displaced,  
121 the rehabilitated foxes would behave differently to their counterparts *in situ*.

122 Specifically, we tested five predictions concerning rehabilitated relative to control  
123 group movements. These were that rehabilitated animals would: i) travel further from  
124 the point of release; ii) cover greater distances on a nightly basis; iii) move over a  
125 larger area; iv) be less likely to establish a stable home range; and v) take longer to  
126 establish a home range. Our findings will help to elucidate the potential impacts of *ex-*  
127 *situ* care of wild foxes on their post-release behaviour.

## 128 **2. Methods**

### 129 **2.1 Study sites**

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

### 143 **2.2 Live-capture and attachment of GPS collars**

144 Foxes were captured in galvanised steel humane cage traps (Pest- Go Limited,  
145 London, [www.pestgo4u.com](http://www.pestgo4u.com)) measuring 5ft x 18' with a mesh size of 2 inches x 2  
146 inches. Up to 10 traps per capture session were deployed in private gardens or public

147 parks with restricted access. Traps were positioned along fox paths, gaps in fences or  
148 hedges, or other known access points, parallel to a wall, fence or tree where possible.  
149 The end of traps were placed against an obstruction or blocked with heavy objects to  
150 prevent foxes or non-target animals digging out the bait without entering the trap.  
151 Traps were baited with eggs, chicken or sausages and bait was also dragged along the  
152 ground in the area immediately surrounding the trap to create a scent trail. Traps were  
153 baited and set in the early evening and checked twice per night to minimise the length  
154 of time a fox was confined.

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

169 Anaesthetised animals were fitted with GPS Tellus collars bearing VHF and GSM  
170 modules (manufactured by FollowIt, Lindesberg AB, Bandygatan 2, SE 711 34,  
171 Lindesberg, Sweden) and remotely-programmable drop-off units for collar retrieval at

172 the end of the study. Collars weighed a maximum of 240g, within the 3% of  
173 minimum body weight guideline for welfare of tagged animals (Kenward, 2001).

## 174 **2.3 Data analysis**

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

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

### 185 **2.3.1 Estimation of error**

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



197 from comparisons between capture status groups (i.e. wild-caught versus rehabilitated  
198 foxes) with similar error.

### 199 **2.3.2 Incremental area analysis**

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

223 truncated accordingly and all subsequent analyses were conducted on truncated data.  
224 Any individual foxes exhibiting unusual behaviour that was considered to be  
225 anomalous were subsequently removed and all analyses re-computed.

### 226 **2.3.3. Time to asymptote and maximum area**

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

### 234 **2.3.4 Home range size**

235 Fixed kernels were used to generate 95% home range isopleths (i.e. all locations,  
236 excluding outliers) defining an area in hectares (ha), for the foxes in each of the CS  
237 groups that reached asymptote. Although Least Squares Cross Validation (LSCV) for  
238 estimating the smoothing parameter ( $h$ ) in KDE is recommended by a number of  
239 authors (e.g. Seaman et al, 1999; Horne and Garton, 2006) it is sensitive to sample  
240 size and can under-smooth kernel isopleths, resulting in artificially fragmented home  
241 ranges, particularly when using data derived from GPS tracking (Kie et al., 2010). In  
242 the current study fox locations were individually assessed by eye and compared to  
243 both LSCV-inflected and fixed KDE, with the latter better representing actual  
244 movement patterns overall. Testing for normality and equal variance was performed  
245 prior to analysis by generating histograms and using Bartlett's test for homogeneity.  
246 Home range size was non-normally distributed with unequal variance (Bartlett's test,

247  $K^2 = 28.281$ ,  $df = 1$ ,  $P < 0.001$ ) hence comparisons between CS groups were  
248 computed using the Kruskal Wallis non-parametric test.

### 249 **2.3.5 Distance travelled**

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

### 264 **2.3.6 Home range overlap**

265 To investigate home range shifts in rehabilitated foxes as a potential consequence of  
266 displacement, fox locations for each CS category were pooled over 3-day periods and  
267 95% home range polygons were generated using fixed kernel density estimators  
268 (KDE). We considered three days to be long enough to generate a sufficient number  
269 of locations to robustly describe the UD, and short enough to be sensitive to changes  
270 over time. Percentage overlap between initial (first 3 days) and last (last 3 days) home  
271 ranges were computed using overlap analysis, and converted into proportions.

