Keywords: behaviour, habitat fragmentation, Sciuridae, spatial ecology, radio telemetry, urbanisation

Introduction

Urbanisation is a process threatening nature conservation. By 2030 the world is predicted to have 41 mega-cities with the percentage of urban inhabitants rising to 66% by 2050 (United Nations, 2014). The expansion of urban areas is rapid and causes habitat loss and degradation (McKinney, 2002). Furthermore, cities introduce a set of novel conditions, including a high level of disturbance, increased habitat fragmentation and diminished availability of natural food sources (Sol et al., 2013; McKinney, 2008; Andrén and Delin, 1994). Thus, animal species must either retreat to remnants of natural habitat or adapt to the challenges posed by urban areas.

Behavioural plasticity appears to be an important characteristic for species’ success in cities because it helps individuals contend with disturbance and environmental change (Hämäläinen et al., 2018; Lowry et al., 2012). It can influence, for example, population density, diet and antipredator behaviour (Ditchkoff et al., 2006; Luniak, 2004). Changes in space use and activity budgets are also common among urban dwelling species. One such measure of wildlife spatial ecology is the home range (HR); the “area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt, 1943). Urban animals generally show a reduction in HR size compared to their rural counterparts; e.g., raccoon Procyon lotor (Prange et al., 2004); key deer Odocoileus virginianus clavium (Harverson et al., 2007) and stone marten Martes foina (Herr et al., 2009). This is thought to be related to larger and more stable, although usually anthropogenic (i.e. unnatural), food resources (Lowry et al., 2012; Prange et al., 2004). Changes in activity patterns are often linked to avoiding peaks of human activity resulting in shifts to crepuscular or nocturnal periods, which can cause a temporal disconnection between carnivores such as bobcats Felis rufus and coyotes Canis latrans and their prey species (Ditchkoff et al., 2006; Tigas et al., 2002). On the other hand, some species lose their sensitivity to human disturbance and switch from nocturnal to diurnal activity, such as the striped field mouse Apodemus agrarius (Gliwicz et al., 1994). Activity budgets can also be influenced by artificial food sources; for example, chipmunks Tamias striatus, which usually reduce activity during summer in natural habitats, stay active longer in urban areas because food availability remains high (Ryan and Larson, 1976).

Therefore, it is important for wildlife management practices to investigate the characteristics of successful urban dwelling species in order to assess which other species are most likely to be threatened by human encroachment.

The Eurasian red squirrel Sciurus vulgaris (herein “red squirrel”) is an example of an apparently successful urban species (Hämäläinen et al., 2018; Jokimäki et al., 2017; Luniak, 2004). This small, diurnal mammal is common and widespread but has been infrequently studied outside its natural habitat to date (Hämäläinen et al., 2018; Jokimäki et al., 2017; Babinski-Werka and Zów, 2008; Lurz et al., 2005; Wauters and Dhondt, 1992), leaving the characteristics enabling its success in cities unclear. Our study was designed to quantify space use and activity budgets of red squirrel populations in semi-natural and urban habitats within a major city. Red squirrels use anthropogenic food (Recher et al., 2016; Bosch and Lurz, 2012; Luniak, 2004; Klausnitzer, 1993; Ga-
jare, Daussmann and Turner, unpublished data) and show reduced space use in fragmented habitats (Wauters et al., 1994). Hence, we hypothesised that, compared to individuals in a semi-natural environment, in urban habitat (1) HRs will be smaller and (2) HR overlap among individuals will be greater. Based on previous red squirrel research conducted during winter, as well as on urban red and grey (Sciurus carolinensis) squirrels (Parker et al., 2014; Bosch and Lurz, 2012; Babińska-Werka and Żółw, 2008), we hypothesised that (3) the timing of red squirrels’ activity patterns during the day will not differ between habitats, given that season influences activity independent of the level of urbanisation and (4) urban red squirrels will spend less time active in total. Finally, we predicted that (5) red squirrel activity duration in both habitats will be positively correlated with ambient temperature ($T_a$), similar to animals in natural habitat (Wauters et al., 1992).

