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1	Title: Managed parks as a refuge for the threatened red squirrel (Sciurus vulgaris) in light of human
2	disturbance
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24 Abstract

25 As the invasive grey squirrel continues to spread, red squirrels are dying out. The result may 26 be isolated populations in managed parks, where access can be controlled. However, recreation can 27 often have a negative effect on wildlife, reducing the conservation potential of parks. Fota Wildlife 28 Park receives over 300,000 visitors each year and is located on an island that is currently free of grey 29 squirrels. We examined the effect of visitors on the existing red squirrel population. Sampling was 30 conducted in the presence and absence of the public. Ten trapping sessions took place from March 2013 to 2014 and faeces were collected to examine stress levels. Squirrels were observed to 31 32 concentrate their activity in non-public areas and move into public areas when the park was closed. 33 Radio tracked squirrels, from the adjacent gardens (intermediate disturbance), also used habitats in the wildlife park (high disturbance) when it was closed but returned when the park had opened. When 34 35 squirrels were observed in public areas, visitors were only visible on 15% of occasions. Levels of 36 faecal cortisol metabolites (FCM) were highest in areas where human disturbance was greatest. 37 However, there was no correlation between visitor numbers and the stress levels of squirrels. FCM 38 levels were however, positively correlated with density of squirrels. The fact that high numbers of 39 squirrels continued to utilise the wildlife park demonstrates that managed parks could provide an 40 important reserve for the maintenance of the species, as long as non-public areas are accessible.

41 **Keywords:** Glucocorticoids; invasive species; reserves; wildlife park

42 Introduction

The increase in tourism and recreational activities in recent times potentially adds to the already increasing pressure on endangered and vulnerable wildlife, (Lowney, 2011; Taylor and Knight, 2003). In the U.S. it is the second leading cause of the decline of federally threatened and endangered species on public lands (Losos et al., 1995). Gill (2007) commented on the potential dilemma this causes, due to the need for public access to wildlife, for educational purposes. However, wild animals often perceive humans as potential predators (Beale and Monaghan, 2004; Gill et al., 1996; Hosey, 2000), which may result in animals avoiding parts of their normal range (Gander and Ingold, 1997; Hamr, 1988) and a cessation of foraging, fleeing or altered reproductive behaviour (Cole and Knight, 1991). For instance, human disturbance was found to have a significant negative effect on the nesting success of guillemots (*Uria aalge*) and kittiwakes (*Rissa tridactyla*) in Scotland (Beale and Monaghan 2003) and reindeer (*Rangifer tarandus*) densities increased in winter, when outdoor activities declined in Lapland (Helle and Särkelä, 1993).

55 However, it has been shown that while certain species may avoid human presence it may 56 have little effect on others with some animals habituating to the predictable nature of human 57 disturbance along trails (Knight and Cole, 1995; Whittaker and Knight, 1998). Well-managed 58 tourism and recreational activities can even have direct benefits to certain wildlife species, as they can reduce both inter- and intraspecific conflict as well as having a disturbance effect on predators 59 (Lowney, 2011). Other animals may not show any behavioural responses to disturbance due to high 60 cost (Frid and Dill, 2002). Thus, Thiel et al. (2008) stated the need for a combination of methods, 61 62 utilitising both behavioural and a physiological measure of stress to evaluate possible responses to 63 human disturbance. This was confirmed in their study on Capercaillie, Tetrao urogallus where the 64 physiological response to winter tourism was more pronounced and obvious than the behavioural 65 response (Thiel et al. 2008).