272 Proportional overlap was approximately normally distributed and variances were  
273 equal (Bartlett's test,  $K^2 = 1.382$ ,  $P > 0.05$ ) hence comparisons between CS groups  
274 were computed using simple linear regression.

### 275 **3. Results**

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

#### 286 **3.1 Proportion reaching asymptote**

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

#### 290 **3.2 Time to asymptote and maximum area**

291 Rehabilitated foxes were more variable than wild-caught ones in the time taken to a)  
292 traverse 100% of the total area covered (i.e. time to reach maximum area) (Figure 1;  
293 Table 2) and; b) time to reach asymptote, where this occurred (Figure 2; Table 2).  
294 Capture status (CS) influenced time to maximum area (GLM, Likelihood ratio  $\chi^2 =$   
295 4.251,  $df=1$ ,  $P<0.05$ ) with RH foxes taking longer to reach maximum area than WC

296 foxes (*Maximum Likelihood Parameter Estimate [MLPE]* = 0.999,  $z=2.835$ ,  $p<0.01$ ).

297 There was an effect of season (GLM, Likelihood ratio  $\chi^2 = 23.427$ ,  $df=3$ ,  $p<0.001$ )

298 where foxes took longer in summer than any other season (winter,  $MLPE= -1.389$ ,

299  $z=-3.939$ ,  $p<0.001$ ; autumn,  $MLPE= -0.999$ ,  $z=-3.225$ ,  $p<0.01$ ; spring,  $MLPE= -$

300  $1.418$ ,  $z=-4.958$ ,  $p<0.001$ ). A significant interaction between season and CS ( $\chi^2 =$

301  $22.570$ ,  $df = 2$ ,  $p<0.001$ ) was also detected. A greater proportion of wild-caught foxes

302 reached asymptote and maximum area simultaneously, i.e. home ranges encompassed

303 the full extent of the area used (Table 2). CS had no effect on time to asymptote

304 (GLM, Likelihood ratio  $\chi^2 = 1.337$ ,  $df=1$ ,  $P>0.05$ ) but there were seasonal differences

305 (GLM, Likelihood ratio  $\chi^2 = 14.262$ ,  $df=2$ ,  $P<0.001$ ) where foxes reached asymptote

306 more quickly in winter than in autumn ( $MLPE= -1.012$ ,  $z=-2.570$ ,  $p<0.05$ ) or spring

307 ( $MLPE= -1.155$ ,  $z=-1.70$ ,  $p<0.01$ ).

### 308 **3.3 Home range size and overlap**

309 For the 15 foxes that reached asymptote, mean 95% home range size ( $\pm$  SE) was

310  $118.5 (\pm 67.23)$  hectares for RH foxes and  $14.2 (\pm 3.26)$  hectares for WC ones, and

311 this difference was statistically significantly (Kruskal Wallis test,  $\chi^2 =7.517$ ,  $df = 1$ ,  $p$

312  $< 0.01$ ). In addition, proportional overlap between the first and last 95% 3-day home

313 ranges differed between CS groups (Linear regression,  $F_{1,12} =4.755$ ,  $df=1$ ,  $P < 0.05$ )

314 and was smaller in RH foxes ( $MLPE = -0.498$ ,  $t = 2.181$ ,  $P < 0.05$ ). Two of the four

315 RH foxes (50%) and one of the 11 WC foxes (9%) showed zero proportional overlap

316 between the ranges (see Figure 3 for examples).

### 317 **3.4 Distance travelled**

318 Mean DPH per night ( $\pm$  SE) for the period until maximum area was reached was

319  $290m (\pm 24.9)$  for RH foxes and  $361.3m (\pm 41.9)$  for WC ones. There was no

320 difference between the two groups (Linear regression,  $F_{1, 179} = 0.4554$ ,  $P > 0.05$ ).

