Research Article

# Degree of urbanisation affects Eurasian red squirrel activity patterns

Lea S. Thomas[1], Edna Teich[1], Kathrin H. Dausmann[1], Stephanie Reher[1], James M. Turner[1,2,*]

[1]*University of Hamburg*
[2]*Charles Sturt University*

## Abstract

With cities growing at a rapid pace, animal species must either retreat to patches of intact natural habitat or adapt to novel conditions in urban areas. While this disturbance causes most species to be in local decline, some show specific behavioural plasticity, facilitating success in a new habitat. The Eurasian red squirrel (*Sciurus vulgaris*) is a common small mammal species which occurs in high numbers in urban environments. To determine which characteristics enable its success, we investigated space use and activity budgets of seven free-ranging individuals living in semi-natural and urban habitats within a large city. We did not find significant differences in animals' space use between habitat types but tendencies towards smaller home ranges and increased home range overlap existed among individuals in the urban site. Squirrels differed between sites in both overall activity levels and temporal activity patterns: urban animals spent less time active and activity onset was later compared to semi-natural conspecifics. This is likely explained by a combination of dense and reliable supplementary food sources in the urban habitat, reducing foraging effort, and restrictions to movement imposed by higher fragmentation. Flexibility in space use and activity budgets, as well as the ability to exploit anthropogenic food sources and tolerate reduced habitat connectivity, are likely the most important factors contributing to the squirrels' success in cities. Accordingly, these traits could be used as indicators of low sensitivity towards urbanisation when assessing other species' potential resilience. However, they do not immunise squirrels against extirpation. Further research on individuals' foraging ecology and population health may reveal possible threats to urban red squirrels and help predict their future persistence in this challenging habitat.

## 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 and challenging 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 remnant patches 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; Babińska-Werka and Żółw, 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 (Reher et al., 2016; Bosch and Lurz, 2012; Luniak, 2004; Klausnitzer, 1993; Ga-

---
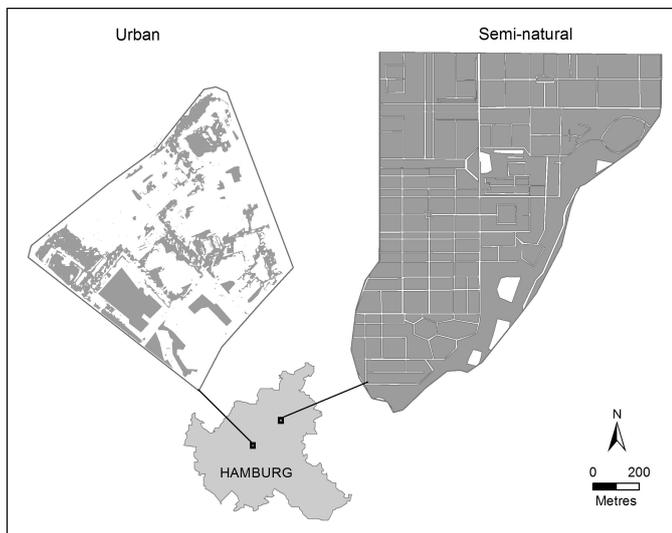
Figure 1 – Maps of the urban (left) and semi-natural (right) study sites within the city of Hamburg, Germany (inset map). Grey shading indicates vegetated areas (e.g., trees, gardens and lawns); white areas are human-made sealed surfaces (e.g., buildings, roads, footpaths and carparks).

jare, Dausmann 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 and 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

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.

| Variable | Site | |
|---|---|---|
| | Urban | Semi-natural |
| Site size (ha) | 77 | 128.4 |
| Vegetated/sealed area (ha) | 20.6/56.4 | 111.1/17.3 |
| Vegetated/sealed area (%) | 26.8/73.2 | 86.8/13.2 |
| No. vegetated patches | 271 | 136 |
| Vegetated patch size (ha) | $0.08 \pm 0.38$ | $0.82 \pm 1.43$ |
| Vegetated patch size, range (ha) | <0.01–3.52 | <0.01–15.6 |
| Distance between vegetated patches (m) | $6.4 \pm 10.0$ | $4.0 \pm 1.8$ |
| Distance between vegetated patches, range (m) | <1–91 | <1–7 |

*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 $T_a$ ($T_{min}/T_{max}$) was measured using temperature-sensitive data loggers (DS1922L-F5 Thermochron iButtons, Maxim Integrated Products, San Jose, USA) placed ≈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 ($20 \times 20 \times 50$ 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 (Pip2SM; 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

semi-natural sites, respectively. A total of 435 fixes were collected in the urban site ($145 \pm 63$/individual) and 472 in the semi-natural site ($118 \pm 23$/individual).