Materials and methods

Study sites

Squirrels were studied in urban and semi-natural habitats. The urban study site (77 ha) was in central Hamburg, Germany (53°34.043' N, 9°58.725' E) (Tab. 1, Fig. 1). The area encompassed a University of Hamburg campus with large buildings, car parks and mostly sealed surfaces. Habitat fragmentation was high, owing to several large roads and inaccessible built-up areas. However, it also included vegetated backyards and gardens; 26.8% of the study site was vegetated while 73.2% was sealed (Tab. 1). Vegetation consisted mainly of deciduous alley trees, garden species and a few conifers (e.g., lime trees Tilia cordata, different maples Acer spp., horse chestnut Aesculus hippocastanum, cherry plum Prunus cerasifera, black pine Pinus nigra and white spruce Picea glauca). There was a high abundance of supplementary food provided by residents, including seed-filled bird feeders, nuts left out on balconies for squirrels and food scraps from local restaurants.

The semi-natural site (128 ha) was located within the 391-ha Ohlsdorf Cemetery, approximately 9 km from the urban site (53°37.393' N, 10°3.516' E) (Tab. 1, Fig. 1). The cemetery is a large, enclosed park crossed by footpaths and roads open to visitors. While resident squirrels were exposed to the presence of humans, there were also isolated, near-natural areas with unbroken tree stands. Hence, habitat fragmentation was lower than in the urban study site and while 86.8% was vegetated, only 13.2% of the area was covered by human-made surfaces (Tab. 1). The cemetery grounds consisted of small lawns, flower beds and planted shrubs, as well as patches of mature coniferous (e.g., Douglas-fir Pseudotsuga menziesii) and Norway spruce Picea abies and broadleaf (e.g., beech Fagus sylvatica and pedunculate oak Quercus robur) trees. This ensured an abundance of natural food sources, supplemented by bird feeders filled by visitors (Reher et al., 2016).

Ambient temperature

Average daily minimum/maximum $T_a$ ($T_{\text{min}}/T_{\text{max}}$) was measured using temperature-sensitive data loggers (DS1922L-F5 Thermochron iButtons, Maxim Integrated Products, San Jose, USA) placed $\approx$1 m above the ground in shaded locations in both habitats. $T_a$ data was not available for the first five and eight days of radio-tracking periods in the urban and semi-natural habitats, respectively.

Trapping and processing

Trapping was conducted during February and March 2015. Red squirrels were caught using cage traps (20×20×50 cm; Tomahawk Live Trap, Hazelhurst, WI, USA) baited with walnuts, hazelnuts, sunflower seeds, peanut butter and apples (Wauters et al., 2007; Curtis and Sullivan, 2001). Red squirrels were transferred to a handling cone modelled after Koprowski (2002), weighed and sexed; only non-reproductive, adult squirrels $>$320 g were used in the study. A passive integrated transponder (trovan ID100, Euro I.D. Usling GmbH, Weilerswist, Germany) was injected between the shoulder blades for individual identification. Each of nine red squirrels was fitted with a temperature-sensitive transmitter (Pip25M; Biotrack Ltd, Wareham, UK) on a cable tie collar padded with heat shrink, with the tie tail trimmed and lock superglued in place. The thermistor was located on the side of the transmitter that faced the animal, to measure surface temperature ($T_s$) and was used to determine activity patterns (see below); a stable, high $T_s$ indicated inactivity (i.e., an animal at rest in curled posture with the thermistor nestled against the animal’s chest), whereas a low, fluctuating $T_s$ indicated activity (i.e., an animal moving with an extended neck, exposing the thermistor to $T_a$). A transmitter with collar weighed 4.3 $\pm$ 0.1 g ($n=8$), which was 1.2 $\pm$ 0.2% of a red squirrel’s body mass and below recommended maxima suggested by Rojas et al. (2010). Transmitters, which changed their signal interval with temperature, were calibrated in a water bath from 5–40 °C at 7 °C steps using a thermometer traceable to the national standard.