321 However there were seasonal differences, with greater distances travelled in spring  
322 than in summer (Table 3). Following removal of RH7 the results changed little; again  
323 there was a seasonal effect and distances were greater in spring (Table 3). Mean DPH  
324 per night ( $\pm$  SE) for the period until asymptote was reached was 204.6 m ( $\pm$ 26.1) for  
325 RH foxes and 374.6 m ( $\pm$  46.5) for WC ones. Wild-caught foxes travelled further than  
326 rehabilitated ones (Table 3) and females travelled further than males. Again, DPH  
327 varied between seasons but in this case foxes travelled further in spring than in  
328 winter. A significant interaction was detected between CS and sex (Table 3).  
329 Following removal of WC12 and WC13, sex became non-significant (Linear  
330 regression,  $F_{1, 139} = 2.0771, P > 0.05$ ) but the effect of CS and season remained  
331 (Table 3). Again the results did not change markedly following removal of RH7.

332

## 333 **4. Discussion**

### 334 **4.1 Evidence of territorial displacement**

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

344 However, for other movement measures we either did not detect a difference between  
345 capture status groups, or found the reverse relationship. Wild-caught foxes travelled

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

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

## 365 **4.2 Seasonal and sex-related patterns**

366 Seasonal patterns in time to establish a stable home range, and nightly distance  
367 travelled, did not vary between capture status groups in our study. For both groups  
368 greater distances were travelled in spring, and the establishment of stable home  
369 ranges was delayed in the summer and accelerated in the winter. This is broadly  
370 consistent with the stages of the fox reproductive cycle, and associated shifts in both  
371 energetic requirements and territorial activity, which themselves reflect changing

372 weather conditions. However, the extent to which seasonal changes in food  
373 availability drive these patterns is unclear. Although food availability is widely  
374 considered to be a limiting factor driving territory size and ranging behaviour in  
375 carnivores (Macdonald, 1983) anthropogenic food sources are significant components  
376 of urban fox diet (e.g. scavenged food comprised 64% of fox diet by weight in Bristol  
377 [Saunders et al., 1993]) and tend to be more consistently available throughout the year  
378 than natural food items (White et al., 1996).

379 Our findings showed interactions between: i) season and capture status in terms of  
380 time to traverse maximum area used; and ii) sex and capture status in terms of nightly  
381 distance travelled for the period until a stable range was reached. There are two well-  
382 documented processes by which male and female movement patterns might be  
383 expected to differ from random over the annual cycle in resident foxes. These are:  
384 increased female activity in spring and summer due initially to lactation and  
385 subsequently to provisioning of semi-dependent cubs (e.g. Saunders et. al, 1993); and  
386 winter expansion of male ranges due to forays in search of extra-group mating  
387 opportunities (e.g. White and Harris, 1994; White et al., 1996; Soulsbury et al., 2011).  
388 In our study the behaviour of the wild-caught female cohort was skewed by breeding  
389 and putative alloparenting exhibited by the two vixens WC12 and WC13. Removal of  
390 these two animals from the main dataset both eliminated the effect of sex on nightly  
391 distance travelled, and lessened the effect of season (presumably by reducing the  
392 breeding spike in activity in spring) resulting in a more uniform effect of capture  
393 status for non-breeding animals. However the greater nightly distances travelled by  
394 wild-caught foxes persisted.

395 Although this at first appears unexpected in the context of prediction two (that  
396 rehabilitated foxes would travel greater distances) the prediction is only logical where  
397 distances represent cumulative trajectories in one direction rather than repetitive



398 movements within a smaller area. The latter are consistent with: i) patrolling of  
399 resident territories; ii) exploiting reliable resources such as food supplied by  
400 householders; and iii) denning, and rearing cubs. Supplementary feeding of foxes by  
401 householders in Brighton and Hove is common whilst fox densities and  
402 corresponding territorial defence are high (Scott and Tolhurst unpublished  
403 observations). Furthermore, home-ranges were small for wild-caught foxes in the  
404 current study and at least two animals were provisioning cubs, supporting the  
405 assertion that greater distance travelled was indicative of resident territorial  
406 behaviour.

### 407 **4.3 Patterns of space use**

408 Three distinct patterns of space use emerged in our study: one where a stable home  
409 range was never established; a second where home range extent was equal to the  
410 maximum area covered; and a third where maximum area peaked at an early stage,  
411 and home range was established later. Under the classification system presented by  
412 Dekker et al (2001), the first pattern is similar to the early stages of dispersal or of  
413 itinerant animals that are non-territorial and range over large areas. The second  
414 pattern suggests that the fox is resident and, either solely or jointly, defends an  
415 existing territory. The third indicates an initial exploratory period where the fox  
416 ranges widely over a large area before ‘settling ’ on a smaller section of that area for  
417 habitual use (i.e. a home range) and is analogous to the two-stage process reported by  
418 Robertson and Harris (1995) for captive-bred juveniles. Based on this classification,  
419 in the current study the relative proportion of dispersing or itinerant foxes was higher  
420 for the rehabilitated group, indicating that for these animals temporary captivity led to  
421 territorial displacement. However this pattern was not universal – for example two of  
422 the wild-caught foxes in the study could also be categorised as dispersing or transient.  
423 As both of these animals were non-breeding vixens of approximately 4-5 years of