## Data analyses

$T_s$ data was used to analyse activity budgets. $T_s$ data associated with observed activity/inactivity was used to determine a $T_s$ 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 $T_s$ data. For individuals in the semi-natural habitat, the two values used were the means of all inactive and active $T_s$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 $T_s$ and the 1st quartile (25th percentile; Q25) of active $T_s$ 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 $T_s$ lower than the calculated cut-off was therefore given the status "active" and data with $T_s$ 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 `maptools` (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 $T_a$ 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 $T_a$ 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.
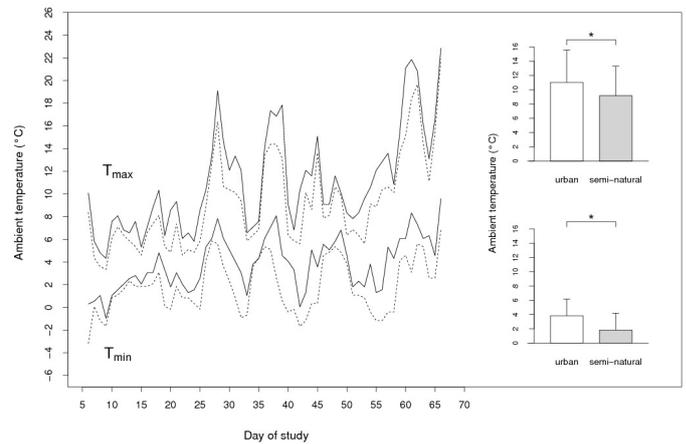


**Figure 2** – Average daily minimum ($T_{min}$) and maximum ($T_{max}$) ambient temperatures during the radio-tracking period (February 14th – April 15th 2015) in urban (solid lines) and semi-natural (dashed lines) habitat in Hamburg, Germany. Inset graphs show pairwise comparisons between urban (white) and semi-natural (grey) habitats; asterisks indicate significant differences in average daily $T_{min}$ (lower graph) and $T_{max}$ (upper graph) between habitat types.

$T_a$ 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 $\pm$ standard deviation (SD) and medians $\pm$ 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: $372.5 \pm 46.7$ g, n=4; semi-natural: $370.0 \pm 10.7$ g, n=5).

### Ambient temperature

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

**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), ΔAICc and the Akaike weights (w) are shown. The random effect was always the individual (1|individual).

| Model | Fixed effects | AICc | ΔAICc | w |
|---|---|---|---|---|
| **M1a** | 1\|individual + $T_{max}$ + habitat + hours after sunrise + habitat × hours after sunrise | 1212.8 | 1.56 | 0.23 |
| **M1b** | 1\|individual + $T_{min}$ + habitat + hours after sunrise + habitat × hours after sunrise | 1213.2 | 1.89 | 0.19 |
| **M1c** | 1\|individual + habitat + hours after sunrise + habitat × hours after sunrise | 1211.3 | 0 | 0.5 |
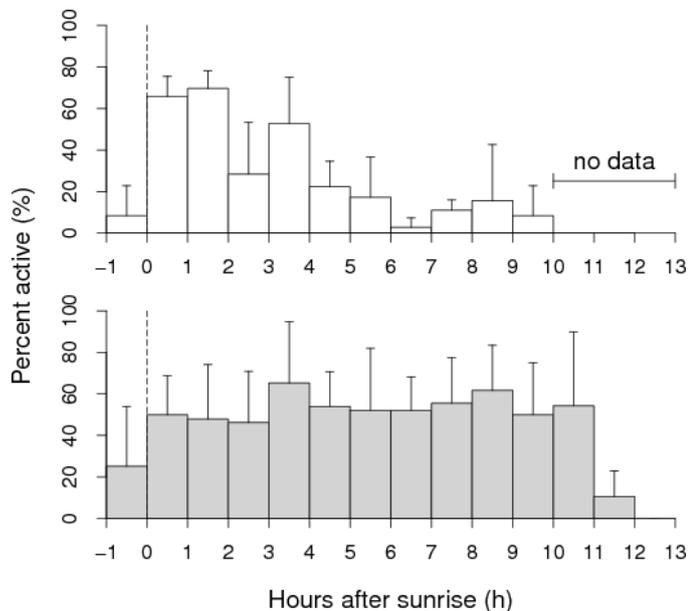
Figure 3 – Activity levels of Eurasian red squirrels in urban (white bars, upper panel; n=3) and semi-natural (grey bars, lower panel; n=4) habitat in Hamburg, Germany. Each column displays the average activity as a percentage of the total time spent either active or at rest within a one-hour time bin 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).