Radio-tracking

Radio-tracking took place in late winter/early spring between February and April 2015, between 5:30 and 18:30 for 3–5 h/day, 5–6 days/week, for 38 and 39 days in the urban (n=4) and semi-natural (n=5) sites, respectively. Two individuals were not included in analyses: one red squirrel at each site lost its collar shortly after deployment, therefore sample sizes in the urban and semi-natural sites were 3 and 4, respectively. Individuals were radio-tracked in rotation starting with a randomly selected individual each day using a combination of homing and triangulation. Upon finding a red squirrel we recorded the time, location, $T_s$ (determined remotely using a stopwatch to measure the transmitter’s interpulse interval) and, if visible, activity status (see below). Fixes were taken every 10 and 15 minutes in the urban and

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**Table 1** – Descriptive statistics of habitat spatial characteristics and measures of fragmentation in the urban and semi-natural study sites in Hamburg, Germany, relevant to the movement patterns of Eurasian red squirrels.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Urban</th>
<th>Semi-natural</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site size (ha)</td>
<td>77</td>
<td>128.4</td>
</tr>
<tr>
<td>Vegetated/sealed area (ha)</td>
<td>20.6/56.4</td>
<td>111.1/17.3</td>
</tr>
<tr>
<td>Vegetated/sealed area (%)</td>
<td>26.8/73.2</td>
<td>86.8/13.2</td>
</tr>
<tr>
<td>No. vegetated patches</td>
<td>271</td>
<td>136</td>
</tr>
<tr>
<td>Vegetated patch size (ha)</td>
<td>$0.08 \pm 0.38$</td>
<td>$0.82 \pm 1.43$</td>
</tr>
<tr>
<td>Vegetated patch size, range (ha)</td>
<td>$&lt;0.01$–3.5</td>
<td>$&lt;0.01$–15.6</td>
</tr>
<tr>
<td>Distance between vegetated patches (m)</td>
<td>$6.4 \pm 10.0$</td>
<td>$4.0 \pm 1.8$</td>
</tr>
<tr>
<td>Distance between vegetated patches, range (m)</td>
<td>$&lt;1–91$</td>
<td>$&lt;1–7$</td>
</tr>
</tbody>
</table>

---

Figure 1 – Maps of the urban (left) and semi-natural (right) study sites within the city of Hamburg, Germany (inset map). Grey shading indicates vegetated areas (e.g., trees, gardens and lawns); white areas are human-made sealed surfaces (e.g., buildings, roads, footpaths and car parks).
semi-natural sites, respectively. A total of 435 fixes were collected in the urban site (145 ± 63/individual) and 472 in the semi-natural site (118 ± 23/individual).

**Data analyses**

$T_x$ data was used to analyse activity budgets. $T_x$ data associated with observed activity/inactivity was used to determine a $T_x$ cut-off value (see below) differentiating activity from inactivity. This was used to identify the activity status of each individual squirrel that was not visible. The cut-off value was calculated as the mean of two values (see below) and applied to all $T_x$ data. For individuals in the semi-natural habitat, the two values used were the means of all inactive and active $T_x$s. Owing to a higher proportion of data with an unknown (i.e., not directly observed) status in the urban habitat, the 3rd quartile (75th percentile; Q75) of inactive $T_x$ and the 1st quartile (25th percentile; Q25) of active $T_x$ for each squirrel was used to calculate a mean as an individual cut-off. For one individual there was not enough data with visible activity or inactivity, so the mean of the cut-offs for the other two urban individuals was used. “Not visible” data with $T_x$ lower than the calculated cut-off was therefore given the status “active” and data with $T_x$ higher than the calculated cut-off was given the status “inactive”. Hence, activity data were binary. The median activity rate in a habitat was calculated using percentages of activity within one-hour time bins. For this calculation and for the analysis of the temporal distribution of daily activity patterns, activity was related to time after sunrise. This relative measure was used because red squirrels link the onset of activity to astronomical sunrise (Wauters et al., 1992) and day length changed considerably from 9.1–13.6 h during the radio-tracking period.