66 Over the past 25 years, non-invasive ways for measuring glucocorticoid metabolites in 67 excreta have been increasingly used to evaluate stress levels in laboratory, domestic, zoo and free-68 ranging animals (Palme et al., 2005; Sheriff et al., 2011). The front-line hormones to overcome 69 stressful situations are the glucocorticoids and catecholamines and these hormones are determined 70 as a parameter of adrenal activity and thus of disturbance (Möstl and Palme, 2002). The consequences 71 of chronic stress may be of particular importance for species inhabiting disturbed landscapes 72 (Macbeth et al., 2010) and in areas of high levels of human activity, as has been recorded in pine 73 martens (Martes martes) in North West Spain (Barja et al., 2007) and elk (Cervus canadensis) in 74 South Dakota (Millspaugh, 1999).

Another leading threat to biodiversity (Wilcove et al., 1998) is the introduction of non-native
 species, which continues to cause global ecological concern (Manchester and Bullock, 2000), with

77 the monitoring of biological invasions being highlighted as a priority (Latombe et al. 2016). In the 78 U.K. the red squirrel has disappeared from most of the areas now occupied by the grey squirrel 79 (Reynolds, 1985) and it has been suggested that continuation at the current rate of decline will result in extinction of the red squirrel throughout the U.K. by 2023 (Tompkins et al., 2003). Following its 80 introduction to Ireland in 1911 (Watt, 1923), the grey squirrel (Sciurus carolinensis) has spread and 81 82 is now found in 26 of the 32 counties (Carey et al., 2007). This has resulted in a 30% contraction in 83 the range of the native red squirrel in Ireland in the last 10 years alone (Poole and Lawton, 2009). 84 Grey squirrels are currently absent from south Cork (Carey et al., 2007). However, Goldstein et al. 85 (2014) confirmed that the southern frontier of the grey squirrel range has progressed in a south westerly distribution since the 2007 survey. Clearly, red squirrel populations in South Cork and Kerry 86 87 are particularly at risk as it is inevitable that the grey squirrel will eventually occupy all counties. 88 Given their inevitable decline, it is likely that red squirrel populations may become isolated to small 89 enclosed parks, where grey squirrel access can be controlled. However, how would the more 90 secretive of the two-species fare in these parks, especially if they are used by the public?

With reserves becoming established within the U.K. to conserve remaining red squirrel populations (Lowney 2011), we aimed to examine the potential of a busy wildlife park as a refuge for red squirrels in an area currently free of the invasive grey. Given the more secretive nature of the red squirrel we hypothesised that squirrels occupying the busy wildlife park may have elevated levels of FCM and may modify their behaviour to reduce human encounters. However, we hypothesised that the park may still offer the potential to sustain healthy populations of this vulnerable species.

97 Materials and Methods

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98 Study site
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99 The study was carried out between December 2012 and March 2014 in Fota wildlife park
100 (51.889585° N, 8.311276° W), 16.7 km from Cork City, Ireland. The wildlife park is located on an
101 island connected to the mainland by two road bridges and a train bridge. The 315-hectare island
102 includes a stately home and gardens (29 hectares), an 18 hole golf course and resort (243 hectares;

including a scout camp) and the wildlife park (32 hectares). An additional 11 hectares of land is
currently being developed to expand the wildlife park and incorporates bordering areas of car park
and woodland patches between the wildlife park and gardens (Fig. 1).

The wildlife park has been open since 1983 and has received over 4 million visitors between 107 1983-2004. The park is open year round with visitor peaks in the summer months. There is a total of 108 26 tree species in the wildlife park comprised of a mixture of native and non-native species. Most 109 trees are mature (>50 years old), some much older trees originate from the original plantings carried 110 out in the 19th century for the Fota estate.

111 Trapping

112 As part of a larger study, thirty squirrel traps (STV076 Defenders-STV International), 113 modified with a nest box were placed around the island in February 2013 and pre-baited for a period 114 of two weeks before trapping commenced. Traps were placed in areas of high public disturbance 115 (wildlife park), intermediate disturbance (gardens and surrounding area) and low levels of human 116 disturbance (woodland within the golf course; Fig. 1). Ten trapping sessions took place between 117 March 2013 and March 2014, resulting in 1080 trap days. On the morning of each trapping session, 118 traps were baited with hazelnuts, whole maize and peanuts. Traps were then checked a maximum of 119 six hours later.