itat (n=4; February 6$^{th}$ – April 2$^{th}$ 2015) was more or less consistent throughout most of the day (Fig. 3). M2 showed that habitat had a significant influence on activity (Tab. 3). Hence, the activity rate differed between habitats.
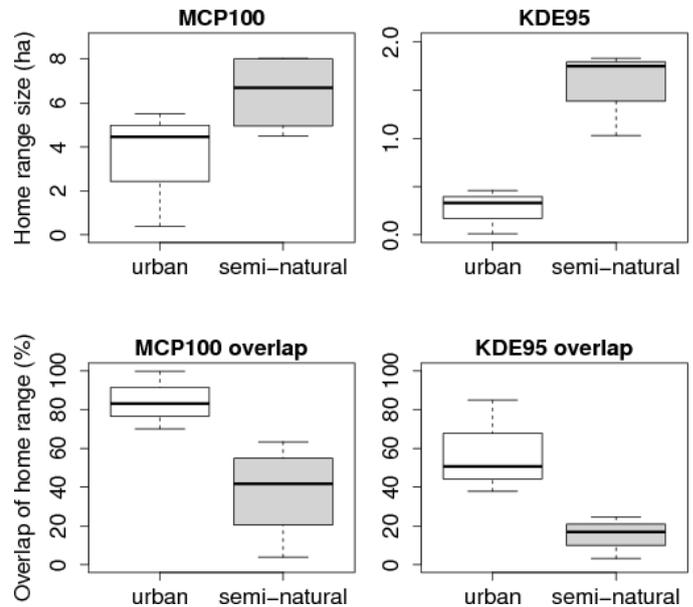
For urban squirrels, the mean activity rate per time bin (i.e., proportion of active data points within one hour) was only 25±13/32% (Fig. 3). In the semi-natural habitat, however, it was 58±49/64% (Fig. 3). In a nutshell, individuals in semi-natural habitat were not only more consistently active throughout the day but also showed a higher activity rate overall.

### Space use

Neither HR size nor overlap differed significantly between habitats (MCP: U=1.0, $p$=0.114; KDE95: U=0.0, $p$=0.057; MCP overlap: U=0.0, $p$=0.057; KDE95 overlap: U=0.0, $p$=0.057; n=7). However, even though our samples sizes were small, the low $p$-values indicate

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.

| Model | Parameter | Estimate | SE | z |
|---|---|---|---|---|
| **M1a** | (intercept) | 0.03 | 0.37 | 0.081 |
| | $T_{max}$ | −0.011 | 0.017 | −0.67 |
| | habitat | −0.34 | 0.5 | −0.68 |
| | hours after sunrise | −0.0038 | 0.028 | −0.14 |
| | habitat×hours after sunrise | 0.38 | 0.059 | 6.3 |
| **M1b** | (intercept) | −0.076 | 0.32 | −0.24 |
| | $T_{min}$ | −0.011 | 0.033 | −0.33 |
| | habitat | −0.31 | 0.5 | −0.61 |
| | hours after sunrise | −0.0035 | 0.028 | −0.13 |
| | habitat×hours after sunrise | 0.37 | 0.059 | 6.3 |
| **M1c** | (intercept) | −0.091 | 0.32 | −0.29 |
| | habitat | −0.32 | 0.5 | −0.65 |
| | hours after sunrise | −0.0044 | 0.028 | −0.16 |
| | habitat×hours after sunrise | 0.37 | 0.059 | 6.3 |
| **M2** | (intercept) | −0.12 | 0.27 | −0.43 |
| | habitat | 1.1 | 0.42 | 2.6 |

a trend: on average MCP HRs in the urban habitat were only half the size of those in semi-natural habitat (3.5±2.7 vs 6.7±1.7 ha; Fig. 4) and KDE95 HRs were one sixth of the size (0.3±0.2 vs 1.6±0.4 ha; Fig. 4). Mean HR overlap for urban squirrels, on the other hand, was more than twice as high for MCP (84.2±14.8 vs 37.6±25.0%; Fig. 4) and almost four times as high for KDE95 (57.8±24.3 vs 15.4±8.9%; Fig. 4).