To analyse space use, 100% minimum convex polygon (MCP) and 95% fixed kernel density estimator (KDE95) were both used as parameters for HR size. MCP assumes even space use so it is considered less accurate than KDE95, which calculates the utilisation distribution density (Worton, 1989). However, MCP is more commonly used and therefore allows comparison with a larger array of previous studies (Powell, 2000). All parameters were calculated in Tinn-R (Fari et al., 2014) using the packages naapools (Bivand and Lewin, 2014), adehabitat (Calenge, 2006), rgeos (Bivand and Rundel, 2014), ade4 (Dray et al., 2007),foreign (R Core Team, 2013), shapefiles (Stabler, 2013) and rgdal (Bivand et al., 2015). Least square cross validation was used as the individual smoothing factor “h” for KDE95s. To calculate the overlap of individual HRs, no double overlaps were included to prevent the value from exceeding 100%. Individual calculations for MCP and KDE95 were transformed into shape files and analysed using QGIS 2.8.2 (QGIS Development Team, 2015).

**Statistics**

$T_{min}$ and $T_{max}$ were tested for a normal distribution using a one-sample Kolmogorov-Smirnov test. Because the data did not follow a normal distribution, a Wilcoxon signed-rank test with continuity correction was used to compare $T_x$ between habitats.

We analysed data from three red squirrels in urban habitat and four red squirrels in semi-natural habitat. Generalized linear mixed models (GLMMs) were used to test for differences in activity patterns and activity rate between habitats, as well as the influence of $T_x$ on the latter. All models used “activity” as the response variable and “individual” as a random effect predictor variable. The first and larger model (M1) included the following fixed effect predictor variables: “$T_{min}$”, “$T_{max}$”, “habitat” and “hours after sunrise”, as well as the interaction between “habitat” and “hours after sunrise”. The second model (M2) only included “habitat” as a fixed effect predictor variable in order to test for effects on activity rate, which could have been masked by time pattern effects in the first model. We then conducted two separate model reductions to test for the contribution of individual fixed effect predictor variables to overall model parsimony.

HR size and percent overlap were compared between habitats using a non-parametric Mann Whitney U test; testing for a normal distribution was not possible owing to small sample sizes.

$T_x$ and HR analyses were conducted using IBM SPSS Statistics v24 and activity GLMMs were created using R 3.4.1 (R Core Team, 2017) with the package lme4 (Bates et al., 2017). Means are reported ± standard deviation (SD) and medians ± Q25/Q75. The significance level used was $p<0.05$. “n” indicates the number of individuals, “N” indicates the number of measurements.

**Results**

**Body mass**

Mean body mass was similar in both habitats (urban: 372.5 ± 46.7 g, n=4; semi-natural: 370.0 ± 10.7 g, n=5).

**Ambient temperature**

$T_{min}$ and $T_{max}$ from February 14th to April 15th, 2015, differed significantly between habitats (M1: $T_{min}$: $W=2672$, $p<0.001$, $N=61$; $T_{max}$: $W=2333$, $p=0.015$, $N=61$); $T_{hr}$ was 2 °C higher in the urban habitat (urban: $T_{min}=3.8±2.3°C/T_{max}=11.0±4.5°C$, semi-natural: $T_{min}=1.8±2.4°C/T_{max}=9.2±4.1°C$; Fig. 2).

**Activity budgets**

The model that best explained red squirrel activity patterns did not include $T_{min}$ or $T_{max}$ as fixed effect predictor variables (M1c: Tab. 2 and 3). However, the interaction between habitat and time after sunrise was included in each model, showing its significant effect on activity (M1; Tab. 2). Therefore, temporal patterns of activity differed between the two habitats. While activity in the urban habitat (n=3; February 9th – April 15th 2015) peaked two hours after sunrise and rapidly declined after around four hours after sunrise, activity in the semi-natural habitat decreased more gradually. The random effect was always the individual (individual).