120 Each trapped squirrel was flushed into a light hessian bag and then put in a wire-mesh 121 'handling cone' to minimize stress during handling. All animals were individually marked using 122 passive integrated transponder tags (MID Fingerprint, Bournemouth, Dorset, UK) inserted into the 123 nape of the neck. The sex and reproductive condition were recorded. An individual was considered 124 to be in breeding condition if the nipples were visible in females and the testes were scrotal and large 125 in males (Wauters and Dhondt, 1993). Each animal was weighed using a Pesola spring scale balance 126 with clip (NHBS, Devon, U.K) and the shin length taken using vernier callipers. All applicable 127 institutional and national guidelines for the care and use of animals were followed and all procedures 128 were carried out in accordance with current regulations. Licenses (S.23-capturing and S.32-tagging) 129 were obtained from the Department of Environment, Heritage and Local Government.

130 Radio-tracking

131 As part of a larger study investigating tree preference (Haigh et al., 2015), ten individuals 132 $(5^{\bigcirc}, 5^{\bigcirc})$ on the island were fitted with radio-collars (Holohil Systems Ltd, Carp, Ontario, Canada). Four $(3^{\circ}_{+}, 1^{\circ}_{\circ})$ of the tagged squirrels were resident in the high disturbance area. Four $(1^{\circ}_{+}, 3^{\circ}_{\circ})$ 133 squirrels were located in the intermediate disturbance area and two (19, 13) were resident at the low 134 135 disturbance area. Once tagged, fixes were obtained on two days each week for a period of six hours 136 per day. A fix was obtained on average every hour, with each fix representing a sighting of the 137 animal. Sampling took place over two time periods, between morning to midday and midday to late 138 afternoon with equal sampling times being conducted in each time segment to examine movement 139 in and out of the wildlife park (high disturbance area). Of the 10 squirrels that were radio-tagged, a 140 mean of 99 (\pm 16) fixes per individual (range 48-183) were obtained, over a mean of 7 (\pm 0.17) months 141 (range 4-12). When located, the behaviour of the animal was recorded for a minimum of ten minutes 142 or until the squirrel was no longer visible. The number of visitors (if any) visible by the observer 143 from that location was also recorded. In addition, daily visitor numbers were obtained from park 144 staff.

145 San

Sampling/Locating squirrels

146 The 32 ha park (high disturbance) consists of non-public areas (8 ha) and areas accessible to the public (24 ha). Two 1 km routes were selected, one encompassing areas in the public domain and 147 148 the other, covering areas that were not accessible to the public (Fig. 2). The park is open from 10 am-149 5 pm daily during the summer, closing at 4 pm in the winter, with staff arriving around 8 am. For the 150 purpose of this study the park was accessible to the authors 24 hours a day. These two transects were 151 walked at a steady pace at times when the park was closed and again when it was open and all squirrel 152 encounters were recorded. When a squirrel was observed, its GPS (Garmin) location was recorded, 153 where possible its behaviour (Table 1), and the number (if any) of visitors that were visible to the 154 observer from that location. Temperatures (°C) were obtained from MET Eireann (www.met.ie).

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Faecal cortisol metabolites (FCM)