Although we did not quantify instances, nest sharing was observed in the urban habitat but not in the semi-natural habitat.

## 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

activity (Wauters and Dhondt, 1987; Tonkin, 1983). Our findings suggest that food provided by humans might have become more important than abiotic factors in both urban and semi-natural habitats compared to natural habitats (Wauters et al., 1992). Similarly, Bacigalupe et al. (2003) found that supplementary feeding increased degu (*Octodon degus*) activity regardless of thermal conditions, and supplementary food reduced overall activity time for red squirrels independently of $T_a$ (Holm, 1990). However, an effect of $T_a$ might still be found during other seasons, over the course of the whole year or under more extreme $T_a$ 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: $3.5 \pm 2.7$ ha; semi-natural $6.7 \pm 1.7$ ha) than in natural habitats where HRs can reach up to 17 ha (Di Pierro et al., 2007; Wauters and Dhondt, 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 Dhondt, 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; Hämäläinen 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 abundant energy source, reduces space use in areas affected by urbanisation (Davison et al., 2009). Additionally, it likely facilitates energy conservation because animal movement is concentrated around only a few locations with provided food, reducing the need for long foraging forays (Reher et al., 2016). When food availability is high, it can reduce intraspecific competition for food (Davison et al., 2009; Wauters and Dhondt, 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 individuals. 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 fragments 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 squirrels' resilience to habitat fragmentation, it remains unclear if this is due to a source-sink system or if urban populations can persist independently. Source-sink systems have been suggested for red squirrels in both fragmented woodland and urban habitats and patch size, quality and isolation determine occupancy (Verbeylen 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 environments 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 not hindered by roads, a source-sink system might make squirrels more resilient to urbanisation (Fey et al., 2016; Hale, 2001). However, increasing fragmentation and habitat destruction in cities could push red squirrels to their tolerable limit, given that they cannot persist when habitat connectivity and patch size is insufficient (Celada et al., 1994; Verboom and Van Apeldoorn, 1990).

## 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 aggression (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 (Bruemmer 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 provided and natural food. For example, in a nature reserve with ad libitum 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 squirrel 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 habitat, 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 quality 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. ✍

## References

Andrén H., Delin A., 1994. Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. Oikos 70(1): 43–48.

Babińska-Werka J., Żółw M., 2008. Urban populations of the Red squirrel (*Sciurus vulgaris*) in Warsaw. Ann. Zool. Fenn. 45(4): 270–276.

Bacigalupe L.D., Rezende E.L., Kenagy G.J., Bozinovic F., 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability? J. Mammal. 84(1): 311–318.

Bates D., Maechler M., Bolker B., Walker S., Christensen R.H.B., Singmann H., Dai B., Grothendieck G., Green P., 2017. `lme4`: linear mixed-effects models using "Eigen" and S4.

Bivand R., Lewin-Koh N., 2014. `maptools`: tools for reading and handling spatial objects. R package version 0.8–29.

Bivand R., Rundel C., 2014. `rgeos`: interface to geometry engine – open source (GEOS). R package version 0.3–3.

Bivand R., Keitt T., Rowlingson B., 2015. `rgdal`: bindings for the geospatial data abstraction library.

Bosch S., Lurz P.W.W., 2012. The Eurasian red squirrel, Westarp Wissenschaften, Hohenwarsleben.

Bruemmer C.M., Rushton S.P., Gurnell J., Lurz P.W.W., Nettleton P., Sainsbury A.W., Duff J.P., Gilray J., McInnes C.J., 2010. Epidemiology of squirrelpox virus in grey squirrels in the UK. Epidemiol. Infect. 138(7): 941–950.

Burt W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24(3): 346–352.

Calenge C., 2006. The package "`adehabitat`" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197: 516–519.

Celada C., Bogliani G., Gariboldi A., Maracci A., 1994. Occupancy of isolated woodlots by the red squirrel *Sciurus vulgaris* L. in Italy. Biol. Cons. 69(2): 177–183.

Curtis P.D., Sullivan K.L., 2001. Tree squirrels. Cornell Cooperative Extension Wildlife Damage Management Fact Sheet Series, Cornell University, Ithaca.

Davison J., Huck M., Delahay R.J., Roper T.J., 2009. Restricted ranging behaviour in a high-density population of urban badgers. J. Zool. (Lond.) 277(1): 45–53.

