Managed parks as a refuge for the threatened red squirrel (Sciurus vulgaris) in light of human disturbance

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

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Abstract

As the invasive grey squirrel continues to spread, red squirrels are dying out. The result may be isolated populations in managed parks, where access can be controlled. However, recreation can often have a negative effect on wildlife, reducing the conservation potential of parks. Fota Wildlife Park receives over 300,000 visitors each year and is located on an island that is currently free of grey squirrels. We examined the effect of visitors on the existing red squirrel population. Sampling was 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 concentrate their activity in non-public areas and move into public areas when the park was closed. 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 squirrels were observed in public areas, visitors were only visible on 15% of occasions. Levels of faecal cortisol metabolites (FCM) were highest in areas where human disturbance was greatest. However, there was no correlation between visitor numbers and the stress levels of squirrels. FCM levels were however, positively correlated with density of squirrels. The fact that high numbers of squirrels continued to utilise the wildlife park demonstrates that managed parks could provide an important reserve for the maintenance of the species, as long as non-public areas are accessible.

Keywords: Glucocorticoids; invasive species; reserves; wildlife park

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).

However, it has been shown that while certain species may avoid human presence it may have little effect on others with some animals habituating to the predictable nature of human disturbance along trails (Knight and Cole, 1995; Whittaker and Knight, 1998). Well-managed 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 (Lowney, 2011). Other animals may not show any behavioural responses to disturbance due to high cost (Frid and Dill, 2002). Thus, Thiel et al. (2008) stated the need for a combination of methods, utilising both behavioural and a physiological measure of stress to evaluate possible responses to human disturbance. This was confirmed in their study on Capercaillie, *Tetrao urogallus* where the physiological response to winter tourism was more pronounced and obvious than the behavioural response (Thiel et al. 2008).

Over the past 25 years, non-invasive ways for measuring glucocorticoid metabolites in excreta have been increasingly used to evaluate stress levels in laboratory, domestic, zoo and free-ranging animals (Palme et al., 2005; Sheriff et al., 2011). The front-line hormones to overcome stressful situations are the glucocorticoids and catecholamines and these hormones are determined as a parameter of adrenal activity and thus of disturbance (Möstl and Palme, 2002). The consequences of chronic stress may be of particular importance for species inhabiting disturbed landscapes (Macbeth et al., 2010) and in areas of high levels of human activity, as has been recorded in pine martens (*Martes martes*) in North West Spain (Barja et al., 2007) and elk (*Cervus canadensis*) in South Dakota (Millsbaugh, 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
the monitoring of biological invasions being highlighted as a priority (Latombe et al. 2016). In the U.K. the red squirrel has disappeared from most of the areas now occupied by the grey squirrel (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 introduction to Ireland in 1911 (Watt, 1923), the grey squirrel (Sciurus carolinensis) has spread and is now found in 26 of the 32 counties (Carey et al., 2007). This has resulted in a 30% contraction in the range of the native red squirrel in Ireland in the last 10 years alone (Poole and Lawton, 2009). Grey squirrels are currently absent from south Cork (Carey et al., 2007). However, Goldstein et al. (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 are particularly at risk as it is inevitable that the grey squirrel will eventually occupy all counties. Given their inevitable decline, it is likely that red squirrel populations may become isolated to small enclosed parks, where grey squirrel access can be controlled. However, how would the more 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.

Materials and Methods

Study site

The study was carried out between December 2012 and March 2014 in Fota wildlife park (51.889585° N, 8.311276° W), 16.7 km from Cork City, Ireland. The wildlife park is located on an island connected to the mainland by two road bridges and a train bridge. The 315-hectare island 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 1983-2004. The park is open year round with visitor peaks in the summer months. There is a total of 26 tree species in the wildlife park comprised of a mixture of native and non-native species. Most trees are mature (>50 years old), some much older trees originate from the original plantings carried out in the 19th century for the Fota estate.