**Table 2** – Details and results of generalized linear mixed models used to examine the effects of average daily minimum and maximum ambient temperatures ($T_{min}$ and $T_{max}$), habitat type (urban and semi-natural) and hours after sunrise on the activity patterns of Eurasian red squirrels (n=7) in Hamburg, Germany. For each model the fixed effects, bias-corrected Akaike Information Criterion (AICc), AICc and the Akaike weights (w) are shown. The random effect was always the individual (individual).

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed effects</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1a</td>
<td>1</td>
<td>individual + $T_{max}$ + habitat + 1212.8 hours after sunrise + habitat × hours after sunrise</td>
<td>1.56</td>
<td>0.23</td>
</tr>
<tr>
<td>M1b</td>
<td>1</td>
<td>individual + $T_{min}$ + habitat + 2113.2 hours after sunrise + habitat × hours after sunrise</td>
<td>1.89</td>
<td>0.19</td>
</tr>
<tr>
<td>M1c</td>
<td>1</td>
<td>individual + habitat + hours after sunrise + habitat × hours after sunrise</td>
<td>1211.3</td>
<td>0.5</td>
</tr>
</tbody>
</table>
Table 3 – Fixed effects estimates ± standard error (SE) and z values for each parameter of the generalized linear mixed models that best explain the activity patterns of Eurasian red squirrels (n=7) in Hamburg, Germany.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(intercept)</td>
<td>0.03</td>
<td>0.37</td>
<td>0.081</td>
</tr>
<tr>
<td>M1a</td>
<td>$T_{max}$</td>
<td>-0.011</td>
<td>0.017</td>
<td>-0.67</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>-0.34</td>
<td>0.5</td>
<td>-0.68</td>
</tr>
<tr>
<td></td>
<td>hours after sunrise</td>
<td>-0.0038</td>
<td>0.028</td>
<td>-0.14</td>
</tr>
<tr>
<td></td>
<td>× hours after sunrise</td>
<td>0.38</td>
<td>0.059</td>
<td>6.3</td>
</tr>
<tr>
<td>M1b</td>
<td>$T_{min}$</td>
<td>-0.076</td>
<td>0.32</td>
<td>-0.24</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>-0.011</td>
<td>0.033</td>
<td>-0.33</td>
</tr>
<tr>
<td></td>
<td>hours after sunrise</td>
<td>-0.0035</td>
<td>0.028</td>
<td>-0.13</td>
</tr>
<tr>
<td></td>
<td>× hours after sunrise</td>
<td>0.37</td>
<td>0.059</td>
<td>6.3</td>
</tr>
<tr>
<td>M1c</td>
<td>$T_{max}$</td>
<td>-0.091</td>
<td>0.32</td>
<td>-0.29</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>-0.32</td>
<td>0.5</td>
<td>-0.65</td>
</tr>
<tr>
<td></td>
<td>hours after sunrise</td>
<td>-0.0044</td>
<td>0.028</td>
<td>-0.16</td>
</tr>
<tr>
<td></td>
<td>× hours after sunrise</td>
<td>0.37</td>
<td>0.059</td>
<td>6.3</td>
</tr>
<tr>
<td>M2</td>
<td>(intercept)</td>
<td>-0.12</td>
<td>0.27</td>
<td>-0.43</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>1.1</td>
<td>0.42</td>
<td>2.6</td>
</tr>
</tbody>
</table>

Figure 3 – Activity levels of Eurasian red squirrels in urban (white bars, upper panel; n=3) and semi-natural (grey bars, lower panel; n=4) habitat in Hamburg, Germany. Each column displays the average activity as a percentage of the total time spent either active or at rest within one-hour time bin relative to sunrise (vertical dashed lines). Radio-tracking in the urban habitat did not extend beyond 16:30 (upper panel).

Figure 4 – Average home range size (ha; upper two panels) and average home range overlap among individuals (%; lower two panels) of Eurasian red squirrels living in urban (white boxes; n=3) and semi-natural (grey boxes; n=4) habitats in Hamburg, Germany. Data is displayed as 100% minimum convex polygons (MCP100; left panels) and 95% fixed kernel density estimators (KDE95; right panels).