Di Pierro E., Molinari A., Tosi G., Wauters L.A., 2007. Exclusive core areas and intrasexual territoriality in Eurasian red squirrels (*Sciurus vulgaris*) revealed by incremental cluster polygon analysis. Ecol. Res. 23(3): 529–542.

Ditchkoff S.S., Saalfeld S.T., Gibson C.J., 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosys. 9(1): 5–12.

Dray S., Lyon U.D., Dufour A., Lyon U.D., 2007. The ade4 package: implementing the duality.

Faria J.C., Grosjean P., Jelihovschi E., Pietrobon R., Farias P.S., 2014. Tinn-R – Editor – GUI for R language and Environment. Editus, Ilhéus.

Fey K., Hämäläinen S., Selonen V., 2016. Roads are no barrier for dispersing red squirrels in an urban environment. Behav. Ecol. 27(3): 741–747.

Gliwicz J., Goszczynski J., Luniak M., 1994. Characteristic features of animal populations under synurbization — the case of the blackbird and of the striped field mouse. Mem. Zoologi. 49: 237–244.

Grimmond S., 2007. Urbanization and global environmental change: local effects of urban warming. Geogr. J. 173(1): 83–88.

Gurnell J., 1987. The natural history of squirrels, Facts on file publications, New York.

Hale M.L., 2001. Impact of landscape management on the genetic structure of red squirrel populations. Science 293(5538): 2246–2248.

Hämäläinen S., Fey K., Selonen V., 2018. Habitat and nest use during natal dispersal of the urban red squirrel (*Sciurus vulgaris*). Landscape Urban Plan. 169(2018): 269–275.

Harveson P.M., Lopez R.R., Collier B.A., Silvy N.J., 2007. Impacts of urbanization on Florida Key deer behavior and population dynamics. Biol. Cons. 134(3): 321–331.

Herr J., Schley L., Roper T.J., 2009. Socio-spatial organization of urban stone martens. J. Zool. 277(1): 54–62.

Holm J.L., 1990. The ecology of the red squirrel (*Sciurus vulgaris*) in deciduous woodlands. PhD thesis, University of London, London, UK.

Jokimäki J., Selonen V., Lehikoinen A., Kaisanlahti-Jokimäki M.-L., 2017. The role of urban habitats in the abundance of red squirrels (*Sciurus vulgaris*, L.) in Finland. Urban For. Urban Gree. 27(2017): 100–108.

Keymer I.F., Hime J.M., 1977. Nutritional osteodystrophy in a free-living red squirrel (*Sciurus vulgaris*). Vet. Rec. 100(2): 31–32.

Klausnitzer B., 1993. Ökologie der Großstadtfauna, Elsevier, Jena. [in German]

Koprowski J.L., 2002. Handling tree squirrels with a safe and efficient restraint. Wildl. Soc. Bull. 30(1): 101–103.

Koprowski J.L., 2005. The response of tree squirrels to fragmentation: a review and synthesis. Anim. Cons. 8(4): 369–376.

Lowry H., Lill A., Wong B.B.M., 2012. Behavioural responses of wildlife to urban environments. Biol. Rev. 88(3): 537–549.

Luniak M., 2004. Synurbization - adaptation of animal wildlife to urban development. Proceedings of the $^{th}$ International Symposium on Urban Wildlife Conservation, University of Arizona, Tucson. 50–55.

Lurz P.W.W., Gurnell J., Magris L., 2005. *Sciurus vulgaris*. Mamm. Spec. 769: 1–10.

Magris L., Gurnell J., 2002. Population ecology of the red squirrel (*Sciurus vulgaris*) in a fragmented woodland ecosystem on the Island of Jersey, Channel Islands. J. Zool. 256(1): 99–112.

McKinney M.L., 2002. Urbanization, biodiversity, and conservation. BioScience 52(10): 883–890.

McKinney M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosys. 11(2): 161–176.

Parker T.S., Nilon C.H., 2008. Gray squirrel density, habitat suitability, and behavior in urban parks. Urban Ecosys. 11(3): 243–255.

Parker T.S., Gonzales S.K., Nilon C.H., 2014. Seasonal comparisons of daily activity budgets of gray squirrels (*Sciurus carolinensis*) in urban areas. Urban Ecosys. 17(4): 969–978.

Parrott D., Quy R., Van Driel K., Lurz P.W.W., Rushton S.P., Gurnell J., Aebischer N., Reynolds J., 2009. Review of red squirrel conservation activity in northern England. Natural England commission report NECR019, Natural England, Sheffield.