424 age, it is possible that they were transient as a consequence of social exclusion from a  
425 group territory. Patterns of space use are however inevitably dynamic where foxes  
426 occur at high-densities in urban areas with high rates of population turnover.

#### 427 **4.4 Welfare implications of displacement**

428 Dispersal is linked to an increase in mortality (e.g. Robertson and Harris, 1995; Baker  
429 et al 2007) and we demonstrate here the similarities between dispersal and the ranging  
430 behaviour of displaced rehabilitated animals. It therefore follows that foxes subject to  
431 rehabilitation might subsequently be at greater risk of death. The single fatality  
432 recorded during our study was a rehabilitated animal but this was believed to have  
433 occurred due to existing disease and was therefore a probable cause rather than  
434 consequence of captivity. Thus we did not find evidence of greater mortality in the  
435 rehabilitated cohort during the study period. However, there are a number of social  
436 and nutritional stressors that dispersing and itinerant foxes are vulnerable to,  
437 including: i) the threat of aggressive extra-group encounters (White and Harris,  
438 1994); the absence of enriching social contact between members of the same social  
439 group (e.g. Hovland et al., 2011); and iii) the higher energetic costs associated with  
440 erratic movements, lack of knowledge of the location of food patches, and the  
441 opportunity costs of foraging time lost (Robertson and Harris, 1995b). The displaced  
442 rehabilitated foxes in our sample are likely to have suffered at least some of these  
443 negative yet sub-lethal effects, with potential long-term implications for survival.  
444 Further research into these effects is necessary to determine the full consequences of  
445 displacement.

#### 446 **4.5 Limitations of the study**

447 Limitations of the study include: i) lack of replication of both capture status groups  
448 across different urban areas and associated potential for bias arising from city-specific

449 factors; and ii) small and unbalanced datasets, particularly when comparing ranging  
450 parameters for foxes that reached home range asymptote. Further work with a larger  
451 sample of rehabilitated animals is advised to determine whether the variability of this  
452 group is an inherent characteristic or an artefact of small sample size.

#### 453 **4.6. Management implications and conclusions**

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

#### 459 **5. Acknowledgements**

460 The study was part-funded and supported by Channel 4, Windfall Films and the  
461 British Broadcasting Corporation (BBC). These sponsors were not involved in study  
462 design, analysis or interpretation of the data, nor writing of the report. We are  
463 especially grateful to Jamie Lochhead and Kelly Neaves (Windfall Films) and Bill  
464 Markham and James Smith (BBC). We also thank Roger and Fleur Musselle at  
465 Roger's Wildlife Rescue. We are indebted to the University of Brighton students who  
466 assisted with trapping foxes, in particular Naomi Charman and Kate Davies. Finally  
467 we extend special thanks to the householders who allowed us to trap foxes in their  
468 gardens and without whom the study would not have been possible.