**Trapping**

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

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

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

Sampling/Locating squirrels

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 the other, covering areas that were not accessible to the public (Fig. 2). The park is open from 10 am-5 pm daily during the summer, closing at 4 pm in the winter, with staff arriving around 8 am. For the purpose of this study the park was accessible to the authors 24 hours a day. These two transects were walked at a steady pace at times when the park was closed and again when it was open and all squirrel encounters were recorded. When a squirrel was observed, its GPS (Garmin) location was recorded, where possible its behaviour (Table 1), and the number (if any) of visitors that were visible to the observer from that location. Temperatures (°C) were obtained from MET Eireann (www.met.ie).
**Faecal cortisol metabolites (FCM)**

At the time of capture, faeces from individual squirrels were collected from all 30 traps on the island. This was to investigate variations in stress levels between the different areas of the island and whether elevated stress levels were correlated with the greater public disturbance in the high disturbance area in comparison to areas of low public disturbance. When faecal matter was present, it was removed using forceps and placed in vials and labelled with the P.I.T tag identification code of that squirrel. Faeces were only collected if that squirrel had not previously been caught in that 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 2014, samples were sent on dry ice to the University of Veterinary Medicine, Vienna and extracted as previously described in detail (Touma et al., 2003; Dantzer et al., 2010; Dantzer et al., 2011; Palme et al., 2013). FCM were analysed with a 5α-pregnane-3ß,11ß,21-triol-20-one enzyme immunoassay (EIA) which measures glucocorticoid metabolites with 5α-3ß,11ß-diol structure (Touma et al. 2003). This EIA has been successfully validated in different squirrel species (Bosson et al., 2009, 2013; Dantzer et al., 2010) including the European red squirrels, *Sciurus vulgaris* (Dantzer et al., 2016).

**Data analysis**

Means are provided with standard errors unless otherwise stated. All analysis was performed on IBM SPSS statistics 22 (IBM, NY). Chi Square tests were used to compare the observed number of squirrel fixes with what would be expected along transects and whether the park was opened or closed to the public. These tests were also used to examine whether there was a significant 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 performed. Factors tested included season, sex, breeding condition, weight, temperature, visitor numbers and whether the area experienced low, intermediate or high public disturbance. Residuals were checked for normality using the Kolmogorov Smirnov test (P>0.05). Due to the low sample size for some months, the year was divided into four seasons (December-February; March-May; 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.

Results

Distribution of radio-tagged squirrels

A total of 481 fixes were collected from four (3♀, 1♂) squirrels in the high disturbance area 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 areas of yew (Taxus baccata) and squirrels were found to select this tree species at all times of the year (Haigh et al. 2015). An exception to this was a yew rich area which was situated in the public 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 ($x^2=33.00$, df=17, p<0.01). For instance, in one public area bordering a non-public zone, up to six squirrels were seen foraging 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♀, 3♂) of the squirrels first trapped in the intermediate disturbance area also entered the high disturbance area, particularly the aforementioned stand of yews (public area). They were observed to utilise this area significantly more at times when the park was closed and occupy the intermediate area when it was open ($x^2=10.15$, df=2, p<0.01). The other squirrels (1♀, 1♂) were resident in the low disturbance area and were never recorded in the area of high disturbance.

All other sightings

Non-radio-tagged squirrel sightings were recorded over 80 days (twice a week) from March 2013 to March 2014, resulting in a total of 299 observations. There was a significantly higher number 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.

**Behaviour**

In the majority of observations squirrels were either foraging (54 (public) and 33 (non-public) %) 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**

Over the ten trapping sessions, 52 faecal samples were collected from 34 separate individuals ($16♀, 18♂$). A mean of $1.6 ± 0.03$ (SE; range 1-5) samples were collected per individual. The mean (± SD) weight of squirrels was $358 ± 26$ g. The general linear model revealed two factors (area and breeding condition) that significantly affected the squirrels FCM levels ($R^2 = 0.494$, $F_{2, 49}=7.917$, $p=0.001$; $F_{1, 50}=6.185$, $p=0.016$; Table 3). Mean FCM levels were higher (mean $14.3 ± 2.64$) in the high disturbance area than in the low disturbance area (mean $6.35± 3.34$). Mean FCM levels ($\mu g/g$ faeces) of squirrels were almost double when they were not in breeding condition ($14.8 ± 2.68$), as opposed to when they were ($7.08 ± 1.58$). This pattern was apparent in both males and females. There was no significant relationship between the stress levels of squirrels and the number of visitors in the 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-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 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).