Powell R.A., 2000. Animal home ranges and territories and home range estimators. In: Boitani L., Fuller T.K. (Eds.) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY. 64–110.

Prange S., Gehrt S.D., Wiggers E.P., 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. J. Mammal. 85(3): 483–490.

Pulliainen E., 1973. Winter ecology of the red squirrel (*Sciurus vulgaris* L.) in northeastern Lapland. Ann. Zool. Fenn. 10(4): 487–494.

QGIS Development Team, 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team, 2013. foreign: read data stored by Minitab, S, SAS, SPSS, Stata, Systat, dBase, ... R package version 0.8–53.

R Core Team, 2017. R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna) Available at https://www.R-project.org/

Reher S., Dausmann K.H., Warnecke L., Turner J.M., 2016. Food availability affects habitat use of Eurasian red squirrels (*Sciurus vulgaris*) in a semi-urban environment. J. Mammal. 97(6): 1543–1554.

Rojas A.D., Körtner G., Geiser F., 2010. Do implanted transmitters affect maximum running speed of two small marsupials? J. Mammal. 91(6): 1360–1364.

Ryan D.A., Larson J.S., 1976. Chipmunks in residential environments. Urban Ecology 2(2): 173–178.

Shuttleworth C.M., 1997. The effect of supplemental feeding on the diet, population density and reproduction of red squirrels (*Sciurus vulgaris*). In: Gurnell J., Lurz P.W.W. (Eds.) The conservation of red squirrels, *Sciurus Vulgaris* L. People's Trust for Endangered Species, London, UK. 13–24.

Shuttleworth C.M., 2000. The foraging behaviour and diet of red squirrels *Sciurus vulgaris* receiving supplemental feeding. Wildl. Biol. 6(3): 149–156.

Sol D., Lapiedra O., González-Lagos C., 2013. Behavioural adjustments for a life in the city. Anim. Behav. 85(5): 1101–1112.

Stabler B., 2013. shapefiles: read and write ESRI shapefiles. R package version 0.7.

Tigas L.A., Van Vuren D.H., Sauvajot R.M., 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biol. Cons. 108(3): 299–306.

Tonkin J.M., 1983. Activity patterns of the red squirrel (*Sciurus vulgaris*). Mamm. Rev. 13(2–4): 99–111.

Turner J.M., Reher S., Warnecke L., Dausmann K.H., 2017. Eurasian red squirrels show little seasonal variation in metabolism in food-enriched habitat. Physiol. Biochem. Zool. 90(6): 655–662.

United Nations, Department of Economic and Social Affairs, Population Division, 2014. World urbanization prospects: the 2014 revision, highlights, United Nations, New York.

Verbeylen G., Wauters L.A., De Bruyn L., Matthysen E., 2009. Woodland fragmentation affects space use of Eurasian red squirrels. Acta Oecol. 35(1): 94–103.

Verboom B., Van Apeldoorn R., 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. Landscape Ecol. 4(2–3): 171–176.

Vieira B.P., Fonseca C., Rocha R.G., 2015. Critical steps to ensure the successful reintroduction of the Eurasian red squirrel. Anim. Biodiv. Conserv. 38(1): 49–58.

Wauters L., and Dhondt A.A., 1987. Activity budget and foraging behaviour of the red squirrel (*Sciurus vulgaris*, Linnaeus, 1758) in a coniferous habitat. Z. Saugetierkd 52(6): 341–353.

Wauters L., Dhondt A.A., 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. Anim. Behav. 43(2): 297–311.

Wauters L.A., Lens L., 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. Ecology 76(8): 2460–2469.

Wauters L.A., Vermeulen M., Van Dongen S., Bertolino S., Molinari A., Tosi G., Matthysen E., 2007. Effects of spatio-temporal variation in food supply on red squirrel *Sciurus vulgaris* body size and body mass and its consequences for some fitness components. Ecography 30(1): 51–65.

Wauters L.A., Swinnen C., Dhondt A.A., 1992. Activity budget and foraging behaviour of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. J. Zool. 227(1): 71–86.

Wauters L.A., Casale P., Dhondt A.A., 1994. Space use and dispersal of red squirrels in fragmented habitats. Oikos 69(1): 140–146.

Wauters L.A., Bertolino S., Adamo M., Van Dongen S., Tosi G., 2005. Food shortage disrupts social organization: the case of red squirrels in conifer forests. Evol. Ecol. 19(4): 375–404.

Worton B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1): 164–168.

*Associate Editor: J. Gurnell*