469

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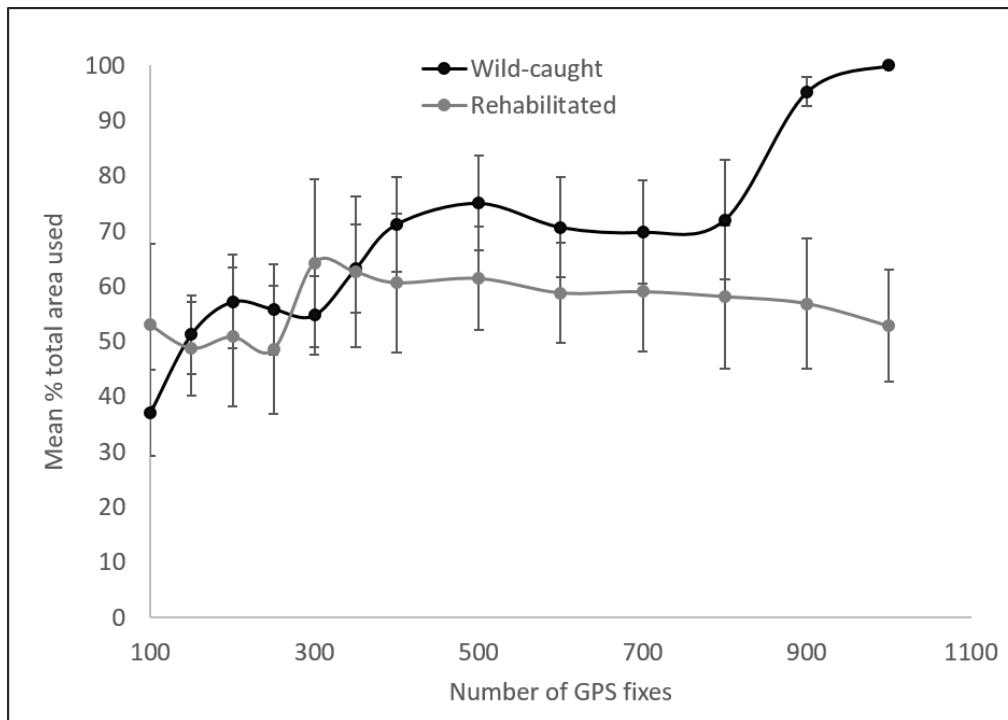
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614 **Figure 1** Incremental Area Analysis (IAA) plot of number of locations to reach  
 615 maximum area (i.e. 100% of Home Range Area) for rehabilitated (n = 7) versus wild-  
 616 caught (n = 13) foxes, expressed as mean % area used ( $\pm$  SE).

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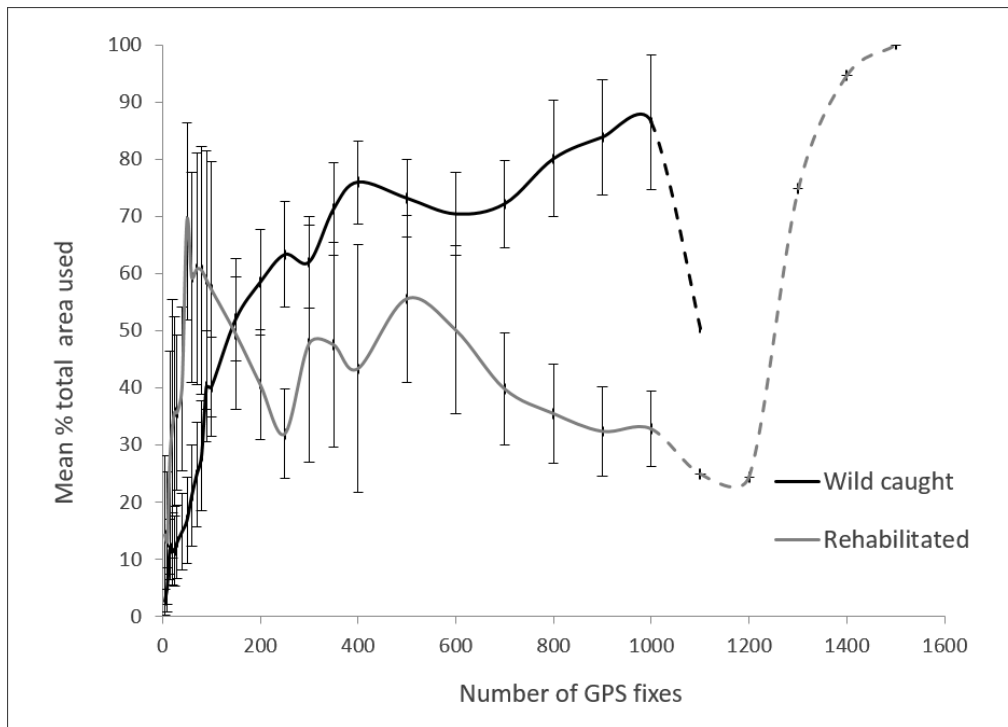
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630 **Figure 2** Incremental Area Analysis (IAA) plots of number of locations to reach  
 631 home range asymptote for rehabilitated (n = 4) versus wild-caught (n = 11) foxes,  
 632 expressed as mean area used ( $\pm$  SE). Dotted lines represent data for a single animal  
 633 (rehabilitated female RH5)