158 At the time of capture, faeces from individual squirrels were collected from all 30 traps on 159 the island. This was to investigate variations in stress levels between the different areas of the island 160 and whether elevated stress levels were correlated with the greater public disturbance in the high 161 disturbance area in comparison to areas of low public disturbance. When faecal matter was present, 162 it was removed using forceps and placed in vials and labelled with the P.I.T tag identification code 163 of that squirrel. Faeces were only collected if that squirrel had not previously been caught in that 164 trapping session, to eliminate recording elevated stress levels due to trapping. Samples were placed in freezer bags and frozen at -20 °C a maximum of four hours later. At the end of trapping in March 165 166 2014, samples were sent on dry ice to the University of Veterinary Medicine, Vienna and extracted 167 as previously described in detail (Touma et al., 2003; Dantzer et al., 2010; Dantzer et al., 2011; Palme 168 et al., 2013). FCM were analysed with a 5α -pregnane-3 β ,11 β ,21-triol-20-one enzyme immunoassay 169 (EIA) which measures glucocorticoid metabolites with 5α -3 β ,11 β -diol structure (Touma *et al.* 2003). 170 This EIA has been successfully validated in different squirrel species (Bosson et al., 2009, 2013; 171 Dantzer et al., 2010) including the European red squirrels, *Sciurus vulgaris* (Dantzer et al., 2016).

172 Data analysis

173 Means are provided with standard errors unless otherwise stated. All analysis was performed 174 on IBM SPSS statistics 22 (IBM, NY). Chi Square tests were used to compare the observed number 175 of squirrel fixes with what would be expected along transects and whether the park was opened or 176 closed to the public. These tests were also used to examine whether there was a significant 177 relationship between the number of squirrel fixes in public and non-public areas. To investigate a number of potential factors that could influence FCM levels, a general linear model (GLM) was 178 179 performed. Factors tested included season, sex, breeding condition, weight, temperature, visitor 180 numbers and whether the area experienced low, intermediate or high public disturbance. Residuals 181 were checked for normality using the Kolmogorov Smirnov test (P>0.05). Due to the low sample 182 size for some months, the year was divided into four seasons (December-February; March-May; 183 June-August and September-November). The mean temperature was 10 ± 4 (SD) °C and the number of visitors per day 428 ± 666 (5 (min)-2467 (max)). All assumptions were met, with for example the data showing independence of residuals (Durbin-Watson-1.729) (Durbin and Watson, 1951, Hocking, 2013), no evidence of multicollinearity (as assessed by tolerance values of >0.1) and a maximum Cooks distance score of 0.168. Stepwise model selection was performed by eliminating parameters with p values >0.05. To investigate whether there was an effect of the number of individual squirrels caught per area and the FCM levels, a spearman rank correlation was performed.

190 **Results**

191 Distribution of radio-tagged squirrels

192 A total of 481 fixes were collected from four $(3^{\bigcirc}, 1^{\bigcirc})$ squirrels in the high disturbance area 193 from March 2013 to March 2014. Significantly more fixes were obtained in non-public (n=397) than public (n=84) areas (x^2 =87.68, df=18, p<0.001; Fig. 3). The non-public areas were dominated by 194 195 areas of yew (Taxus baccata) and squirrels were found to select this tree species at all times of the 196 year (Haigh et al. 2015). An exception to this was a yew rich area which was situated in the public 197 area at the entrance of the park. There was significantly more radio-fixes obtained in public areas when the park was closed as opposed to when it was open to the public ($x^2=33.00$, df=17, p<0.01). 198 199 For instance, in one public area bordering a non-public zone, up to six squirrels were seen foraging 200 on the ground beneath a stand of yew just prior to the park's opening. However, as soon as the park opened they either left the park or retreated to non-public areas (pers. obs.). Four $(1^{\circ}_{+}, 3^{\circ}_{\circ})$ of the 201 202 squirrels first trapped in the intermediate disturbance area also entered the high disturbance area, 203 particularly the aforementioned stand of yews (public area). They were observed to utilise this area 204 significantly more at times when the park was closed and occupy the intermediate area when it was 205 open (x²=10.15, df=2, p<0.01). The other squirrels (1 \bigcirc , 1 \bigcirc) were resident in the low disturbance 206 area and were never recorded in the area of high disturbance.