Discussion

Activity

We found that habitat type had a significant influence on both activity rate and activity time patterns because urban red squirrels were generally less active than conspecifics in the semi-natural cemetery. Reduced activity is typical for red squirrels in winter and early spring in most natural habitats (Bosch and Lurz, 2012; Wauters et al., 1992) owing to the high thermoregulatory cost of foraging at low $T_a$ and shorter day length (Bosch and Lurz, 2012; Wauters et al., 1992; Pulliainen, 1973). However, in urban parks in Poland red squirrels displayed no extended periods of inactivity during the day in winter (Babińska-Werka and Żółw, 2008). This was true for individuals in our semi-natural site, but not for the urban individuals. It is likely that an increased abundance of artificial food sources in the urban site is evidenced by the reduced activity because the red squirrels were able to maintain a high body mass (see Turner et al., 2017) and satisfy energy intake while spending less time foraging. Similarly, winter food supplementation led red squirrels to spend less time outside the drey and forage less (Gurnell, 1987). They also reduce activity and foraging time if food items were easier to handle and energy-rich (Wauters and Dhondt, 1992), which could also help them decrease daily energy expenditure and maintain a positive energy balance (Turner et al., 2017).

The environmental conditions red squirrels were exposed to differed with the degree of urbanisation: higher $T_a$ occurred towards the city centre (Grimmond, 2007). However, $T_a$ did not affect the overall level of activity. In the literature, the primary abiotic environmental cue influencing red squirrel activity timing is contentious, but appears to be $T_a$ (Wauters et al., 1992), photoperiod (i.e., day length; Wauters and Dhondt, 1987; Tonkin, 1983) or a combination of both (Holm, 1990). Food availability, on the other hand, affects the duration of

Tables and Figures

Table 3 – Fixed effects estimates ± standard error (SE) and z values for each parameter of the generalized linear mixed models that best explain the activity patterns of Eurasian red squirrels (n=7) in Hamburg, Germany.
activity (Wauters and Dhome, 1987; Tonkin, 1983). Our findings sug-
gest that food provided by humans might have become more important
than abiotic factors in both urban and semi-natural habitats com-
pared to natural habitats (Wauters et al., 1992). Similarly, Baccaloupe
et al. (2003) found that supplementary feeding increased degu (Octo-
don degus) activity regardless of thermal conditions, and supplement-
ary food reduced overall activity time for red squirrels independently of
T_e (Holm, 1990). However, an effect of T_e might still be found during
other seasons, over the course of the whole year or under more extreme
T_e than that which occurred during this study.