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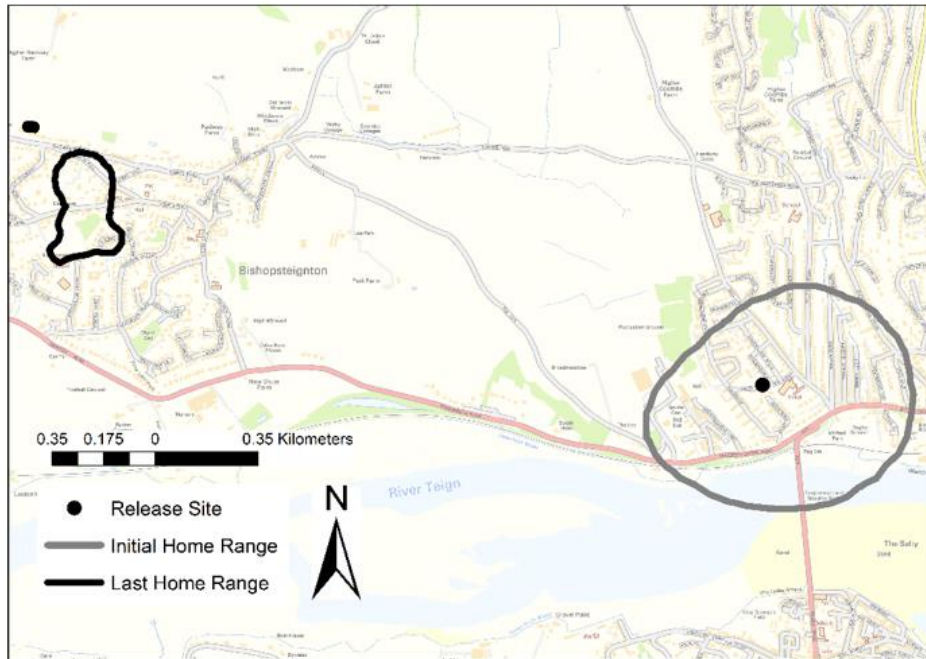
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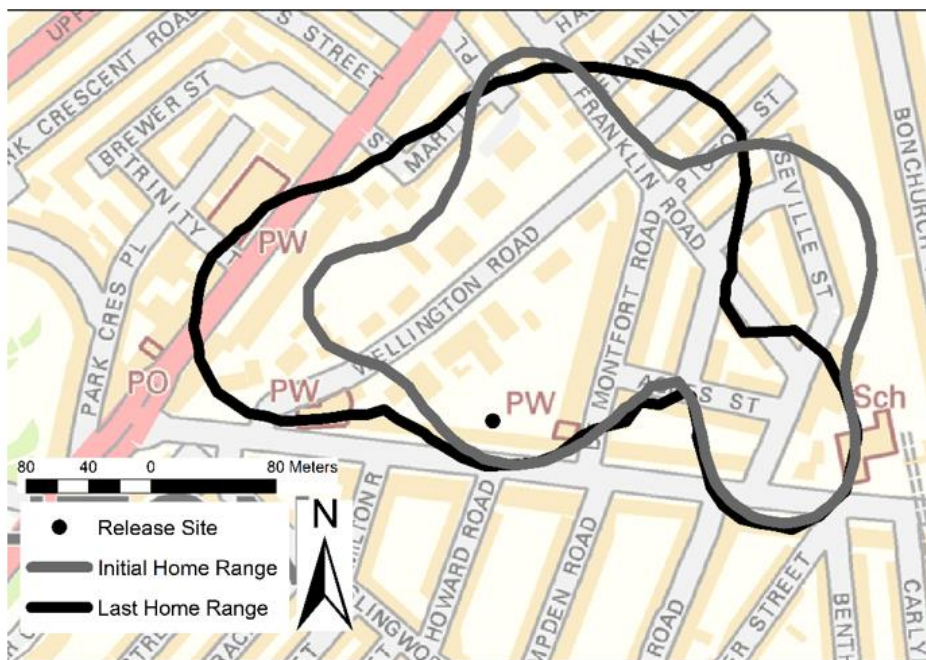
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646 **Figure 3** Examples of variation in percentage overlap between initial (first 3 days)