207 All other sightings

Non-radio-tagged squirrel sightings were recorded over 80 days (twice a week) from March 209 2013 to March 2014, resulting in a total of 299 observations. There was a significantly higher number 210 of observations ($x^2 = 24.49$, df=15, p<0.05) in non-public areas (n=200) than public areas (n=99) but there was no significant difference in the number of observations along the transects, when the park was open or closed to the public ($x^2 = 17.3$, df=15, p>0.05). However, activity was concentrated in non-public areas with more incidences of them being in public areas when the park was closed (46 vs. 32 observations) and in non-public areas when the park was open (168 vs. 53). When squirrels were observed in public areas during open times, visitors were observed on only 15% of occasions.

216 Behaviour

In the majority of observations squirrels were either foraging (54 (public) and 33 (nonpublic) %) or jumping and climbing (20 and 35%). There was little difference in the behaviour of squirrels in the public and non-public areas and depending on whether visitors were present or not (Table 2). Notably, there was no difference in vigilance behaviour when people were present or absent (Table 2).

FCM levels

223 Over the ten trapping sessions, 52 faecal samples were collected from 34 separate individuals $(16^{\circ}_{\pm}, 18^{\circ}_{\circ})$. A mean of 1.6 ± 0.03 (SE; range 1-5) samples were collected per individual. The mean 224 225 $(\pm$ SD) weight of squirrels was 358 \pm 26 g. The general linear model revealed two factors (area and breeding condition) that significantly affected the squirrels FCM levels ($R^2 = 0.494$, $F_{2, 49} = 7.917$, 226 p=0.001; F_{1, 50} =6.185, p=0.016; Table 3). Mean FCM levels were higher (mean 14.3 ±2.64) in the 227 228 high disturbance area than in the low disturbance area (mean 6.35 ± 3.34). Mean FCM levels (µg/g 229 facees) of squirrels were almost double when they were not in breeding condition (14.8 ± 2.68) , as 230 opposed to when they were (7.08 ± 1.58) . This pattern was apparent in both males and females. There 231 was no significant relationship between the stress levels of squirrels and the number of visitors in the 232 park (p=0.370) and this was therefore excluded from the model. For instance, the lowest FCM levels were found in June-August when the park was at its busiest (Fig. 4) and highest in September-233 234 November when the park was quietest. Instead the density of other squirrels had an effect with a significant correlation ($r_s=0.813$, p<0.01, Spearman's rank) between FCM levels and the number of 235 236 different individuals that were caught in that trap over the study period, suggesting that squirrels in

areas where there was a higher number of captures/squirrel density, also had elevated stress levels(Fig. 5).

239 Discussion

240 This study hypothesised that red squirrel densities would be lower in areas exhibiting the 241 highest levels of human disturbance and that squirrels would avoid human encounters, as has been 242 found in previous studies on red squirrels (Lowney 2011), mountain hares Lepus timidus; (Rehnus 243 et al., 2014) and black grouse, Tetrao tetrix; (Arlettaz et al., 2007; Formenti et al., 2015). In contrast 244 to what was hypothesised, squirrel densities in the current study were higher in the areas with the 245 highest levels of human disturbance. However, while densities were higher in these areas, squirrels 246 did show avoidance behaviour. For instance, when squirrels were observed in public areas during 247 open times, they were always near non-public areas and the public were only visible on 15% of 248 occasions. Similarly, Thiel et al. (2008) stated that capercaillie probably use skiing areas only when 249 undisturbed refuges are also available within their home ranges.

250 In accordance with the hypothesis, there was also evidence that squirrels altered their activity 251 to avoid human encounters and may have habituated to the opening hours of the park. Blanc et al. 252 (2006) recorded how habituation can occur frequently among species, if as Conomy et al. (1998) 253 stated animals experience a regular and predictable stimulus which does not represent a lethal threat. 254 In the same manner, the red squirrels in the high disturbance area, may have adapted to the routine 255 of visitor times, something which is suggested by their movement into public areas during times 256 when the park was closed. Furthermore, squirrels that inhabited adjacent areas of the park were also 257 observed to enter the park during closed periods.