Space use
We did not detect a significant difference in space use between the
sites. However, HRs tended to be smaller, and HR overlap greater,
in the urban site. MCP HRs in both sites were considerably smaller
(urban: 3.5 ± 2.7 ha; semi-natural 6.7 ± 1.7 ha) than in natural habitats
where HRs can reach up to 17 ha (Di Pierro et al., 2007; Wauters and
Dhome, 1992). While our measured HRs were most similar to those
of individuals inhabiting a coniferous forest with a predictable seed crop
(2.8–3.9 ha; Wauters and Dhome, 1992), they were also in the range of
red squirrels in fragmented woodlands (2.8–6.8 ha; Wauters et al.,
1994) and females in urban areas (6.9 ha; Hämmäläinen et al., 2018).
Food availability prescribes HR size in natural habitat (Wauters et al.,
2005), therefore we suggest that the spatial ecology of animals affected
by urbanisation reflects the combination of food availability and habitat
structure. It seems that supplementary food, as a reliable and abund-
ant energy source, reduces space use in areas affected by urbanisation
(Davison et al., 2009). Additionally, it likely facilitates energy con-
servation because animal movement is concentrated around only a few
locations with provided food, reducing the need for long foraging for-
as (Reher et al., 2016). When food availability is high, it can reduce
intraspecific competition for food (Davison et al., 2009; Wauters and
Dhome, 1992), and presumably support higher population densities
in non-territorial species (Jokimäki et al., 2017), indicated by the high
level of HR overlap and nest-sharing that we found among individu-
als. Additionally, if landscape fragmentation is high, suitable habitat is
scarcer and travel between fragments is costly, which helps explain the
tendency towards smaller HRs and increased HR overlap in our urban
site. It is probable that the red squirrels inhabited the few suitable frag-
ments available and within these fragments they were able to access
dependable food sources and fulfill their energetic needs quickly and
with minimal effort.
Even though it seems that supplementary food (Koprowski, 2005;
Magris and Gurnell, 2002) and reduced space use increases red squir-
rels’ resilience to habitat fragmentation, it remains unclear if this is due
to a source–sink system or if urban populations can persist independ-
ently. Source-sink systems have been suggested for red squirrels in both
fragmented woodland and urban habitats and patch size, quality and
isolation determine occupancy (Verbylen et al., 2009; Celada et al.,
1994; Verboom and Van Apeldoorn, 1990). A dependency on a source
population would indicate that habitat quality in highly urbanised en-
vironments might be below a critical minimum required for long-term
red squirrel persistence. Nonetheless, because squirrels use stepping-
stone fragments, and gene flow is likely aided through dispersal that is
stepped across urban boroughs and road crossings (Reher et al., 2016),
the ability to judge the urgency of conservation issues and develop manage-
ment practices will benefit from further research into individual health,
longevity and reproductive success, as well as the demography of urban populations.

Urbanisation hazards
Taking advantage of the often high-energy content of supplemented
food does not come without risk. It leads to high population densities
and, in turn, decreased breeding success and increased intraspecific ag-
gression (Vieira et al., 2015; Bosch and Lurz, 2012; Parker and Nilon,
2008; Ditchkoff et al., 2006; Wauters and Lens, 1995). It can also lead
to high rates of disease transmission among local individuals and feed-

ing stations may facilitate the transmission of squirrelpox virus from
invasive grey squirrels to red squirrels in the United Kingdom (Bruem-
mer et al., 2010; Parrott et al., 2009). Furthermore, an unbalanced diet
resulting from excess consumption of supplemented food can lead to
calcium deficiencies (Shuttleworth, 1997; Keymer and Hime, 1977)
and metabolic bone disease (Bosch and Lurz, 2012). Red squirrels are
opportunistic foragers (Gurnell, 1987) and appear to be able to balance
and provide natural food. For example, in a nature reserve with
and with supplemented food, peanuts were the most important food
item but red squirrels nevertheless consumed natural food in accordance
with seasonal availability (Shuttleworth, 2000). Such flexibility
was possible at our semi-natural site (see Reher et al., 2016) but squir-
rel populations living in highly urbanised areas, with far fewer natural
food resources, are at a greater risk of malnutrition and health decline.
While providing food for wildlife is a popular way for people interested
in nature to interact with animals, the broad dissemination of additional
publicly available information clearly stating the potential problems
for wildlife is needed.

Conclusions
Although our sample size was small, we are confident that our results
reflect squirrels’ natural ecological patterns as we were able to identify
statistical differences among activity variables and identified trends in
spatial ecology that were consistent with published data.
Our study indicates that squirrels may be able to adjust their space
use and activity budgeting to cope with urban conditions and the ability
to exploit anthropogenic food sources likely plays a large role in
their success in cities. Resulting energy savings would enable squirrels
to tolerate the high degree of fragmentation in this challenging hab-
itat, up to a point. This could help explain their persistence and be a
good indicator of a low sensitivity to urbanisation for other species.
However, this does not mean that red squirrels live in cities without
difficulties. Nutritional deficiencies and disease dispersal caused by
supplementary food could be a potential hazard to urban populations,
as well as light pollution and introduced predators. Also, patch qual-
ity and connectivity must remain above a threshold level. While our
findings provide important data on factors influencing the presence of
urban squirrels, the ability to judge the urgency of conservation issues
and develop management practices will benefit from further research
into individual health, longevity and reproductive success, as well as
the demography of urban populations.


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