**Discussion**

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

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

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

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

Conclusions

In Ireland, the range expansion of the grey squirrel has been up to 13.4 km/year (Teangana
et al., 2000). Similarly, in Italy, following introductions from 1948 to 2000 the grey squirrel has
colonised at a mean rate of 17.2 km² per year and it is estimated that it could reach France in 2026-
2031 and Switzerland in 2031-2041 (Bertolino et al., 2008). With this rapid spread of the grey,
managed parks will take on a greater importance for the maintenance of red squirrel populations.
While Southern (1964) commented how the red squirrel favours seclusion, Tittensor (1970) observed
that in city parks in Stockholm, red squirrels were as tame as grey squirrels in British cities. Similarly,
Rezouki et al. (2014) observed that an urban park near Paris, successfully maintained a viable
population of red squirrels and provided an important potential refuge for the species. In the case of
mountain hares, Rehnus et al. (2014) asserted that there should be regulations in areas where
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
human disturbance, as long as non-public areas are also available. Forest patches that are inaccessible
to humans might provide a visual and acoustic shield from recreation activities in adjacent areas
(Thiel et al. 2008). It is therefore essential that management strategies are implemented to provide
these undisturbed areas for the maintenance of red squirrel populations in parks. Not only could these
parks provide important refuges for the maintenance and conservation of this endangered species but
these reserves could also provide important source populations for the recolonisation of other areas,
ensuring the long term survival of this species in the wild.

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**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.

**Figure 3:** Radio tracking fixes ($n=481$) from March 2013-March 2014, showing the squirrels locations during visitor times and when the park was closed.

**Figure 4:** Mean ($\pm SD$) number of visitors to Fota Wildlife Park per month and mean ($\pm SD$) FCM levels ($\mu g/g$ faeces) of squirrels during the same period.

**Figure 5:** Mean FCM levels ($\mu g/g$ faeces) per trap and the trapping density over nine trapping sessions.
Table 1: Ethogram of behaviours displayed by the squirrels.

<table>
<thead>
<tr>
<th>Recorded behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging/Eating</td>
<td>This includes eating, digging at the ground, manipulating branches with forelimbs, and engagement in searching for food.</td>
</tr>
<tr>
<td>Vigilant</td>
<td>The animal is frozen, flat on the branch, staring downwards</td>
</tr>
<tr>
<td>Climbing/jumping</td>
<td>The squirrel is moving through the branches or between the trees without stopping to forage.</td>
</tr>
<tr>
<td>Other</td>
<td>This includes grooming, courtship behaviour, running, walking, vocalisations or when the squirrel was stationary</td>
</tr>
</tbody>
</table>
Table 2: The percentage of time that squirrels were observed engaged in each of the recorded behaviours in non-public and public areas and in the presence and absence of the public.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Public areas (n=252)</th>
<th>Non-public areas (n=145)</th>
<th>Public</th>
<th>No people present (n=402)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging/Eating</td>
<td>54</td>
<td>33</td>
<td>63</td>
<td>40</td>
</tr>
<tr>
<td>Vigilant</td>
<td>3</td>
<td>9</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Climbing/jumping</td>
<td>20</td>
<td>35</td>
<td>25</td>
<td>28</td>
</tr>
<tr>
<td>Other</td>
<td>23</td>
<td>23</td>
<td>6</td>
<td>26</td>
</tr>
</tbody>
</table>
Table 3: The results of the general linear model, showing the factors significantly impacting on the FCM levels of squirrels (B=unstandardised regression coefficient, SE= standard error of the coefficient; ß=standardised co-efficient).

<table>
<thead>
<tr>
<th></th>
<th>B</th>
<th>SE_B</th>
<th>ß</th>
<th>P value</th>
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<td>Intercept</td>
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<td>6.121</td>
<td>.401</td>
<td>0.003</td>
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<tr>
<td>Area</td>
<td>8.596</td>
<td>2.707</td>
<td>.373</td>
<td>0.005</td>
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<tr>
<td>Breeding condition</td>
<td>9.660</td>
<td>3.275</td>
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