The immediate response of many animals to disturbance is a change in behaviour, which can result in a trade-off between avoiding perceived risk and other fitness enhancing activities such as feeding, parental care and mating (Frid and Dill, 2002). Some animals may compensate for energy losses by increasing their food intake after the disturbance event (Blanc et al. 2006; Arlettaz et al. 2014). Experimental disturbance of black grouse resulted in an extension of feeding duration during the following evening foraging bout, confirming the prediction that black grouse must compensate for the extra energy expenditure elicited by human disturbance (Arlettaz et al., 2014). However, the fact that squirrels did not change behaviours such as foraging and vigilance in public and non-public areas and at times when the park was open and closed, suggests that the squirrels were displaying habituation rather than compensatory strategies.

268 In the current study, we hypothesized that squirrels occupying areas of the highest visitor 269 numbers would have associated elevated FCM levels, as for instance has been observed in 270 capercaillie who showed markedly increased stress hormone levels closer to locations with winter 271 recreation activity (Thiel et al. 2008, 2011). However, while FCM levels of squirrels were higher in 272 the high disturbance areas, than in the intermediate and low disturbance areas, there was no 273 correlation between visitor numbers and stress levels. Visitor numbers were highest in June-August 274 and at this time FCM levels were low amongst the squirrels in the park. Martin and Reale (2008) 275 observed that human frequentation did not affect cortisol levels in chipmunks suggesting that it was 276 not the main factor responsible for their stress reaction. Instead they stated that other factors such as 277 intraspecific aggression and predation might play a role in cortisol secretion. A higher number of 278 individuals were caught in traps in the high disturbance areas and higher FCM levels were observed 279 in those animals. Dantzer et al. (2013) observed that experimental elevation of actual and perceived 280 density induced higher maternal glucocorticoid levels. Squirrel densities were higher in the high 281 disturbance area (mean of 0.35 (\pm 0.03) (S.E) per ha) than in the intermediate (0.17 \pm 0.03 per ha) 282 and low disturbance areas (0.009 ± 0.007 per ha; Haigh et al. submitted) and this could potentially 283 result in an increased competition for resources from conspecifics and a subsequent increase in stress 284 levels. FCM levels in the current study were observed to be highest in September-November and 285 when the squirrels of both sexes were not in breeding condition. This is in accordance with some of 286 the findings of Dantzer et al. (2016) who described that the lowest FCM levels were present in 287 pregnant females. Wauters and Dhondt (1993) observed that after the breeding season, adult females 288 started to forage more intensively over the whole home range. This consequently results in more 289 frequent interactions with transients, and potential elevated stress levels through competition, which 290 may result in a 'stress of subordination' (Blanchard et al., 1993). Dantzer et al. (2016) also observed

elevated FCM levels in the autumn/winter period, something they attributed to more frequent
intraspecific interactions linked to dispersal, higher predation risk when foraging on the ground and
reduced food quality and/or more extreme weather conditions in winter. This pattern was also
observed in alpine chamois, *Rupicapra rupicapra* (Corlatti et al. 2014).

295 From a conservation perspective, human disturbance of wildlife is important only if it affects 296 survival or fecundity and hence causes a population to decline (Gill et al., 2001). Rehnus et al. (2014) 297 observed that female hares failed to reproduce following stress experiments and that higher FCM 298 levels observed as a result of tourism could negatively affect the reproduction of wild mountain hares 299 in the subsequent breeding season. This can have long term impacts with lower body masses and 300 lipid reserves as observed in disturbed chamois (Schnidrig-Petrig et al., 1998). However, in the 301 current study all squirrels caught exhibited weights that were in line with what was defined as healthy 302 in other studies (Wauters & Dhondt, 1989). In addition, no differences were observed between the 303 body or breeding condition of squirrels in disturbed versus undisturbed areas of the island (Haigh et 304 al. submitted) or in the vigilance of squirrels in public/non-public areas and in the presence of the 305 public.