647 and final (last 3 days) 95% home range kernel isopleths for rehabilitated and wild-

648 caught foxes; showing a) rehabilitated female RH5; and b) wild-caught male WC9,

649 tracked in Autumn 2013

Code	Sex	Approx. age	Capture status	Season tracked	Year tracked	Area Tracked	Total locations	Total nights
WC1	Male	2 years	WC	Spring	2012	Brighton	4181	17
WC2	Male	2 years	WC	Spring	2012	Brighton	1620	65
WC3	Female	4 years	WC	Spring	2012	Brighton	1558	19
WC4	Female	1 year	WC	Spring	2012	Brighton	1515	30
WC5	Male	2 years	WC	Spring	2013	Brighton	1341	22
WC6	Male	1 year	WC	Spring	2013	Brighton	2637	20
WC7	Male	2 years	WC	Spring	2013	Hove	2854	45
WC8	Male	2 years	WC	Autumn	2013	Hove	1002	133
WC9	Male	10 months	WC	Autumn	2013	Brighton	681	147
WC10	Female	5 years	WC	Winter	2013	Brighton	968	87
WC11	Female	8 months	WC	Winter	2014	Brighton	784	86
WC12	Female	2 years	WC	Spring	2014	Brighton	209	17
WC13	Female	4 years	WC	Spring	2014	Brighton	245	16
RH1	Male	1 year	RH	Spring	2012	Newport	1718	32
RH2	Male	2 years	RH	Spring	2012	Brixham	2327	31
RH3	Male	1 year	RH	Spring	2012	Manchester	1047	19
RH4	Female	18 months	RH	Spring	2012	London	1141	16
RH5	Male	3 years	RH	Summer	2013	Rustington	2220	36
RH6	Female	8months	RH	Autumn	2013	Teignmouth	1629	110
RH7	Male	11 months	RH	Winter	2014	Woodingdean	102	9

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651 **Table 1** List of foxes that were GPS-tracked during the 2-year study, showing capture  
652 status (WC = wild-caught; RH = rehabilitated), approximate age and sex, season,  
653 location and length of time tracked in terms of both nights and number of locations.

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Capture Status (CS)	Mean nights to maximum area ( $\pm$ SE)	Mean nights to asymptote ( $\pm$ SE)	Proportion asymptote equals max. area
Rehabilitated	8.43 ( $\pm$ 3.44)	15.00 ( $\pm$ 2.66)	2/4* = 50% 1/4**= 33%
Wild-caught	9.54 ( $\pm$ 2.64)	11.73 ( $\pm$ 1.03)	7/11= 64%

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

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

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687 **Table 3** Significant variables predicting distance travelled by foxes in metres per hour

688 per night for the time period until: i) asymptote was reached; and ii) maximum area

689 was reached, using linear fixed effects models. ANOVA = Analysis of Variance; CS

690 = capture status; x operator indicates interaction term. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ;691 \*\*\*  $P < 0.001$ .

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Time period until maximum area reached				Time period until asymptote reached			
	<i>MLPE</i>	<i>t</i>	<i>P</i>		<i>MLPE</i>	<i>t</i>	<i>P</i>
Spring v. Summer	0.167	2.43	*	WC v. RH	0.32	5.25	***
				Spring v. Winter	0.26	2.59	*
				♀ v. ♂	0.53	3.93	***
<b>Results after fox RH7 removed</b>							
Spring v. Summer	0.167	2.45	*	WC v. RH	0.33	5.27	***
				Spring v. Winter	0.30	2.69	**
				♀ v. ♂	0.55	4.01	***
<b>Results after foxes WC12 and WC13 removed</b>							
				WC v. RH	0.27	4.52	***
				Summer v. Spring	0.16	2.40	*
				Summer v. Winter	0.28	2.43	*

698 **Table 4** Post-hoc tests for significant variables predicting distance travelled by foxes  
699 in metres per hour per night for the time period until: i) asymptote was reached; and  
700 ii) maximum area was reached, using linear fixed effects models. MLPE = Maximum  
701 Likelihood Parameter Estimate; WC = wild-caught, RH = rehabilitated; v. = versus;  
702 direction of difference indicated by positive or negative operator. \*  $P < 0.05$ ; \*\*  $P <$   
703  $0.01$ ; \*\*\*  $P < 0.001$ .

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