306 Conclusions

307 In Ireland, the range expansion of the grey squirrel has been up to 13.4 km/year (Teangana 308 et al., 2000). Similarly, in Italy, following introductions from 1948 to 2000 the grey squirrel has 309 colonised at a mean rate of 17.2 km² per year and it is estimated that it could reach France in 2026-310 2031 and Switzerland in 2031-2041 (Bertolino et al., 2008). With this rapid spread of the grey, 311 managed parks will take on a greater importance for the maintenance of red squirrel populations. 312 While Southern (1964) commented how the red squirrel favours seclusion, Tittensor (1970) observed 313 that in city parks in Stockholm, red squirrels were as tame as grey squirrels in British cities. Similarly, 314 Rezouki et al. (2014) observed that an urban park near Paris, successfully maintained a viable 315 population of red squirrels and provided an important potential refuge for the species. In the case of 316 mountain hares, Rehnus et al. (2014) asserted that there should be regulations in areas where 317 mountain hare habitats overlap with human winter recreational activities, with tourists being confined

to marked trails. Likewise, the results of this study would suggest that red squirrels can habituate to 318 319 human disturbance, as long as non-public areas are also available. Forest patches that are inaccessible 320 to humans might provide a visual and acoustic shield from recreation activities in adjacent areas 321 (Thiel et al. 2008). It is therefore essential that management strategies are implemented to provide 322 these undisturbed areas for the maintenance of red squirrel populations in parks. Not only could these 323 parks provide important refuges for the maintenance and conservation of this endangered species but 324 these reserves could also provide important source populations for the recolonisation of other areas, 325 ensuring the long term survival of this species in the wild.

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474 Figure titles

- **Figure 1:** The 315 ha of Fota Island displaying the main recreational areas of the island.
- **Figure 2:** Public and non-public transects walked through the wildlife park.
- 477 Figure 3: Radio tracking fixes (n=481) from March 2013-March 2014, showing the squirrels
- 478 locations during visitor times and when the park was closed.
- **Figure 4:** Mean (±SD) number of visitors to Fota Wildlife Park per month and mean (±SD) FCM
- 480 levels (μ g/g faeces) of squirrels during the same period.
- 481 Figure 5: Mean FCM levels (µg/g faeces) per trap and the trapping density over nine trapping
 482 sessions.

Table 1: Ethogram of behaviours displayed by the squirrels. Recorded behaviour Description					
Necolucu I		This includes eating, digging at the ground, manipulating branches with			
Foraging/Ea	ting	forelimbs, and engagement in searching for food.			
Vigilant		The animal is frozen, flat on the branch, staring downwards			
		The squirrel is moving through the branches or between the trees without			
Climbing/ju	mping	stopping to forage.			
		This includes grooming, courtship behaviour, running, walking, vocalisations			
Other		or when the squirrel was stationary			
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 Table 1: Ethogram of behaviours displayed by the squirrels.

513	Table 2: The percentage of time that squirrels were observed engaged in each of the	e recorded
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514	behaviours in non-	public and public are	as and in the prese	ence and absend	ce of the public.
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			Public	
	Public areas (n=252)	Non-public areas (n=145)	People present (n=16)	No people presen (n=402)
Foraging/Eating	54	33	63	40
Vigilant	3	9	6	6
Climbing/jumping	20	35	25	28
Other	23	23	6	26

Table 3: The results of the general linear model, showing the factors significantly impacting on the

531	FCM levels of squirrels (B=unstandardised regression co-efficient, SE= standard error of the co-						
532	efficient; ß=standardised co-efficient).						
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		В	$\mathbf{SE}_{\mathbf{B}}$	ß	P value
]	Intercept	9.596	6.121		
	Area	8.596	2.707	.401	0.003
	Breeding condition	9.660	3.275	.373	0.005

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